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Research article

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On new genera and species of crack-leg spiders (Araneae, Udubidae) from Madagascar

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Abstract. Two new genera, *Tabiboka* gen. nov. and *Zorascar* gen. nov., are described to accommodate five new Udubidae species from Madagascar: *Tabiboka milleri* gen. et sp. nov. (type species; ♂♀), *T. milloti* gen. et sp. nov. (♂♀), *T. polotowae* gen. et sp. nov. (♂♀), *Zorascar pasunepipe* gen. et sp. nov. (type species; ♂♀) and *Z. pasunepomme* gen. et sp. nov. (♀). In addition, two new species of *Zorodictyna* Strand, 1907 are described: *Zorodictyna almae* sp. nov. (♂♀) and *Z. silvadavilae* sp. nov. (♂♀). *Uduba inhonesta* Simon, 1906 is declared to be a junior synonym of *Zorodictyna oswaldi* (Lenz, 1891). The descriptions of the new species are complemented with a phylogenetic analysis to tentatively place them into an existing phylogenetic framework. Phylogenetic analyses based on COI and 16S rRNA genes and morphological data show that they are separate species and confirm their familial and supraspecific placement within the Udubidae. The new species are further described using high quality colored photographs, drawings, SEM and (for *Zorascar* gen. nov. ssp.) by the use of X-Ray micro-computed tomography to recreate virtual 3D models without destroying the original specimens. A dichotomous key to identify Malagasy Ububidae is provided. Whereas many undescribed Udubidae remain in Madagascar, the phylogenetic and generic arrangement that we present here succinctly summarizes the higher classification of Madagascar Udubidae.

Keywords. Oval calamistrum clade, new taxa, phylogeny, *Zorodyctina*, micro-CT scans.

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Introduction

The spider family Udubidae Griswold & Polotow (described in Polotow *et al.* 2015: 151), commonly called crack-leg spiders, currently comprises four genera occurring in Africa (*Raecius* Simon, 1892), Sri Lanka (*Campostichomma* Karsch, 1892) and Madagascar (*Uduba* Simon, 1880 and *Zorodictyna* Strand, 1907). The four genera of Udubidae plus *Zorocrates* Simon, 1888 were formerly placed in the family Zorocratidae Dahl, 1913, which is no longer accepted and was defined as a synonym of Zoropsidae Bertkau, 1882 by Polotow *et al.* (2015). After several attempts to elucidate the relationships of lycosoid spiders and relatives (Lehtinen 1967; Raven & Stumkat 2005; Platnick & Ubick 2007; Jocqué 2009; Piacentini *et al.* 2013; Polotow *et al.* 2015), the family Udubidae was eventually created, almost ten years ago, based on the results of both morphological and molecular analyses (Polotow *et al.* 2015). These authors provided a total evidence phylogeny of exemplars of the oval-calamistrum clade of spiders, which suggested that new genera remain to be described from Madagascar. More recently, fresh material containing new udubid spiders was collected from Madagascar during an Expedition organized in collaboration with BINCO (Biodiversity Inventory for Conservation, details in Jocqué & Jocque 2021). We took the opportunity to describe these newly collected species as well as some other unknown udubid '*Zorodyctina*' with sequences available from GenBank and published in previous studies (Polotow *et al.* 2015; Wheeler *et al.* 2017). We have seized the occasion to bring these unknown udubids out of the shadows and describe new taxa, including two new genera and five new species, and place these within a key to the genera of Madagascar Udubidae.

Material and methods

The specimens sequenced during this study were collected during the "Expedition Mahimborondro" organized in collaboration with Biodiversity Inventory for Conservation (BINCO) organization (see Jocqué & Jocque 2021). All biological samples collected on this expedition are labeled with the code BINCO_MAD_19_0079_2, which is a standardized format allowing easily tracking where the material is deposited, who identified it and what was used in publications. We include sequence data from previous studies (Polotow *et al.* 2015; Wheeler *et al.* 2017): protocols for extraction and sequencing are detailed in those studies.

