

First evidence of aggressive chemical mimicry in the Malagasy orb weaving spider *Exechocentrus lancearius* Simon, 1889 (Arachnida: Araneae: Araneidae) and description of a second species in the genus

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> Abstract

The araneid genus *Exechocentrus* Simon, 1889 and its type species *Exechocentrus lancearius* were originally described based on a single female specimen from Madagascar, which was missing the abdomen. The first complete adult specimen, a female, of *Exechocentrus lancearius* was collected in 2000. A second adult female of *Exechocentrus* sp. was discovered in 2009, about 300 km away from the first locality. We redescribe the neotype of *Exechocentrus lancearius* and describe the second adult female as *Exechocentrus madilina* new species. We also report some observations on the natural history of *Exechocentrus lancearius*, including photographs of its highly modified foraging web, which provide indirect evidence of aggressive chemical mimicry.

> Key words

Systematics, taxonomy, bolas spiders, spider webs, silk, Madagascar.

Introduction

The spider family Araneidae comprises more than 3000 species in 171 genera (PLATNICK 2012; see also DIMITROV et al. 2012), and includes the well known common orb-weavers, which produce geometric orbicular snares to capture a wide variety of airborne prey. No less than 48 of the 171 described genera (28%) are monotypic (i.e., include only one species; PLATNICK 2012) and many species are rare and have been collected only a few times since their original description. Although the vast majority of spiders are generalist predators, Araneidae includes a number of specialists that target a very narrow range of prey items. Spectacular examples of such prey specialization are provided by *Mastophora* spp., which prey on

selected species of male moths that are lured by sex pheromones (EBERHARD 1977, 1980; YEARGAN 1988; STOWE et al. 1987), or by the highly modified ladder orb webs of *Scoloderus* spp. (STOWE 1986).

The Malagasy genus *Exechocentrus* is rare and monotypic. It was recently placed in the araneid subfamily Cyrtarachninae (EMERIT 2000), which includes genera that have reduced webs (or have entirely abandoned foraging webs) and includes members that use aggressive chemical mimicry to lure male moths as prey, such as the aforementioned genus *Mastophora* Holmberg, 1876 (JOCQUÉ & DIPPENAAR-SCHOEMAN 2006; DIPPENAAR-SCHOEMAN 1997; GRISWOLD 2003), which Emerit placed in the tribe Mastophoreae, under the

subfamily Cyrtarachninae. Other authors have suggested that Mastophoreae should be considered its own subfamily (STOWE 1986; SCHARFF & CODDINGTON 1997), Mastophorinae, and this is followed herein.

The genus *Exechocentrus* and its type species *Exechocentrus lancearius* were originally described by SIMON (1889) based on a single female specimen from Madagascar, which was missing the abdomen (and therefore the genitalia, assuming that it was an adult specimen). Simon probably felt compelled to describe this species, despite the incompleteness of the specimen, because of its unusual carapace, covered with bizarre spines and projections. Simon redescribed the same specimen in 1895 and added the first illustrations of the cephalothorax and leg I (SIMON 1895: figs. 951–953). No other species of *Exechocentrus* has been described since Simon's original description. In fact, it took 83 years before more specimens of *Exechocentrus* were 'discovered' (EMERIT 1978). EMERIT (2000) provided an illustration of a juvenile specimen from Ambohivoangy, Madagascar. He suggested that it was conspecific with *Exechocentrus lancearius* based on the unusual morphology of the cephalothorax. A more detailed description of *Exechocentrus*, based on immature females collected by J. Millot in 1946 and M. Emerit in 1963, was presented by EMERIT (1980), who also compared the juvenile specimens to the holotype (which consists of only a cephalothorax). The juvenile specimens all came from forest areas east and northeast of the capital Antananarivo (Forêt d'Ambohivoangy, Forêt de la Mandraka and Forêt de Périnet). Emerit (2000) also suggested that *Exechocentrus* could be related to the mastophorines (Araneidae-Cyrtarachninae, Mastophoreae – bolas spiders), particularly to the genus *Acantharachne* Tullgren, 1910 from Madagascar and Africa, whose members also have bizarre spines on the carapace and large abdominal tubercles. EMERIT (2000) thereby suggested that this Malagasy species may forage using a bola, although no direct observations supported the implied hunting strategy.

During our world-wide search for specimens in museums we discovered a juvenile *Exechocentrus* in the Museum für Naturkunde of the Humboldt University in Berlin. The museum catalogue entry reads "23919 *Exechocentrus lancearius* Sim.*, 1female, S. Centr. Madagaskar, Hildebrandt Typus, Ann. Soc. ent. France (6) 8 p. 227, 1889." According to the curator (Dr. Jason Dunlop), a '*' in the catalogue entry usually denotes a type specimen, and the museum therefore assumed that it represented an original syntype. This is however impossible because Simon's original description (SIMON 1889) only mentioned the cephalothorax and legs. Later, SIMON (1895: p. 887) specifically mentioned that the only known specimen of *Exechocentrus lancearius* is missing the abdomen. The

juvenile from Berlin is complete, with abdomen, and had Simon known this specimen, he would certainly have described the peculiar abdomen, with two long dorsal apophyses. The specimen in Berlin was collected by Johann Maria Hildebrandt (1847–1881), a German explorer who collected plants and animals in the Afrotropical region from 1872 until he died of yellow fever in Madagascar in 1881, at the age of 34. The original label data does not reveal collecting date, but from Hildebrandt's collecting itineraries (BEENTJE 1998), we know that he collected in Madagascar from 1879 until his death in 1881, and that South Central Madagascar was visited between last half of 1880 to early 1881. The juvenile specimen in Hamburg could therefore, in theory, have been available to Simon when he described *Exechocentrus lancearius* in 1889, but no direct or indirect evidence suggests that Simon ever examined Hildebrandt's specimen.

