Research article

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Caerostris (Araneidae: Araneae) cryptic diversity highlights the need for taxonomic expertise in the genomic era

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Abstract. Bark spiders (*Caerostris* Thorell, 1868, Araneidae Clerck, 1757) are large spiders distributed across the Old-World tropics. This genus was understudied until recently, but received more attention following the discovery of unique web evolution and biomaterial properties of its species. *Caerostris* are characterized by web gigantism, reaching extremes in Darwin's Bark spider (*C. darwini* Kuntner & Agnarsson, 2010), which employs the toughest known silk. Due to the exceptional silk of *C. darwini*, recent research provided whole-genome sequencing and silk-gene mapping for *C. darwini* and a sympatric congener misassigned, due to cryptic diversity, to *C. extrusa* Butler, 1882. We describe a case of convergent evolution in somatic morphology that further hinders species identification in the field. Conducting a morphological and molecular investigation of exemplars that share the "*C. extrusa* morphotype", we conclude they belong to four distinct species. We redescribe the two valid ones, *C. extrusa* and *C. hirsuta* (Simon, 1895), elevate the previously synonymized *C. bankana* Strand, 1915 to species level, and newly describe *C. kuntneri* sp. nov., the species used in the assembly of its genome. We argue this to be an example of how the global taxonomic impediment can lead to errors in rapidly advancing fields such as genomics.

Keywords. Bark spiders, taxonomic impediment, cryptic species, convergent evolution, somatic morphology.

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Introduction

Bark spiders of the genus *Caerostris* Thorell, 1868 (Fig. 1) are large spiders of the family Araneidae Clerck, 1757 that are widespread in the Old-World tropics. Although known for over one and a half centuries, these spiders were understudied until recently, when it became clear they represent a particularly interesting case of biomaterial and web evolution (Agnarsson *et al.* 2010), spawning a lively decade of research related to web gigantism and silk mechanics.

The genus *Caerostris* represents the most striking case of web gigantism with several species building orb webs considerably larger than those of other spiders, reaching extremes in Darwin's Bark spider, *C. darwini* Kuntner & Agnarsson, 2010 (Kuntner & Agnarsson 2010; Gregorič *et al.* 2011a, 2015a). This species uniquely suspends its webs across small rivers and lakes, while employing major ampullate

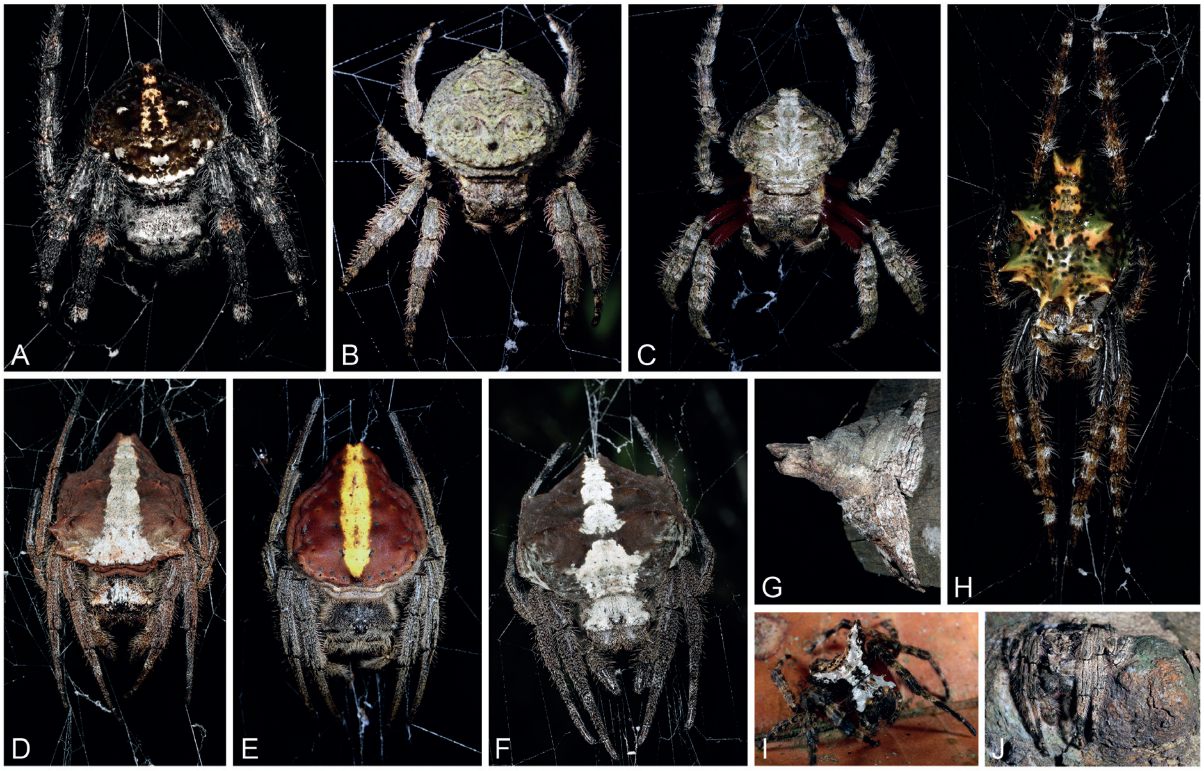

Fig. 1. Some female *Caerostris* Thorell, 1868 from Madagascar and Africa. **A**. *C. darwini* Kuntner & Agnarsson, 2010, Madagascar. **B**. *C. bojani* Gregorič, 2015, Madagascar. **C**. *C. almae* Gregorič, 2015, Madagascar. **D**. *C. extrusa* Butler, 1882, Madagascar. **E**. *C. hirsuta* (Simon, 1895), Madagascar. **F**. *C. kuntneri* Gregorič & Yu sp. nov., Madagascar. **G**. *C. linnaeus* Gregorič, 2015, Mozambique. **H**. *C. pero* Gregorič, 2015, Madagascar. **I**. *C. cowani* Butler, 1882, Madagascar. **J**. *C. sexcuspidata* (Fabricius, 1793), South Africa. Note similarity in *C. extrusa*, *C. kuntneri*, and *C. hirsuta* that we term the "*C. extrusa* morphotype".

silk that outperforms all other known silks in toughness, giving the genus *Caerostris* the potential of becoming a model lineage in research of silk mechanics and web evolution (Agnarsson *et al.* 2010; Gregorič *et al.* 2011b). The major ampullate silk of *C. darwini* has an unusual protein secondary structure (Htut *et al.* 2021) and includes a highly expressed proline-rich silk protein (Garb *et al.* 2019). Together with an unusually long duct in its silk gland (Garb *et al.* 2019), all these potentially contribute to the higher toughness of *C. darwini* major ampullate silk.

The recent increased availability of high-throughput sequencing sparked a number of genome and transcriptome assemblies of spiders. Due to the exceptional mechanical properties of *C. darwini*'s major ampullate silk, recent genomic research provided whole-genome sequencing and silk gene mapping for two representatives of the genus, Darwin's bark spider *C. darwini* and a sympatric congener misassigned to *C. extrusa* Butler, 1882 (Kono *et al.* 2021; Babb *et al.* 2022). Many fields of biological research, including biomaterial and genomic research, are addressing urgent human problems and research agendas, e.g., climate change, biodiversity conservation, and the development of new or improved materials. However, the global taxonomic impediment – the decline in species discovery and description (Agnarsson & Kuntner 2007) – can lead to errors in such rapidly advancing fields of research. Here, we report on the erroneous determination of species whose newly assembled genome is attributed to *C. extrusa* (published by Kono *et al.* 2021), due to undiscovered cryptic species diversity and challenging species diagnosis in the genus *Caerostris*. While this genus is known to be variable in genital and somatic morphology (Grasshoff 1984; Gregorič *et al.* 2015b), we here describe a case of convergent evolution in somatic morphology that further hinders species identification in the field. Namely, the specimens associated with the "*C. extrusa* morphotype" in fact belong to several species. By conducting a morphological and molecular investigation on exemplars of this morphotype, we describe four distinct species of the "*extrusa* morphotype". *Caerostris extrusa*, *C. hirsuta* (Simon, 1895), and *C. bankana* Strand, 1915 (reestablished) are valid and redescribed here, while *C. kuntneri* sp. nov. is described here and the previously published genome assigned to it.

Material and methods

Taxonomic sampling

On 21 Dec. 2022, we downloaded all 58 *Caerostris cox1* (cytochrome c oxidase subunit I) sequences, standard animal DNA barcodes (Hebert *et al.* 2003), publicly available in the BOLD Systems database (Ratnasingham & Hebert 2007; Appendix 1). Additionally, we obtained *cox1* sequences of 31 *Caerostris* specimens of the *C. extrusa* morphotype, collected in expeditions to Madagascar between 2010 and 2022, and added the voucher *cox1* sequence from the Kono *et al.* (2021) draft genome. The final data matrix contained 90 *Caerostris* specimens and eight selected outgroups (downloaded from the BOLD Systems database) of the families Araneidae, Nephilidae, Phonognathidae, and Tetragnathidae (sensu Kuntner *et al.* 2023; Appendix 1).

Institutional abbreviations

BMNH = The Natural History Museum, London, UK
SMF = Senckenberg Naturmuseum, Frankfurt, Germany
USNM = National Museum of Natural History, Smithsonian Institution, Washington DC, USA
ZRC SAZU = Research Centre of the Slovenian Academy of Sciences and Arts, Ljubljana, Slovenia

Anatomical abbreviations in text and figures

ALE = anterior lateral eyes
AME = anterior median eyes
C = conductor
CB = cymbium

PME = posterior median eyes
ST = subtegulum
T = tegulum

Morphological examination and imaging

We performed all measurements and imaging under a Leica M205C stereo microscope equipped with a Leica DMC5400 camera through the Leica Application Suite X software (Leica Microsystems, Wetzlar, Germany). We report all measurement in millimeters.