Types and other specimens examined are deposited in the Royal Museum for Central Africa, Tervuren, Belgium (RMCA; spider collection acronym BE_RMCA_ARA.Ara.), California Academy of Sciences, San Francisco, USA (CAS), Field Museum of Natural History, Chicago, USA (FMNH), Museum of Comparative Zoology at Harvard University, Cambridge, USA (MCZ), Muséum national d'Histoire naturelle, Paris, France (MNHN), National Museum of Natural History, Washington, D.C., USA (USNM) and Zoological Museum, Hamburg, Germany (ZMH).

Remarks: the acronym_numbers "CASENT_###", represent identifiers for this specimen level database and do not always identify the institutional ownership of specimens. For example, the holotype male of *Tabiboka milloti* gen. et sp. nov., which was collected in the Analamazaotra special reserve, Aug. 1946 by J. Millot, and which is deposited in MNHN Paris, is also assigned the specimen number CASENT_9016063 in this paper.

Specimens from RMCA were observed, drawn and measured with a WILD M 10 stereo microscope. Photographs of the habitus, details of mouthparts, detached male palps, female genitalia and measurements were taken with a DFC500 camera mounted on a Leica MZ16A and piloted with the LAS automontage software (ver. 4.13). The epigyne was dissected and digested using half a tablet of Total Care Enzima product (protein removal system originally for cleaning contact lenses and containing subtilisin A – 0,4 mg per tablet; Abbott Medical Optics, Santa Ana, CA) in a few milliliters of distilled water for several hours or overnight, then immersed in 75% ethanol. For scanning electron micrographs (SEM), some juvenile specimens were first dried in Hexamethyldisilazane (24h), gold coated and then examined and photographed with a JEOL 6480 LV scanning electron microscope. For the micro-computed tomography (micro-CT) analyses, the genitalia were stained with a 1% LUGOL iodine solution for 42 hours. After washing in few milliliters of pure acetone for few hours, the sample was air-dried for

24 hours, then gently fixed with a piece of tape on a carbon stick. The palp was scanned with an XRE-UniTOM (Tescan XRE, Ghent, Belgium) piloted with Acquila software, at 70 keV and 1–2 W (additional settings: exposure time: 800 ms, voxel size: 1–2 µm, and total of 2000 projections). The obtained data were first processed with the Acquila reconstruction software ver. 1.1, followed by segmentation and mesh generation in the 3D analysis software Dragonfly 2019 (Object Research Systems (ORS), Canada, https://www.theobjects.com/dragonfly/index.html). The model was further processed in GOM Inspect (now ZEISS INSPECT https://www.zeiss.com/metrology/en/software/metrology-software.html). Final 3D model, micro-CT scans and further photographs of the RMCA specimens are visible on the RMCA Virtual Collection website (https://virtualcol.africamuseum.be).

For specimens assigned under "CASENT_###" acronym, measurements were taken using a reticule in Olympus SZH, Leica MZ12.5 or Leica MZ16 stereo microscopes. Morphological observations and drawings were made using a Leica MZ12 or Leica MZ16 stereo microscope with a camera lucida. SEM were taken on a Hitachi S-520, Leo 1450VP or Hitachi SU3500S SEM at the Department of Entomology at the California Academy of Sciences. Specimens were critical-point dried, sputter coated with gold-palladium, and mounted on copper wire with white glue. Specimen preparation follows Álvarez-Padilla & Hormiga (2008), except as indicated below. Vulvae were cleaned by immersion in a trypsin solution for three to five days at room temperature or by digestion with contact lens cleaner overnight (Sierwald 1990) or cleared with clove oil or with Chlorox® bleach. Drawings of the vulvae were taken with the specimen cleared in lactic acid. Photographs of somatic morphology and female genitalia were taken with a Nikon DXM 1200 digital camera mounted on a Leica MZ16A stereo microscope. Multiple images were combined with software from Syncroscopy® and also the Helicon Focus®. Illustrations of male genitalia were sketched using a camera lucida mounted on a Leica MZ12.5 stereo microscope, rendered on coquille board, scanned and finished in Adobe Illustrator® (ver. CS3). Drawings are by Jenny Speckels (JS) and Charles Griswold (CEG).