The first adult specimen, a female, of *Exechocentrus* was collected by researchers from the California Academy of Sciences near Andranomay in 2000. A second adult female was collected by us in the vicinity of Ranomafana National Park in 2009 (this specimen was designated as the neotype of *Exechocentrus lancearius* Simon, 1889 by SCHARFF & HORMIGA 2012). As far as we have been able to determine, no other specimens of *Exechocentrus* exist in collections. These two localities are 300 km apart and the two adult specimens clearly represent two different species. Given the high diversity of spiders in Madagascar and how poorly known most of its arthropods are (GRISWOLD 2003) it is very likely that further species of *Exechocentrus* exist on the island. We describe here the neotype for *Exechocentrus lancearius* and the foraging web of this species based on our field observations. We also describe the specimen from Andranomay as a new species of *Exechocentrus*.

Materials and methods

Specimens were examined and illustrated using a Leica M205A stereoscopic microscope equipped with a Leica DFC420 camera and LAS software. Further details were studied and illustrated using a Leica DMRM compound microscope with a drawing tube. Photographs were taken with a BK+ Imaging System from Visionary Digital (<http://www.visionarydigital.com>) equipped with a Canon EOS 7D camera. Single images were combined with Helicon Focus version 5.0 to increase depth of field (www.heliconsoft.com, Helicon Soft Ltd.). All morphological measurements



Fig. 1. *Exechocentrus* “*lancearius*” Simon, 1889 – Simon’s specimen (MNHN 8339). A: cephalothorax and legs, ventral view; B: cephalothorax and legs, dorsal view. Scale bars: 1 mm.



Fig. 2. *Exechocentrus* “*lancearius*” Simon, 1889 – Simon’s specimen (MNHN 8339). A: cephalothorax and legs, fronto-lateral view; B: cephalothorax and legs, dorso-lateral view. Scale bars: 1 mm.

are in millimeters. Somatic morphological measurements were taken using a scale reticule in the dissecting microscope. The epigynum was excised using a breakable surgical blade and sharpened needles and then transferred to methyl salicylate (HOLM 1979) for examination under the microscope using the mounting method described by GRANDJEAN (1949) and CODDINGTON (1983).

Taxonomy

Family Araneidae Clerck, 1758

Genus *Exechocentrus* Simon, 1889

Type species: *Exechocentrus lancearius* Simon, 1889: 227.

Diagnosis. *Exechocentrus* species can be distinguished from all other known araneids by the presence of a long cephalic projection (Figs. 1A,B, 2A,B, 3A–C, 6A–C), originating from the median eye rectangle, and three long dorsal projections on thorax, just in front of the fovea (Fig. 2A,B).

Description. Females: Medium sized araneid spiders; total length 3.90–5.38 (margin of clypeus to posterior end of abdomen), cephalothorax piriform, hirsute, covered with short dense translucent setae almost as wide as long, provided with a long cephalic projection, originating from median eye rectangle, and three dorsal (long or short) projections on thorax, just in front of the fovea (Figs. 1A,B, 2A,B, 3A–C, 6A–C). Labium wider than long and strongly rebordered. Endites longer than wide. Cephalothorax yellowish white with brown pattern radiating from fovea (Figs. 1B, 3A, 6A). Legs pale yellowish white, with dark brown patterns. Tibiae, metatarsi and tarsi with prolateral row of short (half diameter of leg segment) pale macrosetae. Macrosetae on legs otherwise absent, except for the apical part of metatarsi IV and proximal part of tarsi IV, which are provided with several serrated dorsal macrosetae (Fig. 3A,B, arrows). Femora I bent, slightly swollen in the middle (Figs. 1B, 3A, 6A). Coxae IV orange brown. Sternum approximately as long as wide and blackish brown. Posterior eye row strongly recurved (dorsal views; Figs. 1B, 3A, 6A), AME, ALE, PLE, and PME approximately same size, lateral eyes (ALE & PLE) close, almost touching. Clypeus high, $2.2\text{--}2.4 \times$ the diameter of AME. Abdomen

creamy white and almost heart-shaped dorsally (Figs. 1B, 3A, 6A). Booklung covers whitish. Colulus present. Epigynum dorsally concave, ventrally projecting and heavily sclerotized lip (Figs. 4A, 7A). Spermathecae large, ovoid, with narrow short copulatory ducts (Figs. 4B, 7B). **Males:** Unknown.

Composition. Two species, *Exechocentrus lancearius* Simon, 1889 and *Exechocentrus madilina* n.sp.

Distribution. Madagascar (Ambohivoangy, Mandraka, Périnet, Andranomay, Ankarafantsika and Ranomafana).

