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Capobula gen. nov., a new Afrotropical dark sac spider genus related to *Orthobula* Simon, 1897 (Araneae: Trachelidae)

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Abstract

A new genus of the spider family Trachelidae L. Koch, 1872 from the Afrotropical Region is described. *Capobula* **gen. nov.** is represented by five species, known from South Africa and Lesotho only. Adults of both sexes of *Orthobula infima* Simon, 1896a, which is widely distributed in the Western Cape, South Africa, are described for the first time, and this species is transferred to *Capobula* **gen. nov.** as its type species. Four new species are described: *C. capensis* **spec. nov.** and *C. neethlingi* **spec. nov.** (South Africa: Western Cape), *C. montana* **spec. nov.** (Lesotho and South Africa: Eastern Cape, Free State and KwaZulu-Natal) and *C. ukhahlamba* **spec. nov.** (South Africa: KwaZulu-Natal). A phylogenetic analysis based on the cytochrome oxidase subunit I (COI) gene, including 14 genera of Trachelidae, one genus of Clubionidae Wagner, 1887 and three genera of Phrurolithidae Banks, 1892, supports the placement of *Capobula* **gen. nov.** in Trachelidae, with *Orthobula* Simon, 1897 as its likely closest relative.

Key words: COI, barcoding, epigeal, endemic, Lesotho, South Africa

Introduction

The Trachelidae Simon, 1897 is a medium-sized spider family recently elevated from subfamily level in Corinnidae Karsch, 1880 (Ramírez 2014). During the last two decades particularly, there has been a considerable increase in taxonomic research on the group, which has seen the generic and species diversity more than double during this period (World Spider Catalog 2020). Most of this research has focused on the fauna of East Asia and the Afrotropical Region. In the latter, eight new genera have been described (Haddad 2006; Haddad & Lyle 2008; Lyle & Haddad 2009, 2010, 2018), and many more new genera allied to *Trachelas* L. Koch, 1872 and *Thysanina* Simon, 1910 still await description.

One enigmatic genus in the Dionycha is *Orthobula* Simon, 1897. Originally, it was described in the subfamily Liocraninae Simon, 1897 of Clubionidae Wagner, 1887, and was later placed in the subfamily Phrurolithinae Banks, 1892 of Liocranidae (Dippenaar-Schoeman & Jocqué 1997; Deeleman-Reinhold 2001) until the subfamily was transferred to Corinnidae (Bosselaers & Jocqué 2002). Ramírez (2014) elevated Phrurolithinae to family level based on a comprehensive morphological phylogeny of Dionycha, and transferred *Orthobula* to it. Wheeler *et al.* (2017) subsequently transferred *Orthobula* to Trachelidae based on the results of a molecular phylogeny using three mitochondrial and three nuclear genes.

Orthobula can be easily recognized from most other Trachelidae by the strong ventral spines on the anterior legs, the strongly pitted carapace, and the male palpal tegulum that is considerably swollen basally (e.g. Platnick 1977; Deeleman-Reinhold 2001). During a revision of the Afrotropical members of the genus, we discovered a

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group of species with a considerably narrowed tegulum, different embolus structure, and very different female genitalia from *Orthobula*.

DNA barcoding initiatives have played a crucial role in providing molecular data for inferring phylogenies (Hedin 2001; Souza *et al.* 2016), determining species boundaries (Robinson *et al.* 2009; Spasojevic *et al.* 2016), species identification (Barrett & Hebert 2005; Blagoev *et al.* 2013), species delineation and description (e.g. Navarro-Rodríguez & Aldez-Mondragón 2020), and community phylogenetics (Boyle & Adamowicz 2015). However, DeSalle *et al.* (2005) highlighted several issues that may hinder the use of COI-only molecular analyses (also see Martinsson *et al.* 2017 and Yao *et al.* 2010), which must be considered when doing such analyses. An integrated taxonomic approach that uses COI in conjunction with other types of evidence, such as traditional morphological evidence, to support the description of new taxa will improve the quality of the hypothesis formed (Pante *et al.* 2015; Xu *et al.* 2015; Spasojevic *et al.* 2016).

Here we describe a new genus, *Capobula* **gen. nov.**, which is represented by five species from South Africa and Lesotho, of which four are described as new. We also present molecular phylogenies based on the DNA barcoding gene (cytochrome oxidase subunit I COI) to test whether the new genus emerges as the sister group of *Orthobula*, and whether there is support for the placement of these two genera in Trachelidae, consistent with multi-gene analyses (Wheeler *et al.* 2017).

Material and methods

Taxonomy

All specimens used for the current study were preserved in 70% ethanol. Descriptions and measurements were taken using a Nikon SMZ800 stereomicroscope with an ocular micrometer. All measurements are given in millimetres and are provided for the specimen indicated, with a range of total length measurements also provided for each sex. Leg measurements were taken from the dorsal side of each segment, and are given in sequence from femur to tarsus, followed by the total length. Digital photographs of the dorsal habitus of each species were taken with a Nikon SMZ800 stereomicroscope with coupled Nikon DS-L3 camera system, with 15–20 images taken and stacked using Combine ZM software (Hadley 2008) to increase the depth of field.

Material of both sexes of *Capobula infima* (Simon, 1896a) **comb. nov.** were examined for electron microscopy (SEM). Three individuals of each sex from De Hoop Nature Reserve, Western Cape, South Africa, were first cleaned in a Labcon 5019U ultrasonic bath in 70% ethanol for 30 seconds. The material was transferred to fresh 100% ethanol for dehydration overnight, after which they were critical-point dried in carbon dioxide gas. After drying, the material was mounted onto aluminium stubs using double-sided tape, sputter-coated with gold three times for two minutes in an argon chamber, and then examined in a JEOL JSM-7800F FE-SEM at 5 kV. Epigynes were removed and cleared in a pancreatin solution (Álvarez-Padilla & Hormiga 2007) and illustrated with a Leica M205A stereomicroscope equipped with an Abbe drawing device.

Material for this study was loaned from or deposited in the following collections, with curators indicated in brackets:

AMNH—American Museum of Natural History, New York, U.S.A. (Lou Sorkin); CAS—California Academy of Sciences, San Francisco, U.S.A. (Lauren Esposito, Darrell Ubick); MHBU—Museum of Hebei University, Baoding, China (Mei Zhang); MNHN—Museum National d'Histoire Naturelle, Paris, France (Christine Rollard); MRAC—Royal Museum for Central Africa, Tervuren, Belgium (Rudy Jocqué); NCA—National Collection of Arachnida, ARC-Plant Health Protection, Pretoria, South Africa (Ansie Dippenaar-Schoeman, Petro Marais); SAMC—Iziko South African Museum, Cape Town, South Africa (Dawn Larsen, Aisha Mayekiso); TMSA—Ditsong National Museum of Natural History, Pretoria, South Africa (Audrey Ndaba).

The following abbreviations are used in the descriptions: AL—abdomen length; AW—abdomen width; CL—carapace length; CW—carapace width; MOQ—median ocular quadrangle; MOQAW—anterior width of median ocular quadrangle; MOQL—median ocular quadrangle length; MOQPW—posterior width of median ocular quadrangle; PERW—posterior eye row width; plv—prolateral ventral spines of anterior legs; rlv—retrolateral ventral spines of anterior legs; TL—total length.

Leg spination follows the format of Bosselaers & Jocqué (2000), but in *Capobula* **gen. nov.** spines are restricted to the ventral aspect of the anterior legs only, so are indicated as plv and rlv (see above).

Where geographical locality co-ordinates were not provided on specimen labels or were unavailable on institutional databases, they were searched for using the Global Gazetteer Version 2.2 (www.fallingrain.com/world/) and are indicated in square brackets. The distribution map of *Capobula* **gen. nov.** species was created using the online mapping software SimpleMappr (Shorthouse 2010).

Phylogenetic taxon sampling

A total of 154 public barcode sequences, representing 41 species of Phrurolithidae and Trachelidae combined, were downloaded in .fasta format from the Barcode of Life Data Systems website (BOLD) (www.boldsystems.org), together with one outgroup sequence belonging to *Clubiona pallidulla* (Clerck, 1757) (Clubionidae). Only cytochrome oxidase subunit I (COI) sequences were used for this study. Sequences were aligned using an online multiple sequence alignment service (https://mafft.cbrc.jp/alignment/server/) that used the software MAFFT (Kuraku *et al.* 2013; Katoh *et al.* 2019). The "auto" strategy was used alongside the default settings. The alignments were double-checked and malalignments were manually corrected using the Mega X software (Kumar *et al.* 2018).

Molecular phylogenetic analyses

Two phylogenetic analyses were performed using the molecular data obtained. Both these analyses were performed on the CIPRES Science Gateway V3.3 infrastructure (Miller *et al.* 2010a).

The first analysis, a maximum likelihood analysis (ML), was performed using the RaxML V8.0 software (Stamatakis 2014) to infer a maximum likelihood phylogeny. A general time-reversible (GTRGAMMAI) model was used as a substitution model with GAMMA model of rate heterogeneity with estimation of proportion of invariable sites. The final maximum likelihood optimisation was -9374.977599 and the analysis was repeated for 1000 bootstraps. Branch support was measured as a bootstrap support percentage (BS%).

Secondly, a Bayesian Inference phylogenetic analysis (BI) was performed on a partitioned dataset (3 partitions) using MrBayes V3.2.7 Parallel version (Ronquist & Huelsenbeck 2003; Altekar *et al.* 2004). Four runs (nruns=4) and six Markov Chain Monte Carlo (MCMC) chains (nchains= 6) were performed simultaneously for a total of 100 000 000 generations (ngen=100000000) at a temperature of 0.7 (temp=0.7). Convergence was validated using the Potential Scale Reduction Factor (PSRF was 1) and an average standard deviation of split frequencies value of 0.008743. Branch support was measured as a bipartition posterior probability support percentage (bpp%).

PartitionFinder2 (Lanfear *et al.* 2016) was used to determine the COI region's codon partitions and the results were entered into the MrBayes block. Furthermore, the partitions were unlinked using the following commands: unlink statefreq= (all), revmat (all), shape= (all), pinvar= (all), tratio= (all). Beagle was enabled (set beagle=yes) during these runs to speed up the analysis on the High-Performance-Computing (HPC) cluster. Summaries of the trees were made using the commands "sump" and "sumt" with a burnin frequency of 25% (burninfrac=0.25). Lastly, a majority rule consensus tree was requested using the "contype=Allcompat" command.

The trees were visualised and rooted using FigTree 1.4 software (Rambaut 2014) and were subsequently edited using Adobe Photoshop CC 2019®.

Phylogenetic results

A total of 154 barcodes were obtained from the BOLD database and analysed (Appendix 1), containing three Phrurolithidae and 14 Trachelidae genera, each with 10 and 31 species, respectively. The phrurolithid genera *Phrurolithus* C.L. Koch, 1839, *Phrurotimpus* Chamberlin & Ivie, 1935 and *Scotinella* Banks, 1911 recovered as a single large monophyletic clade depicting the Phrurolithidae (Clade A), the family sister to Trachelidae (Clades B–I). This was true for both the BI and ML analyses (Figs 1 & 2, respectively). The Phrurolithidae clade showed that the genus *Scotinella* recovered as sister to a clade formed by *Phrurotimpus* and *Phrurolithus*, with 100% support in both analyses (Figs 1 & 2). Contrary to expectations, we failed to obtain monophyletic Trachelidae and Phrurolithidae

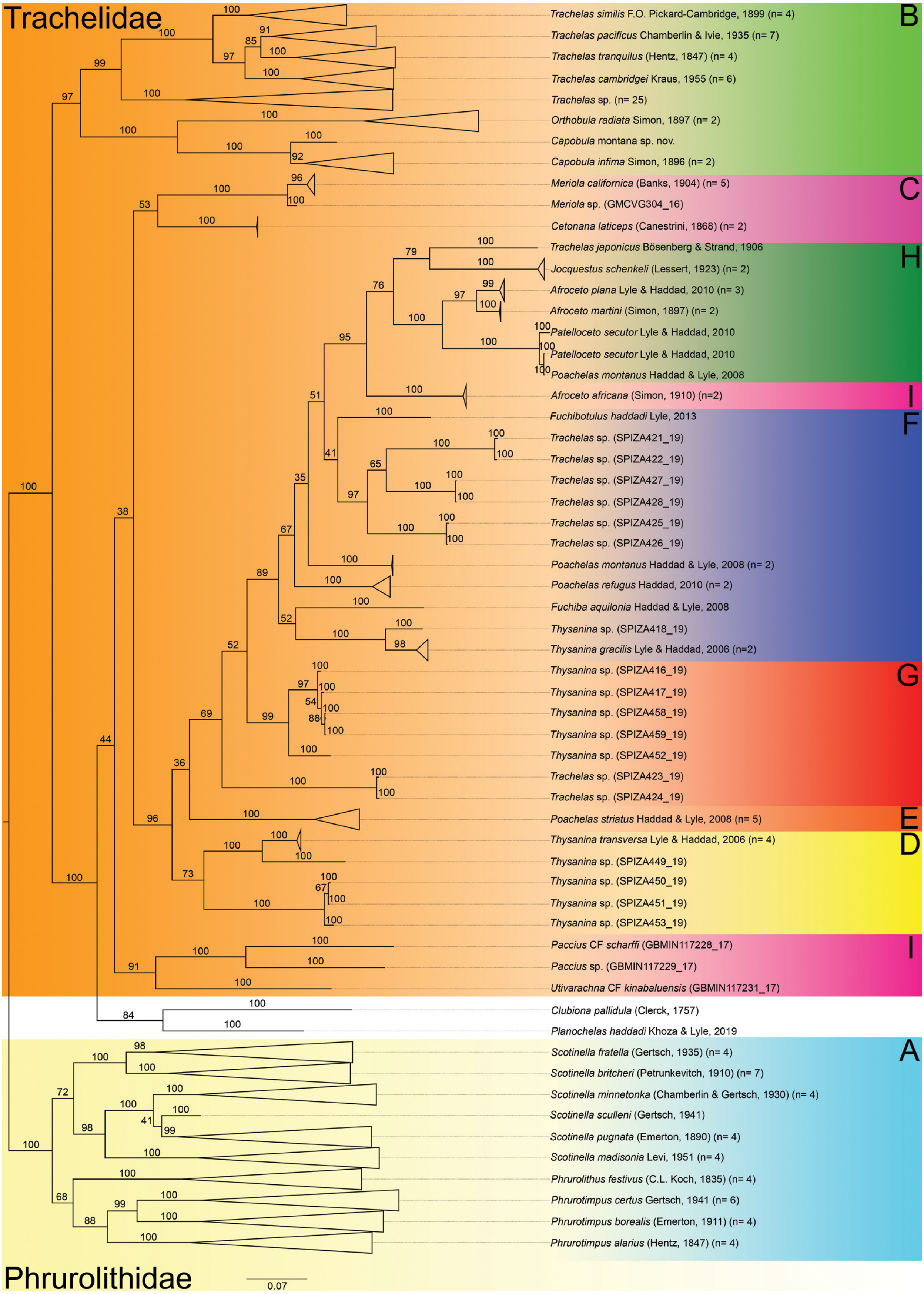


FIGURE 1. Bayesian Inference phylogenetic analyses results based on cytochrome c oxidase subunit 1 (COI) sequences showing the two familial clades, Phrurolithidae and Trachelidae, with Clades A-I distributed throughout them, and *Clubiona pallidula* (Clerck, 1757) as the outgroup. Branch support measured as bipartition posterior probability percentage (% bpp).