Maps were created with the online tool SimpleMappr (Shorthouse 2010). All illustrations were assembled and edited in Photoshop CS5 (white balance and level adjusted, sharpness improved). All measurements in the text are in mm. Measurements are based on one specimen of each sex, where available; this specimen is listed at the beginning of the description. Variation for each sex is reported separately. All palp illustrations are from left palps, excepted for (1) *Zorascar pasunepipe* gen. et sp. nov. and (2) SEMs of non-RMCA specimens, for which the right palp was scanned and images were reversed to make them appear as if they are the left palp.

Terminology of genitalic features follows Griswold (1993), Polotow *et al.* (2015) and Griswold *et al.* (2022) (except for "paraconductor" (Pc) = membranous tegular process (MTP) in Griswold 1993).

As suggested by Agnarsson & Kuntner (2007), we consider it important to cite original species descriptions in the references: the convention of not citing such original works undervalues the primary literature of taxonomy.

DNA extraction, amplification and sequencing

A few legs of five freshly collected udubid specimens were detached for molecular analyses (see Table 1). The DNA of each sample was extracted with a Macherey-Nagel NucleoSpin tissue kit, slightly adapted from the manufacturer's protocol. Partial fragments of two mitochondrial markers, the cytochrome oxidase I (COI) and the large subunit ribosomal RNA (16S rRNA), were amplified with polymerase chain reactions (PCRs) using the primers displayed in Appendix 1. All amplifications were performed in a 20 µL reaction mixture containing 2 µL of extracted DNA (regardless of initial concentrations), 2 µL of 10 X buffer, 0.5 mm $MgCl_2$, 0.2 mm dNTP, 0.8 µM of each primer, and 0.02 units/µL of PlatinumTM Taq DNA Polymerase (Invitrogen™, Waltham, MA, USA). PCR conditions comprised an initial denaturation at 94°C for 3 min followed by 35 cycles with, per cycle, a denaturation at 94°C for 45 s followed by an

Table 1. List of the *Zorascar* gen. nov. specimens sequenced for this study, with information on the sex / stage (M = male adult; F = female adult; juv. = juvenile), type specimen (Ht = holotype; Pt = paratype) collection number, DNA working code and GenBank accession number for COI and 16S rRNA markers.

					GenBank number	
Species	**Stage**	**Type**	**RMCA number**	**DNA**	**COI**	**16S**
Z. pasunepipe	M	Ht	BE_RMCA_ARA.Ara.247343	RJ5	OK561858	OK564657
Z. pasunepipe	juv.	Pt	BE_RMCA_ARA.Ara.247344	RJ1	OK561857	OK564656
Z. pasunepomme	F	Ht	BE_RMCA_ARA.Ara.247346	RJ4	OK561861	OK564660
Z. pasunepomme	juv.	Pt	BE_RMCA_ARA.Ara.247349	RJ2	OK561859	OK564658
Z. pasunepomme	juv.	Pt	BE_RMCA_ARA.Ara.247348	RJ3	OK561860	OK564659

annealing step of 45 s at 48°C and an extension step at 72°C (1 min) and with a final extension at 72°C for 10 min followed by 10 min at 4°C. PCR products (and negative controls) were checked on a 1.5% agarose gel containing 0.03% of MidoriGreenTM Direct (NIPPON Genetics Europe, Dueren, Germany) using a UV transilluminator. Positive amplifications were purified using the ExoSAP-ITTM protocol (following manufacturer's instructions) and then sequenced in both directions, using the same couples of primers (0.05 mm each), by Macrogen Inc. (Seoul, South Korea).