Molecular procedures

For DNA extraction, we used the QIAGEN DNeasy Blood & Tissue Kit and the QIAamp DNA Micro Kit (both QIAGEN N.V., The Netherlands) using standard protocols. To amplify around 1200 bp of the *cox1* gene, under standard PCR conditions (Čandek *et al.* 2013; Gregorič *et al.* 2015b), we used either the forward LCO1490 (Folmer *et al.* 1994) and the reverse C1-N-2776 aka "Maggy" (Hedin & Maddison 2001) primers, or a combination of the forward LCO1490 and reverse Chelicerate-R2 (Barrett & Hebert 2005) or the forward C1-J-2123 aka "Tom" (Vidergar *et al.* 2014) and the reverse C1-N-2776.

We aligned the sequences using ClustalW in the software MEGA 11 (Tamura *et al.* 2021). We conducted Bayesian inference using the model GTR+G+I, determined by jModel Test 2 (Darriba *et al.* 2012), implementing the Akaike information criterion, as the statistically best-fitting model of nucleotide substitutions. We conducted the Bayesian analysis using MrBayes on XSEDE (ver. 3.2.7a) via the CIPRES Science Gateway (Miller *et al.* 2010). We performed two independent runs with four simultaneous Markov Chain Monte Carlo chains, with random starting trees, running for 50 million generations. We discarded 25% generations as burnin.

To test the species hypotheses based on morphological diagnoses, we performed two species delimitation analyses, the multi-rate Poisson tree analysis under ML and Markov chain Monte Carlo (mPTP; (Kapli *et al.* 2017) run online at https://mptp.h-its.org/#/tree, and the Assemble Species by Automatic Partitioning that is based on genetic distance (ASAP; https://bioinfo.mnhn.fr/abi/public/asap/; Puillandre *et al.* 2021), using the K80 substitution model.

Results

Phylogenetic inference and species delimitation

Our analysis strongly supported the monophyly of the genus *Caerostris* and its African clade (Fig. 2). The two species delimitation analyses recovered *C. extrusa*, *C. hirsuta*, and *C. kuntneri* as distinct and they can therefore be considered as 'valid' species (note that molecular data for *C. bankana* is unavailable). However, the analyses also suggested a different total number of operational taxonomic units (OTUs) at different parts of the phylogenetic tree (Fig. 2). The mPTP analysis on our phylogenetic tree favored multi coalescent rate over single coalescent rate and recovered 14 OTUs. The ASAP analysis on the dataset of 90 ingroup sequences recovered 10 best partitions, of which the highest confidence one (asap-score = 2.50, P-val = 3.41×10^{-1}, W = 5.53×10^{-4}, Threshold dist. = 0.022041) recovered 21 OTUs.

The molecular voucher specimen used in the genome assembly by Kono *et al.* (2021) was clearly nested within the *C. kuntneri* sp. nov. The specimens of the *C. extrusa* morphotype, represented by *C. extrusa*, *C. hirsuta*, and *C. kuntneri* are not monophyletic. The results imply that the *C. extrusa* morphotype evolved more than once (Fig. 2). The species delimitation methods indicate possible further cryptic diversity in the specimens identified as *C. cowani* Butler, 1882, *C. mitralis* (Vinson, 1863), *C. sexcuspidata* (Fabricius, 1793), and *C. sumatrana* Strand, 1915.

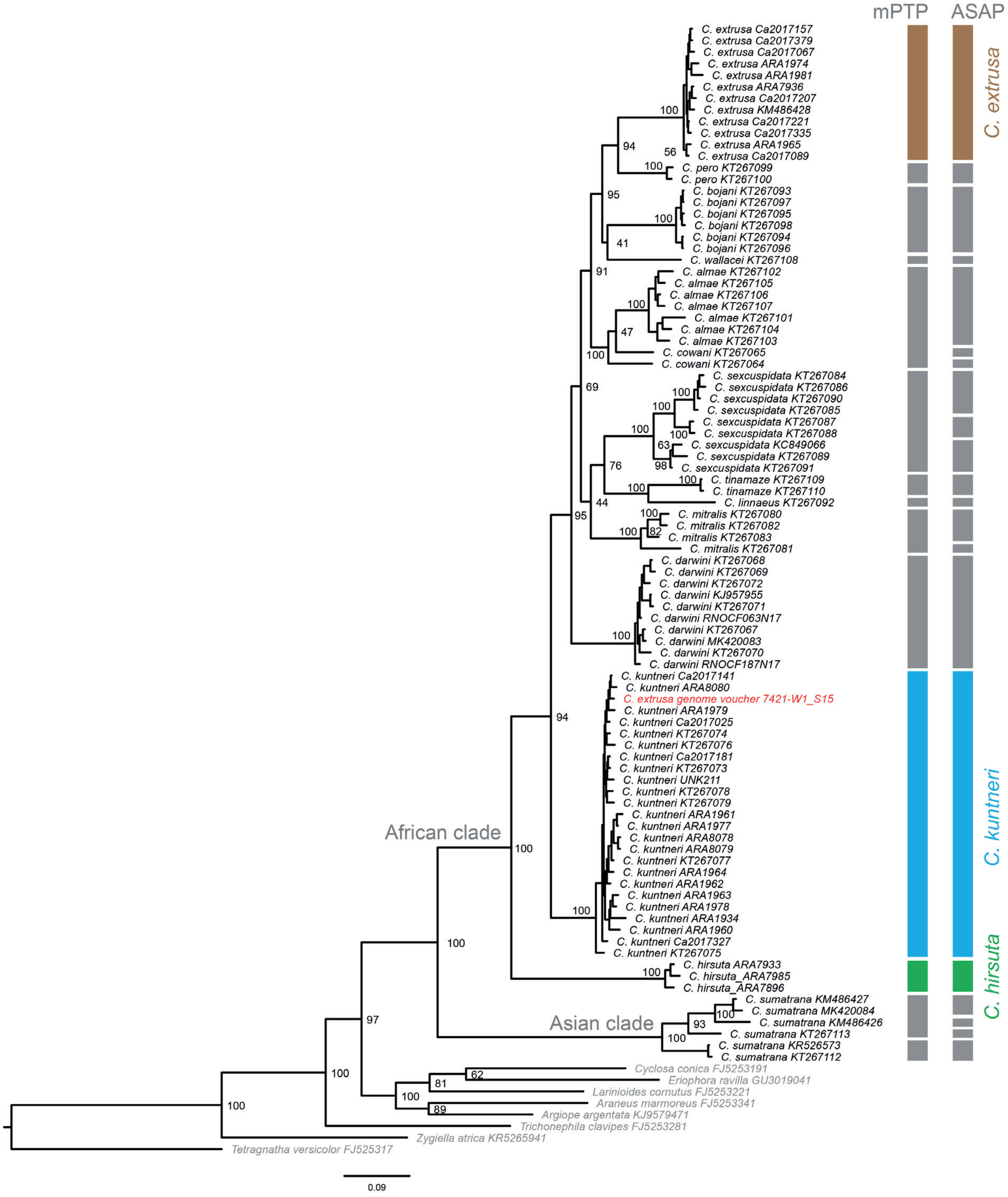

Fig. 2. Phylogeny of *Caerostris* Thorell, 1868 with specimen codes (for specimens from this study) and BOLD identifiers (for specimens obtained from the BOLD database) next to species names, and with Bayesian inference posterior probabilities at nodes. Vertical bars summarize the results of the mPTP and ASAP species delimitations methods. The specimen in red highlights the voucher specimen used for obtaining the genome of "*C. extrusa*" (Kono *et al.* 2021).

Taxonomy

Class Arachnida Lamarck, 1801
Order Araneae Clerck, 1757
Family Araneidae Clerck, 1757

Genus ***Caerostris*** Thorell, 1868

Caerostris Thorell, 1868: 4, 7–8.
Trichocharis Simon, 1895 by Grasshoff 1984: 727 (transfer of type species).

Type species

Epeira mitralis Vinson, 1863, designated by Thorell, 1868: 4.

Diagnosis

Caerostris spiders of both sexes differ from other araneids by the following combination of somatic characteristics: prosoma and opisthosoma wider than long, head region of the prosoma wide and elevated from the thoracic region, prosoma with a frontal rostrum, cheliceral furrow smooth rather than denticulated, females with two pairs of median prosomal projections (one pair or none in males), sternal tubercule adjacent to coxae IV, median and lateral eyes grouped on separate tubercules, presence of abdominal sigillae, legs I, II, and IV with flattened and hairy patellae, tibiae, and metatarsi, femur IV with spatulate setae, the ventro-lateral abdominal sclerotization in several rather than one line of small dots (Grasshoff 1984; Kuntner *et al.* 2008; Kuntner & Agnarsson 2010; Gregorič *et al.* 2015b). *Caerostris* differ from other araneids by the following genital features: female epigynum with paired epigynal hooks anteriorly (Figs 3–7), male palp with large subtegulum, cymbial ectal margin sclerotized as cymbium rather than transparent, absence of paracymbium (Figs 4, 7) (Kuntner *et al.* 2008; Kuntner & Agnarsson 2010; Gregorič *et al.* 2015b).

Species composition (reestablished and newly described species in bold)

Caerostris almae Gregorič, 2015; ***Caerostris bankana* Strand, 1915**; *Caerostris bojani* Gregorič, 2015; *Caerostris corticosa* Pocock, 1902; *Caerostris cowani* Butler, 1882; *Caerostris darwini* Kuntner & Agnarsson, 2010; *Caerostris ecclesiigera* Butler, 1882; *Caerostris extrusa* Butler, 1882; *Caerostris hirsuta* (Simon, 1895); *Caerostris indica* Strand, 1915; ***Caerostris kuntneri* Gregorič sp. nov.**; *Caerostris linnaeus* Gregorič, 2015; *Caerostris mayottensis* Grasshoff, 1984; *Caerostris mitralis* (Vinson, 1863); *Caerostris pero* Gregorič, 2015; *Caerostris sexcuspidata* (Fabricius, 1793); *Caerostris sumatrana* Strand, 1915; *Caerostris tinamaze* Gregorič, 2015; *Caerostris vicina* (Blackwall, 1866); *Caerostris wallacei* Gregorič, 2015.

Caerostris bankana Strand, 1915
Fig. 3; Appendix 1

Caerostris bankana Strand, 1915: 225 (♀).