Key to females of *Exechocentrus* (males unknown)

- 1 Abdomen with two long digitiform dorsal abdominal apophyses (Fig. 3A) and U-shaped epigynal lip (Fig. 4A) ***Exechocentrus lancearius* Simon**
- 1' Abdomen with many small dorsal protuberances, but no long digitiform apophyses (Fig. 6A) and V-shaped epigynal lip (Fig. 7A) ***Exechocentrus madilina* n.sp.**

Exechocentrus lancearius Simon, 1889

Figs. 3A–C, 4A,B, 5A,B

Exechocentrus lancearius Simon, 1889: 227.

Exechocentrus lancearius: SIMON 1895: 888, figs. 951–953.

Exechocentrus lancearius: EMERIT 1980: 14, pl. 1A.

Material examined. 1 female neotype from Madagascar, Fianarantsoa province. 3.62 km ENE of Ranomafana, Parc National Ranomafana, Vohiparara, $21^{\circ}14'26''\text{S}$ $47^{\circ}23'34''\text{E}$, 3.3 km WNW (297.2°) of the Centre ValBio Research Station adjacent to Ranomafana National Park, 1115 m a.s.l. Evergreen rainforest, along road, 11.i.2009, G. Hormiga & N. Scharff leg. (deposited at ZMUC; Cat no. ZMUC00021482). – 1 juvenile female, S. Centr. Madagascar, Hildebrandt leg. (ZMB 23919); 1 juvenile female, Madagascar, Mahajanga Province, Parc National d'Ankarafantsika, $16^{\circ}19'15''\text{S}$ $46^{\circ}48'38''\text{E}$, 130 m a.s.l., 26.iii.–01.iv.2001, J.J. Rafanomezantsoa et al. leg. (JJR0142/CASENT 9002635).

Remarks on type(s). An adult female was designated as neotype by SCHARFF & HORMIGA (2012) (Figs. 3–5) and is here redescribed in detail. Simon's original type is a female cephalothorax missing the abdomen and most legs (Figs. 1, 2; deposited in MNHN, examined; Cat. no. 8339). It is not possible to determine where on Madagascar Simon's specimen came from