The sequences were checked using Geneious R11 (Biomatters Ltd., Auckland, New Zealand): paired bi-directional strands were trimmed, assembled, edited and consensus sequences were extracted for each specimen and each DNA marker. As control, consensus sequences were compared against the Identification System of BOLD (www.boldsystems.org) and the BLAST web application of GenBank (https://blast.ncbi.nlm.nih.gov/Blast.cgi; accessed Oct. 2021).

Phylogenetic analyses

Morphology-based

The morphological analyses were based on those of Polotow *et al.* (2015). The data matrix was adapted by addition of two extra taxa; *Zorascar pasunepipe* gen. et sp. nov. (male and female) and *Z. pasunepomme* gen. et sp. nov. (female only). The final morphological matrix included 63 taxa and 96 characters.

The scoring for the two new species of *Zorascar* gen. nov. is as follows:

Zorascar_pasunepipe 003001001110033021101000110010100100001000?010010100000001111001111 201100?200021100?????000?0000

Zorascar_pasunepomme 0030010011100330211??????????????????????????????10000001111001111 201100?2000111000010?1?00?0000

The scoring for *Tabiboka polotowae* gen. et sp. nov. was updated with the addition of male information:

Tabiboka_polotowae_DP2014b 0030010011100331111011001100101001000010010120010100???020 110011103?1000?200?10010?0??01?10?000?

Tabiboka_polotowae_DP2014a 0030010011100331111011001100101001000010010120010100???020 110011103?1000?200?10010001001?10?000?

The parsimony analysis was carried out in TNT 1.1 (Goloboff *et al.* 2003, 2008) run through NONA 2.0 (Goloboff 1993). All multistate characters were coded as non-additive and equally weighted, and the tree search was as in Polotow *et al.* 2015. The most parsimonious trees were found using the 'ratchet' search with default setting (except the number of iterations, set to 500, and 1000 replicates of random addition sequences). The majority rule consensus tree was then estimated with a cut off value of 50. The resulting trees were then imported into WINCLADA 1.00.08 (Nixon 1999–2002), which was used to show the character changes. Following Polotow *et al.* (2015), ambiguous character optimizations were solved so as to favor reversal or secondary loss over convergence (fast optimization option).

Molecular-based

For phylogenetic analyses, we included additional sequences from GenBank of Udubidae and Zoropsidae representatives studied in Polotow *et al.* (2015) and Wheeler *et al.* (2017), which were selected to broadly represent Madagascar Udubidae and relatives (see Appendix 2). The present study follows the family limits defined by previous analysis. The Udubidae is treated as the ingroup and Zoropsidae + Senoculidae were included as outgroups for testing the placement of the new taxa. The distantly-related lycosoid exemplar *Ancylometes bogotensis* (Keyserling, 1877) was chosen as the outgroup to root the trees.

All sequences of each marker were aligned with MAFFT ver. 7 implemented online (Server available at https://mafft.cbrc.jp/alignment/server; accessed Oct. 2021 (Katoh & Standley 2013) with default settings. Both COI and 16S alignments were cured using the least stringent settings in Gblocks 0.91b online (Castresana 2000; Talavera & Castresana 2007; Gblocks Server available online at http://molevol.cmima.csic.es/castresana/Gblocks_server.html; accessed Oct. 2021). Finally, a partitioned COI-16S alignment (1464 sites and 38 taxa) was created with Mesquite ver. 3.5 (Maddison & Maddison 2018) by concatenating the Gblocks curated alignments of the two markers (COI: 1029 sites; 16S: 435 sites). Best partition scheme and best-fit substitution models (see Appendix 3) were then estimated using PartitionFinder 2 (Lanfear *et al.* 2016) on the basis of one partition for 16S and three for COI (protein coding gene partitioned into single codon positions).