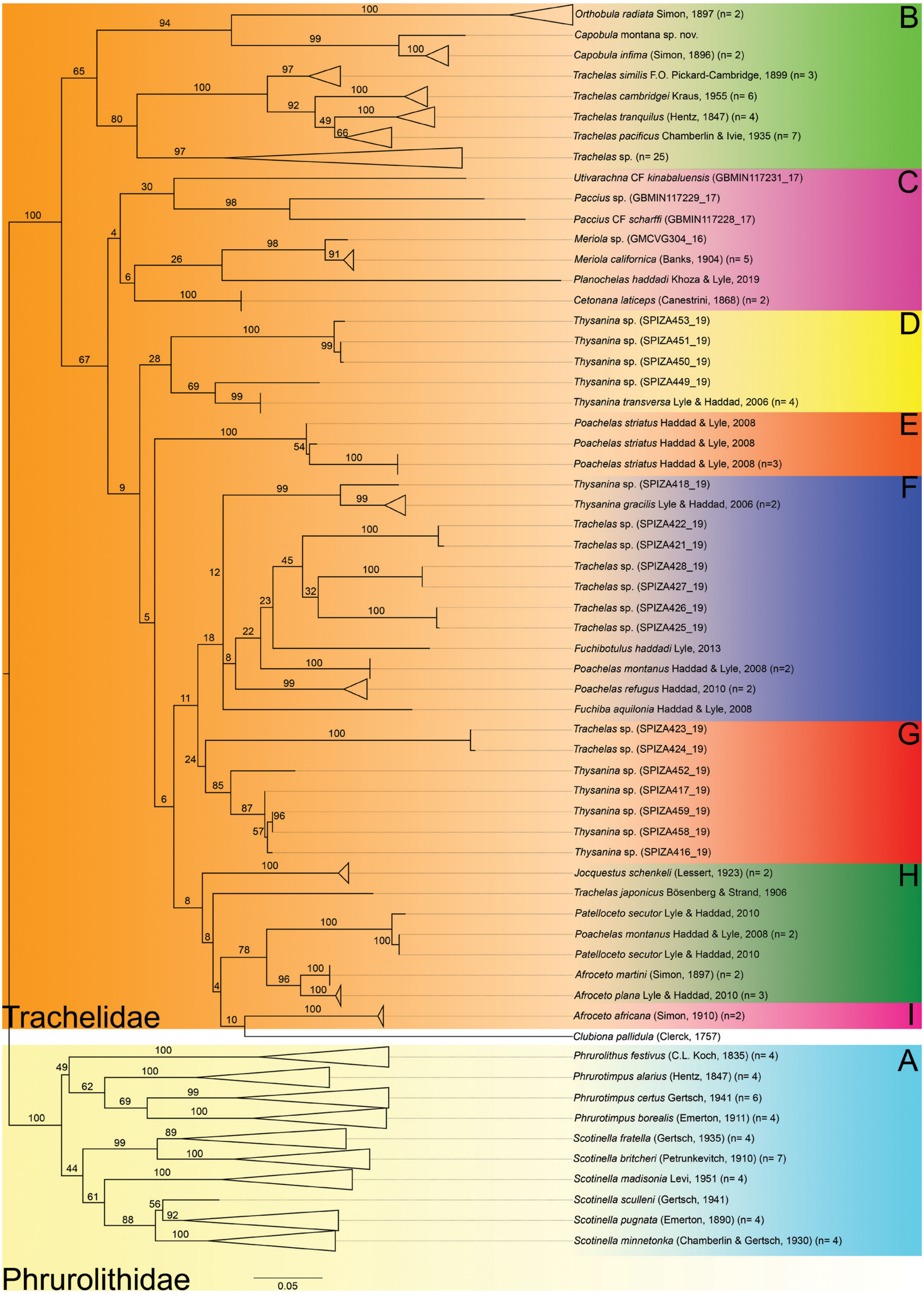


FIGURE 2. Maximum likelihood phylogenetic analyses results based on cytochrome c oxidase subunit 1 (COI) sequences showing the two familial clades, Phrurolithidae and Trachelidae, with Clades A-I distributed throughout them, and *Clubiona pallidula* (Clerck, 1757) as the outgroup. Branch support measured as bootstrap support percentage (% BS).

using the intended outgroup, *Clubiona*, and instead rooted our tree between Phrurolithidae and the remaining taxa. Regarding the Trachelidae, several genera were recovered as polyphyletic in both the analyses, namely *Afroceto* Lyle & Haddad, 2010 (Clades H and I), *Poachelas* Haddad & Lyle, 2008 (Clades E, F and H), *Trachelas* (Clades B, F and H) and *Thysanina* (Clades D–G). *Trachelas japonicus* Bösenberg & Strand, 1906 recovered as sister to *Jocquestus schenkeli* (Lessert, 1923) in the BI analysis (Clade H) (Fig. 1), but in the ML analysis (Fig. 2) *J. schenkeli* was placed basal to *T. japonicus*.

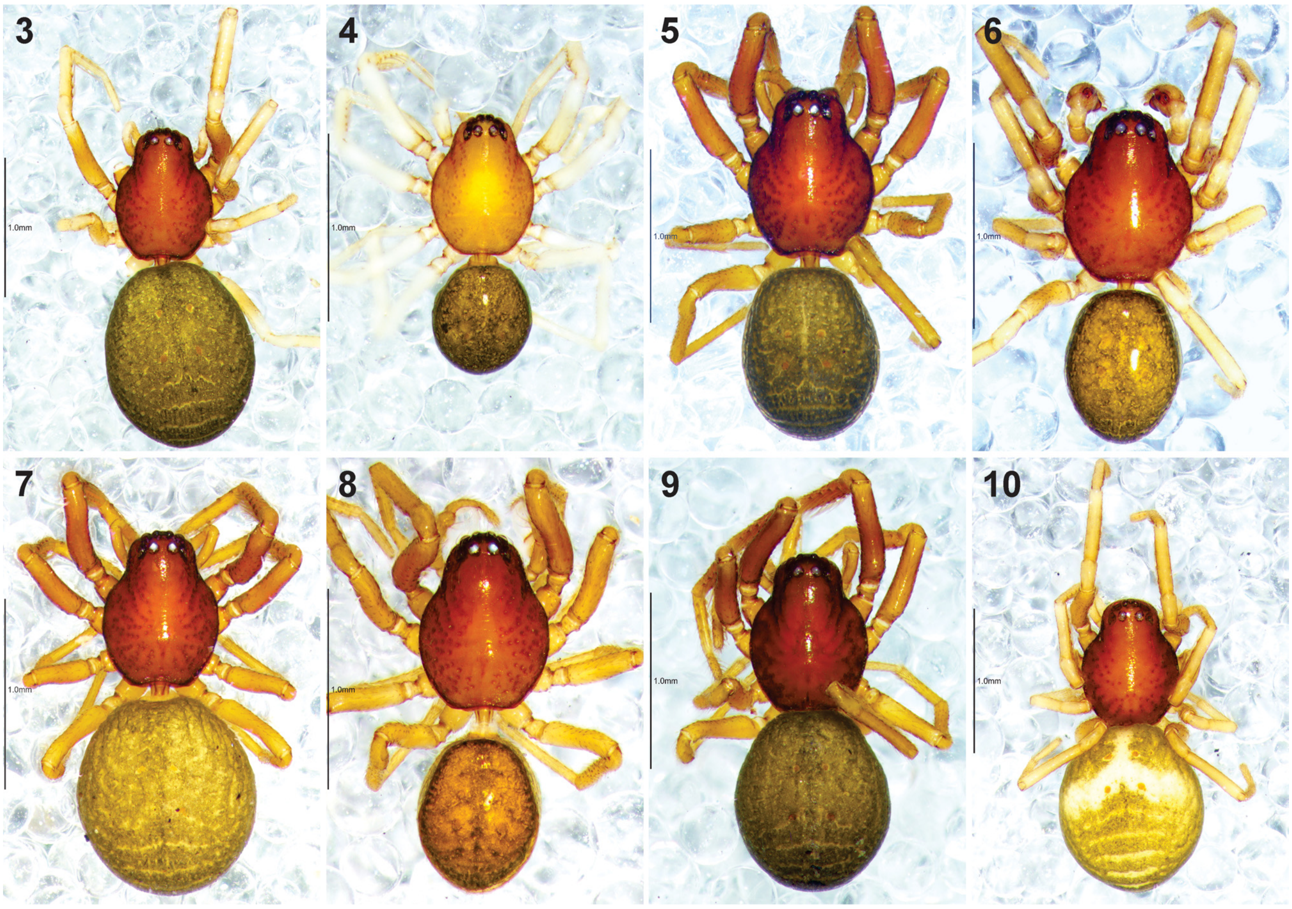
Capobula **gen. nov.** (represented by two species, *C. infima* **comb. nov.** and *C. montana* **spec. nov.**) recovered as sister to *Orthobula radiata* Simon, 1897, both genera together forming a clade sister to a group of New World *Trachelas* spp. in clade B. Clade B also was placed sister to Clades C–I in both analyses. Clade C contained several trachelid genera, namely *Meriola* Banks, 1895, *Cetonana* Strand, 1929, *Paccius* Simon, 1898, *Utivarachna* Kishida, 1940 and *Planochelas* Lyle & Haddad, 2009 in the ML analyses, but were divided into two smaller clades in the BI analyses, separating *Meriola* and *Cetonana* from *Paccius* and *Utivarachna*. Furthermore, *Planochelas haddadi* Khoza & Lyle, 2019 was excluded from Clade C in the BI analysis and was placed with the outgroup taxon, *Clubiona pallidula*.

Taxonomy

Family Trachelidae Simon, 1897

Genus *Capobula* gen. nov.

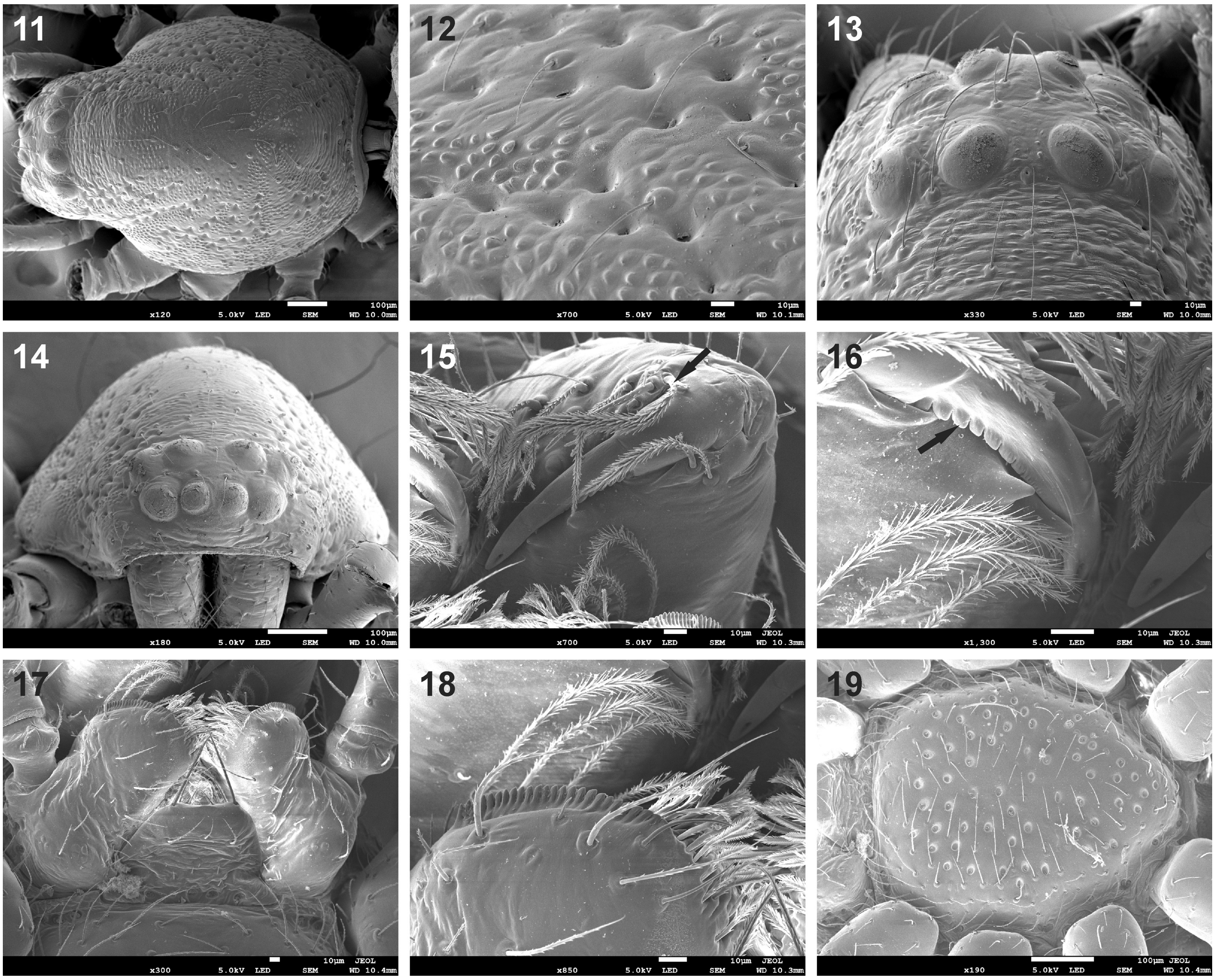
Type species: *Orthobula infima* Simon, 1896a



FIGURES 3–10. *Capobula* **gen. nov.** dorsal habitus photographs: 3 *C. capensis* **spec. nov.**, female holotype from Pakhuis Pass; 4 Same, paratype male from Pakhuis Pass; 5 *C. infima* (Simon, 1896) **comb. nov.**, female from Fisherhaven; 6 Same, male from De Hoop Nature Reserve; 7 *C. montana* **spec. nov.**, female holotype from Mount Coke State Forest; 8 Same, paratype male from Shamwari Game Reserve; 9 *C. neethlingi* **spec. nov.**, female holotype from Saasveld Pass; 10 *C. ukhahlamba* **spec. nov.**, paratype female from Royal Natal National Park.

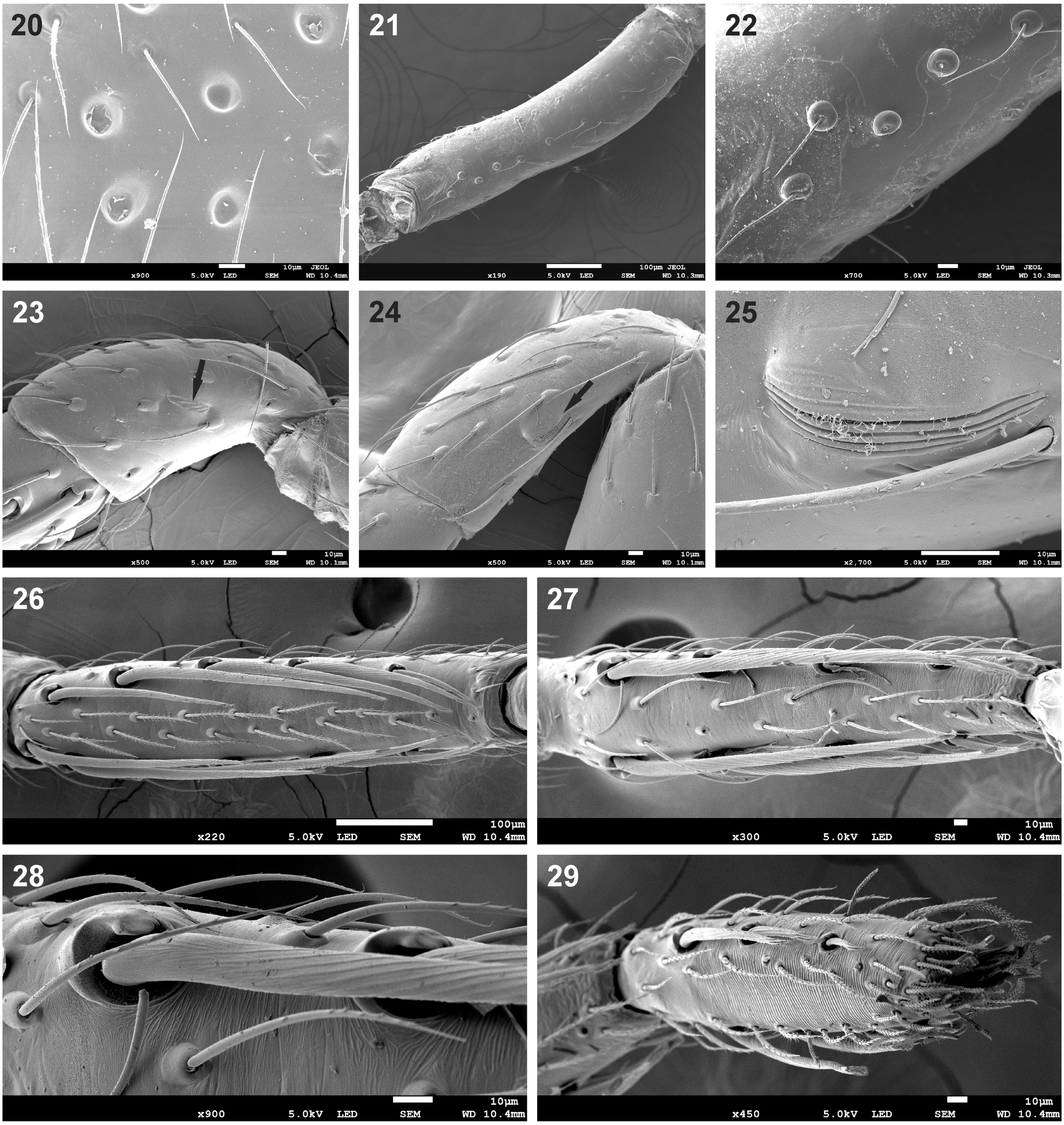
Diagnosis. *Capobula* **gen. nov.** can be recognized from all other trachelid genera except *Orthobula* by the combination of a large number of paired ventral spines on the anterior tibiae, metatarsi and tarsi, the absence of ventral cusps in both sexes, the deep pits on the carapace, and the presence of a large ventral sclerite on the abdomen of males. Although *Spinotrachelas* Haddad, 2006 and *Poachelas* also have heavily spined anterior legs, both have ventral cusps on the anterior legs, lack carapace pits, and lack a ventral abdominal scutum (Haddad 2006; Haddad & Lyle 2008). Female *Capobula* **gen. nov.** can be recognized by the laterally positioned, teardrop-shaped primary spermathecae that are in the same transverse plane as the copulatory openings, while in *Orthobula* the spermathecae are oval and positioned posteriorly, close to the midline of the epigyne, and far from the anteriorly positioned copulatory openings (e.g. Marusik *et al.* 2013: figs 19–22). Further, *Capobula* **gen. nov.** lack pits along the midline of the carapace (Figs 3–11), which are present in *Orthobula* (e.g. Marusik *et al.* 2013: figs 1, 4; Ramírez 2014: fig. 6A). *Capobula* **gen. nov.** can be separated from *Orthobula* by the male palpal tegulum being pear-shaped and approximately as broad as the cymbium, and the embolus with a broad base, clear bend near its midpoint, and tip directed retrodistally (e.g. Fig. 52). In *Orthobula* the tegulum is subtriangular and strongly swollen basally towards the prolateral side, and the embolus usually straight, narrow, finely coiled and directed distally (e.g. Marusik *et al.* 2013: figs 11–16).