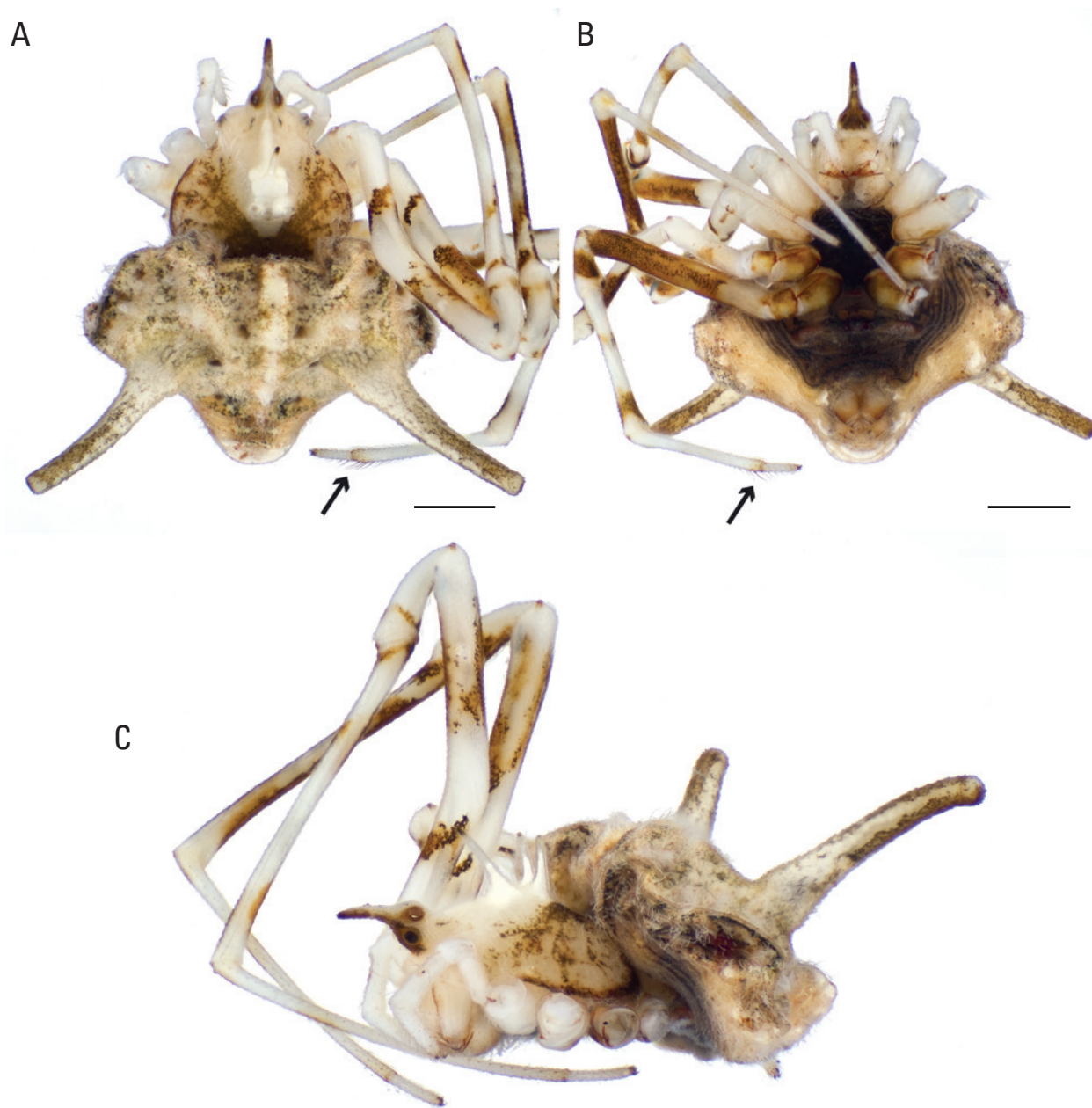


Fig. 3. *Exechocentrus lancearius* Simon, 1889 – Female neotype from near Ranomafana National Park (ZMUC00021482). Left legs detached. **A:** dorsal view; **B:** ventral view; **C:** lateral view. Scale bars: 1 mm.

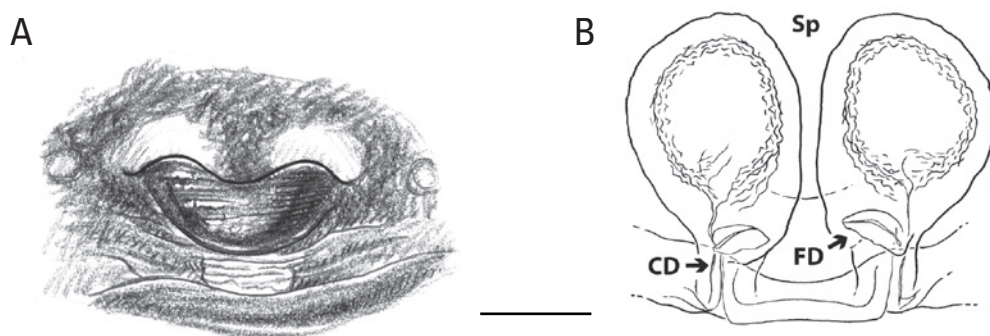


Fig. 4. *Exechocentrus lancearius* Simon, 1889 – Female neotype from Ranomafana National Park (ZMUC00021482). **A:** epigynum, ventral view; **B:** female vulva, cleared, dorsal view. Abbreviations: Sp, spermathecae; CD, copulatory ducts; FD, fertilization ducts. Scale bar: 1 mm.

or whether it was adult. Simon's specimen probably represents a juvenile specimen, since all measurements on cephalothorax and legs are considerably shorter than the measurements presented here for adult specimens. The measurements of cephalothorax, sternum and tibia, metatarsus & tarsus of leg I of Simon's original type specimen agree well with the measurements presented by EMERIT (1980: p. 17) for a juvenile that he identified as *E. lancearius* (cat. no. CEM5013). Except for size, the two adult females of *Exechocentrus* described in this paper and the original type of Simon cannot be distinguished based on cephalothorax and leg morphology. Therefore, it is impossible to say which of these adult specimens, if any, is conspecific with Simon's type specimen of *E. lancearius*. In absence of genitalic data, and diagnostic somatic characters on the cephalothorax, critical for species identification, we designated a neotype (SCHARFF & HORMIGA 2012). After this nomenclatural act, Simon's type specimen for *E. lancearius* cannot be assigned to a species of *Exechocentrus*; we therefore put "*lancearius*" in inverted commas when referring to this specimen, which is now officially *Exechocentrus* sp. indet., and we keep the redescription of this specimen (see below) separate from the species redescription of *Exechocentrus lancearius*, which is based on the neotype.

Diagnosis. The female of *Exechocentrus lancearius* differs from that of *Exechocentrus madilina* n.sp. by having a pair of long digitiform dorsal abdominal apophyses (Fig. 3A–C) and by details of the genitalia (Fig. 4A,B), with a dorsally concave, ventrally projecting and heavily sclerotized U-shaped epigynal lip. The spermathecae are ovoid, with short posteriorly projecting copulatory ducts and mesally oriented dorsal fertilization ducts.

Description. Female neotype (from Ranomafana – ZMUC00021482; Figs. 3–5): Total length 3.90 (margin of clypeus to posterior end of abdomen). Cephalothorax 2.02 long (margin of clypeus to posterior end of cephalothorax), 2.02 wide. Sternum 1.04 long, 0.96 wide. Abdomen 2.65 long, 3.91 wide. Abdominal projections 2.52 long. Cephalothorax piriform, hirsute, covered with short dense translucent setae; with one slightly antieriad-bent spiniform projection (Fig. 3A–C), originating from median eye rectangle, and three long characteristic similarly shaped projections anterior to fovea, one on mid-point and one on each side of the midline axis (Fig. 3A,C). Carapace and chelicerae yellowish white with dark brown pattern radiating from fovea (Fig. 3A–C) and a white line running from fovea to ocular area. Margin of carapace blackish brown, projections with black tips and median eye rectangle dark brown. Legs yellowish white,