Phylogenetic reconstructions were evaluated using statistical approaches including maximum likelihood (MLi) using GARLI ver. 2.01 (Zwickl 2006) and Bayesian inferences, the latter utilizing MrBayes ver. 3.2.7a (Ronquist *et al.* 2012) (MB), all performed on the CIPRES Science Gateway ver. 3.3 (Miller *et al.* 2010). For the MB analysis, two parallel runs (with four chains each) were executed for ten million generations. Parameters were estimated independently for each partition using the following command: unlink statefreq = (all) revmat = (all) shape = (all) pinvar = (all) tratio = (all). Trees were sampled every 1000th generation and were used to reconstruct a 50% majority rule consensus tree after having discarded the first 25% as 'burn-in'. Analyses using the MLi method were conducted in GARLI with 1000 bootstrap replicates. Values were then summarized on the best MLi tree using SumTree ver. 4.0.0 (Sukumaran & Holder 2015), run in DendroPy ver. 4.0.0 (Sukumaran & Holder 2010).

Edition and annotation of trees

Trees were first displayed and drawn in programs such as WINCLADA 1.00.08 (Nixon 1999–2002) or FigTree ver. 1.4.2 (Rambaut 2006–2014) then exported in a vector image format (.emf or\.svg) and edited in Inkscape for final publication.

Genetic distance calculations

In addition, estimations of the average evolutionary divergences for each marker were calculated in MEGA-X (Kumar *et al.* 2018; Stecher *et al.* 2020) as the number of base differences per site (p-distance) from between sequences and species group. The analyses are based on a Gblocks curated alignments of Udubidae representatives (Polotow *et al.* 2015; Wheeler *et al.* 2017) and the sequenced specimens of *Zorascar* gen. nov., which involved 15 nucleotide sequences for COI and nine sequences for 16S. There were a total of 1020 positions in the final dataset for COI and 436 positions in the final dataset for 16S.

The rate variation among sites was modeled with a gamma distribution (shape parameter = 4) and all ambiguous positions were removed for each sequence pair (pairwise deletion option).

Abbreviations

AER	=	anterior eye row
ALE	=	anterior lateral eyes
ALS	=	anterior lateral spinnerets
AME	=	anterior median eyes
a.s.l.	=	above sea level
AW	=	anterior width
BC	=	basal concavity of the RTA
C	=	conductor (hyaline = Sierwald conductor of Polotow *et al.* 2015)
CD	=	copulatory duct
CE	=	cymbial retrobasal extension
CI	=	consistency index
CO	=	copulatory opening
d	=	dorsal
disp	=	dispersed
dRTA	=	retrodorsal tibial apophysis
E	=	embolus
EBP	=	embolus basal process
F	=	femur
FD	=	fertilisation duct
L	=	length
LL	=	lateral lobe
LP	=	lateral process
MA	=	median apophysis
MB	=	Bayesian inference performed with MrBayes
ML	=	median lobe
MLi	=	maximum likelihood analysis
MOQ	=	median ocular quadrangle
MS	=	median sector
Mt	=	metatarsus
OAL	=	ocular area length
OC	=	Oval Calamistrum (clade)
OQA	=	ocular quadrangle, anterior
OQL	=	ocular quadrangle length
OQP	=	ocular quadrangle, posterior
P	=	patella
Pc	=	paraconductor (additional tegular process, STP, Griswold 1993)
pl	=	prolateral
PER	=	posterior eye row
PLE	=	posterior lateral eyes
PLS	=	posterior lateral spinnerets
PME	=	posterior median eyes
PMS	=	posterior median spinnerets
PP	=	paracymbial process
PPr	=	posterior probabilities
PW	=	posterior width
RI	=	retention index

rl	=	retrolateral
RTA	=	retrolateral tibial apophysis
S	=	spermatheca
SEM	=	scanning electronic microscope (microscopy)
SL	=	subtegular locking lobe
t	=	tarsus
T	=	tibia
TA1	=	proapical tegular apophysis, *Uduba*
TA2	=	proapical tegular apophysis, arising just prolaterad of distal notch, *Uduba*
TA3	=	retroapical tegular apophysis, apex extending to prolateral, *Uduba*
TL	=	tegular locking lobe
UTA	=	tibia-patella palpal apophysis of male *Uduba*
v	=	ventral
vRTA	=	retroventral tibial apophysis
VTA	=	ventral tibial apophysis
W	=	width