Etymology. The genus name is a combination of Cape, referring to the Western and Eastern Cape Provinces of South Africa from where the majority of the species have been recorded, and *Orthobula*, to which it is closely related. Gender is feminine.



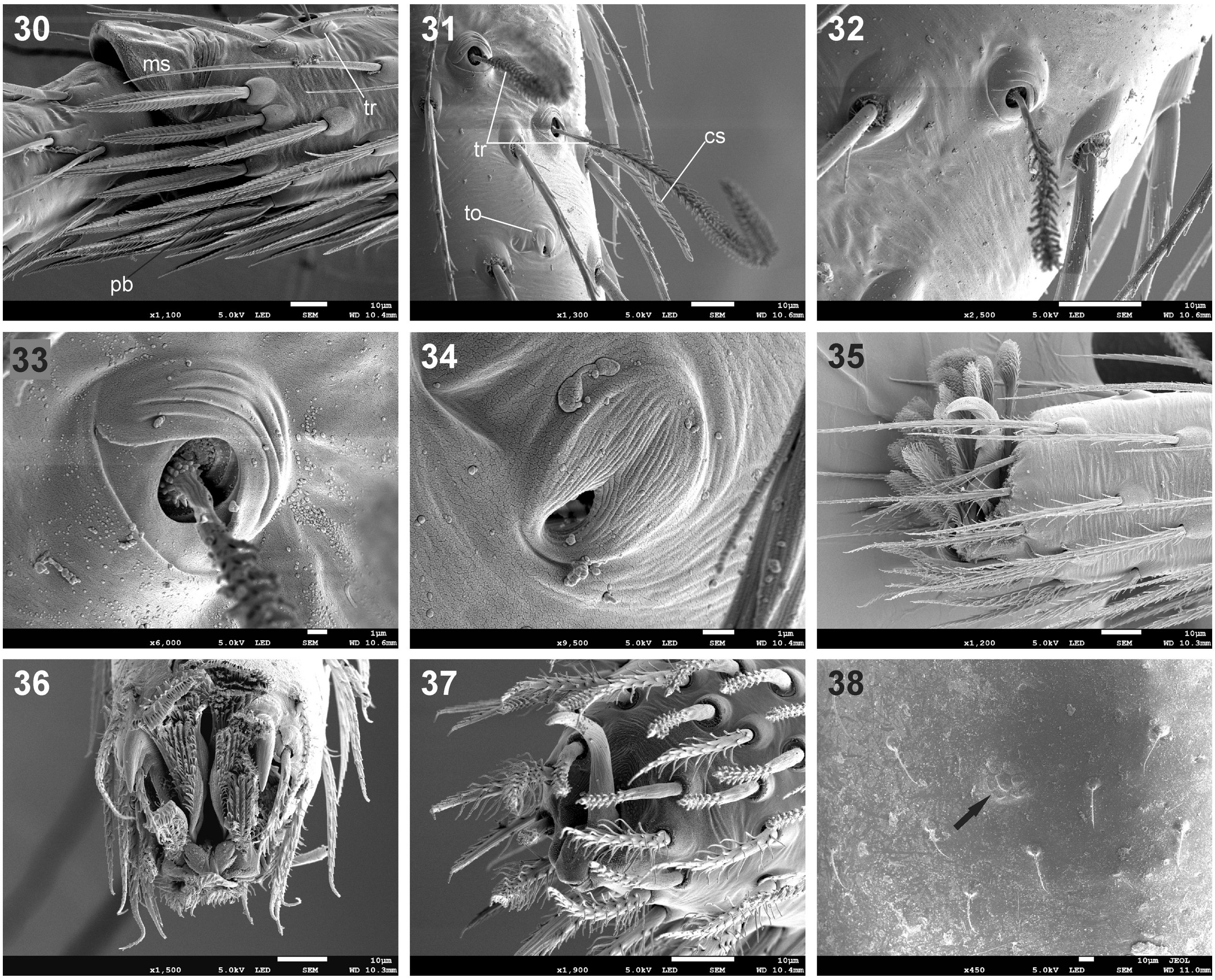
FIGURES 11–19. *Capobula infima* (Simon, 1896) **comb. nov.**, female from De Hoop Nature Reserve, SEM photographs: 11 Carapace, dorsal; 12 Same, detail of carapace texture, showing pits and fine tubercles on striae, dorsal; 13 Eye region, dorsal; 14 Eye region, frontal; 15 Chelicerae, ventral (arrow indicating promarginal escort seta); 16 Fang, ventral (arrow indicating fang serrula); 17 Endites and labium, ventral; 18 Detail of endite serrula, ventral; 19 Sternum, ventral.

Description. Small spiders, 1.70–2.35 mm in total length; carapace bright orange to deep red-brown (Figs 3–10); carapace oval, broadest at middle of coxae II, eye region narrow, fovea indistinct, a short shallow depression (Fig. 11); posterior margin very slightly concave; carapace surface finely granulose, with series of deep pits forming striae, pits absent from midline of carapace (Figs 11, 12), each pit with central pore; surface sparsely covered with scattered fine curved setae (Figs 12, 13). All eyes surrounded by black rings (Figs 3–10); anterior eye row procurved in anterior view, recurved in dorsal view, anterior median eyes approximately ¾ anterior lateral eye diameter; anterior median eyes separated by approximately ½ their diameter, nearly touching anterior lateral eyes (Figs 13, 14); posterior eye row recurved in dorsal view, posterior median eyes oval, posterior lateral eyes round; posterior median eyes approximately 1¼ times posterior lateral eye diameter; MOQ narrower anteriorly than posteriorly, length and



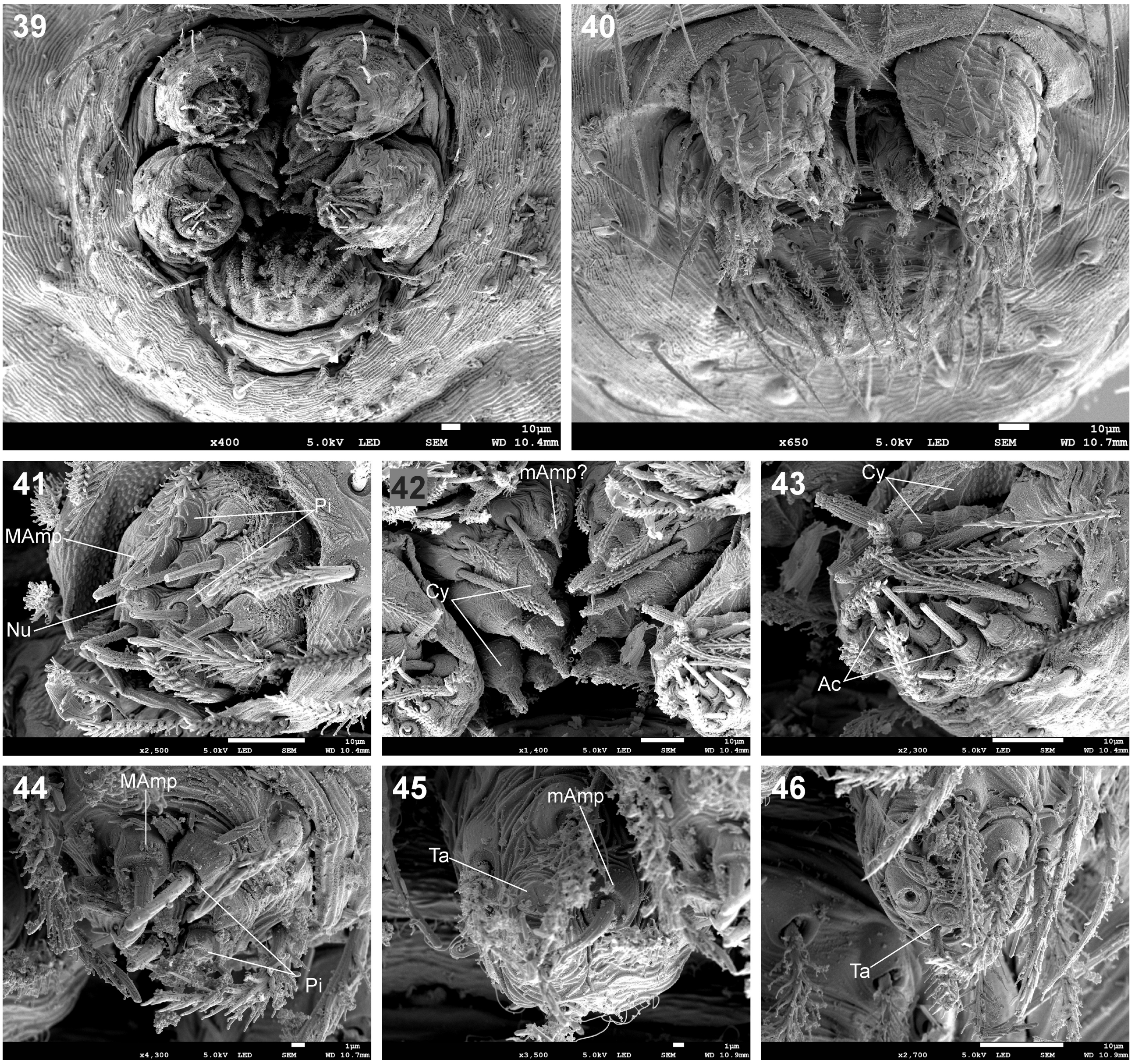
FIGURES 20–29. *Capobula infima* (Simon, 1896) **comb. nov.**, female (20, 23–29) and male (21, 22) from De Hoop Nature Reserve, SEM photographs: 20 Detail of sternum texture; 21 Femur I, ventral; 22 Femur I, detail of fine distal tubercles on ventral surface, ventral; 23 Patella III, prolateral (arrow indicating lyriform organ); 24 Patella IV, retrolateral (arrow indicating lyriform organ at end of patellar indentation: PI); 25 Detail of lyriform organ at end of PI, retrolateral ventral; 26 Tibia I spines, ventral; 27 Metatarsus I spines, ventral; 28 Metatarsus I, detail of spine bases, ventral; 29 Tarsus I spines, ventro-distal.

posterior width approximately equal. Chilum indistinct, a tiny transverse sclerite; cheliceral promargin and retromargin with two teeth each, cheliceral escort seta present (Figs 15, 16); fang with distinct serrula (Fig. 16); endites convergent, not sexually dimorphic, slightly notched laterally (Fig. 17), with distinct serrula comprising sharp, ventrally curved denticles (Fig. 18); dense maxillar hair tuft on mesal margins (Fig. 17); labium trapezoidal, slightly wider than long. Pleural bars sclerotised, isolated; sternum shield-shaped, longer than broad, surface smooth with deep pits without pores, sparsely covered in long straight setae (Figs 19, 20); precoxal triangles present, intercoxal sclerites present between all coxal pairs. Leg formula 4132, sparsely covered in long fine setae; femora I with mesal convex curvature, all femora strongly constricted proximally, with sparse ventral tubercles in basal half (Figs 21, 22); patellae with small lyriform organ on prolateral side (Fig. 23), patellar indentation on retrolateral side narrow, with lyriform organ at proximal end (Figs 24, 25); anterior legs with strong paired ventral spines on tibiae, metatarsi and tarsi (Figs 26–29); metatarsi IV with sparse chemosensory setae and trichobothria dorsally, ventral preening brush at distal end (Fig. 30); tarsi with sparse tactile hairs, few dorsal trichobothria and chemosensory setae (Figs 31, 32); trichobothria with sunken distal plate, distal margin of hood overlapping plate, hood with four curved ridges, roughly concentric (Fig. 33); tarsal organ oval, very slightly elevated from integument, surface finely wrinkled, opening oval and distally placed (Figs 31, 34); paired tarsal claws short, with two teeth and moderately dense tenant setae forming claw tufts in between (Figs 35, 36); palpal claw simple, sharply curved distally (Fig. 37). Abdomen oval, clearly larger in females than males, with dorsal scutum in males only; dorsum with very sparse fine setae



FIGURES 30–38. *Capobula infima* (Simon, 1896) **comb. nov.** female from De Hoop Nature Reserve, SEM photographs: 30 Metatarsus IV, distal preening brush and metatarsal stopper, retrolateral; 31 Tarsus I, dorsal, indicating chemosensory seta (cs), trichobothria (tr) and tarsal organ (to); 32 Tarsus I, trichobothrium, dorsal; 33 Same, detail of trichobothrium base, dorsal; 34 Tarsus I, detail of tarsal organ, dorsal; 35 Tarsal claws, leg IV, prolateral; 36 Tarsal claws, leg III, distal; 37 Palpal claw, prolateral distal; 38 Dorsal abdominal setae, dorsal, arrow indicating sigillum.

and two pairs of sigilla, prominent in females, barely distinguishable on scutum in males (Figs 3–10, 38); venter without post-epigastric sclerites, with large ventral sclerite in males that is wider than long, absent in females; small, weakly sclerotized inframamillary sclerite present in females, indistinct in males. Spinnerets (observed in *C. infima* **comb. nov.** only): female (Figs 39, 41–43): anterior lateral spinnerets of female each with one major ampullate gland spigot, one nubbin and approximately ten piriform gland spigots; posterior median spinnerets of female each with one small minor ampullate gland spigot and five large cylindrical gland spigots; posterior lateral spinnerets of female each with two large cylindrical gland spigots and approximately ten aciniform gland spigots; male (Figs 40, 44–46): anterior lateral spinnerets of male each with one major ampullate gland spigot and five piriform gland spigots; posterior median spinnerets of male each with only one minor ampullate gland spigot and one tartipore evident; posterior lateral spinnerets of male each with only a single tartipore discernible. Female epigyne with small paired copulatory openings positioned anteriorly in epigyne (Fig. 47), in same transverse plane as teardrop-shaped laterally positioned primary spermathecae (e.g. Figs 54, 59); copulatory ducts directed posteriorly along midline, with