with orange brown patterns on all legs (particularly pronounced on distal half of femora). Coxae III and IV orange brown. Sternum blackish brown (Fig. 3A). Posterior eye row strongly recurved (dorsal view; Fig. 3A). Eye measurements: AME 0.12, ALE 0.10, PLE 0.10, PME 0.11, AME–AME 0.16, PME–PME 0.20, AME–ALE 0.15, ALE–PLE 0.01, PLE–PME 0.46. Clypeus 0.29 high. Pedipalps: tarsal claw provided with three small teeth; tibia with a proximal group of eight trichobothria. Legs: leg formula (longest to shortest) I,II,IV,III; length of segments (femur + patella + tibia + metatarsus + tarsus): I: 12.37 (3.99+1.09+3.36+3.36+0.57), II: 11.37 (3.78+1.05+2.86+3.15+0.53), III: 5.47 (1.89+1.12+0.67+1.31+0.48), IV: 7.50 (2.72+0.77+1.83+1.73+0.45). First femora bent (Fig. 3A), slightly swollen in the middle. Tibiae, metatarsi and tarsi with prolateral row of short (half diameter of leg segment) pale macrosetae. Macrosetae on legs otherwise absent, except for the apical part of metatarsus IV and proximal part of tarsi IV, which are provided with several serrated dorsal macrosetae (Fig. 3A,B, arrows). Abdomen (Fig. 3A–C): almost heart-shaped dorsally (Fig. 3A) with two long digitiform dorsal abdominal apophyses (Fig. 3A–C) but otherwise no other protuberances. Abdomen creamy white dorsally with dark brownish black sigilla, yellowish brown ventrally with a broad black median band that runs from anterior to posterior. Booklung covers white and spinnerets brown. Colulus present, with macrosetae. Spinnerets: Details not visible on neotype. Epigynum (Fig. 4A,B): with a dorsally concave, ventrally projecting and heavily sclerotized U-shaped lip (Fig. 4A). Spermathecae (Sp) large, ovoid, juxtaposed and with short, narrow, posteriorly projecting copulatory ducts (CD) and mesally oriented short dorsal fertilization ducts (FD) (Fig. 4B). **Male:** Unknown.

Distribution. Only known from Madagascar (Ambohivoangy, Mandraka, Périnet, Ankarafantsika and Ranomafana). The specimens from Ambohivoangy, Mandraka, and Périnet are all juveniles and based on literature records. We have listed these as *Exechocentrus lancearius* since they all have the characteristic long digitiform dorsal abdominal apophyses.

Natural history. The specimen described above was observed live near Ranomafana National Park, where it was found actively hunting on the forest edge shortly after sundown (Fig. 5C, white arrow; at approx. 19:30). The spider was found hanging on a horizontal silk line underneath a narrow leaf approximately 1.5 meters above ground. It had already produced a bola with two sticky droplets and was in foraging mode, with the bola hanging/swinging from the horizontal silk line. The bola was manipulated with the second pair of legs (Fig. 5A,B). The bola was approx. 26 mm