Diagnosis

As in *C. extrusa* (Figs 4E, 6C), *C. darwini* (Kuntner & Agnarsson 2010: fig. 6e), *C. kuntneri* (Figs 6I, 7E), *C. mitralis* (Grasshoff 1984: figs 19–20, 29–30), *C. tinamaze* (Gregorič *et al.* 2015b: fig. 9c), and *C. wallacei* (Gregorič *et al.* 2015b: fig. 10c), and in contrast to other Afrotropical species of *Caerostris*, the epigynal hooks in *C. bankana* (Fig. 3E) are short rather than long, positioned medially on the epigynal plate rather than anteriorly and pointing laterally rather than posteriorly. As in *C. kuntneri* but in contrast to the above mentioned species of *Caerostris*, *C. bankana* has short and stout epigynal hooks that are about as wide as long, while longer in other species of *Caerostris*. In contrast to all species of *Caerostris*, the anterior epigynal margin in *C. bankana* is S-shaped and perpendicular to the longitudinal body axis (Fig. 3E).

Type material

Holotype

MADAGASCAR • ♀; Nosy Be; SMF3618 SMF.

Description

Female (holotype, Fig. 3A–E)

MEASUREMENTS AND COLORATION. Total body length 23.36. Prosoma 7.81 long, 8.05 wide, 6.97 high. Carapace and chelicerae reddish brown, covered with whitish to yellowish setae. Sternum 3.65 long, 3.46 wide, widest between coxae of second legs, brown with whitish setae. AME diameter 0.40, PME diameter 0.34, AME separation 0.52, PME separation 1.22, PME–PLE separation 3.00, ALE–PLE separation 0.07. Clypeus height 1.48. Appendages: palps brown. All leg segments uniformly reddish brown. Leg I femur 6.53, patella 3.71, tibia 5.51, metatarsus 6.55, tarsus 2.47. Opisthosoma 14.96 long, 14.58 wide, 10.22 high. Base color of dorsum light reddish brown, covered with dark reddish-brown spots, with several small, pointy tubercules on anterior half and pair of large posterior tubercules, pointing posteriorly and protruding past spinnerets. Anterior dorsum with broad, whitish speck. Venter light brown with several dark brown spots, two paler, grey, longitudinal bands. Epigynum as diagnosed (Fig. 3E).

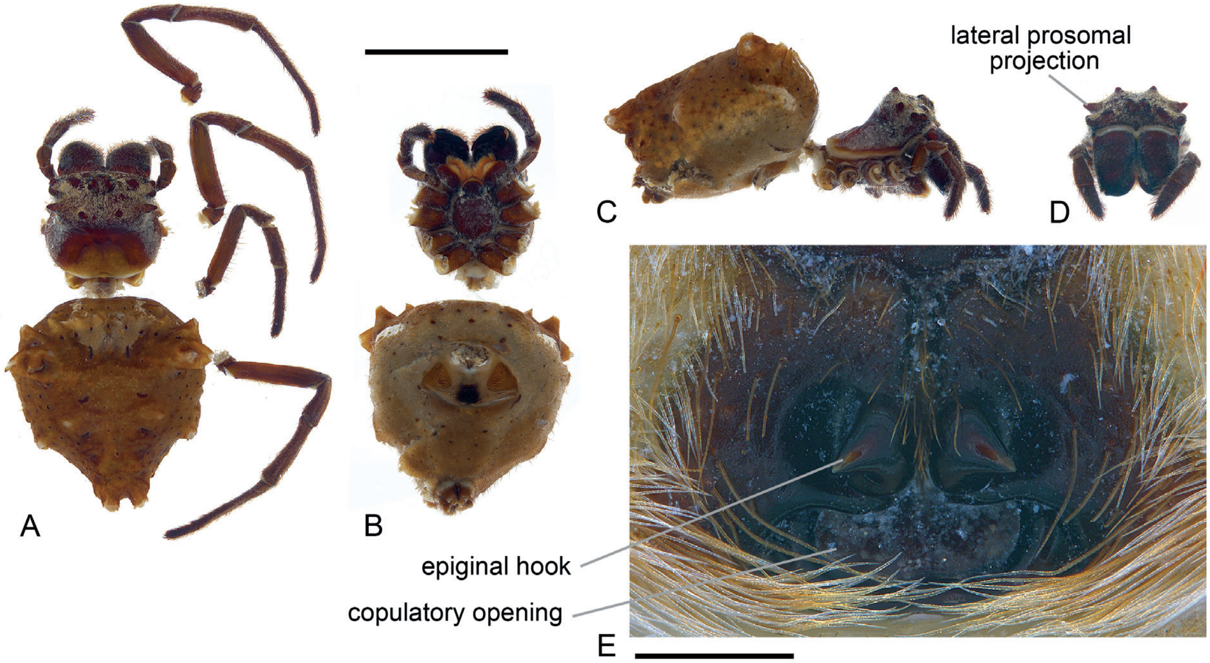

Fig. 3. *Caerostris bankana* Strand, 1915, ♀ (SMF3618), somatic and genital morphology, Nosy Be, Madagascar. **A–D**. Somatic morphology. **E**. Epigynum, ventral view. Scale bars: A–D = 10 mm; E = 1 mm.

Distribution

Strand (1915) described the female he believed to be collected in Bandar Kwala, North Sumatra, Indonesia. However, the specimen closely resembles Malagasy species in morphology, and at the SMF was kept together with two resembling specimens from Nosy Be, Madagascar. As a similar specimen was never again found in Indonesia, Grasshoff (1984) concluded a confusion of specimen locality the most likely. We agree with this assessment and find Nosy Be, Madagascar as the most likely type locality and known distribution of this species.

Remark

Caerostris bankana Strand, 1915 was synonymized with *C. extrusa* Butler, 1882 by Grasshoff (1984). In epigynal morphology, the type of *C. bankana* is clearly different from both *C. extrusa* and *C. kuntneri*, as well as all other described species of *Caerostris*. Due to the lack of molecular data for this species, its phylogenetic position within the genus is unclear.

Caerostris extrusa Butler, 1882

Figs 1D, 4, 6A–C; Appendix 1

Caerostris extrusa Butler, 1882: 100 (♀), plate 6 fig. 3.

Caerostris extrusa – Grasshoff 1984: 752 (♀), figs 28–30.

Diagnosis

As in *C. kuntneri* (Figs 6I, 7E), *C. darwini* (Kuntner & Agnarsson 2010: 6e), *C. mitralis* (Grasshoff 1984: figs 19–20, 29–30), *C. tinamaze* (Gregorič *et al.* 2015b: fig. 9c), and *C. wallacei* (Gregorič *et al.* 2015b: fig. 10c), and in contrast to other Afrotropical species of *Caerostris*, the epigynal hooks in *C. extrusa* (Figs 4E, 6C) are short rather than long, positioned medially on the epigynal plate rather than anteriorly and pointing laterally rather than posteriorly. Different to all other species and as in *C. darwini*, the epigynal hooks in *C. extrusa* have an anteriorly pointing base that is longer than the hook length, but the hooks are wide and heavily sclerotized in *C. extrusa* but shorter and narrower in *C. darwini*. Male *C. extrusa* (Fig. 4K–M) differ from those of other Afrotropical *Caerostris*, except *C. tinamaze* (Gregorič *et al.* 2015b: fig. 9j–k), by the relatively small palpal bulbus, and from all *Caerostris* by the twisted conductor positioned at a perpendicular axis to the cymbium.

Type material

Holotype

MADAGASCAR • ♀; specimen photographs examined; BMNH, BMNH1882.26.

Other material examined

MADAGASCAR • 1 ♀; Toamasina Province, Mantadia National Park; lat. -18.783784, lon. 48.427617; 26. Feb. 2010; M. Kuntner, I. Agnarsson and M. Gregorič leg.; *Cox1* not obtained; USNM, ARA4270 • 1 ♂; Toamasina Province, Analamazoatra National Park; lat. -18.937172, lon. 48.4200538; Dec. 2017; M. Gregorič, M. Kuntner, I. Agnarsson and P. Babb leg.; GenBank accession number PP403861; ARA1965; USNM • 1 ♀; Antsiranana Province, Marojejy National Park; lat. -14.437629, lon. 49.775602, 30. Mar. 2022; M. Gregorič, M. Kuntner, K.P. Yu and M. Bedjanič leg.; GenBank accession number PP403853; ARA7936; ZRC SAZU • 1 ♀; Toamasina Province, Andasibe-Mantadia National Park; lat. -18.8255 lon. 48.4349; 6. Dec. 2017; M. Gregorič, M. Kuntner, I. Agnarsson and P. Babb leg.; GenBank accession number PP403854; CA2017067; ZRC SAZU • 1 ♀; Toamasina Province, Analamazoatra National Park; lat. -18.937172 lon. 48.420053; 10–16. Dec. 2017; M. Gregorič, M. Kuntner, I. Agnarsson and P. Babb