Repositories

CAS	=	California Academy of Sciences, San Francisco, USA
FMNH	=	Field Museum of Natural History, Chicago, USA
MCZ	=	Museum of Comparative Zoology, Harvard, USA
MNHN	=	Muséum national d'Histoire naturelle, Paris, France
RMCA	=	Royal Museum for Central Africa, Tervuren, Belgium
USNM	=	United States National Museum, Smithsonian, Washington D. C., USA
ZMH	=	Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Hamburg, Germany

Results

Phylogeny

Parsimony analysis

The analysis in TNT resulted in 38 equally long trees of length 566, all with consistency index (CI) 23 and retention index (RI) 60. The majority consensus (Fig. 1), of length 575, CI 22, RI 59, shows the Udubidae recovered, with *Zorascar* gen. nov. sister to the remaining representatives used in this study. *Tabiboka* gen. nov. appears sister to *Zorodictyna*, *Raecius* Simon, 1892 and *Uduba* (the latter two forming a sister-group relationship).

Zorascar gen. nov. is distinguished by one synapomorphic character, the male palp with embolus base originating in center of tegulum (char. 45:1 in Polotow *et al.* 2015) and nine homoplasic characters (see Fig. 1). *Tabiboka* gen. nov. is distinguished by one homoplasic character: the serrate texture of the fang's proximal edge (char. 16:1).

The analysis based on the data matrix of Polotow *et al.* 2015 allowed us at least to test the phylogenetic placement of *Zorascar* gen. nov. and *Tabiboka* gen. nov. The relationships among the other groups are not the primary focus of the present study, and results on their relationships will not be described nor tested with statistics. One can however note that Zoropsidae are not recovered, Udubidae are recovered, and Senoculidae Simon, 1890 are nested within Lycosoidea Mello-Leitão, 1941.

Partitioned COI-16S analysis

Both MLi and MB phylogenetic analyses based on the COI–16S alignment provided congruent results, with similar tree topologies. Figure 2 presents the tree resulting from the MLi analysis on which the support values of MB are also summarized.

The Udubidae represent a well-supported monophyletic clade that includes the genera *Raecius*, *Uduba*, *Zorodictyna*, *Tabiboka* gen. nov. and *Zorascar* gen. nov. The last is strongly supported and is represented by two distinct representatives: *Zorascar pasunepipe* gen. et sp. nov. and *Z. pasunepomme* gen. et sp. nov. *Zorascar* is placed as the sister-group (with moderate support) to the newly erected genus *Tabiboka*, which include three species *Tabiboka milleri* gen. et sp. nov., *T. milloti* gen. et sp. nov. and *T. polotowae* gen. et sp. nov. *Zorodictyna* is sister to the two latter groups and is recovered with strong support, including the two new species: *Zorodictyna almae* sp. nov. and *Z. silvadavilae* sp. nov. The latter three genera, *Zorascar*, *Tabiboka* and *Zorodictyna* form a clade moderately supported, sister-group to *Uduba* + *Raecius* (the latter group not supported).