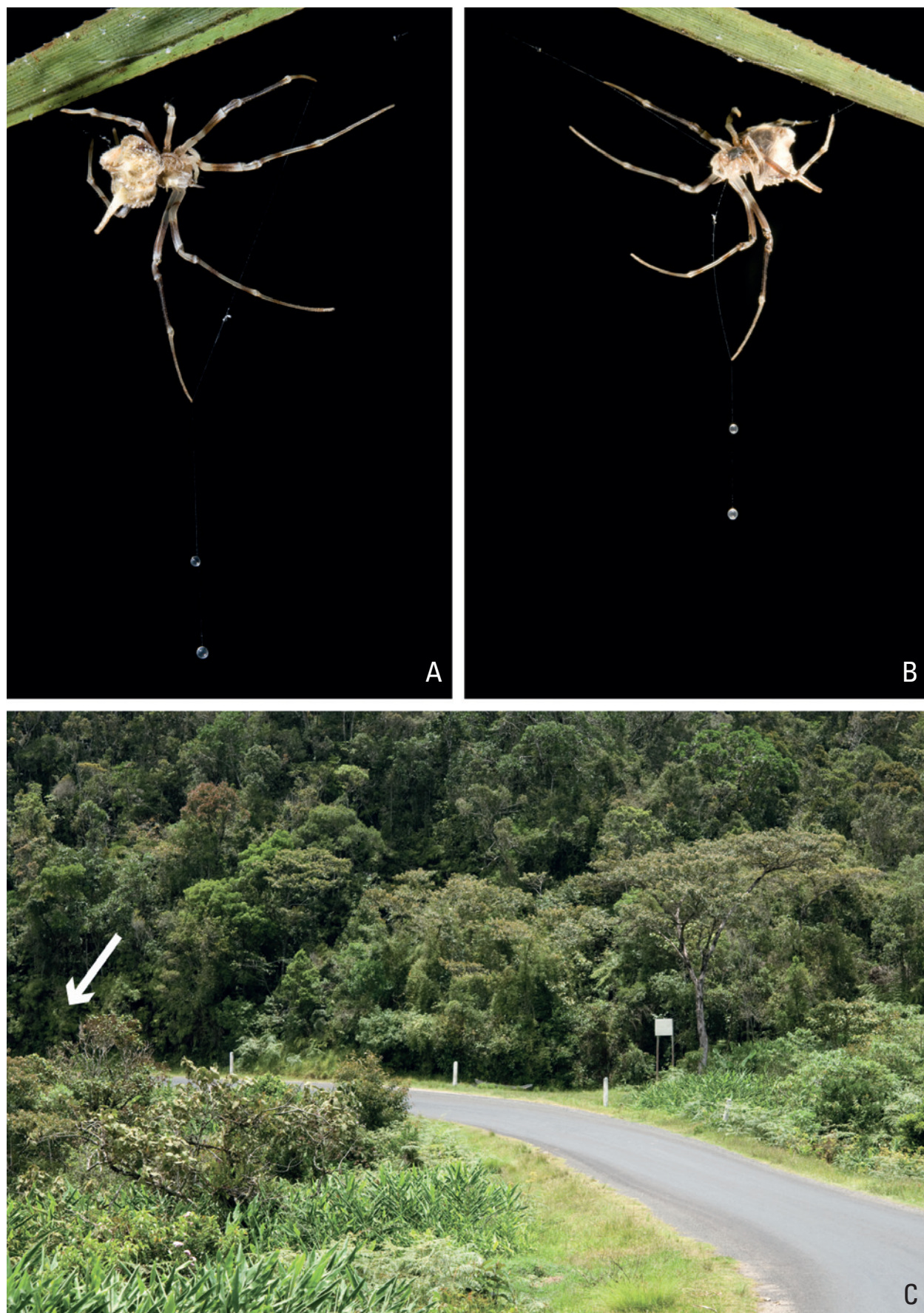


Fig. 5. *Exechocentrus lancearius* Simon, 1889 – Female neotype from near Ranomafana National Park (ZMUC00021482). **A:** dorsal view; **B:** ventral view; **C:** habitat, daytime (white arrow indicates where spider was found at night). Photos: Gustavo Hormiga (A), Nikolaj Scharff (B,C).

long ($6.5 \times$ the total length of the spider) from the attachment point on the horizontal silk line to the glue droplet at the end of the bola and was grabbed by the second pair of legs approx. 6–10 mm from the end of the bola. The two glue droplets were positioned approx. 4 mm apart. When swinging the foraging line, the bola is whirled in a horizontal direction. We did not observe any prey during this swinging behaviour, but observed that the behaviour could be elicited by vibrations caused by passing cars on the road next to the forest.

Redescription of Simon's original specimen of *Exechocentrus "lancearius"*

Figs. 1A,B, 2A,B

Note that due to the missing abdomen of this specimen and the consequently required designation of a neotype for *E. lancearius* (SCHARFF & HORMIGA 2012), this specimen can no longer be assigned to a species of *Exechocentrus*.

Female from Madagascar (catalogue number MNHN 8339). Cephalothorax 1.50 long (margin of clypeus to posterior end of carapace), 1.50 wide. Sternum 0.85 long, 0.82 wide. Cephalothorax piriform with long cephalic projection (Figs. 1A,B; 2A,B), originating from median eye rectangle, and three long projections on thorax, just in front of the fovea (Fig. 2A,B). Cephalothorax and chelicerae yellowish white with darker orange brown pattern radiating from fovea (Figs. 1B, 2B) and a white line running from fovea to ocular area. Cephalic projections with black tips (Figs. 1B, 2A). Legs yellowish white, with orange brown patterns on distal half of femora and tibiae (most legs broken, several legs segments lost) (Figs. 1A,B, 2A,B). Coxae IV orange brown (Fig. 1A). First femora bent, slightly swollen in the middle (Fig. 1B). The prolateral row of spines on the tibiae and metatarsi of leg I and II mentioned in the original description (SIMON 1889), and later illustrated by SIMON (1895: fig. 953), is impossible to verify, as most legs are broken and lost. Only half of tibia II (proximal part) has been preserved and here it is possibly to recognize a short row of 3–4 prolateral spines. Sternum dark brown with yellowish white margins (Fig. 1A). Posterior eye row strongly recurved (dorsal view) (Fig. 1B). Eye measurements: AME 0.09, ALE 0.10, PLE 0.08, PME 0.09, AME–AME 0.18, PME–PME 0.17, AME–ALE 0.20, ALE–PLE 0.02, PLE–PME 0.25. Clypeus 0.20 high. Abdomen and most legs absent.

Exechocentrus madilina new species

Figs. 6A–C, 7A,B

Material examined. 1 female holotype from Madagascar, Prov. Antananarivo, 3 km NE (41°) Andranomay, 11.5 km SSE (147°) Anjozorobe, 18°28'24"S 47°57'36"E, 1300 m a.s.l., general collection in montane rainforest, 5.–13.xii.2000, C. Griswold & J. Ledford leg., BLF 2545 (CAS cat. no. CASENT9003001).

Etymology. The species epithet is a name in apposition taken from the contraction of the Malagasy words for "sticky" (*madity*) and "ball" (*baolina*).

Diagnosis. *Exechocentrus madilina* n.sp. differs from *Exechocentrus lancearius* Simon, 1889 by having short digitiform dorsal abdominal apophyses (Fig. 6A,C) and by the details of the genitalia (Fig. 4A,B), with a dorsally concave, ventrally projecting and heavily sclerotized V-shaped epigynal lip. The spermathecae are ovoid, juxtaposed, and very similar to those of *E. lancearius*.