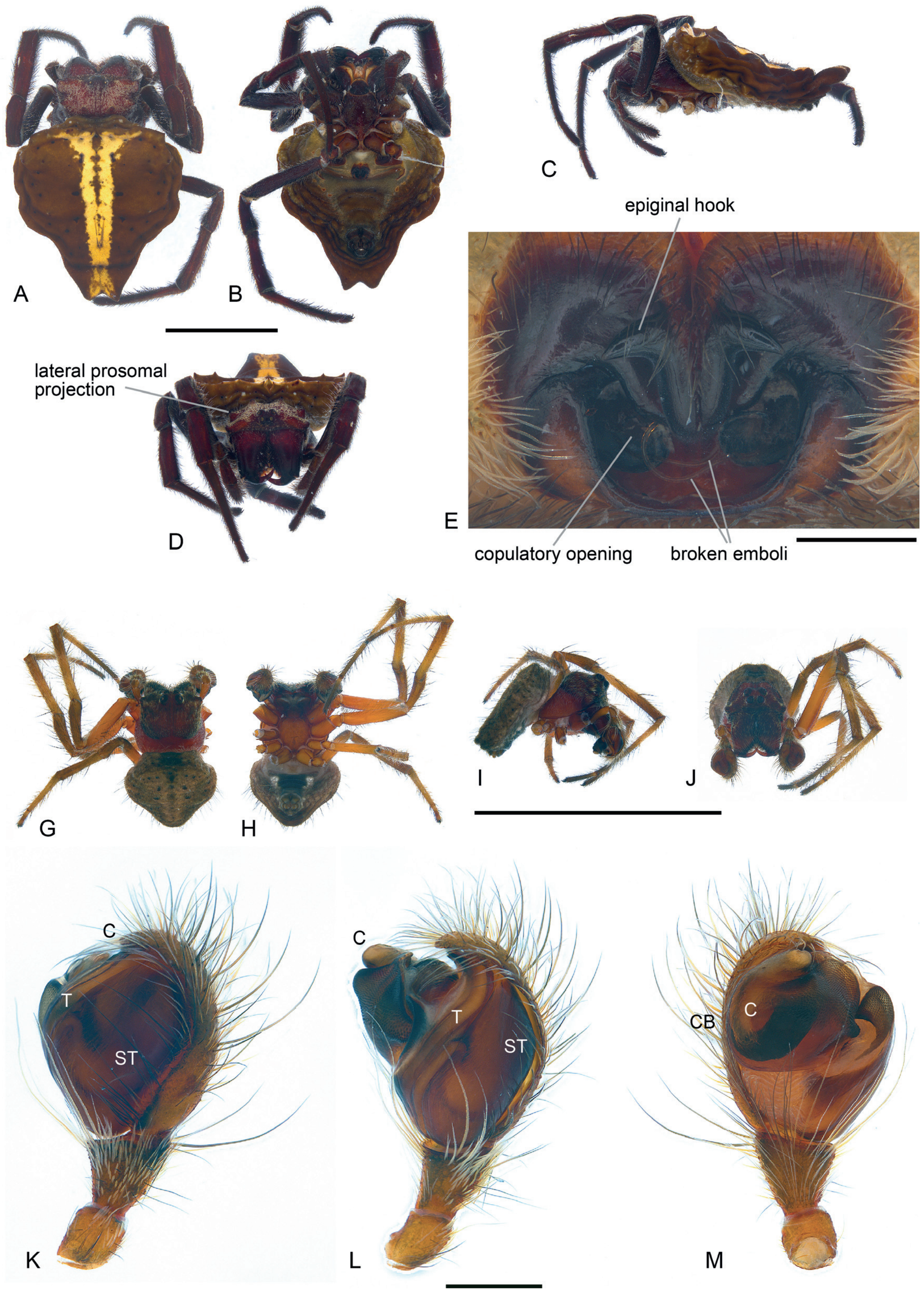

Fig. 4. *Caerostris extrusa* Butler, 1882, ♀ (ARA4270) and ♂ (ARA1965), somatic and genital morphology, Andasibe-Mantadia National Park, Madagascar. **A–D**. ♀, somatic morphology. **E**. ♀, epigynum, ventral view. **G–J**. ♂, somatic morphology. **K**. ♂, left palp, lateral view. **L**. ♂, left palp, mesal view. **M**. ♂, left palp, ventral view. Scale bars: A–D, G–J = 10 mm; E, K–M = 1 mm.

leg.; GenBank accession number PP403855; CA2017089; ZRC SAZU • 1 ♀; same locality, date, and leg. data as for preceding; GenBank accession number PP403856; CA2017157; ZRC SAZU • same locality, date, and leg. data as for preceding; GenBank accession number PP403857; CA2017207; ZRC SAZU • 1 ♀; same locality, date, and leg. data as for preceding; GenBank accession number PP403858; CA2017221; ZRC SAZU • 1 ♀; same locality, date, and leg. data as for preceding; GenBank accession number PP403859; CA2017335; ZRC SAZU • 1 ♀; same locality, date, and leg. data as for preceding; GenBank accession number PP403860; CA2017379; ZRC SAZU • 1 ♂; same locality, and leg. data as for preceding; 9. Dec. 2017; GenBank accession number PP403862; ARA1974; ZRC SAZU • 1 ♂; Toamasina Province, Analamazoatra National Park; lat: -18.932779, lon. 48.413215; 7; Dec. 2017; M. Gregorič, I. Agnarsson, M. Kuntner and P. Babb leg.; GenBank accession number PP403863; ARA1981; ZRC SAZU • 1 ♀; Toamasina Province, Analamazoatra National Park; lat. -18.786784, lon. 48.427617; 26. Feb. 2010; M. Gregorič, I. Agnarsson and M. Kuntner leg.; *Cox1* not obtained; ARA5603; ZRC SAZU.

Description

Female (ARA4270 from Andasibe-Mantadia National Park, Madagascar, Fig. 4A–E)

Measurements and coloration. Total body length 20.11. Prosoma 7.84 long, 8.54 wide, 4.06 high. Carapace and chelicerae reddish brown, covered with whitish setae. Sternum 4.17 long, 3.76 wide, widest between coxae of second legs, dark brown with pale band in posterior half. AME diameter 0.36, PME diameter 0.32, AME separation 0.51, PME separation 1.07, PME–PLE separation 2.93, ALE–PLE separation 0.11. Clypeus height 1.22. Appendages: palps dark reddish brown. All leg segments uniformly dark reddish brown. Leg I femur 7.81, patella 4.21, tibia 6.15, metatarsus 7.55, tarsus 2.92. Opisthosoma 16.84 long, 14.94 wide, 5.08 high. Base color of dorsum light brown, with yellowish longitudinal band, covered with black spots, and with several small, pointy tubercules on anterior half and pair of large posterior tubercules, pointing posteriorly and protruding past spinnerets. Venter brown with several dark brown and black spots, two paler, grey, longitudinal bands. Epigynum as diagnosed (Fig. 4E).

Male (ARA1965 from Andasibe-Mantadia National Park, Madagascar, Fig. 4G-M)

Measurements and coloration. Total body length 4.90. Prosoma 2.48 long, 2.37 wide, 2.12 high. Carapace and chelicerae dark reddish brown, covered with whitish to yellowish setae. Sternum 1.25 long, 1.14 wide, widest between coxae of second legs, orange, sparsely covered with white setae. AME diameter 0.23, PME diameter 0.21, AME separation 0.21, PME separation 0.49, PME–PLE separation 0.81, ALE–PLE separation 0.02. Clypeus height 0.42. Appendages: palps orange. Coxae, trochanters, and femurs orange, patellae, tibiae, metatarsi, and tarsi greenish orange. Leg I femur 3.20, patella 1.41, tibia 2.93, metatarsus 3.44, tarsus 1.26. Opisthosoma 3.46 long, 3.07 wide, 1.36 high. Base color of dorsum greenish brown, covered with black spots and areas, without small, pointy tubercules on anterior half. Venter greyish with black middle area and pair of white spots. Palp as diagnosed (Fig. 4K–M).

Variation

Female total length 18.9–25.1, prosoma length 7.65–8.55. Base color of opisthosoma dorsum light brown to dark brown, with anterior tubercules from small to pronounced. Some individuals with light median band, others without or with light anterior speck (Figs 4A, 6A). Males with little variation in appearance.

Distribution

Eastern Madagascar, known from Andasibe-Mantadia National Park (Toamasina Province), Ranomafana National Park (Fianarantsoa Province), and Marojejy National Park (Antsiranana Province).

Natural history

This species occurs in montane rainforests of eastern Madagascar. The web is typical of *Caerostris* (Gregorič *et al.* 2011a), suspended at day and night. Several individuals have embolic plugs in copulatory openings (Kuntner *et al.* 2015), but never more than one per copulatory opening.

Caerostris hirsuta (Simon, 1895)

Figs 1E, 5, 6D–F; Appendix 1

Trichocharis hirsuta Simon, 1895: 835 (♀).

Caerostris hirsuta – Grasshoff 1984: 756 (♀), fig. 4.

Diagnosis

Caerostris hirsuta differs from all known species of *Caerostris* by the lack of lateral prosomal projections (Figs 5A, E, 6D). The female copulatory openings in *C. hirsuta* (Figs 5E, 6F) are elliptical in shape and relatively larger than in all other Afrotropical species of *Caerostris*. The epigynal hooks in *C. hirsuta* (Figs 5E, 6F) are positioned anteriorly on the epigynal plate, resembling *C. corticosa* (Grasshoff 1984: fig. 26), *C. vicina* (Grasshoff 1984: figs 23–24), and *C. linnaeus* (Gregorič *et al.* 2015b: fig. 7d) from mainland Africa. As in *C. corticosa* and *C. vicina*, these hooks point posteriorly, but are narrow and short in *C. hirsuta* rather than narrow and long as in the other two species. In *C. linnaeus* the hooks are narrow and short as in *C. hirsuta*, but point laterally rather than posteriorly. In contrast to *C. hirsuta*, all other known species of *Caerostris* from Madagascar, as well as others from mainland Africa, have the epigynal hooks positioned medially on the epigynal plate rather than anteriorly, they are wide rather than narrow, and point laterally rather than posteriorly (Grasshoff 1984; Gregorič *et al.* 2015b).

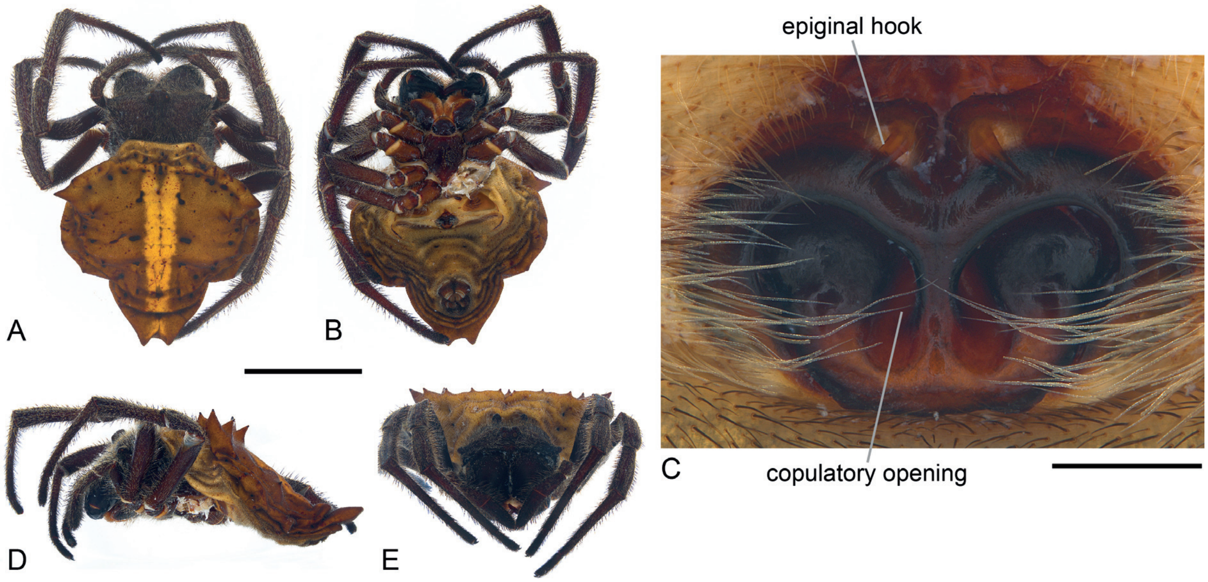

Fig. 5. *Caerostris hirsuta* (Simon, 1895), ♀ (ARA7894), somatic and genital morphology, Marojejy National Park, Madagascar. **A–D**. Somatic morphology. **E**. Epigynum, ventral view. Scale bars: A–B, D, E = 10 mm; C = 1 mm.