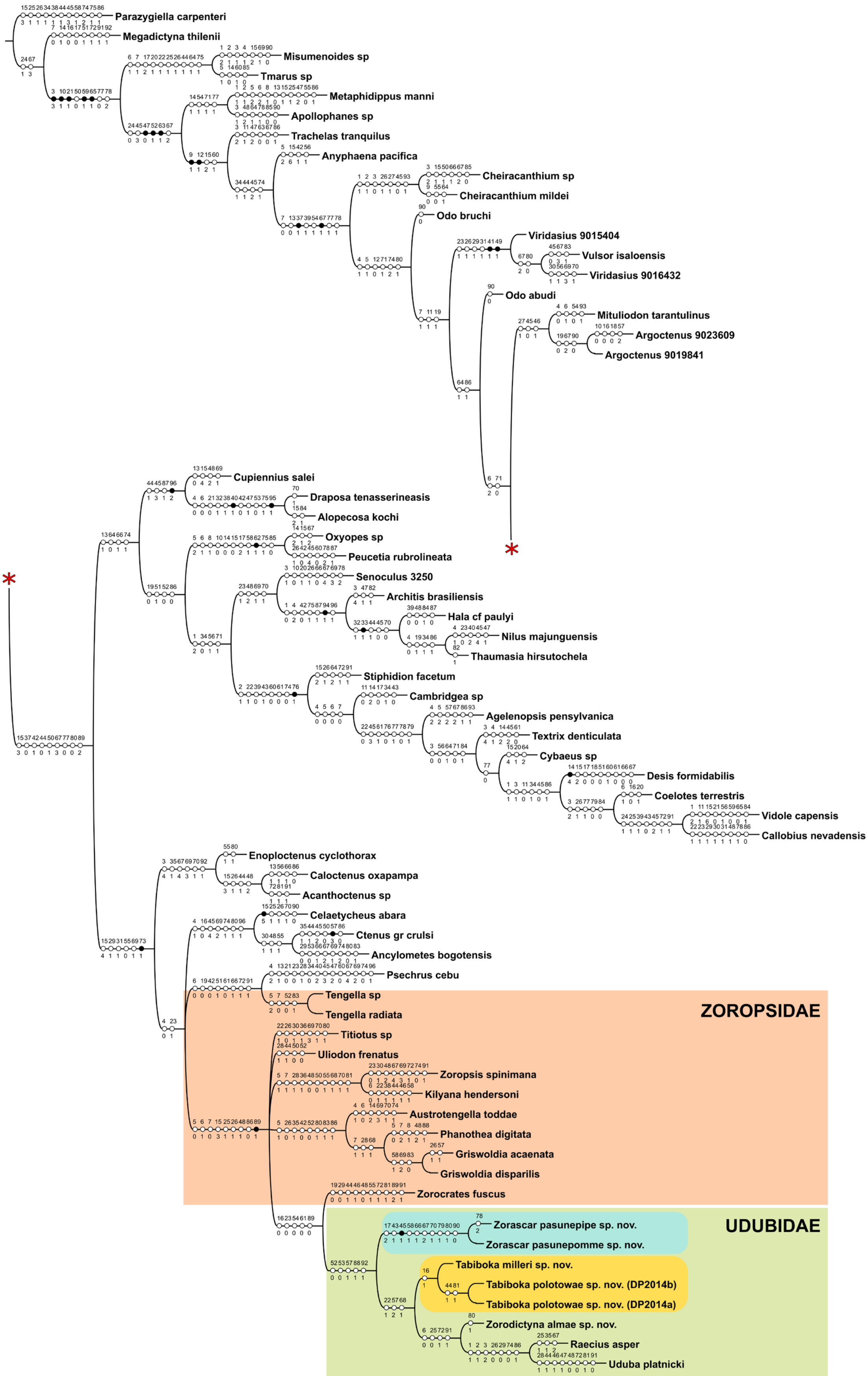
Inside Udubidae, relationships between the different genera cannot be considered as fully resolved (especially considering the MLi analysis).

The relationships among the outgroups are not the primary focus of the present study and will not be discussed further. We only briefly describe here the results obtained in Fig. 2. Zoropsidae is placed as the sister group to Udubidae but received no support for its monophyly, and some shallow relationships within Zoropsidae are also unresolved. *Uliodon* L. Koch, 1873 and *Kilyana* Raven & Stumkat, 2005 form a strongly supported group. *Tengella* Dahl, 1901 and *Zorocrates* Simon, 1888 are sister-groups, *Liocranoides* Keyserling, 1881 and *Titiotus* Simon, 1897 as well, and both groups are sister of each other, all with relatively high support values. *Griswoldia* Dippenaar-Schoeman & Jocqué, 1997 and *Phanotea* Simon, 1896 appear as a sister-group, with high support. Placement of *Austrotengella* Raven, 2012, *Zoropsis* Simon, 1878 and *Ciniflella* Mello-Leitão, 1921 is not resolved at all. Zoropsidae + Udubidae received high support, and have Senoculidae as sister group (as rooted using *Ancylometes bogotensis*).