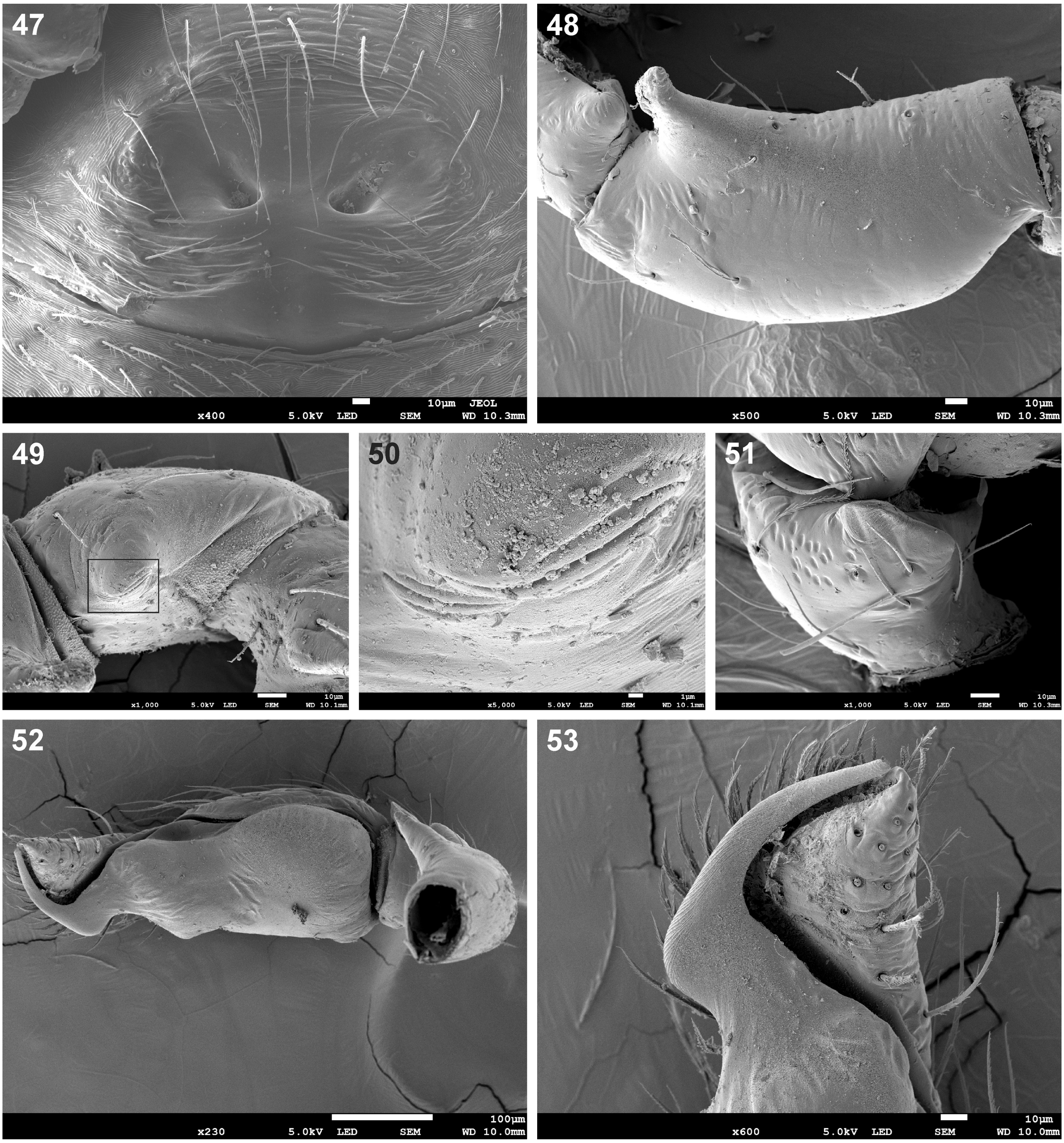


FIGURES 39–46. *Capobula infima* (Simon, 1896) **comb. nov.**, female (39, 41–43) and male (40, 44–46) from De Hoop Nature Reserve, SEM photographs: 39–40 Spinnerets, general view; 41, 44 Anterior lateral spinnerets; 42, 45 Posterior median spinnerets; 43, 46 Posterior lateral spinnerets. Abbreviations: Ac—aciniform gland spigot; Cy—cylindrical gland spigot; mAmp—minor ampullate gland spigot; MAmp—major ampullate gland spigot; Nu—nubbin; Pi—piriform gland spigot; Ta—tartipore.

membranous anterior bursae originating near initial part of ducts; posteriorly, copulatory ducts bend laterally to enter spermathecae along their mesal margin (e.g. Figs 55, 60); secondary spermathecae not distinguished. Male palpal femur, patella and tibia all with ventral apophyses (Figs 48–52), patella with lyriform organ associated with apophysis (Figs 49, 50); tegulum pear-shaped, broadest basally, tapering distally, slightly broader than cymbium, with narrow sperm duct running down centre of tegulum in ventral view, with single basal loop (e.g. Fig. 57); embolus distal, curving retrodistally (Fig. 53), tegulum without any other structures.

Composition. *Capobula infima* (Simon, 1896a) **comb. nov.** (type species) and four new species, *C. capensis* **spec. nov.**, *C. montana* **spec. nov.**, *C. neethlingi* **spec. nov.** and *C. ukhahlamba* **spec. nov.**

Distribution. Only known from South Africa and the enclave of Lesotho.



FIGURES 47–53. *Capobula infima* (Simon, 1896) **comb. nov.**, female (47) and male (48–53) from De Hoop Nature Reserve, SEM photographs: 47 Epigyne, ventral; 48 Left palpal femur and patella, ventral; 49 Left palpal patella, retrolateral (rectangle indicating lyriform organ associated with patellar apophysis); 50 Lyriform organ, enlarged; 51 Right palp, detail of retrolateral tibial apophysis; 52 Left palp, ventral; 53 Embolus, ventral.

Key to the species of *Capobula* gen. nov.

1 Females. 2
– Males (males of *C. neethlingi* **spec. nov.** and *C. ukhahlamba* **spec. nov.** unknown). 6
2 Abdomen grey, with cream inverted Y-shaped marking dorsally (Fig. 10); epigyne with large circular depressions incorporating copulatory openings (Fig. 73). . . . . *C. ukhahlamba* **spec. nov.**
– Abdomen uniformly grey dorsally, without marking (e.g. Fig. 3); epigyne with curved epigynal ridges incorporating copulatory openings 3
3 Copulatory openings in anterolateral corners of faint M-shaped ridges (Fig. 54); bursae clearly much larger than primary spermathecae (Fig. 55) . . . . *C. capensis* **spec. nov.**
– Copulatory openings in small C- or J-shaped ridges (e.g. Fig. 59); bursae same size or smaller than primary spermathecae (e.g. Fig. 60) 4
4 Anterior margin of ridges incorporating copulatory openings in same transverse plane as anterior margin of primary spermathecae; initial 2/3 of copulatory ducts before posterior bend heavily sclerotized and darker than last 1/3 (Fig. 55) . . . . *C. infima* **comb. nov.**
– Anterior margin of primary spermathecae clearly in front of anterior margin of ridges incorporating copulatory openings; only initial 1/3 of copulatory ducts before posterior bend heavily sclerotized, last 2/3 clearly lighter in colour (Figs 65, 71). 5
5 Ridges incorporating copulatory openings large and almost transverse to longitudinal plane of epigyne (Fig. 71); heads of bursae converging (Fig. 72) (South Africa: Western Cape, Fig. 75) . . . . *C. neethlingi* **spec. nov.**
– Ridges incorporating copulatory openings small and obliquely orientated, at 45 degrees to longitudinal plane of epigyne (Fig. 65); heads of bursae diverging (Fig. 66) (eastern half of South Africa, Fig. 75) . . . . *C. montana* **spec. nov.**
6 Embolus as wide as 1/2 of tegulum width at midpoint, tip sharply curved and almost transverse to longitudinal plane of palp (Fig. 62) . . . . *C. infima* **comb. nov.**
– Embolus narrow, width less than ¼ of tegulum width at midpoint, tip directed disto-retrolaterally (Figs 57, 68)…7
7 Embolus short, with stout tip (Fig. 57); femoral apophysis a sharp retrolateral spike (Fig. 58) (South Africa: Western Cape, Fig. 75). . . . . *C. capensis* **spec. nov.**
– Embolus longer, with slender tip (Fig. 68); femoral apophysis a stout ventral lobe (Fig. 69) (eastern half of South Africa, Fig. 75). . . . . *C. montana* **spec. nov.**

Capobula capensis spec. nov.

Figs 3–4, 54–58

Type material. Holotype ♀: **SOUTH AFRICA:** *Western Cape*: Cederberg Wilderness Area, Pakhuis Pass, 12.6 km 70° E of Clanwilliam, 32°08.419'S, 19°01.034'E, 773 m a.s.l., 9.X.2011, leg. L. Almeida, C. Griswold & T. Meikle (general collecting, Restionaceae fynbos) (CAS, CASENT 9043323, SA11-109). **Paratypes: SOUTH AFRICA:** *Western Cape*: Cederberg, leg. G. Smith, 1♂ (MRAC 133613); Cederberg, 32°21'S, 19°10'E, VII.1962, leg. N. Leleup (litter), 1♂ 5♀ (MRAC 131897); Cederberg Wilderness Area, Pakhuis Pass, 12.6 km 70° E of Clanwilliam, 32°08.419'S, 19°01.034'E, 773 m a.s.l., 9.X.2011, leg. L. Almeida, C. Griswold & T. Meikle (general collecting, Restionaceae fynbos), 1♂ (CAS, CASENT 9043335, SA11-112); Same locality, 13.5 km 76° E of Clanwilliam, 32°09.014'S, 19°01.793'E, 900 m a.s.l., 9.X.2011, leg. L. Almeida, C. Griswold & T. Meikle (general collecting, Restionaceae fynbos), 1♀ (CAS, CASENT 9043334, SA11-112); Same locality, VII.1962, leg. N. Leleup (litter), 4♂ 35♀ (MRAC 131979); Klein-Dassenberg Road, Farm Trinity, 33°34.94'S, 18°36.08'E, 25–27.XII.2012, leg. D. Ubick, 1♂ (CAS, CASENT 9055498); 17 km N Citrusdal, road on E bank of Olifants River, 32°35'S, 19°01'E, 7.I.1989, leg. R. Jocqué, 1♀ (MRAC 169745); Touws River [33°20'S, 20°01'E], 1953, leg. J. Gordon, 5♂ 9♀ (MRAC 127791).

Diagnosis. Females are distinct from congeners by the M-shaped atrial margins, with the copulatory openings positioned in the anterolateral corners (Fig. 54). Males of this species share with *C. infima* **comb. nov.** the broad, ridge-like retrolateral tibial apophysis, but can be distinguished by the spike-shaped femoral apophysis and short, stout distal section of the embolus that is directed retro-distally (Figs 57, 58), while in *C. infima* **comb. nov.** the femoral apophysis is lobate and the distal section of the embolus long, narrow and curved (Figs 62, 63). Males are also similar to *C. montana* **spec. nov.**, but have a clearly thicker embolus (compare Figs 57 and 68).

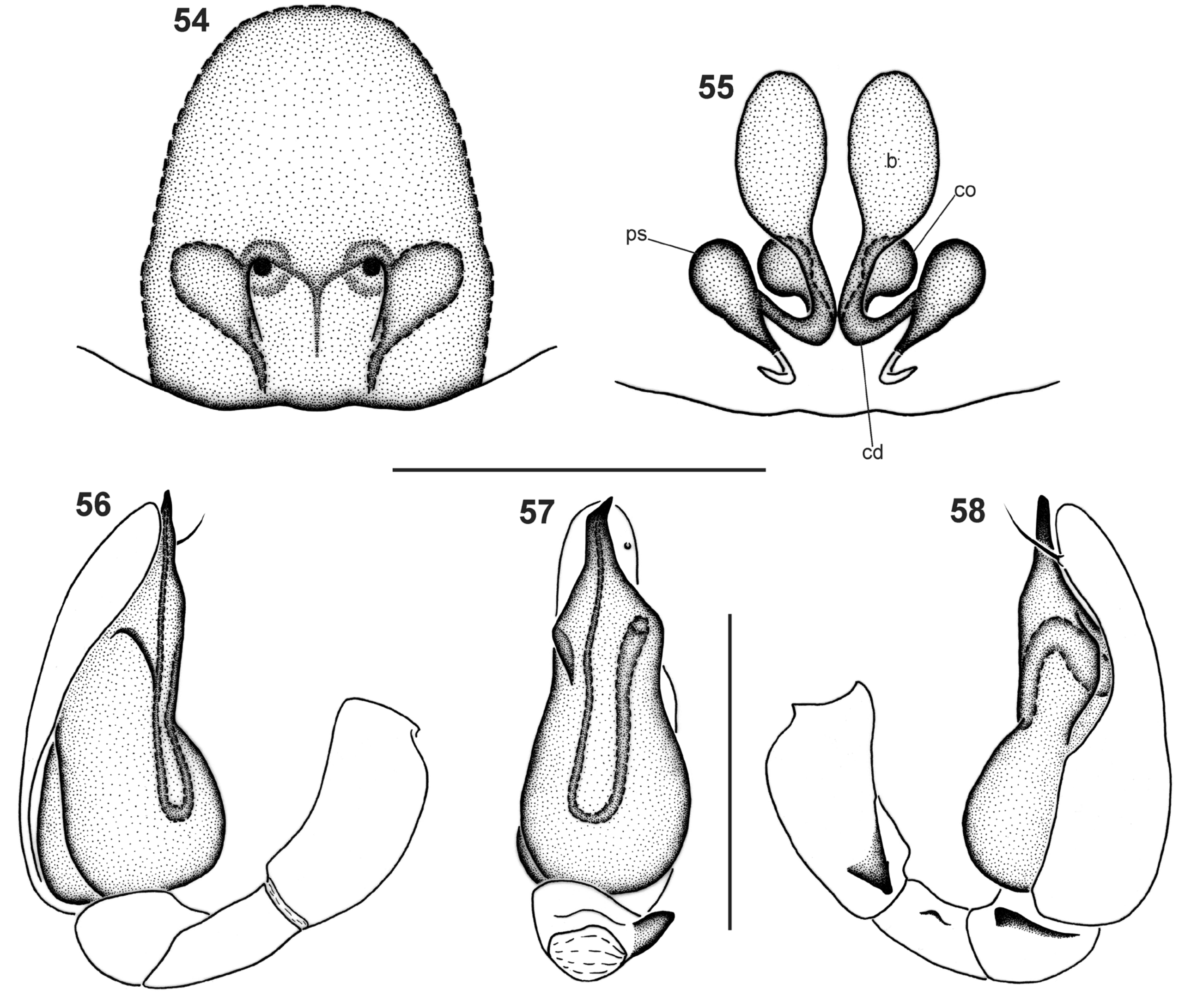
Etymology. Named for the Western Cape Province, from which it originates; Latin adjective.

Female (holotype, CAS, CASENT 9043323). Measurements: CL 0.90, CW 0.70, AL 1.24, AW 1.06, TL 2.35 (1.90–2.35), PERW 0.30, MOQAW 0.11, MOQPW 0.16, MOQL 0.17. Length of leg segments: I 0.67 + 0.27 + 0.57 + 0.51 + 0.28 = 2.30; II 0.59 + 0.23 + 0.48 + 0.44 + 0.27 = 2.01; III 0.51 + 0.21 + 0.33 + 0.43 + 0.25 = 1.73; IV 0.68 + 0.25 + 0.54 + 0.60 + 0.29 = 2.36.

Colour: carapace deep orange-brown, pits and lateral margins brown; chelicerae yellow-brown; endites and labium yellow-brown proximally, distal ends cream; sternum bright yellow-orange, pit margins yellow-brown, lateral margins deep yellow-brown; palps creamy-yellow; legs with femora I and II pale yellow-brown, becoming progressively paler on III and IV, remaining segments creamy-yellow; abdomen dark grey dorsally and laterally, dorsally with seven fine cream chevrons in posterior half to spinnerets; venter paler mottled grey; spinnerets cream.

Leg spination: femora and patellae: spineless; tibiae: I plv 6 rlv 5, II plv 5 rlv 4; metatarsi: I plv 4 rlv 4, II plv 4 rlv 4; tarsi: I plv 3 rlv 3, II plv 3 rlv 3.

Epigyne with small copulatory openings positioned anterolaterally in shallow M-shaped ridges (Fig. 54); copulatory ducts short and C-shaped, initially curving mesally, then laterally before entering teardrop-shaped lateral primary spermathecae along their interior margin; bursae large, elongate-oval, almost twice the size of primary spermathecae (Fig. 55).



FIGURES 54–58. *Capobula capensis* **spec. nov.**, genitalic morphology of female (54–55) and male (56–58) paratypes from Pakhuis Pass: 54 Epigyne, ventral; 55 Vulva, dorsal; 56–58 Left palp (56 prolateral, 57 ventral, 58 retrolateral). Scale bars = 0.25 mm. Abbreviations: b—bursa; cd—copulatory duct; co—copulatory opening; ps—primary spermatheca.

Male (paratype, CAS, CASENT 9043335). Measurements: CL 0.83, CW 0.60, AL 0.77, AW 0.60, TL 1.61 (1.58–1.82), PERW 0.27, MOQAW 0.10, MOQPW 0.14, MOQL 0.15. Length of leg segments: I 0.57 + 0.22 + 0.46 + 0.41 + 0.27 = 1.93; II 0.50 + 0.22 + 0.38 + 0.39 + 0.25 = 1.74; III 0.41 + 0.21 + 0.29 + 0.37 + 0.24 = 1.52; IV 0.56 + 0.22 + 0.46 + 0.51 + 0.26 = 2.01.

Colour: carapace deep yellow, pits pale yellow-brown, lateral margins dark yellow-brown; chelicerae pale yellow-brown; endites yellow-brown medially, cream proximally and distally; labium yellow-brown, cream at distal end; sternum bright creamy-yellow, pit margins yellow, lateral margins yellow-brown; palps and legs creamy-yellow; abdomen with yellow dorsal scutum covered in dark grey mottling, cream with grey mottling laterally; venter with creamy-yellow epigastric and ventral sclerites, latter with faint grey mottling; spinnerets cream.