Material examined

Material examined

MADAGASCAR • 1 ♀; Antsiranana Province, Marojejy National Park; lat. -18.8255, lon. 48.4349; 29. Mar. 2022; M. Gregorič, M. Kuntner, K.P. Yu and M. Bedjanič leg.; *Cox1* not obtained; ARA7894; USNM • 1 ♀; Antsiranana Province, Marojejy National Park; lat. -14.437629, lon. 49.775602; 24. Mar. 2022; M. Gregorič, M. Kuntner, K.P. Yu and M. Bedjanič leg.; GenBank accession number PP403864; ARA7933; ZRC • 1 ♀; same locality, date, and leg. data as for preceding; *Cox1* not obtained; ARA7987; ZRC • 1 ♀; same locality and leg. data as for preceding; 25. Mar. 2022; GenBank accession number PP403865; ARA7896; ZRC SAZU • 1 ♀; same locality, date, and leg. data as for preceding; GenBank accession number PP403866; ARA7985; ZRC SAZU • 1 ♀; same locality and leg. data as for preceding; 26. Mar. 2022; *Cox1* not obtained; ARA7931; ZRC SAZU • 1 ♀; same locality, date, and leg.data as for preceding; *Cox1* not obtained; ARA7928; ZRC SAZU.

Description

Female (ARA7894 from Marojejy National Park, Madagascar, Fig. 5A–E)

MEASUREMENTS AND COLORATION. Total body length 21.93. Prosoma 9.70 long, 9.09 wide, 5.36 high. Carapace and chelicerae dark reddish brown, covered with long and dense yellowish setae. Sternum 4.40 long, 3.86 wide, widest between coxae of second legs, dark brown and sparsely covered with yellowish setae. AME diameter 0.45, PME diameter 0.35, AME separation 0.57, PME separation 1.28, PME–PLE separation 3.54, ALE–PLE separation 0.12. Clypeus height 1.72. Appendages: palps dark reddish brown. All leg segments uniformly dark reddish brown. Leg I femur 8.41, patella 6.47, tibia 6.85, metatarsus 8.62, tarsus 3.19. Opisthosoma 18.11 long, 16.87 wide, 6.92 high. Base color of dorsum light brown, with a yellowish longitudinal band, covered with black spots, and with several small, pointy tubercules on anterior half and pair of large posterior tubercules, pointing posteriorly and protruding past the spinnerets. Venter brown with several dark brown and black spots, two paler, grey, longitudinal bands. Epigynum as diagnosed (Fig. 5E).

Variation

Female total length 21.93–23.30, prosoma length 8.71–9.70. Base color of opisthosoma dorsum light brown to dark brown, with anterior tubercules from small to pronounced. Some individuals with light median band, others without (Figs 5A, 6D).

Distribution

Toamasina (Tamatave), eastern Madagascar, is designated as the locality of the holotype. However, the species today does not occur in eastern Madagascar, and Toamasina as a major port-city was often designated as the locality in museum collections in the past. Therefore, the holotype might not have been collected there. This species is likely restricted to the northern wet montane forests of Madagascar.

Natural history

This species occurs in montane rainforests of northeastern Madagascar. The web is typical of *Caerostris* (Gregorič *et al.* 2011a), suspended at day and night.

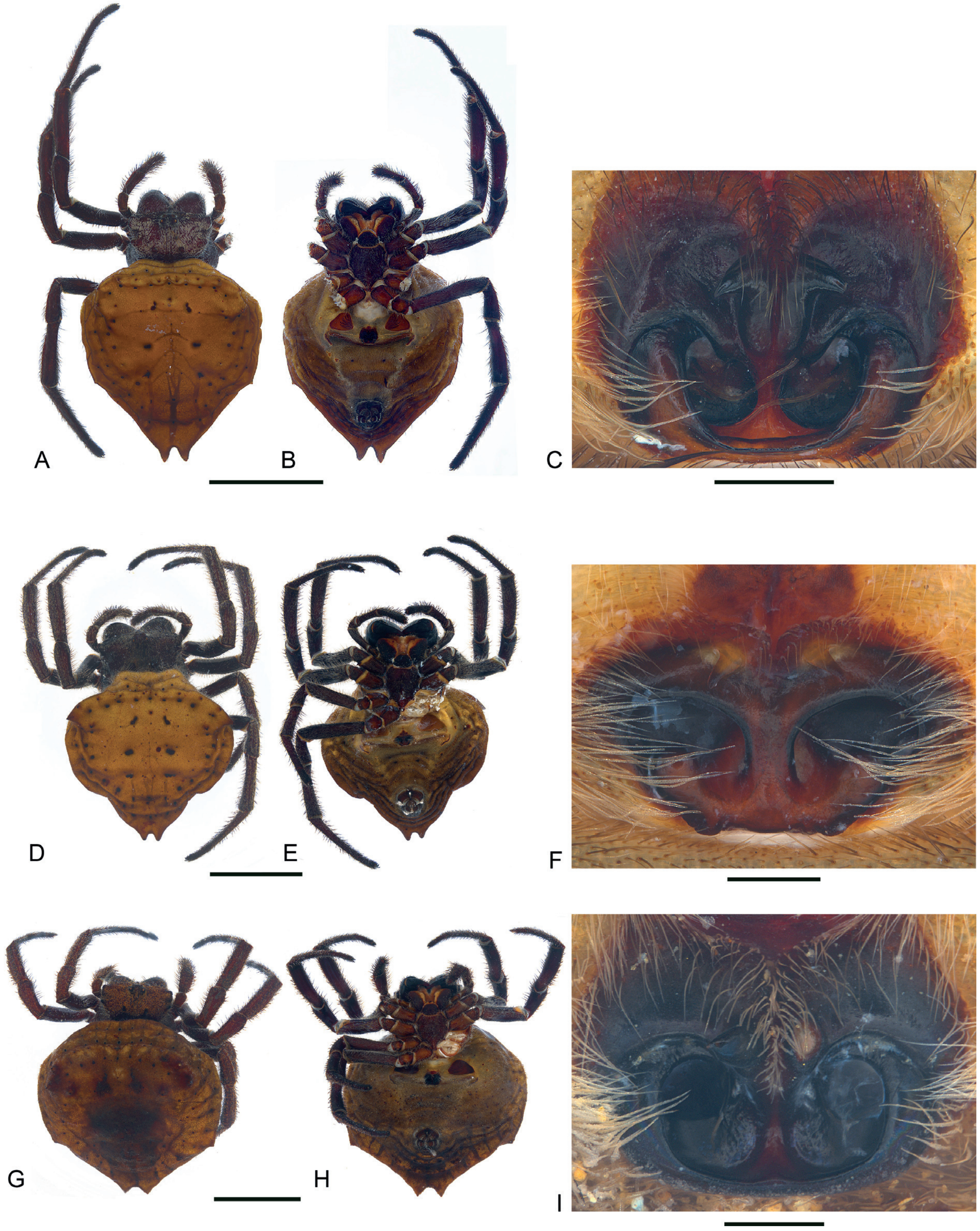

Fig. 6. *Caerostris extrusa* Butler, 1882, ♀ (ARA5603), *C. hirsuta* (Simon, 1895), ♀ (ARA7931), and *C. kuntneri* Gregorič & Yu sp. nov., ♀ (ARA7952), somatic and genital morphology. **A–B**. *C. extrusa*, somatic morphology. **C**. *C. extrusa*, epigynum, ventral view. **D–E**. *C. hirsuta*, somatic morphology. **F**. *C. hirsuta*, epigynum, ventral view. **G**. *C. extrusa*, epigynum, ventral view. **G–H**. *C. kuntneri*, somatic morphology. **I**. *C. kuntneri*, epigynum, ventral view. Scale bars: A–B, D–E, G–H = 10 mm; C, F, I = 1 mm.

Caerostris kuntneri Gregorič & Yu sp. nov.

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Figs 1F, 6G–I, 7; Appendix 1

Diagnosis

As in *C. extrusa* (Figs 4E, 6C), *C. darwini* (Kuntner & Agnarsson 2010: fig. 6e), *C. mitralis* (Grasshoff 1984: figs 19–20, 29–30), *C. tinamaze* (Gregorič *et al.* 2015b: fig. 9c), and *C. wallacei* (Gregorič *et al.* 2015b: fig. 10c), and in contrast to other Afrotropical species of *Caerostris*, the epigynal hooks in *C. kuntneri* (Figs 6I, 7E) are short rather than long, positioned medially on the epigynal plate rather than anteriorly and pointing laterally rather than posteriorly. *Caerostris kuntneri* is similar to *C. almae* and *C. mitralis* but different from the abovementioned species of *Caerostris* by the anterior epigynal margin that circles around the copulatory openings; however, the hooks are small in *C. mitralis* (Grasshoff 1984: figs 19–20), heavily sclerotized, relatively wide, and longer than wide in *C. almae* (Gregorič *et al.* 2015b: figs 3d, 4d, f), and short, about as long as wide in *C. kuntneri* (Figs 6I, 7E). Male *C. kuntneri* (Fig. 7K–M) differ from those of other Afrotropical *Caerostris*, except *C. almae* (Gregorič *et al.* 2015b: fig. 3i–k), by the relatively large palpal bulbus with a large and blunt conductor. The conductor in *C. kuntneri* is large, pointing anteriorly, while mesally in *C. almae*.