Description. **Female holotype** (from Andranomay – CASENT9003001; Figs. 6, 7): Total length 5.38 (margin of clypeus to posterior end of abdomen). Cephalothorax 2.02 long (margin of clypeus to posterior end of cephalothorax), 2.14 wide. Sternum 1.05 long, 0.99 wide. Abdomen 3.46 long, 5.44 wide. Abdominal projections short, only 0.38 long. Cephalothorax piriform, hirsute, covered with short dense translucent setae; with one slightly anteriad-bent spiniform projection (Fig. 6A,C), 0.71 long, originating from median eye rectangle, and three long similarly shaped projections anterior to fovea, one on the mid-point and one on each side of the midline axis (Fig. 6C). Carapace and chelicerae pale yellowish white with indistinct dark brown pattern radiating from fovea (Fig. 6A,C) and a short white line anterior to the mid-point projection (Fig. 6A). Margin of carapace same colour as carapace, projections with black tips and median eye rectangle and anteriad spiniform projection dark brown. Legs pale yellowish white, with blackish brown annuli on all legs (particularly pronounced on tibiae and femora). Coxae IV orange brown. Sternum blackish brown (Fig. 6B). Posterior eye row strongly recurved (dorsal view; Fig. 6A). Eye measurements: AME 0.11, ALE 0.12, PLE 0.09, PME 0.10, AME–AME 0.18, PME–PME 0.20, AME–ALE 0.30, ALE–PLE 0.01, PLE–PME 0.44. Clypeus 0.24 high. Pedipalps: tarsal claw provided with six small teeth; tibia with a proximal group of six trichobothria. Legs: leg formula (longest to shortest) I,II,IV,III; length of segments (femur + patella + tibia + metatarsus + tarsus): I: 11.15 ($3.61+1.09+2.88+3.02+0.55$), II: 9.78 ($3.23+1.05+2.35+2.65+0.50$), III: 5.21 ($1.81+0.63+1.13+1.18+0.46$), IV: 6.97 ($2.56+0.80+1.64+1.55+0.42$). First femora bent (Fig.



Fig. 6. *Exechocentrus madilina* n.sp. – Female holotype from Andranomay (CASENT9003001). **A:** dorsal view; **B:** ventral view; **C:** lateral view. Scale bars: 1 mm.

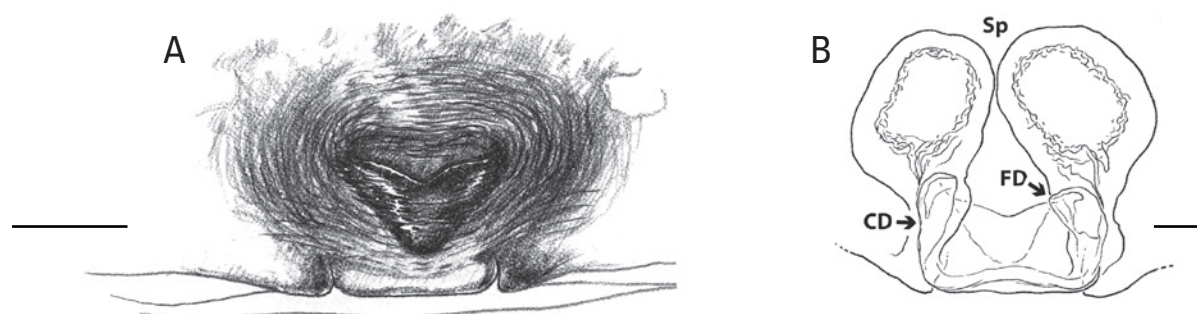


Fig. 7. *Exechocentrus madilina* n.sp. – Female holotype from Andranomay (CASENT9003001). **A:** epigynum, ventral view; **B:** female vulva, cleared, dorsal view. Abbreviations: Sp, spermathecae; CD, copulatory ducts; FD, fertilization ducts. Scale bars: 1 mm.

6A), slightly swollen in the middle. Tibiae, metatarsi and tarsi with prolateral row of short (half diameter of leg segment) pale macrosetae. Macrosetae on legs otherwise absent, except for the apical part of metatarsus IV and proximal part of tarsi IV, which are provided with several serrated dorsal macrosetae. Abdomen (Fig. 6A–C): almost heart-shaped dorsally (Fig. 6A), with many small blunt dorsal protuberances and one pair of short pointed projections (Fig. 6C) at the same position where *E. lancearius* have long projections (Figs. 3C versus 6C). Abdomen creamy white dorsally and ventrally with dark brownish black transversal band between epigastric furrow and spinnerets and on the lateral side of the abdomen. Booklung covers and spinnerets whitish with orange brown tips. Colulus present, with macrosetae. Spinnerets (only investigated with light microscope): ALS with long slender major ampullate and more than 60 piriform spigots. PMS with one minor ampullate, a nubbin, at least one cylindrical and less than 10 aciniform spigots. PLS with two cylindrical (both marginal) and more than 30 aciniform spigots; triad not visible (covered in dirt/silk). Epigynum (Fig. 7A,B): Similar to *Exechocentrus lancearius*, but with heavily sclerotized V-shaped lip (Fig. 7A). Spermathecae (Sp) large, ovoid, juxtaposed and with short, narrow, posteriorly projecting copulatory ducts (CD) and mesally oriented short dorsal fertilization ducts (FD) (Fig. 7B). **Male:** Unknown.