Leg spination: femora and patellae: spineless; tibiae: I plv 6 rlv 5, II plv 5 rlv 4; metatarsi: I plv 4 rlv 4, II plv 4 rlv 4; tarsi: I plv 3 rlv 3, II plv 3 rlv 3.

Palpal femur with spike-like retrolateral apophysis; patella with very faint retrolateral ridge; tibia with retrolateral tibial apophysis triangular in ventral view, broad and ridge-like in retrolateral view; embolus short and stout, tip directed retrodistally (Figs 56–58).

Habitat and biology. Mainly collected from litter or by hand in fynbos habitats.

Distribution. Only known from a few localities in the Western Cape, South Africa (Fig. 75).

Capobula infima **(Simon, 1896a) comb. nov.**

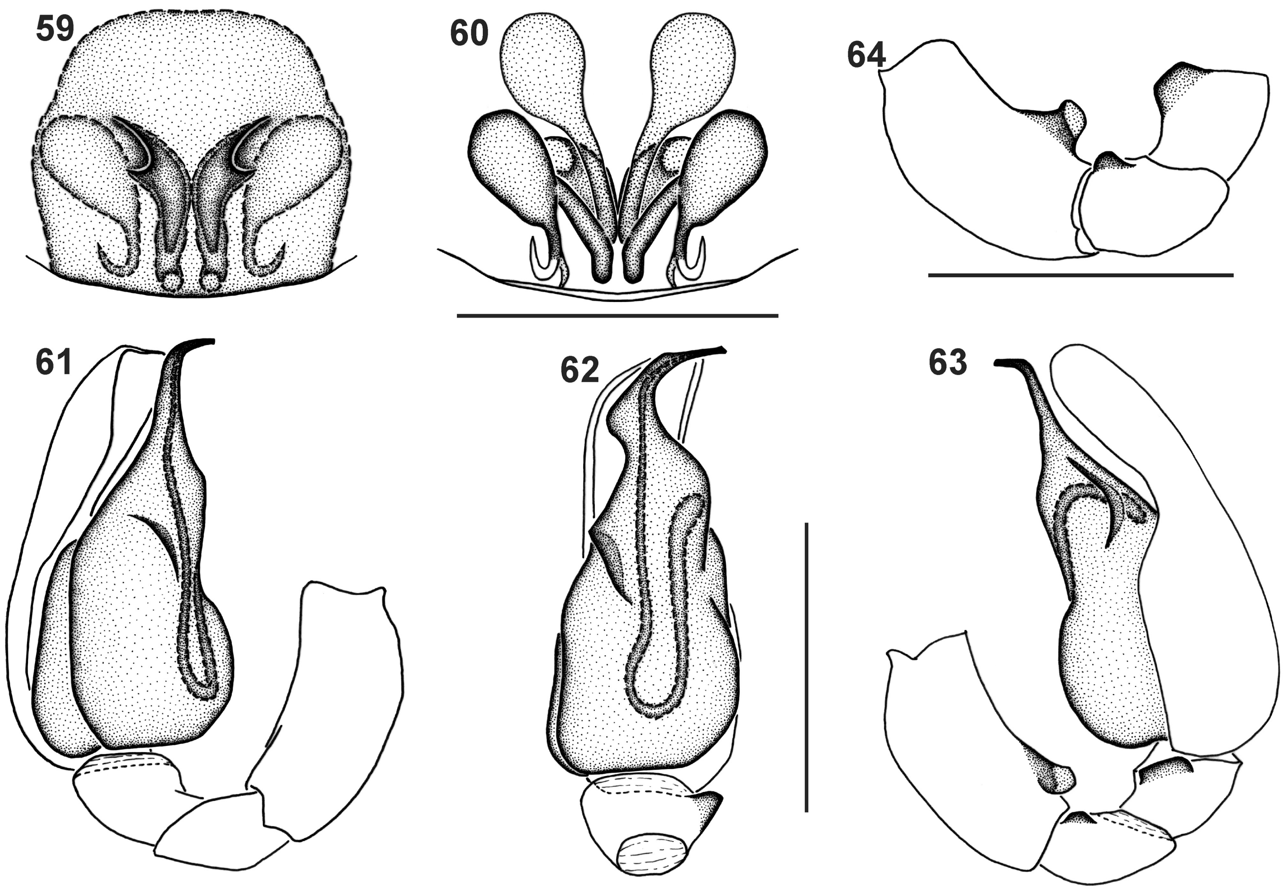
Figs 5, 6, 11–53, 59–64

Orthobula infima Simon, 1896a: 402 (Description of juvenile in generic *nomen nudum*; holotype juvenile: "Prom. Bonae Spei" {per original description, "Cap!" on label}, = Cape of Good Hope, MNHN 16457; examined).

Remarks. This species was described from a juvenile specimen from the Cape of Good Hope (Prom. Bonae Spei), i.e. the vicinity of modern-day Cape Town. Only a single species of *Capobula* has been sampled from this part of the Western Cape, and these specimens are presented here as the previously undescribed adults of *C. infima* **comb. nov.**

Additional material examined. SOUTH AFRICA: *Western Cape*: Brenton-on-Sea, 34°04'S, 23°02'E, 17.XI.1998, leg. H.G. Robertson (butterfly site, Winkler sample #4), 1♀ (SAMC ENW-C006112); Same locality, 19.XI.1998, leg. H.G. Robertson (forest site, Winkler sample #6), 1♀ (SAMC ENW-C006114); Same locality, 23.XI.1998, leg. H.G. Robertson (Old Strandveld site, Winkler sample #16), 1♀ (SAMC ENW-C006115); Cape Flats Nature Reserve [33°56'S, 18°37'E], III.1993, leg. A. Fortuin & M. Hendricks (pitfalls), 1♀ (SAMC C3217); Cape of Good Hope Nature Reserve, Olifantsbos nr Skaife Centre, Teeberg, Strandveld Mountain, 34°15.76'S, 18°23.13'E, X.1998, leg. H.G. Robertson (Winkler bag leaf litter, fynbos ecotone-dense bush), 1♀ (SAMC ENW-C005373), 1♀ (SAMC ENW-C005374); Same locality, X.1998, leg. H.G. Robertson (Winkler bag leaf litter, mesic mountain fynbos), 1♀ (SAMC ENW-C005371), 2♀ (SAMC ENW-C005372); Same locality, Smitswinkelvlakte, 34°15.6'S, 18°27.6'E, X.1998, leg. H.G. Robertson (Winkler bag leaf litter, mesic mountain fynbos on low-lying flat land), 1♂ (SAM-ENW-C005375); Cape Town, Robben Island [33°48'S, 18°22'E], 20.VIII.2004, leg. University of Cape Town (open range), 1♀ (NCA 2005/2001); De Hoop Nature Reserve, De Hoop Vlei, 34°29.425'S, 20°25.762'E, 8.IV.2004, leg. C. Haddad (milkwood leaf litter), 5♂ 14♀ (NCA 2008/1903); Same locality, Koppie Alleen, 34°28.534'S, 20°30.349'E, 5.IV.2004, leg. C. Haddad, 1♀ (SAMC ENW-C005351); Same locality, Lekkerwater road, 34°24.002'S, 20°33.151'E, 26.IX.2007, leg. C. Haddad (under *Thamnochortis*), 1♀ (NCA 2007/3654); Same locality, Potberg, *Eucalyptus* forest 34°22.237'S, 20°32.482'E, 8.IV.2004, leg. C. Haddad (leaf litter and creepers), 3♂ 2♀ (MHBU); Same data as previous but hand collecting, 2♂ 4♀ (MHBU); Fernkloof Nature Reserve, 2.81 km 43º NE of Hermanus, 34°23.677'S, 19°15.967'E, 97 m a.s.l., 12.X.2011, leg. L. Almeida (hand sorting of concentrated leaf litter from fynbos and riparian vegetation), 2♀ (CAS, CASENT 9043228, SA11-120); Same locality, 4.18 km 92º E of Hermanus, 34°24.857'S, 19°17.445'E, 13 m a.s.l., 13.X.2011, leg. L. Almeida & C. Griswold (general collecting in coastal white milkwood forest and bushes), 1♀ (CAS, CASENT 9043214, SA11-125); Fisherhaven, near Hermanus, 34°21.430'S, 19°07.557'E, 30.IX.2007, leg. R. Lyle & C. Haddad (sifting leaf litter), 3♀ (NCA 2008/219); Same locality, 19.III.2004, leg. C. Haddad (sifting leaf litter), 2♂ 2♀ (SAMC ENW-C005352); Same locality, 24.VI.2019, leg. C. Haddad (base of *Restio* spp. in fynbos), 4♀ (NCA 2019/429); Hartenbos, Bolandpark, 34°09.807'S, 22°06.388'E, 4.XII.2012, leg. J.A. Neethling (leaf litter, coastal fynbos), 1♀ (NCA 2019/1001); Langeberge, Grootvadersbosch, Honeywood Farm, 34°00.38'S, 20°49.69'E, 5–6.I.2013, leg. D. Ubick, 1♀ (CAS, CASENT 9055435); Table Mountain National Park, Cecilia, Rooikat, 33°59'S, 18°25'E, 4.X.2008, leg. C. Uys (site 10, leaf litter, fynbos), 1♀ (NCA 2011/879); Table Mountain National Park, Cecilia, Spilhaus, 34°00'S, 18°25'E, 23.I.2009, leg. C. Uys (site 14, pitfall trap, fynbos), 1♀ (NCA 2011/878); Table Mountain National Park, Kirstenbosch, 33°59'S, 18°25'E, 12.IX.2008, leg. C. Uys (site 6, leaf litter, fynbos), 1imm. 1♀ (NCA 2011/851); Table Mountain National Park, Newlands, 33°58'S, 18°26'E, 15.I.2009, leg. C. Uys (site 2, sugar-baited ant trap, pine plantation), 1♀ (NCA 2011/875); Same locality, 15.I.2009, leg. C. Uys (site 2, pitfall trap, pine plantation), 1♀ (NCA 2011/883); Same locality, 12.IX.2008, leg. C. Uys (site 4, leaf litter, pine plantation), 1♀ (NCA 2011/873); Table Mountain National Park, Orange Kloof, 34°05'S, 18°14'E, 18.XI.2008, leg. C. Uys (site 22, leaf litter, pine plantation), 1♀ (NCA 2011/850); Same locality, 28.I.2009, leg. C. Uys (site 23, pitfall traps, felled pine), 1♀ (NCA 2011/874); Table Mountain National Park, Tokai South, 34°04'S, 18°24'E, 9.I.2009, leg. C. Uys (site 30, pitfall trap, fynbos), 1♀ (NCA 2011/877); Same locality, 19.I.2009, leg. C. Uys (site 32, pitfall trap, felled pine), 1♀ (NCA 2011/876).

Diagnosis. Females have a similar epigyne to *C. montana* **spec. nov.** and *C. neethlingi* **spec. nov.**, but the initial 2/3 of the copulatory ducts are heavily sclerotized and much darker than the posterior 1/3, while in the other two species only the initial 1/3 of the copulatory ducts is heavily sclerotized. Further, the anterior margin of the ridges incorporating the copulatory openings is in the same transverse plane as the anterior margin of the primary spermathecae, while more posteriorly positioned in the other two species (compare Fig. 59 with Figs 65 and 71). Males of *C. infima* **comb. nov.** can be distinguished from *C. capensis* **spec. nov.** and *C. montana* **spec. nov.** by the considerably longer and more strongly curved distal section of the embolus (compare Fig. 62 with Figs 57 and 68).



FIGURES 59–64. *Capobula infima* (Simon, 1896) **comb. nov.**, genitalic morphology of female (59, 60) and male (61–64) from De Hoop Nature Reserve: 59 Epigyne, ventral; 60 Vulva, dorsal; 61–63 Left palp (61 prolateral, 62 ventral, 63 retrolateral); 64 Palpal femur, patella and tibia, retro-dorsal. Scale bars = 0.25 mm.

Female (De Hoop, NCA 2008/1903). Measurements: CL 0.90, CW 0.70, AL 1.19, AW 1.02, TL 2.25 (1.70–2.25), PERW 0.30, MOQAW 0.13, MOQPW 0.18, MOQL 0.17. Length of leg segments: I 0.63 + 0.24 + 0.56 + 0.48 + 0.28 = 2.19; II 0.57 + 0.24 + 0.44 + 0.41 + 0.25 = 1.91; III 0.50 + 0.22 + 0.38 + 0.40 + 0.23 = 1.73; IV 0.62 + 0.24 + 0.51 + 0.57 + 0.29 = 2.23.

Colour: carapace deep orange-brown, pits slightly darker, lateral margins brown; chelicerae orange-brown; endites and labium yellow-brown proximally, distal ends cream; sternum yellow-orange, pits slightly darker, lateral margins yellow-brown; palps pale yellow-brown; legs with femora and tibiae I and II pale orange-brown, other segments yellow; legs III and IV yellow, distal segments slightly paler than proximal; abdomen dark grey dorsally and laterally, with cream spots at setal bases, dorsally with eight fine cream chevrons in posterior half to spinnerets; venter paler mottled grey medially; spinnerets cream.

Leg spination: femora and patellae: spineless; tibiae: I plv 6 rlv 5, II plv 5 rlv 4; metatarsi: I plv 4 rlv 4, II plv 4 rlv 4; tarsi: I plv 3 rlv 3, II plv 3 rlv 2.

Epigyne with copulatory openings in large J-shaped epigynal ridges (Fig. 59); copulatory ducts relatively thick, initially curving mesally, then directed posteriorly along midline, looping dorsally and laterally before entering lateral teardrop-shaped primary spermathecae along their interior margin; bursae oval, similar in size to primary spermathecae (Fig. 60).

Male (De Hoop, NCA 2008/1903). Measurements: CL 0.89, CW 0.67, AL 0.83, AW 0.62, TL 1.78 (1.75–1.90), PERW 0.29, MOQAW 0.12, MOQPW 0.17, MOQL 0.16. Length of leg segments: I 0.62 + 0.24 + 0.52 + 0.43 + 0.26 = 2.07; II 0.52 + 0.23 + 0.41 + 0.40 + 0.25 = 1.81; III 0.44 + 0.19 + 0.35 + 0.37 + 0.23 = 1.58; IV 0.59 + 0.23 + 0.48 + 0.52 + 0.27 = 2.09.

Colour: carapace deep orange-brown, pits and lateral margins brown; chelicerae dark yellow-brown; endites pale yellow-brown medially, cream distally; labium yellow-brown, darker than endites, cream at distal end; sternum bright yellow-orange, pit margins orange, lateral margins orange-brown; palps yellow-brown; legs with femora and tibiae I and II pale orange-brown, patellae and metatarsi yellow-brown, tarsi creamy-yellow; legs III and IV pale yellow-brown, progressively paler distally; abdomen with bright yellow dorsal scutum covered in dark grey mottling, cream with grey mottling laterally; venter with creamy-yellow epigastric and ventral sclerites, latter covered in grey mottling; spinnerets cream.

Leg spination: femora and patellae: spineless; tibiae: I plv 6 rlv 5, II plv 6 rlv 5; metatarsi: I plv 5-7 rlv 4, II plv 5 rlv 4; tarsi: I plv 4 rlv 3, II plv 4 rlv 2-3.

Palpal femur with stout thumb tip-like ventral apophysis; patella with small subtriangular retrolateral ridge; tibia with tibial apophysis short and triangular in ventral view, broad and ridge-like in retrolateral view; embolus larger than in congeners, S-shaped, width larger than ½ width of tegulum at midpoint, tip curved and directed retrolaterally (Figs 61–63).

Habitat and biology. Commonly found in leaf litter in fynbos habitats, particularly in litter of broadleaved plants such as milkwood (*Sideroxylon inerme*) and dune guarri (*Euclea racemosa*) in coastal regions and *Protea* spp. away from coastal habitats.

Distribution. Only known from the Western Cape Province of South Africa (Fig. 75).