Etymology

The species epithet, a noun in the genitive case, honors the arachnologist Matjaž Kuntner, whose discoveries initiated recent research efforts on the genus *Caerostris*.

Type material

Holotype

MADAGASCAR • ♀, labeled “ARA5602, Andasibe-Mantadia, Madagascar”; Toamasina Province, Mantadia National Park; lat. -18.783784, lon. 48.427617; 28. Feb. 2010; M. Kuntner, I. Agnarsson and M. Gregorič leg.; *Cox1* not obtained; ARA5602; USNM.

Paratype

MADAGASCAR • 1 ♂, labeled “ARA1961, Andasibe-Mantadia, Madagascar”; Toamasina Province, Analamazoatra National Park; lat. -18.937172, lon. 48.420053; 8. Dec. 2017; M. Gregorič, M. Kuntner and I. Agnarsson leg.; GenBank accession number PP403877; ARA1961; USNM.

Other material examined

MADAGASCAR • 1 ♀; sequence obtained from Kono *et al.* (2021), sequence voucher 7421-W1_S15; Toamasina Province, Andasibe-Mantadia National Park; GenBank accession number PP403852 • 1 ♀; Toamasina Province, Analamazoatra National Park; lat. -18.932779 lon. 48.413215; 6. Dec. 2017; M. Gregorič, I. Agnarsson, M. Kuntner and P. Babb leg.; GenBank accession number PP403867; CA2017025; ZRC SAZU • 1 ♀; same locality, date, and leg. data as for preceding; GenBank accession number PP403869; CA2017141; ZRC SAZU • 1 ♂; same locality, and leg. data as for preceding; 7. Dec. 2017; GenBank accession number PP403881; ARA1977; ZRC SAZU • 1 ♂; same locality, date, and leg. data as for preceding; GenBank accession number PP403882; ARA1978; ZRC SAZU • 1 ♂; same data as for preceding; GenBank accession number PP403883; ARA1979; ZRC SAZU • ♂; same locality as for preceding; 11. Apr. 2022; M. Gregorič, M. Kuntner, K.P. Yu and M. Bedjanič leg.; GenBank accession number PP403872; ARA8078; ZRC SAZU • 1 ♂; same locality, date, and leg. data as for preceding; GenBank accession number PP403873; ARA8079; ZRC SAZU • 1 ♂; same locality, date, and leg. data as for preceding; GenBank accession number PP403874; ARA8080; ZRC SAZU • 1 ♀; Toamasina Province, Analamazoatra National Park; lat. -18.937172 lon. 48.420053; 8. Dec. 2017; M. Gregorič, I. Agnarsson, M. Kuntner and P. Babb leg.; GenBank accession number PP403868; CA2017327; ZRC

SAZU • 1 ♂; same locality, date, and leg. data as for preceding; GenBank accession number PP403876; ARA1960; ZRC SAZU • 1 ♂; same locality, date, and leg. data as for preceding; GenBank accession number PP403877; ARA1961; ZRC SAZU • 1 ♂; same locality, date, and leg. data as for preceding; GenBank accession number PP403878; ARA1962; ZRC SAZU • 1 ♂; same locality, date, and leg. data as for preceding; GenBank accession number PP403879; ARA1963; ZRC SAZU • 1 ♂; same locality, date, and leg. data as for preceding; GenBank accession number PP403880; ARA1964; ZRC SAZU • 1 ♀; same locality and leg. data as for preceding; 10–16. Dec. 2017; GenBank accession number PP403870; CA2017181; ZRC SAZU • 1 ♀; same locality and leg. data as for preceding; 4. Dec. 2017; GenBank accession number PP403871; CA2017211; ZRC SAZU • 1 ♂; same locality and leg. data as for preceding; 3. Dec. 2017; GenBank accession number PP403875; ARA1934; ZRC SAZU • 1 ♀; Toamasina Province, Analamazoatra National Park; lat. -18.937703, lon. 48.371233; 5. Apr. 2022; M. Gregorič, M. Kuntner, K.P. Yu and M. Bedjanič leg.; *Cox1* not obtained; ARA7923; ZRC SAZU • 1 ♀; same locality, date, and leg. data as for preceding; *Cox1* not obtained; ARA7913; ZRC SAZU • 1 ♀; same locality and leg. data as for preceding; 5. Apr. 2022; *Cox1* not obtained; ARA7937; ZRC SAZU • 1 ♀; same locality and leg. data as for preceding; 8. Apr. 2022; *Cox1* not obtained; ARA7874; ZRC SAZU • 1 ♀; Toamasina Province, Analamazoatra National Park; lat. -18.825368, lon. 48.434792; 6. Apr. 2022; M. Gregorič, M. Kuntner, K.P. Yu and M. Bedjanič leg.; *Cox1* not obtained; ZRC SAZU ARA7967 • 1 ♀; Toamasina Province, Analamazoatra National Park; lat. -18.889361, lon. 48.433165; 10. Apr. 2022; M. Gregorič, M. Kuntner, K.P. Yu and M. Bedjanič leg.; *Cox1* not obtained; ARA7884; ZRC SAZU • 1 ♀; Toamasina Province, Analamazoatra National Park; lat. -18.786784, lon. 48.427617; 28. Feb. 2010; M. Kuntner, I. Agnarsson and M. Gregorič leg.; *Cox1* not obtained; ARA5602; ZRC SAZU • 1 ♀; same locality and leg. data as for preceding; 27. Feb. 2010; *Cox1* not obtained; ARA5608; ZRC SAZU • 1 ♀; Antsiranana Province, Marojejy National Park; lat. -14.437629, lon. 49.775602; 24. Mar. 2022; M. Gregorič, M. Kuntner, K.P. Yu and M. Bedjanič leg.; *Cox1* not obtained; ARA7924; ZRC SAZU • 1 ♀; same locality and leg. data as for preceding; 25. Mar. 2022; *Cox1* not obtained; ARA7925; ZRC SAZU.

Description

Female (holotype, Fig. 7A–E)

Measurements and coloration. Total body length 26.21. Prosoma 9.64 long, 9.67 wide, 7.91 high. Carapace and chelicerae dark reddish brown, covered with whitish to yellowish setae. Sternum 4.59 long, 4.22 wide, widest between coxae of second legs, dark brown with pale band in posterior half. AME diameter 0.39, PME diameter 0.40, AME separation 0.59, PME separation 1.21, PME–PLE separation 3.42, ALE–PLE separation 0.10. Clypeus height 1.70. Appendages: palps dark reddish brown. All leg segments uniformly dark reddish brown. Leg I femur 7.26, patella 4.38, tibia 6.63, metatarsus 7.69, tarsus 2.93. Opisthosoma 17.07 long, 19.24 wide, 10.24 high. Base color of dorsum light brown, covered with black spots, with several small, pointy tubercules on anterior half and pair of large posterior tubercules, pointing posteriorly and protruding past spinnerets. Venter brown with several dark brown and black spots, two paler, grey, longitudinal bands. Epigynum as diagnosed (Fig. 7E).

Male (paratype, Fig. 7G–M)

Measurements and coloration. Total body length 5.15. Prosoma 2.96 long, 2.48 wide, 2.28 high. Carapace and chelicerae dark reddish brown, covered with whitish to yellowish setae. Sternum 1.27 long, 1.24 wide, widest between coxae of second legs, orange brown, sparsely covered with white setae. AME diameter 0.24, PME diameter 0.25, AME separation 0.22, PME separation 0.53, PME–PLE separation 0.92, ALE–PLE separation 0.03. Clypeus height 0.52. Appendages: palps orange. All leg segments uniformly orange. Leg I femur 2.70, patella 1.35, tibia 2.30, metatarsus 2.81, tarsus 1.05. Opisthosoma 3.76 long, 3.61 wide, 1.83 high. Base color of dorsum greenish brown, covered with dark brown spots and black amorphous areas, with several small, pointy tubercules on anterior half. Venter black with white spots. Palp as diagnosed (Fig. 7K–M).