Distribution. Only known from Andranomay, Madagascar.

Natural history. Unknown.

Discussion

Based on the presence of prolateral rows of macrosetae on the tibiae and metatarsi of legs I and II, SIMON (1889) originally suggested a close relationship between the mimetid *Gelanor* Thorell, 1869 and *Exechocentrus*. Later, in 1895, Simon placed *Exechocentrus lancearius* together with the African araneid species *Coelossia aciculata* Simon, 1895 in a separate group that he named Exechocentreae, but emphasized the similarity between species in his Exechocentreae and those in his other group named Glyptocranieae. The latter group included those species that we now call bolas spiders (tribe Mastophoreae or subfamily Mastophorinae). At least four of the five known mastophorine genera produce bolas for prey capture. These are: *Mastophora* (North- and South America, 50 species),

Cladomelea Simon, 1895 (Africa, 4 species), *Ordgarius* Keyserling, 1886 (South East Asia and Australia, 11 species) (STOWE 1986; LEVI 2003), and *Exechocentrus* (Madagascar, 2 species), which can now be added to the list of bolas spider taxa. The possible use of bolas for *Exechocentrus* was already implied by EMERIT (1980) when he suggested placement in the Mastophoreae and by GRISWOLD (2003: p. 585). The webs of the last genus, *Acantharachne* (Africa and Madagascar, 8 species) is unknown, but its general morphology with long dorsal spines on the carapace and various tubercles on the abdomen, strongly suggests that it belongs in the mastophorines (EMERIT 1978; STOWE 1986; YEARGAN 1994; EMERIT 2000). LEVI (2003) suggested that when males are found of *Acantharachne* it should probably be synonymized with *Cladomelea* or *Ordgarius*.

A phylogenetic analysis based on morphology found mastophorines (*Mastophora*) deeply nested within the family Araneidae (SCHARFF & CODDINGTON 1997) and this position was also supported by the molecular phylogenies of BLACKLEDGE et al. (2009) and DIMITROV et al. (2012). The monophyly of mastophorines is supported by a behavioural synapomorphy: orb web modified to single silk line provided with terminal glue globule(s) (SCHARFF & CODDINGTON 1997). A sistergroup relationship to the cyrtarachnines is supported by two synapomorphies: the presence of sticky silk that is so adhesive that a single sticky silk line can withhold large prey items, such as moths (SCHARFF & CODDINGTON 1997), and a bridge thread of the future web that is spun with extensive combing action of leg IV (STOWE 1986).

The foraging web of *Exechocentrus lancearius* was provided with two glue globules (Fig. 5A,B). The foraging line of *Cladomelea* and *Mastophora* normally holds only one glue globule, but can occasionally have two (LEROY et al. 1998) or more (LEVI 2003). The webs of *Ordgarius* may have more than two glue globules (YEARGAN 1994). Interestingly, the foraging silk line with the bola is manipulated with the second pair of legs in the Old World genera (*Cladomelea*, *Ordgarius*, and *Exechocentrus*) and with the first pair of legs in the New World genus *Mastophora* (LEVI 2003; LEROY et al. 1998; STOWE 1986).

HUTCHINSON (1903) was the first to suggest that prey was probably attracted to the bolas spider (*Mastophora*) by an odour, but it was the elegant experiments of EBERHARD (1977) that first showed that aggressive chemical mimicry was used for foraging by *Mastophora*. Eberhard demonstrated that the seemingly ineffective foraging line of *Mastophora* derives its success from the use of volatile chemicals that mimic the sex pheromones of its moth prey. Among other things, he showed that only male moths were captured by *Mastophora* and that prey always approached slowly from

directly downwind of the spider. More recent studies have demonstrated aggressive chemical mimicry for *Mastophora bisaccata* (Emerton, 1884) (YEARGAN & QUATE 1996), *M. cornigera* (Hentz, 1850) (STOWE et al. 1987), *M. dizzydeani* Eberhard, 1981, *M. hutchinsoni* Gertsch, 1955 (GEMENO et al. 2000; HAYNES et al. 2001, 2002) and *M. phrynosoma* Gertsch, 1955 (YEARGAN & QUATE 1996, 1997) and the chemical compounds have been identified for *Mastophora cornigera* (STOWE et al. 1987) and *Mastophora hutchinsoni* (GEMENO et al. 2000). The chemical compounds found correspond to the sex pheromones of the prey of choice and thereby demonstrate aggressive chemical mimicry for the investigated *Mastophora* species. No similar studies have been carried out for other mastophorine species in the Old World, many of which are extremely rare and difficult to find. The aforementioned phylogenetic position of *Exechocentrus* as a member of the Mastophorinae clade combined with the presence of a bolas web (Fig. 5) provide strong indirect evidence that members of the this Malagasy genus use pheromone analogues to lure their prey, that is, aggressive chemical mimicry. Since all mastophorine species studied so far use aggressive chemical mimicry, the presence of a highly modified foraging web, a bolas web as it turns out, is hardly surprising and it had been anticipated by EMERIT (1980) and by GRISWOLD (2003).

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