Capobula montana **spec. nov.**

Figs 7, 8, 65–70

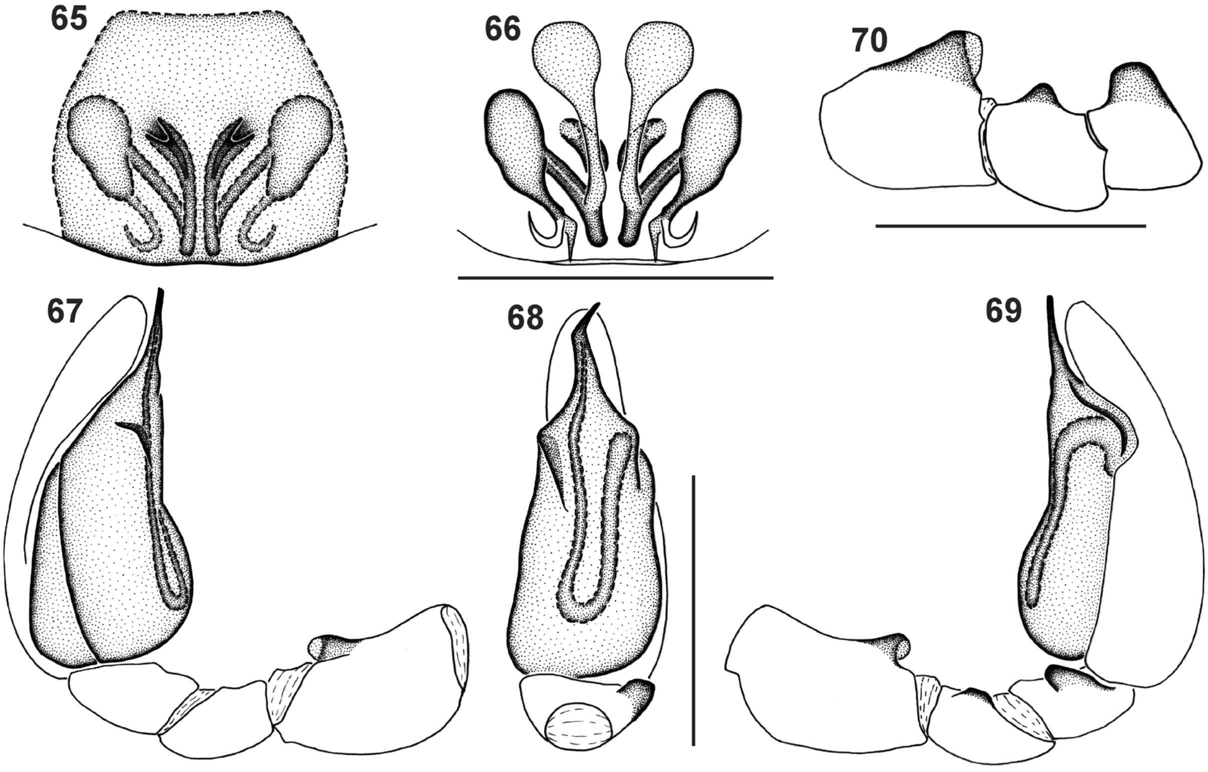
Type material. Holotype ♀: **SOUTH AFRICA:** *Eastern Cape*: Mount Coke State Forest, 32°59.452'S, 27°28.740'E, 395 m a.s.l., 29.XI.2013, leg. J. Neethling (leaf litter, Afromontane forest) (NCA 2013/4565). **Paratypes**: **LESOTHO:** *Butha Buthe district*: Valley near Butha Buthe, 28°48'S, 28°16'E, 2150 m a.s.l., 31.VII.2012, leg. J. van Niekerk (under rocks on mountainside), 1♂ (MHBU). *Maseru district*: Mohale Dam, Island 2, 29°25.396'S, 28°05.903'E, 2025 m a.s.l., 14.XII.2003, leg. C. Haddad (under rocks on hillside), 1♀ (MHBU). *Quthing district*: Ha Lazaro, Letšeng-le-Letsie, 30°18.207'S, 28°07.872'E, 2355 m a.s.l., 11.XI.2005, leg. C. Haddad (under rocks on hillside), 1♀ (NCA 2020/102). **SOUTH AFRICA:** *Eastern Cape*: Amatola Mountains, Hogsback, 32°36.285'S, 26°56.580'E, 27.III.2007, leg. C. Haddad (active searching, knee down), 3♀ (NCA 2007/1191); Cradock, 32°09.535'S, 25°35.496'E, 23.IV.2010, leg. C. Haddad (base of grass tussocks, roadside), 2♀ (TMSA 23765); Grahamstown Municipal Caravan Park, 33°19.166'S, 26°31.326'E, 580 m a.s.l., 10–19.II.2006, leg. J. Miller, H. Wood & L. Lotz (forest), 1♂ (CAS, CASENT 9068190); Humansdorp District, Tsitsikamma Forest, 33°50'S, 24°30'E, I.1961, leg. N. Leleup, 1♂ (MRAC 139801); Shamwari Game Reserve, 33°27.983'S, 26°03.033'E, 13.VII.2005, leg. C. Haddad & R. Lyle (under logs), 1♂ (NCA 2008/2014); Somerset East, Bestershoek Nature Reserve, 32°42.475'S, 25°34.293'E, 882 m a.s.l., 2.XII.2012, leg. J.A. Neethling (leaf litter, montane thicket), 1♀ (NCA 2020/101). *Free State*: Harrismith, Platberg Nature Reserve, 28°16.842'S, 29°12.024'E, 2040 m a.s.l., 13.XI.2015–26.I.2016, leg. C. Haddad, D. Fourie & Z. Mbo (pitfall traps, alpine grassland), 1♂ (NCA 2015/2312); Same locality, 28°16.900'S, 29°12.015'E, 13.III.2012, leg. J.A. Neethling (leaf litter, dry mountain runoff, thicket), 1♂ 1♀ (MHBU).

Additional material examined. LESOTHO: *Butha Buthe*: Near Butha Buthe, 28°47'S, 28°15'E, 1780 m a.s.l., 14.XII.2012, leg. J. van Niekerk (under rocks on mountainside), 1♀ (NCA 2019/1004). **SOUTH AFRICA:**

Eastern Cape: Baviaanskloof, Keurkloof, Farm Ferndale, 33°41'S, 24°50'E, 21–24.III.2008, leg. A.S. Honiball & S. Hohowsky (pitfalls), 1♂ (NCA 2020/104); Greater Addo Elephant National Park, 33°27.783'S, 25°47.017'E, IV.2011, leg. B. Milne (pitfall traps), 1♀ (NCA 2020/105). *Free State*: Bloemfontein, Free State National Botanical Gardens, 29°03'S, 26°12'E, 1380 m a.s.l., 8.V–8.VII.2018, leg. C. Haddad & L. Mosese (pitfalls, *Searsia lancea* and grassland), 1♀ (NCA 2019/514); Clocolan district, Mpetsane Conservation Estate, 28°48'S, 27°39'E, 9.III.2007, leg. C. Haddad (*Eucalyptus* leaf litter), 1♀ (NCA 2008/557); Same locality, 17.III.2010, leg. C. Haddad (base of grass tussocks), 1♀ (NCA 2010/345); Golden Gate Highlands National Park, 28°26.157'S, 28°43.560'E, 1771 m a.s.l., 19–21.III.2019, leg. J. Botham (shrubland patch 1, soil sampling 10 m inside patch), 1♀ (NCA 2019/1006); Same locality, 28°31.081'S, 28°34.528'E, 1880 m a.s.l., 19–21.III.2019, leg. J. Botham (shrubland patch 6, leaf litter sifting), 1♀ (NCA 2019/1005); Harrismith, Platberg Nature Reserve, 28°16.137'S, 29°11.172'E, 14.III.2012, leg. J.A. Neethling (leaf litter, mountain runoff, *Eucalyptus* plantation), 1♀ (NCA 2020/103); Luckhof district, Farm Bankfontein, 30°03.466'S, 24°53.653'E, 1235 m a.s.l., 25–28.IV.2019, leg. H. Badenhorst & C. Haddad (Berlese-Tullgren extraction, kloof litter), 1♀ (NCA 2019/887); Tussen-die-Riviere Nature Reserve, 30°27.797'S, 26°07.849'E, 1280 m a.s.l., 14.IV.2012, leg. University of the Free State students (leaf litter, shrubs in open grassland), 3♀ (NCA 2019/1003).

Diagnosis. Females of *C. montana* **spec. nov.** have a similar epigyne to that of *C. neethlingi* **spec. nov.**, but can be distinguished by the V- rather than J-shaped ridges containing the copulatory openings, the slightly separated copulatory ducts (touching medially in *C. neethlingi* **spec. nov.**), and the bursae that are separated by approximately half their diameter, while almost touching in *C. neethlingi* **spec. nov.** (compare Figs 65 and 66 with Figs 71 and 72). Males of *C. montana* **spec. nov.** share with *C. capensis* **spec. nov.** the relatively short distal section of the embolus, but can be distinguished by the lobate rather than spike-like femoral apophysis, and the subtriangular rather than ridge-like retrolateral tibial apophysis (compare Figs 67–70 and 56–58).

Etymology. The species name reflects the predominantly montane habitats that this species has been sampled from; Latin adjective.



FIGURES 65–70. *Capobula montana* **spec. nov.**, genitalic morphology of female (65, 66) and male (67–70) paratypes from Platberg Nature Reserve: 65 Epigyne, ventral; 66 Vulva, dorsal; 67–69 Left palp (67 prolateral, 68 retrolateral, 69 retrolateral); 70 Palpal femur, patella and tibia, retro-dorsal. Scale bars = 0.25 mm.

Female (holotype, Mount Coke, NCA 2013/4565). Measurements: CL 0.87, CW 0.69, AL 1.08, AW 0.94, TL 2.15 (1.73–2.30), PERW 0.30, MOQAW 0.11, MOQPW 0.17, MOQL 0.16. Length of leg segments: I 0.63 + 0.24

+ 0.52 + 0.47 + 0.27 = 2.13; II 0.54 + 0.22 + 0.43 + 0.39 + 0.25 = 1.83; III 0.46 + 0.21 + 0.36 + 0.38 + 0.24 = 1.65; IV 0.62 + 0.24 + 0.51 + 0.59 + 0.29 = 2.25.

Colour: carapace deep orange-brown, pits and lateral margins brown; chelicerae dark yellow-brown; endites and labium yellow-brown proximally, distal ends cream; sternum orange-brown, pits slightly darker, lateral margins brown; palps pale yellow-brown; legs with femora and tibiae I and II dark yellow-brown, other segments paler yellow-brown, similar to legs III and IV; all tarsi lightly paler; abdomen dark grey dorsally and laterally, with cream spots at setal bases, dorsally with seven indistinct fine cream chevrons in posterior half to spinnerets; venter paler mottled grey; spinnerets cream.

Leg spination: femora and patellae: spineless; tibiae: I plv 6 rlv 5, II plv 5 rlv 4; metatarsi: I plv 4 rlv 4, II plv 4 rlv 4; tarsi: I plv 4 rlv 3, II plv 4 rlv 2.

Epigyne with copulatory openings in small cup-shaped ridges (Fig. 65); copulatory ducts thin, initially curving mesally, then directed posteriorly along midline, looping dorsally and laterally before entering lateral teardrop-shaped primary spermathecae along their interior margin; bursae globular, slightly smaller than primary spermathecae (Fig. 66).

Male (paratype, Shamwari, NCA 2008/2014). Measurements: CL 0.83, CW 0.62, AL 0.83, AW 0.60, TL 1.78 (1.73–1.94), PERW 0.29, MOQAW 0.11, MOQPW 0.16, MOQL 0.15. Length of leg segments: I 0.54 + 0.22 + 0.49 + 0.43 + 0.25 = 1.93; II 0.51 + 0.22 + 0.38 + 0.37 + 0.24 = 1.72; III 0.43 + 0.19 + 0.34 + 0.36 + 0.24 = 1.56; IV 0.53 + 0.23 + 0.46 + 0.52 + 0.28 = 2.02.

Colour: carapace orange-brown, pits and lateral margins brown; chelicerae dark yellow-brown; endites and labium yellow-brown proximally and medially, cream distally; sternum bright yellow-orange, pit margins orange, lateral margins orange-brown; palps pale yellow-brown; legs with femora I yellow-brown, remaining segments yellow, except tarsi creamy-yellow; abdomen with bright yellow dorsal scutum covered in dark grey mottling, sides mottled dark grey; venter mottled pale grey, with bright yellow epigastric and ventral sclerites; spinnerets cream.

Leg spination: femora and patellae: spineless; tibiae: I plv 6 rlv 5, II plv 6 rlv 4; metatarsi: I plv 6 rlv 4, II plv 6 rlv 4; tarsi: I plv 4 rlv 4, II plv 4 rlv 3.

Palpal femur with short thumb tip-like ventral apophysis; patella with small, broad subtriangular retrolateral ridge; tibia with tibial apophysis short and triangular in ventral view, triangular and proximally directed in retrolateral view; embolus shorter and narrower than in congeners, tip slightly bent and directed retrodistally (Figs 67–70).

Habitat and biology. A litter-dwelling species mainly sampled from the litter of shrubs and trees in various biomes, including Grassland, Thicket, Fynbos, Nama Karoo and Afromontane Forests. This is the species that occupies the greatest altitudinal range, from approximately 250–2350 m a.s.l.

Distribution. Widespread in the central and south-eastern parts of South Africa (Fig. 75).

Capobula neethlingi **spec. nov.**

Figs 9, 71, 72

Type material. Holotype ♀: **SOUTH AFRICA:** *Western Cape*: George, Saasveld Pass, 33°58.198'S, 22°31.778'E, 149 m a.s.l., 7.XII.2012, leg. J. Neethling (leaf litter, indigenous forest) (NCA 2019/1002a). **Paratypes**: together with holotype, 1♀ (NCA 2019/1002b). **SOUTH AFRICA:** *Western Cape*: Laingsburg, Anysberg Nature Reserve, 33°27.300'S, 20°34.862'E, 735 m a.s.l., 8.IX–8.X.2015, leg. Z. Mbo (pitfall traps, karoo veld) (NCA 2016/2464); Swartberg Nature Reserve, Gamkaskloof, 33°21'S, 21°41'E, 15.I.2001, leg. Z. van der Walt (on ground), 2♀ (NCA 2002/198).

Diagnosis. Females of *C. neethlingi* **spec. nov.** have a similar epigyne to that of *C. montana* **spec. nov.**, but can be distinguished by the V- rather than J-shaped ridges containing the copulatory openings, the slightly separated copulatory ducts (touching medially in *C. neethlingi* **spec. nov.**), and the bursae that are separated by approximately half their diameter, while almost touching in *C. neethlingi* **spec. nov.** (compare Figs 71 and 72 with Figs 65 and 66). Male unknown.

Etymology. Named for arachnologist Jan Andries Neethling, who collected the holotype; name in genitive case.

Female (holotype, NCA 2019/1002). Measurements: CL 0.84, CW 0.64, AL 1.02, AW 0.87, TL 1.95 (1.80–1.98), PERW 0.30, MOQAW 0.12, MOQPW 0.15, MOQL 0.16. Length of leg segments: I 0.60 + 0.24 + 0.52 +

0.45 + 0.25 = 2.06; II 0.54 + 0.23 + 0.41 + 0.38 + 0.24 = 1.80; III 0.46 + 0.21 + 0.33 + 0.38 + 0.23 = 1.61; IV 0.59 + 0.24 + 0.49 + 0.56 + 0.27 = 2.15.

Colour: carapace deep orange-brown, with black mottling at centre, pits and lateral margins with black edges; chelicerae deep yellow-brown, with faint black mottling; endites and labium yellow-brown, cream at distal ends; sternum bright orange, pits slightly darker, lateral margins orange-brown; palps pale yellow-brown; legs with femora and tibiae I and II pale orange-brown, yellow-brown distally; patellae, metatarsi and tarsi I and II, and legs III and IV yellow-brown; abdomen dark grey dorsally and laterally, dorsally with eight fine cream chevrons in posterior half to spinnerets; venter slightly paler mottled grey; spinnerets cream.

Leg spination: femora and patellae: spineless; tibiae: I plv 6 rlv 6, II plv 6 rlv 5; metatarsi: I plv 4 rlv 4, II plv 4 rlv 4; tarsi: I plv 3 rlv 3, II plv 3 rlv 2.

Epigyne with small copulatory openings in J-shaped epigynal ridges (Fig. 71); copulatory ducts initially curving medially, then posteriorly, looping dorsally and anterolaterally before entering teardrop-shaped primary spermathecae along their interior margin; bursae subtriangular, apices converging mesally, similar in size to primary spermathecae (Fig. 72).

Habitat and biology. This species was recorded in two very contrasting biotopes, *viz*. moist Afromontane Forest and xeric Nama Karoo.

Distribution. Only known from three localities in the Western Cape Province, South Africa (Fig. 75).

Capobula ukhahlamba spec. nov.