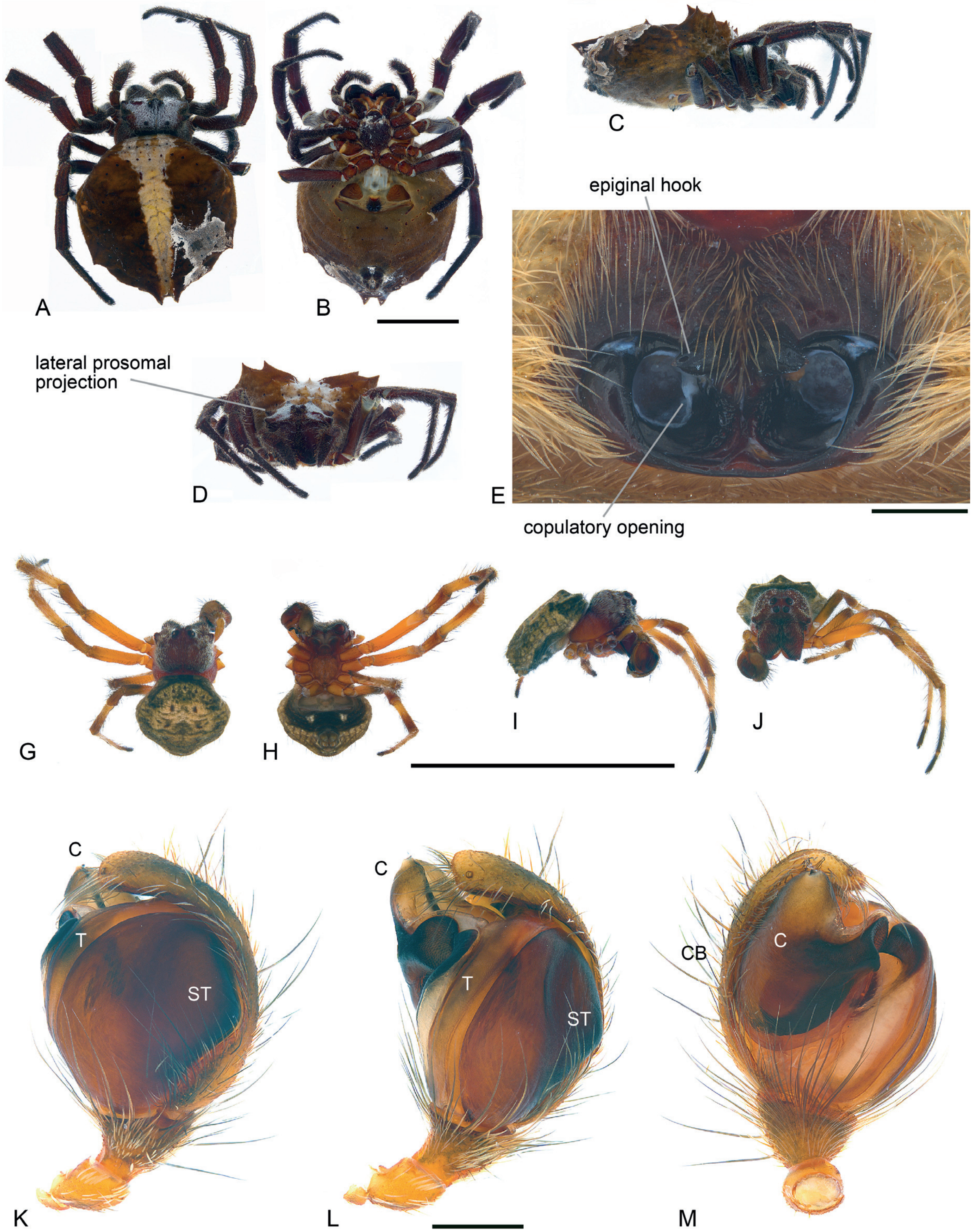

Fig. 7. *Caerostris kuntneri* Gregorič & Yu sp. nov., ♀ (ARA5602) and ♂ (ARA1961) somatic and genital morphology, Andasibe-Mantadia National Park, Madagascar. **A–D**. ♀, somatic morphology. **E**. ♀, epigynum, ventral view. **G–J**. ♂ somatic morphology. **K**. ♂, left palp, lateral view. **L**. ♂, left palp, mesal view. **M**. ♂, left palp, ventral view. Scale bars: A–D, G–J = 10 mm; E, K–M = 1 mm.

Variation

Female total length 19.6–26.2, prosoma length 7.85–9.64. Base color of opisthosoma dorsum light brown to dark brown, with anterior tubercules from small to pronounced. Some individuals with light median band, others without or with light anterior speck (Figs 6G, 7A).

Distribution

Eastern Madagascar, known from Andasibe-Mantadia National Park (Toamasina Province), Ranomafana National Park (Fianarantsoa Province), and Marojejy National Park (Antsiranana Province).

Natural history

This species occurs in montane rainforests of eastern Madagascar. The web is typical of *Caerostris* (Gregorič *et al.* 2011a), suspended at day and night. Several individuals have embolic plugs in copulatory openings (Kuntner *et al.* 2015), but never more than one per copulatory opening. Of the here investigated material, we observed mating in nature, where a male engaged in opportunistic mating (Kuntner & Coddington 2020) with a freshly molted female.

Discussion

Based on the molecular and morphological data, the *C. extrusa* morphotype encompasses four Malagasy species whose distributions in part overlap. While *C. bankana* and *C. hirsuta* seem to be restricted to north Madagascar, and *C. extrusa* to central-east Madagascar, *C. kuntneri* overlaps with them throughout this range. Even though not each other's sister species (Fig. 2), all four species look highly similar in somatic morphology (Figs 1, 3–7) and are often indistinguishable in the field. While *C. extrusa*, *C. bankana*, and *C. kuntneri* can be identified only by inspecting their genital morphology under a microscope, *C. hirsuta* can be identified in the field by the lack of the lateral prosomal projection.

In general, species of the genus *Caerostris* range from very large to fairly small-sized, are all sexually dimorphic in size, and morphologically diverse (Grasshoff 1984; Gregorič *et al.* 2015b). Some species show a stunning resemblance to bark and others a contrasting coloration. Abdomen shape also varies among species: several species have rounded abdomens while others have differently shaped abdominal humps. In some species, there is intraspecific variability in both abdomen color and shape (Gregorič *et al.* 2015b). Interestingly, the four species constituting the *C. extrusa* morphotype match in body size, body coloration, and abdomen shape and even share the variability in dorsal abdomen coloration ranging from completely brown, to brown with an anterior light speck or a full longitudinal light band. This unusual convergent morphotype evolution likely led to the in-field misidentification of specimens used by Kono *et al.* (2021), who missasigned the genome assembly and silk-gene mapping to *C. extrusa*, while *C. kuntneri* sp. nov. is the species they used.

Uncovering the cryptic diversity within the charismatic genus *Caerostris*, whose species are important subjects in studies of the evolution of silk material properties (Agnarsson *et al.* 2010; Gregorič *et al.* 2011b; Garb *et al.* 2019; Htut *et al.* 2021; Kono *et al.* 2021; Babb *et al.* 2022), highlights the need for taxonomic expertise in an era of scientific publishing where taxonomy was in a decades-long decline (Agnarsson & Kuntner 2007; Drew 2011; Sluys 2013). However, in recent years, taxonomy is adopting modern practices that are transforming it into a precise science (Liu *et al.* 2019; Bond *et al.* 2022). As the resources needed to discover and describe new species, as well as to phylogenetically evaluate existing species and groups, are much too low, we hope that the world's scientific community and funding agencies move towards the important goal of increasing funding for taxonomy. Ultimately, understanding global environmental problems like climate change and biodiversity loss, as well as aiding in the discovery of new products like biomaterials and drugs, rely on accurate species identification, making taxonomy an integral part of our scientific endeavors.

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References

Agnarsson I. & Kuntner M. 2007. Taxonomy in a changing world: seeking solutions for a science in crisis. *Systematic Biology* 56: 531–539. https://doi.org/10.1080/10635150701424546

Agnarsson I., Kuntner M. & Blackledge T.A. 2010. Bioprospecting finds the toughest biological material: extraordinary silk from a giant riverine orb spider. *PLoS ONE* 5: e11234. https://doi.org/10.1371/journal.pone.0011234

Babb P.L., Gregorič M., Lahens N.F., Nicholson D.N., Hayashi C.Y., Higgins L., Kuntner M., Agnarsson I. & Voight B.F. 2022. Characterization of the genome and silk-gland transcriptomes of Darwin's bark spider (*Caerostris darwini*). *PLoS ONE* 17: e0268660. https://doi.org/10.1371/journal.pone.0268660

Barrett R.D.H. & Hebert P.D.N. 2005. Identifying spiders through DNA barcodes. *Canadian Journal of Zoology* 83 (3): 481–491. https://doi.org/10.1139/z05-024

Blackwall J. 1866. A list of spiders captured in the south-east region of equatorial Africa, with descriptions of such species as appear to be new to arachnologists. *Annals and Magazine of Natural History* 18 (108): 451–468. https://doi.org/10.1080/00222936608679683

Bond J.E., Godwin R.L., Colby J.D., Newton L.G., Zahnle X.J., Agnarsson I., Hamilton C.A. & Kuntner M. 2022. Improving taxonomic practices and enhancing its extensibility; an example from araneology. *Diversity* 14: 5. https://doi.org/10.3390/d14010005

Butler A.G. 1882. On some new species of the genus *Caerostris* from Madagascar. *Annals and Magazine of Natural History* 10: 100–106. https://doi.org/10.1080/00222938209459680

Clerck C. 1757. *Aranei Svecici. Svenska Spindlar, uti Sina Hufvud-Slågter Indelte Samt Under Några och Sextio Särskildte Arter Beskrefne och med Illuminerade Figurer Uplyste*. Laurentius Salvius, Stockholmiae, Stockholm. https://doi.org/10.5962/bhl.title.119890

Čandek K., Gregorič M., Kostanjšek R., Frick H., Kropf C. & Kuntner M. 2013. Targeting a portion of central European spider diversity for permanent preservation. *Biodiversity Data Journal* 1: e980. https://doi.org/10.3897/BDJ.1.e980

Darriba D., Taboada G.L., Doallo R. & Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772–772. https://doi.org/10.1038/nmeth.2109

Drew L.W. 2011. Are we losing the science of taxonomy?: As need grows, numbers and training are failing to keep up. *BioScience* 61: 942–946. https://doi.org/10.1525/bio.2011.61.12.4

Fabricius J.C. 1793. *Entomologiae Systematica Emendata et Aucta, Secundum Classes, Ordines, Genera, Species Adjectis Synonimis, Locis, Observationibus, Descriptionibus*. Tom. II. Christian Gottlieb Proft, Hafniae, Copenhagen. https://doi.org/10.5962/bhl.title.125869

Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.

Garb J.E., Haney R.A., Schwager E.E., Gregorič M., Kuntner M., Agnarsson I. & Blackledge T.A. 2019. The transcriptome of Darwin's bark spider silk glands predicts proteins contributing to dragline silk toughness. *Communications Biology* 2: 275. https://doi.org/10.1038/s42003-019-0496-1

Grasshoff M. 1984. Die Radnetzspinnen-Gattung *Caerostris* (Arachnida: Araneae). *Revue zoologique Africaine* 98: 725–765.