Figs 10, 73, 74

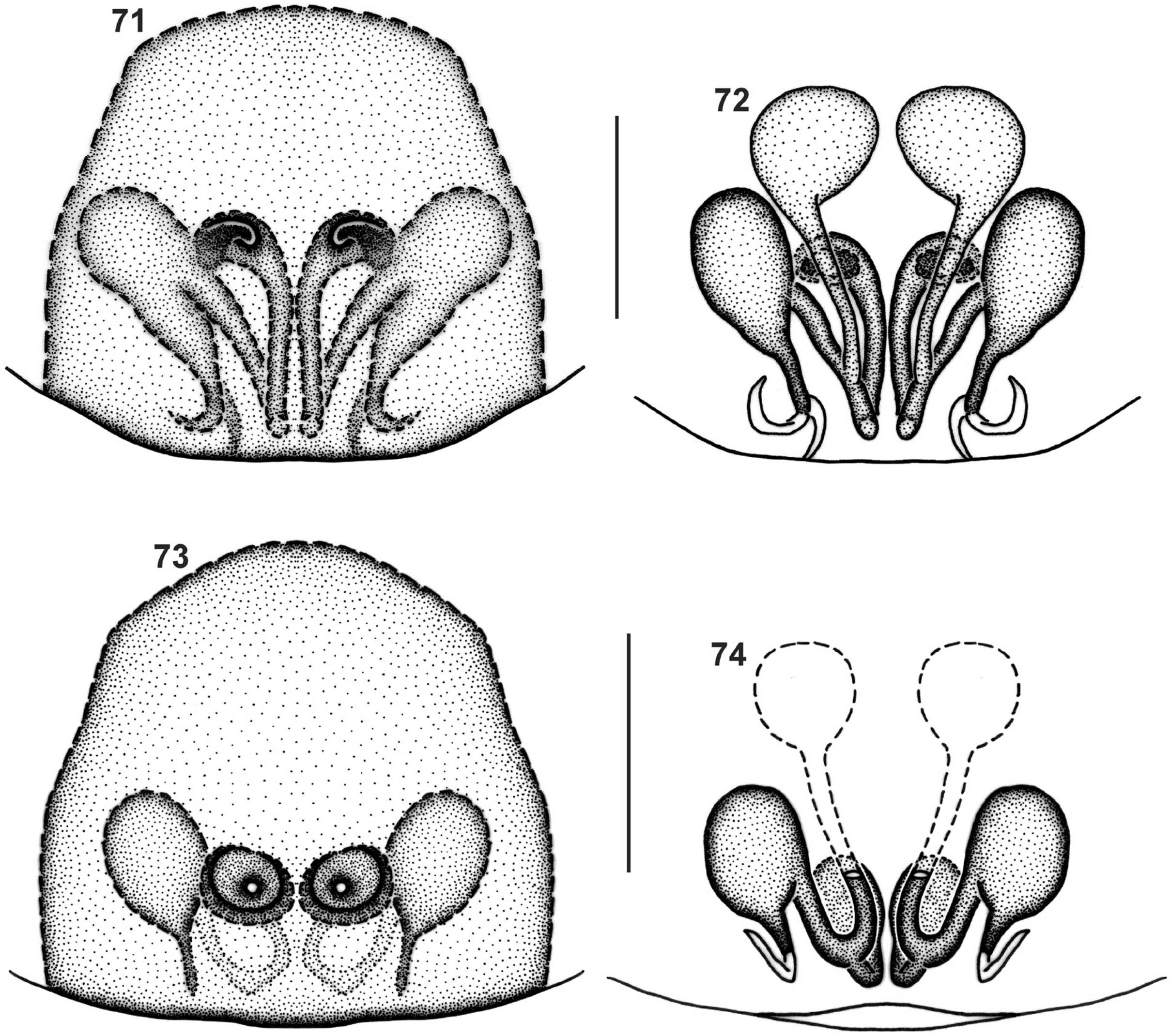
Type material: Holotype ♀: **SOUTH AFRICA:** *KwaZulu-Natal*: Champagne Castle, Hlathikulu Forest, 29°02.366’S, 29°23.421’E, 1560 m a.s.l., 20.I.2011, leg. C. Haddad (base of grass tussocks, grassland-forest ecotone) (NCA 2018/35). **Paratypes**: **SOUTH AFRICA:** *KwaZulu-Natal*: Cathedral Peak Forest Station, 75 km WSW Estcourt, 1380 m a.s.l., 14.XII.1979, leg. S. & J. Peck (*Leucosidea* boulder bush scrub, night sweeping), 1♀ (AMNH); Didima National Park, Cathedral Peak area, Rainbow Gorge, 33.5 km WSW of Winterton, 28°57.600’S, 29°13.635’E, 1518 m a.s.l., 19.I.2011, leg. H. Wood & C. Griswold (sifting leaf litter, Afromontane forest), 1♀ (CAS, CASENT 9043022, SA11-041); Same locality, 28°56.982’S, 29°13.874’E, 1400 m a.s.l., 19.I.2011, leg. C. Haddad (base of grasses and ferns), 1♀ (MHBU); Royal Natal National Park, 38.6 km W of Bergville, 28°41.137’S, 28°57.425’E, 1403 m a.s.l., 21.I.2011, leg. H. Wood, C. Haddad & C. Griswold (general collecting in ferns and grass tussocks), 1♀ (CAS, CASENT 9043423, SA11-046); Sani Pass, IX.2006, leg. D. Prentice (pitfall traps), 1♀ (NCA 2008/1982); Sani Pass elevational project, Ixopo, 30°11.010’S, 30°09.130’E, 900 m a.s.l., 1.I.2009, leg. Univ. of Pretoria students (pitfall traps, site 8a), 1♀ (NCA 2011/774).

Diagnosis. Females can be easily distinguished by the large circular ridges surrounding the copulatory openings (Fig. 73), the oval rather than teardrop-shaped primary spermathecae (Fig. 74), and the presence of a cream Y-shaped marking on the abdominal dorsum (Fig. 10), which is absent in the other species (Figs 3–9). Male unknown.

Remarks. Although the male of this species is unknown and the female has an inverted Y-shaped cream marking that it absent in congeners, we place this species in *Capobula* and not *Orthobula* because of the absence of pits along the dorsal midline of the carapace and the anterolaterally-positioned spermathecae; name in apposition.

Etymology. Taken from the name of the Ukhahlamba-Drakensberg Transfrontier Conservation Park, a conservation initiative between South Africa and Lesotho, which includes the distribution range of this species. Ukhahlamba is the isiZulu word meaning “barrier of spears”; noun in apposition.

Female (holotype, NCA 2018/35). Measurements: CL 0.89, CW 0.67, AL 1.06, AW 0.89, TL 2.15 (2.03–2.15), PERW 0.39, MOQAW 0.12, MOQPW 0.16, MOQL 0.15. Length of leg segments: I 0.54 + 0.22 + 0.48 + 0.41 + 0.27 = 1.92; II 0.48 + 0.22 + 0.37 + 0.37 + 0.25 = 1.69; III 0.41 + 0.19 + 0.33 + 0.33 + 0.24 = 1.50; IV 0.57 + 0.24 + 0.48 + 0.54 + 0.30 = 2.13.



FIGURES 71–74. *Capobula neethlingi* **spec. nov.** (71, 72) and *C. ukhahlamba* **spec. nov.** (73, 74), genitalic morphology of paratype females from Anysberg Nature Reserve and Cathedral Peak, respectively: 71, 73 Epigyne, ventral; 72, 74 Vulva, dorsal. Scale bars = 0.1 mm.

Colour: carapace orange-brown, pits and lateral margins brown; chelicerae yellow-brown; endites and labium yellow-brown proximally, distal third cream; sternum yellow, pit margins and lateral margins yellow-brown; palps and legs creamy-yellow; abdomen dark grey dorsally and laterally, dorsally with diverging cream Y-shaped marking in anterior half, narrow cream chevrons in posterior half; venter cream, with faint grey mottling; spinnerets cream.

Leg spination: femora and patellae: spineless; tibiae: I plv 6 rlv 5, II plv 5 rlv 4; metatarsi: I plv 4 rlv 4, II plv 4 rlv 4; tarsi: I plv 3 rlv 3, II plv 3 rlv 2.

Epigyne with tiny copulatory openings in round epigynal ridges (Fig. 73); copulatory ducts initially curving medially, looping posteriorly, then laterally, before entering anterolateral primary spermathecae along mesal margin; bursae small and spherical (Fig. 74).

Habitat and biology. Distributed in montane grasslands at elevations between 900–1600 m a.s.l.

Distribution. Only known from KwaZulu-Natal, South Africa, with most records from the Drakensberg Mountains (Fig. 75).

Discussion

Phylogenetic analyses

The molecular analyses performed in this study were the first to focus on the Trachelidae and Phrurolithidae families and some of their associated genera. Even though only a single gene was used, an indication of species-level and, to some extent, genus-level relationships were provided. Overall, both phylogenetic analyses (Figs 1–2) showed similar tree topologies, but differ in the placement of *Jocquestus schenkeli*, *Trachelas japonicus* and *Planochelas haddadi*. Both phylogenetic analyses placed *Capobula* **gen. nov.** as a close relative of *Orthobula* (100% bpp and 94% BS, respectively; Figs 1–2), complementing the morphological findings and supporting the hypothesis that these two genera are closely related.

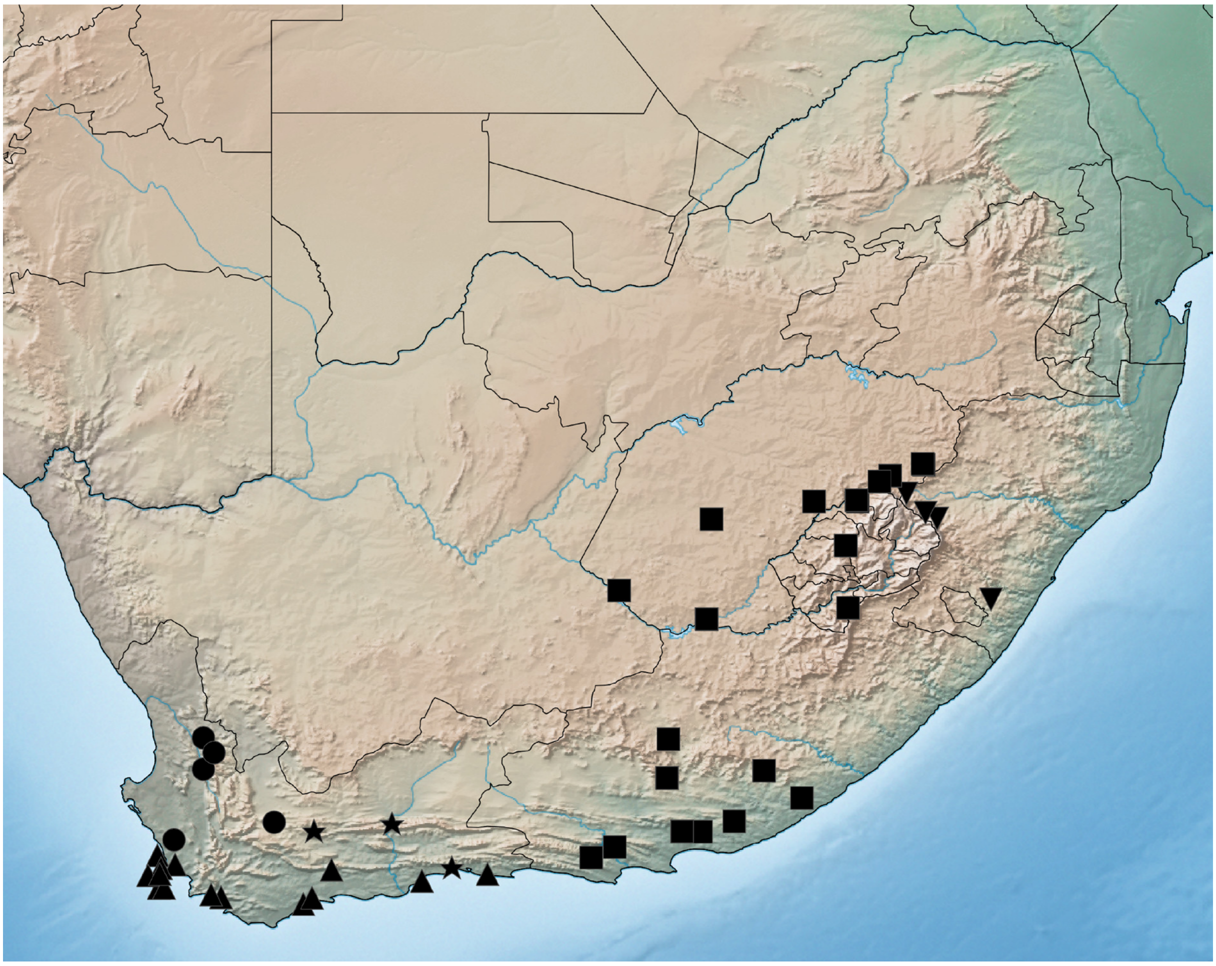


FIGURE 75. Distribution of *Capobula capensis* **spec. nov.** (circles), *C. infima* (Simon, 1896) **comb. nov.** (triangles), *C. montana* **spec. nov.** (squares), *C. neethlingi* **spec. nov.** (stars) and *C. ukhahlamba* **spec. nov.** (inverted triangles) in southern Africa.

However, due to the limitations of using a single gene for a phylogenetic analysis, the molecular analyses alone would not, in this instance, be sufficient to establish a new genus (DeSalle *et al.* 2005), and thus the establishment of *Capobula* **gen. nov.** was based only on their unique somatic and genitalic morphology. Nonetheless, *Orthobula* and *Capobula* **gen. nov.** were recovered as part of the Trachelidae, confirming the results of Wheeler *et al.* (2017) that used six genes in total and placed *Orthobula* in Trachelidae, sister to *Utivarachna*. In our analysis, these two genera formed part of a clade also including several New World *Trachelas* species (Clade B).

In contrast, Afrotropical trachelids that could be broadly placed into *Trachelas* (Clade F and G), *Thysanina* (Clades D, F & G) and *Poachelas* (Clades E & F), as currently defined, were recovered as polyphyletic and show genetic variation, but the support values for these placements are variable and were not strong, with generally less than 70% support in bootstrap and posterior probabilities. However, consideration of the morphology of the representatives of these genera placed in different clades is actually quite informative. In the case of *Thysanina*, for example, the species included in Clade D are characterized by the presence of true leg spines, cusps on the anterior tibiae, metatarsi and tarsi, an oval abdomen and variable genitalic structure (i.e. *T. transversa* Lyle & Haddad, 2006 and undescribed species). Those in clade F lack leg spines, possess cusps on the anterior tibiae, metatarsi and tarsi, have an oval abdomen, and have variable genitalic morphology (i.e. *T. gracilis* Lyle & Haddad, 2006 and undescribed species); these characteristics are shared with the type species, *T. serica* Simon, 1910, and would therefore represent *Thysanina sensu stricto* (Lyle & Haddad 2006). Lastly, the species in clade G (all undescribed) lack leg spines and tibial cusps (but have metatarsal and tarsal cusps), have an elongate-oval abdomen, and have very conservative genitalic morphology.

In summary, although the use of a single gene in making taxonomic decisions should be avoided, there is adequate and congruent morphological evidence that supports the new genus described in this paper. Even in the absence of the COI-based phylogenies produced here, the new genus' description would have been strongly supported by its unique somatic and genitalic morphology. The COI-based phylogeny was nonetheless useful in identifying the plausible sister group of the new genus and potential problem areas in trachelid systematics that require further investigation. It will be interesting to compare these results with future multigene analyses of Trachelidae and assess to what extent the COI marker is useful to infer phylogenetic relationships.

Biogeography

The distribution of *Capobula* **gen. nov.**, currently only known from South Africa and the enclave of Lesotho, shows some overlap with other genera endemic to the subregion (Foord *et al.* 2020). Three of the five species (*C. capensis* **spec. nov.**, *C. infima* **comb. nov.** and *C. neethlingi* **spec. nov.**) show a narrow affinity to the Cape Floristic Region and Succulent Karoo biodiversity hotspots in the south-western part of the country, while a fourth species (*C. ukhahlamba* **spec. nov.**) is restricted to alpine grasslands in the Maputaland-Pondoland-Albany biodiversity hotspot (*sensu* Myers *et al.* 2000). Only one species, *C. montana* **spec. nov.**, has a distribution extending into the central plateau of South Africa; this species also displays the greatest altitudinal range, having been collected between 250 and 2350 m a.s.l., the latter in the Maluti-Drakensberg Mountains.