Gregorič M., Agnarsson I., Blackledge T.A. & Kuntner M. 2011a. Darwin's bark spider: giant prey in giant orb webs (*Caerostris darwini*, Araneae: Araneidae)? *Journal of Arachnology* 39: 287–295. https://doi.org/10.1636/CB10-95.1

Gregorič M., Agnarsson I., Blackledge T.A. & Kuntner M. 2011b. How did the spider cross the river? Behavioral adaptations for river-bridging webs in *Caerostris darwini* (Araneae: Araneidae). *PLoS ONE* 6: e26847. https://doi.org/10.1371/journal.pone.0026847

Gregorič M., Agnarsson I., Blackledge T.A. & Kuntner M. 2015a. Phylogenetic position and composition of Zygiellinae and *Caerostris*, with new insight into orb-web evolution and gigantism. *Zoological Journal of the Linnean Society* 175: 225–243. https://doi.org/10.1111/zoj.12281

Gregorič M., Blackledge T.A., Agnarsson I. & Kuntner M. 2015b. A molecular phylogeny of bark spiders reveals new species from Africa and Madagascar (Araneae: Araneidae: *Caerostris*). *Journal of Arachnology* 43: 293–312. https://doi.org/10.1636/0161-8202-43.3.293

Hebert P.D.N., Cywinska A., Ball S.L. & deWaard J.R. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society B: Biological Sciences* 270: 313–321. https://doi.org/10.1098/rspb.2002.2218

Hedin M.C. & Maddison W.P. 2001. A combined molecular approach to phylogeny of the lumping spider subfamily Dendryphantinae (Araneae : Salticidae). *Molecular Phylogenetics and Evolution* 18: 386–403. https://doi.org/10.1006/mpev.2000.0883

Htut K.Z., Alicea-Serrano A.M., Singla S., Agnarsson I., Garb J.E., Kuntner M., Gregorič M., Haney R.A., Marhabaie M., Blackledge T.A. & Dhinojwala A. 2021. Correlation between protein secondary structure and mechanical performance for the ultra-tough dragline silk of Darwin's bark spider. *Journal of the Royal Society Interface* 18: e20210320. https://doi.org/10.1098/rsif.2021.0320

Kapli P., Lutteropp S., Zhang J., Kobert K., Pavlidis P., Stamatakis A. & Flouri T. 2017. Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. *Bioinformatics* 33: 1630–1638. https://doi.org/10.1093/bioinformatics/btx025

Koch C.L. 1850. *Übersicht des Arachnidensystems. Heft 5*. J.L. Lotzbeck, Nürnberg. https://doi.org/10.5962/bhl.title.39561

Kono N., Ohtoshi R., Malay A.D., Mori M., Masunaga H., Yoshida Y., Nakamura H., Numata K. & Arakawa K. 2021. Darwin's bark spider shares a spidroin repertoire with *Caerostris extrusa* but achieves extraordinary silk toughness through gene expression. *Open Biology* 11: e210242. https://doi.org/10.1098/rsob.210242

Kuntner M. & Agnarsson I. 2010. Darwin's bark spider: Web gigantism in a new species of bark spiders from Madagascar (Araneidae: *Caerostris*). *Journal of Arachnology* 38: 346–356. https://doi.org/10.1636/B09-113.1

Kuntner M. & Coddington J.A. 2020. Sexual size dimorphism: Evolution and perils of extreme phenotypes in spiders. *Annual Review of Entomology* 65: 57–80. https://doi.org/10.1146/annurev-ento-011019-025032

Kuntner M., Coddington J.A. & Hormiga G. 2008. Phylogeny of extant nephilid orb-weaving spiders (Araneae, Nephilidae): testing morphological and ethological homologies. *Cladistics* 24: 147–217. https://doi.org/10.1111/j.1096-0031.2007.00176.x

Kuntner M., Agnarsson I. & Li D.Q. 2015. The eunuch phenomenon: adaptive evolution of genital emasculation in sexually dimorphic spiders. *Biological Reviews* 90: 279–296. https://doi.org/10.1111/brv.12109

Kuntner M., Čandek K., Gregorič M., Turk E., Hamilton C.A., Chamberland L., Starrett J., Cheng R.C., Coddington J.A., Agnarsson I. & Bond J.E. 2023. Increasing information content and diagnosability in family-level classifications. *Systematic Biology* 72 (4): 964–971. https://doi.org/10.1093/sysbio/syad021

Liu Y., Dietrich C., Braxton S. & Wang Y. 2019. Publishing trends and productivity in insect taxonomy from 1946 through 2012 based on an analysis of the *Zoological Record* for four species-rich families. *European Journal of Taxonomy:* 504. https://doi.org/10.5852/ejt.2019.504

Miller M.A., Pfeiffer W. & Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010*: 1–8. 14 Nov. 2010, New Orleans, LA. https://doi.org/10.1109/GCE.2010.5676129

Pocock R.I. 1902. Some new African spiders. *Annals and Magazine of Natural History* 10: 315–330. https://doi.org/10.1080/00222930208678678

Puillandre N., Brouillet S. & Achaz G. 2021. ASAP: assemble species by automatic partitioning. 21: 609–620. https://doi.org/10.1111/1755-0998.13281

Ratnasingham S. & Hebert P.D.N. 2007. bold: The Barcode of Life Data System. *Molecular Ecology Notes* 7: 355–364. Available from https://www.barcodinglife.org [accessed 22 Mar. 2025]. https://doi.org/10.1111/j.1471-8286.2007.01678.x

Simon E. 1895. *Histoire naturelle des araignées* 1: 761–1084. Paris.

Sluys R. 2013. The unappreciated, fundamentally analytical nature of taxonomy and the implications for the inventory of biodiversity. *Biodiversity and Conservation* 22: 1095–1105. https://doi.org/10.1007/s10531-013-0472-x

Strand E. 1915. Indoaustralische, papuanische und polynesische Spinnen des Senckenbergischen Museums, gesammelt von Dr E. Wolf, Dr J. Elbert u. a. *In: Wissenschaftliche Ergebnisse der Hanseatischen Südsee-Expedition 1909. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 36: 179–274.

Tamura K., Stecher G. & Kumar S. 2021. MEGA11: Molecular Evolutionary Genetics Analysis version 11. *Molecular Biology and Evolution* 38 (7): 3022–3027. https://doi.org/10.1093/molbev/msab120

Thorell T. 1868. Araneae. Species novae minusve cognitae. *In*: Virgin C.A. (ed.) *Kongliga Svenska Fregatten Eugenies Resa omkring Jorden*: 1–34. Almqvist & Wiksells,Uppsala / Stockholm.

Vidergar N., Toplak N. & Kuntner M. 2014. Streamlining DNA barcoding protocols: Automated DNA extraction and a new cox1 primer in arachnid systematics. *PLoS ONE*: e113030. https://doi.org/10.1371/journal.pone.0113030

Vinson A. 1863. *Aranéides des Îles de La Réunion, Maurice et Madagascar*. Librairie Classique Eugène Belin, Berlin. https://doi.org/10.5962/bhl.title.125517

Walckenaer C.A. 1805. *Tableau des Aranéides ou Caractères Essentiels des Tribus, Genres, Familles et Races que Renferme le Genre Aranea de Linné, avec la Désignation des Espèces Comprises dans Chacune de ces Divisions*. Dentu, Paris.

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Appendix 1 (continued on next page).

Information of the 58 ingroup and 8 outgroup taxa, downloaded for this study from the BOLD database, given as our species identification, their BOLD identifiers, and the species identification at BOLD if different to ours.

Species	**BOLD identifier**	**Species ID at BOLT if different**
Caerostris almae Gregorič, 2015	KT267101	
Caerostris almae	KT267102	
Caerostris almae	KT267103	
Caerostris almae	KT267104	
Caerostris almae	KT267105	
Caerostris almae	KT267106	
Caerostris almae	KT267107	
Caerostris bojani Gregorič, 2015	KT267093	
Caerostris bojani	KT267094	
Caerostris bojani	KT267095	
Caerostris bojani	KT267096	
Caerostris bojani	KT267097	
Caerostris bojani	KT267098	
Caerostris cowani Butler, 1882	KT267064	
Caerostris cowani	KT267065	
Caerostris darwini Kuntner & Agnarsson, 2010	KJ957955	
Caerostris darwini	KT267067	
Caerostris darwini	KT267068	
Caerostris darwini	KT267069	
Caerostris darwini	KT267070	
Caerostris darwini	KT267071	
Caerostris darwini	KT267072	
Caerostris darwini	MK420083	*Caerostris* sp.
Caerostris darwini	RNOCF063-17	
Caerostris darwini	RNOCF187-17	
Caerostris extrusa Butler, 1882	KM486428	*Caerostris* sp.
Caerostris kuntneri Gregorič & Yu sp. nov.	KT267073	*Caerostris extrusa*
Caerostris kuntneri	KT267074	*Caerostris extrusa*
Caerostris kuntneri	KT267075	*Caerostris extrusa*
Caerostris kuntneri	KT267076	*Caerostris extrusa*
Caerostris kuntneri	KT267077	*Caerostris extrusa*
Caerostris kuntneri	KT267078	*Caerostris extrusa*

Appendix 1 (continued).

Species	**BOLD identifier**	**Species ID at BOLT if different**
Caerostris kuntneri	KT267079	*Caerostris extrusa*
Caerostris linnaeus Gregorič, 2015	KT267092	
Caerostris mitralis (Vinson, 1863)	KT267080	
Caerostris mitralis	KT267081	
Caerostris mitralis	KT267082	
Caerostris mitralis	KT267083	
Caerostris pero Gregorič, 2015	KT267099	
Caerostris pero	KT267100	
Caerostris sexcuspidata (Fabricius, 1793)	KC849066	
Caerostris sexcuspidata	KT267084	
Caerostris sexcuspidata	KT267085	
Caerostris sexcuspidata	KT267086	
Caerostris sexcuspidata	KT267087	
Caerostris sexcuspidata	KT267088	
Caerostris sexcuspidata	KT267089	
Caerostris sexcuspidata	KT267090	
Caerostris sexcuspidata	KT267091	
Caerostris sumatrana Strand, 1915	KM486426	*Caerostris* sp.
Caerostris sumatrana	KM486427	*Caerostris* sp.
Caerostris sumatrana	KR526573	
Caerostris sumatrana	KT267112	
Caerostris sumatrana	KT267113	
Caerostris sumatrana	MK420084	*Caerostris* sp.
Caerostris tinamaze Gregorič, 2015	KT267109	
Caerostris tinamaze	KT267110	
Caerostris wallacei Gregorič, Blackledge, Agnarsson & Kuntner, 2015	KT267108	
Araneus marmoreus Clerck, 1757 (Araneidae Clerck, 1757)	FJ525334	
Argiope argentata (Fabricius, 1775) (Araneidae)	KJ957947	
Cyclosa conica (Pallas, 1772) (Araneidae)	FJ5253191	
Eriophora ravilla (C.L. Koch, 1844) (Araneidae)	GU3019041	
Larinioides cornutus Clerck, 1757 (Araneidae)	FJ5253221	
Trichonephila clavipes (Linnaeus, 1767) (Nephilidae Simon, 1894)	FJ5253281	
Zygiella atrica (C.L. Koch, 1845) (Phonognathidae Simon, 1894)	KR5265941	
Tetragnatha versicolor Walckenaer, 1841 (Tetragnathidae Menge, 1866)	FJ525317	