The distribution of the genus, which conspicuously excludes the more arid and undersampled north-western parts of South Africa (Northern Cape and North West provinces; Foord *et al.* 2020), is mirrored by several other presumed endemic genera, including the endemic family Penestomidae (Miller *et al.* 2010b), amaurobiid genus *Chumma* Jocqué, 2001 (Jocqué & Alderweireldt 2018), the archaeid genus *Afrarchaea* Forster & Platnick, 1984 (e.g. Lotz 1996, 2003, 2006), the gallieniellid genera *Austrachelas* Lawrence, 1938 (Haddad *et al.* 2009; Haddad & Mbo 2017) and *Drassodella* Hewitt, 1916 (Mbo & Haddad 2019), and the zoropsid genera *Phanotea* Simon, 1896b (Griswold 1994) and *Griswoldia* Dippenaar-Schoeman & Jocqué, 1997 (Griswold 1991), amongst others. However, in most of these genera there are species occurring to the north-east of the country, while *Capobula* **gen. nov.** is restricted to more temperate latitudes south of 28°S, a pattern shared among these examples with *Chumma*. Further studies of presumed South African endemics are necessary to provide baseline data to better explain the overriding influence of climatic and topographical factors in shaping spider distributions and patterns of endemism.

Acknowledgments

This paper is dedicated to the memory of co-author Norman Platnick, without whom we will have to complete the Afrotropical *Orthobula* revisions following his untimely passing on 8 April 2020. Norm helped conceptualize this series of papers in collaboration with C.H. and C.J., examined type material of several *Orthobula* from Africa and Asia, and identified a large number of specimens deposited in American and European museums. Without his contribution, considerable gaps in our knowledge of the Afrotropical species, particularly, would exist, or take far longer to resolve. We would also like to thank his son, Will Platnick, for recognizing the effort his father put into this work and giving his blessing for us to see this series of papers to completion. Norm leaves a legacy as arguably the greatest arachnologist of his generation, and will be sorely missed by all that had the pleasure of knowing or working with him.

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APPENDIX 1. All cytochrome c oxidase subunit 1 (COI) sequences of Clubionidae, Phrurolithidae and Trachelidae used for the Bayesian Inference (BI) and maximum likelihood (ML) analyses.

Species	**BOLD ID**	**GenBank Accession #**	**Reference or Provider and date**	**Locality**
Afroceto africana	SPIZA393		Haddad 2019 (unpubl.)	Amanzi Private Game Reserve, R.S.A.
Afroceto africana	SPIZA394		Haddad 2019 (unpubl.)	Amanzi Private Game Reserve, R.S.A.
Afroceto martini	SPIZA391		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Afroceto martini	SPIZA392		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Afroceto plana	SPIZA388		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Afroceto plana	SPIZA389		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Afroceto plana	SPIZA390		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Capobula infima	SPIZA403		Haddad 2019 (unpubl.)	Hermanus, R.S.A.
Capobula infima	SPIZA404		Haddad 2019 (unpubl.)	Hermanus, R.S.A.
Capobula montana	SPIZA402		Haddad 2019 (unpubl.)	Bankfontein Farm, R.S.A.
Cetonana laticeps	FBARB678	KX537479	Astrin *et al.* 2016	Wittenberg, Germany
Cetonana laticeps	GBBSP2147	KY268719	Astrin *et al.* 2016	Wittenberg, Germany
Clubiona pallidula	ARONT247	GU682712	Blagoev 2009 (unpubl.)	Ontario, Canada
Fuchiba aquilonia	SPIZA397		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Fuchibotulus haddadi	SPIZA395		Haddad 2019 (unpubl.)	Golden Gate Highlands National Park, R.S.A.
Jocquestus schenkeli	SPIZA398		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Jocquestus schenkeli	SPIZA399		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Meriola californica	CNGAJ580	MF815067	CBG Collections Unit 2015 (unpubl.)	Guld Islands National Park Reserve, Canada
Meriola californica	CNGIF086	KM835023	Blagoev *et al.* 2016	Guld Islands National Park Reserve, Canada
Meriola californica	CNGUN133	MF811948	CBG Collections Unit 2015 (unpubl.)	Guld Islands National Park Reserve, Canada
Meriola californica	CNGUN134	MF814285	CBG Collections Unit 2015 (unpubl.)	Guld Islands National Park Reserve, Canada
Meriola californica	GMCVE540	MG045777	CBG Collections Unit 2015 (unpubl.)	Victoria, Canada
Meriola decepta	ARONW1719	MG048772	CBG Collections Unit 2015 (unpubl.)	Windsor, Canada
Meriola sp.	GMCVG304	MG043274	CBG Collections Unit 2015 (unpubl.)	Victoria, Canada
Orthobula radiata	SPIZA400		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Orthobula radiata	SPIZA401		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Paccius cf. scharffi	GBMIN117228	KY018021	Wheeler *et al.* 2017	Foret d`Antsirakambiaty, Madagascar
Paccius sp.	GBMIN117229	KY018022	Wheeler *et al.* 2017	Ranomafana, Madagascar
Patelloceto secutor	SPIZA405		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Patelloceto secutor	SPIZA406		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Phrurolithus festivus	NLARA237		Vorst 2012 (unpubl.)	Overjissel, Netherlands
Phrurolithus festivus	NLARA283		Vorst 2013 (unpubl.)	North Holland, Netherlands
Phrurolithus festivus	SMNKA141		Hoefer 2013 (unpubl.)	Karlsruhe, Germany
Phrurolithus festivus	SMNKA160		Hoefer 2013 (unpubl.)	Karlsruhe, Germany
Phrurotimpus alarius	RBINA5179	KP646814	Blagoev *et al.* 2016	Rouge National Urban Park, Canada
Phrurotimpus alarius	RBINA5183	KP649381	Blagoev *et al.* 2016	Rouge National Urban Park, Canada
Phrurotimpus alarius	SSROA3583	KP646944	Blagoev *et al.* 2016	Rouge National Urban Park, Canada

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APPENDIX 1. (continued)

Species	BOLD ID	GenBank Accession #	Reference or Provider and date	Locality
Phrurotimpus alarius	SSROC8081	MF809540	CBG Collections Unit 2015 (unpubl.)	Rouge National Urban Park, Canada
Phrurotimpus borealis	SPICA392	JF885587	Blagoev 2010 (unpubl.)	Kootney National Park, Canada
Phrurotimpus borealis	SPICA394	JF885589	Blagoev 2010 (unpubl.)	Kootney National Park, Canada
Phrurotimpus borealis	SSROC6883	MF811761	CBG Collections Unit 2015 (unpubl.)	Rouge National Urban Park, Canada
Phrurotimpus borealis	TDWGB939	HQ979359	CBG Collections Unit 2010 (unpubl.)	Barnstable Country, United States
Phrurotimpus certus	PPELE643	JN308782	Blagoev *et al.* 2016	Point Pelee National Park, Canada
Phrurotimpus certus	PPELE650	KM837504	Blagoev *et al.* 2016	Point Pelee National Park, Canada
Phrurotimpus certus	PPELE673	JN308799	Blagoev *et al.* 2016	Point Pelee National Park, Canada
Phrurotimpus certus	PPELE692	JN308811	Blagoev *et al.* 2016	Point Pelee National Park, Canada
Phrurotimpus certus	SPRMA162		De Waard 2010 (unpubl.)	British Columbia, Canada
Phrurotimpus certus	SPRMA961	KP649354	Blagoev *et al.* 2016	British Columbia, Canada
Planochelas haddadi	SPIZA430		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Poachelas montanus	SPIZA407		Haddad 2019 (unpubl.)	Hogsback, R.S.A.
Poachelas montanus	SPIZA408		Haddad 2019 (unpubl.)	Hermanus, R.S.A.
Poachelas montanus	SPIZA409		Haddad 2019 (unpubl.)	Hermanus, R.S.A.
Poachelas refugus	SPIZA410		Haddad 2019 (unpubl.)	Tembe Elephant Park, R.S.A.
Poachelas refugus	SPIZA411		Haddad 2019 (unpubl.)	Tembe Elephant Park, R.S.A.
Poachelas striatus	SPIZA365		Haddad 2019 (unpubl.)	Platberg Nature Reserve, R.S.A.
Poachelas striatus	SPIZA366		Haddad 2019 (unpubl.)	Platberg Nature Reserve, R.S.A.
Poachelas striatus	SPIZA464		Haddad 2019 (unpubl.)	Bloemfontein, R.S.A.
Poachelas striatus	SPIZA465		Haddad 2019 (unpubl.)	Bloemfontein, R.S.A.
Poachelas striatus	SPIZA466		Haddad 2019 (unpubl.)	Bloemfontein, R.S.A.
Scotinella britcheri	ARONW1964	MG042797	Blagoev 2015 (unpubl.)	Ontario, Canada
Scotinella britcheri	ARONW352	KP648571	Blagoev *et al.* 2016	Guelph, Canada
Scotinella britcheri	ERSPI272	GU682551	Blagoev 2009 (unpubl.)	Wellington Co., Canada
Scotinella britcheri	ERSPI283	GU682538	Blagoev 2009 (unpubl.)	Wellington Co., Canada
Scotinella britcheri	GMOOG094	MG042729	CBG Collections Unit 2015 (unpubl.)	St. Marys, Canada
Scotinella britcheri	PPELE661	JN308787	Blagoev *et al.* 2016	Point Pelee National Park, Canada
Scotinella britcheri	SMTPD1629	KP654105	Blagoev *et al.* 2016	Teeswater, Canada
Scotinella fratrella	ARONW1780	MG048960	Blagoev 2015 (unpubl.)	Windsor, Canada
Scotinella fratrella	ARONW1800	MG048225	Blagoev 2015 (unpubl.)	Windsor, Canada
Scotinella fratrella	BBUSE2353		CBG Collections Unit 2012 (unpubl.)	Gentry Creek, United States

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APPENDIX 1. (continued)

Species	BOLD ID	GenBank Accession #	Reference or Provider and date	Locality
Scotinella fratrella	BBUSE2354		CBG Collections Unit 2012 (unpubl.)	Gentry Creek, United States
Scotinella madisonia	SMTPB15672	KP649356	Blagoev *et al.* 2016	London, Canada
Scotinella madisonia	SMTPB15673	KP656706	Blagoev *et al.* 2016	London, Canada
Scotinella madisonia	SMTPB15674	KP650459	Blagoev *et al.* 2016	London, Canada
Scotinella madisonia	SMTPM123	MG045329	CBG Collections Unit 2015 (unpubl.)	London, Canada
Scotinella minnetonka	ELPCG920		CBG Collections Unit 2017 (unpubl.)	South Frontenac, Canada
Scotinella minnetonka	ELPCG9326		CBG Collections Unit 2017 (unpubl.)	South Frontenac, Canada
Scotinella minnetonka	SSROA3559	KP654935	Blagoev *et al.* 2016	Rouge National Urban Park, Canada
Scotinella minnetonka	SSROC8978	MF816875	CBG Collections Unit 2015 (unpubl.)	Rouge National Urban Park, Canada
Scotinella pugnata	SPICA703	JF885883	Blagoev 2010 (unpubl.)	Jasper National Park, Canada
Scotinella pugnata	SPICA749	JF885927	Blagoev 2010 (unpubl.)	Kootney National Park, Canada
Scotinella pugnata	SSBAD5956	MG511996	CBG Collections Unit 2013 (unpubl.)	Banff National Park, Canada
Scotinella pugnata	SSPAA6039	KM836777	Blagoev *et al.* 2016	Prince Albert National Park, Canada
Scotinella sculleni	NGSFT1096		De Waard 2015 (unpubl.)	Saturna Island, Canada
Thysanina gracilis	SPIZA418		Haddad 2019 (unpubl.)	Bankfontein Farm, R.S.A.
Thysanina sp.	SPIZA416		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Thysanina sp.	SPIZA417		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Thysanina sp.	SPIZA419		Haddad 2019 (unpubl.)	Bankfontein Farm, R.S.A.
Thysanina sp.	SPIZA420		Haddad 2019 (unpubl.)	Bankfontein Farm, R.S.A.
Thysanina sp.	SPIZA449		Haddad 2019 (unpubl.)	Grahamstown District, R.S.A.
Thysanina sp.	SPIZA450		Haddad 2019 (unpubl.)	Somerset East, R.S.A.
Thysanina sp.	SPIZA451		Haddad 2019 (unpubl.)	Somerset East, R.S.A.
Thysanina sp.	SPIZA452		Haddad 2019 (unpubl.)	Golden Gate Highlands National Park, R.S.A.
Thysanina sp.	SPIZA453		Haddad 2019 (unpubl.)	George, R.S.A.
Thysanina sp.	SPIZA458		Haddad 2019 (unpubl.)	Hopefield Farm, R.S.A.
Thysanina sp.	SPIZA459		Haddad 2019 (unpubl.)	Hopefield Farm, R.S.A.
Thysanina sp.	SPIZA467		Haddad 2019 (unpubl.)	10 km South of Hogsback on R345, R.S.A.
Thysanina transversa	SPIZA412		Haddad 2019 (unpubl.)	Hogsback, R.S.A.
Thysanina transversa	SPIZA413		Haddad 2019 (unpubl.)	Hogsback, R.S.A.
Thysanina transversa	SPIZA414		Haddad 2019 (unpubl.)	Hogsback, R.S.A.
Thysanina transversa	SPIZA415		Haddad 2019 (unpubl.)	Hogsback, R.S.A.
Trachelas cambridgei	GMCCC161		CBG Collections Unit 2014 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas cambridgei	GMCRN3471		CBG Collections Unit 2013 (unpubl.)	Area de Conservación Guanacaste, Costa Rica

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APPENDIX 1. (continued)

Species	BOLD ID	GenBank Accession #	Reference or Provider and date	Locality
Trachelas cambridgei	GMCRQ090		CBG Collections Unit 2013 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas cambridgei	GMCRS320		CBG Collections Unit 2014 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas cambridgei	GMCRT1004		CBG Collections Unit 2014 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas cambridgei	GMCZZ1375		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas japonicus	GBCH11046	JN817224	Blagoev *et al.* 2016	-
Trachelas pacificus	BBUSE412		CBG Collections Unit 2011 (unpubl.)	Great Valley Grasslands State Park, United States
Trachelas pacificus	BBUSE466		CBG Collections Unit 2011 (unpubl.)	Great Valley Grasslands State Park, United States
Trachelas pacificus	BBUSE467		CBG Collections Unit 2011 (unpubl.)	Great Valley Grasslands State Park, United States
Trachelas pacificus	BBUSU278		CBG Collections Unit 2015 (unpubl.)	Lee County, United States
Trachelas pacificus	GMRMM179		CBG Collections Unit 2014 (unpubl.)	San Diego, United States
Trachelas pacificus	NBINS1047		CBG Collections Unit 2017 (unpubl.)	San Diego County, United States
Trachelas pacificus	NBINS1059		CBG Collections Unit 2017 (unpubl.)	San Diego County, United States
Trachelas similis	BBUSE1494		CBG Collections Unit 2012 (unpubl.)	Brazos Bend State Park, United States
Trachelas similis	BBUSE2106		CBG Collections Unit 2012 (unpubl.)	Brazos Bend State Park, United States
Trachelas similis	BBUSU304		CBG Collections Unit 2012 (unpubl.)	Collier County, United States
Trachelas sp.	GMAAI616		CBG Collections Unit 2016 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMAAM016		CBG Collections Unit 2016 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMAAR127		CBG Collections Unit 2016 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMAAS035		CBG Collections Unit 2016 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMAAT065		CBG Collections Unit 2016 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMAAW115		CBG Collections Unit 2016 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMAAZ358		CBG Collections Unit 2016 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACB018		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACB1612		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACD828		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica

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APPENDIX 1. (continued)

Species	BOLD ID	GenBank Accession #	Reference or Provider and date	Locality
Trachelas sp.	GMACE1076		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACH047		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACJ1146		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACN753		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACO253		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACQ095		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACQ096		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACR050		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACT013		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACW012		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMACZ032		CBG Collections Unit 2015 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMCCG1309		CBG Collections Unit 2014 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMCCW022		CBG Collections Unit 2018 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMCCZ053		CBG Collections Unit 2018 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	GMCCZ055		CBG Collections Unit 2018 (unpubl.)	Area de Conservación Guanacaste, Costa Rica
Trachelas sp.	SPIZA421		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Trachelas sp.	SPIZA422		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Trachelas sp.	SPIZA423		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Trachelas sp.	SPIZA424		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Trachelas sp.	SPIZA425		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Trachelas sp.	SPIZA426		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Trachelas sp.	SPIZA427		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Trachelas sp.	SPIZA428		Haddad 2019 (unpubl.)	Ndumo Game Reserve, R.S.A.
Trachelas tranquillus	SMTPI10007	MG046501	De Waard 2015 (unpubl.)	Teeswater, Canada
Trachelas tranquillus	SMTPI1012	MG045184	De Waard 2015 (unpubl.)	Guelph, Canada
Trachelas tranquillus	SMTPI4130	MG046149	De Waard 2015 (unpubl.)	Brandtford, Canada
Trachelas tranquillus	SMTPI839	MG049197	De Waard 2015 (unpubl.)	Brampton, Canada
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