Genetic distances

Genetic divergences, as calculated with MEGA-X, result in p-distance of 10.7% (COI) and 10.1% (16S) between *Zorascar pasunepipe* gen. et sp. nov. and *Z. pasunepomme* gen. et sp. nov. (see also Appendix 4). No or little genetic variation is observed between sequenced specimens of *Z. pasunepipe* (0.0% for each marker) or *Z. pasunepomme* (0.7% for COI and 0.0% for 16S). Only two COI sequences were available for the following species: *Tabiboka milleri* gen. et sp. nov. (within variation 0.32%) and *Tabiboka polotowae* gen. et sp. nov. (within variation 2.45%). Genetic distances between species of *Tabiboka* gen. nov. varies from 10.77% and 13.05% (COI only). Genetic variations between *Zorodictyna almae* sp. nov. and *Z. silvadavilae* sp. nov. are 12.08% (COI only). Estimates of average evolutionary divergence over sequence pairs within *Zorascar* gen. nov. are 6.6% for COI and 6.1% for 16S, within *Tabiboka* gen. nov. 9.20% (COI only), within *Zorodictyna* 10.08% (COI only) and within *Uduba* 9.50% (COI only). The genetic divergence between *Zorascar* and other groups analyzed varies from 11.78–15.53 % for COI and 18.00–21.58% for 16S (Table 2).

Fig. 1 (on next page). Result of morphological analysis (63 taxa, 96 characters) – Majority consensus tree (cut 50) out of 38, of length 575, CI 22, RI 59. The blue area indicates the position of *Zorascar* gen. nov and the yellow area indicates the position of *Tabiboka* gen. nov within the family Udubidae Griswold & Polotow, 2015 (green area). The Zoropsidae Bertkau, 1882 (orange area) are not recovered as monophyletic group. Black circles indicate non-homoplasic synapomorphies and white circles indicate homoplasic changes, depicted under fast optimisation option in WINCLADA. Character numbers (see Polotow *et al.* 2015) are placed above the circles and the states are shown under the circles.



Parazygiella carpenteri
Megadictyna thilenii
Misumenoides sp
Tmarus sp
Metaphidippus manni
Apollophanes sp
Trachelas tranquilus
Anyphaena pacifica
Cheiracanthium sp
Cheiracanthium mildei
Odo bruchi
Viridasius 9015404
Vulsor isaloensis
Viridasius 9016432
Odo abudi
Mituliodon tarantulinus
Argoctenus 9023609
Argoctenus 9019841
Cupiennius salei
Draposa tenasserineasis
Alopecosa kochi
Oxyopes sp
Peucetia rubrolineata
Senoculus 3250
Architis brasiliensis
Hala cf paulyi
Nilus majunguensis
Thaumasia hirsutochela
Stiphidion facetum
Cambridgea sp
Agelenopsis pensylvanica
Textrix denticulata
Cybaeus sp
Desis formidabilis
Coelotes terrestris
Vidole capensis
Callobius nevadensis
Enoploctenus cyclothorax
Caloctenus oxapampa
Acanthoctenus sp
Celaetycheus abara
Ctenus gr crulsi
Ancylometes bogotensis
Psechrus cebu
Tengella sp
Tengella radiata
ZOROPSIDAE
Titiotus sp
Uliodon frenatus
Zoropsis spinimana
Kilyana hendersoni
Austrotengella toddae
Phanothea digitata
Griswoldia acaenata
Griswoldia disparilis
Zorocrates fuscus
UDUBIDAE
Zorascar pasunepipe sp. nov.
Zorascar pasunepomme sp. nov.
Tabiboka milleri sp. nov.
Tabiboka polotowae sp. nov. (DP2014b)
Tabiboka polotowae sp. nov. (DP2014a)
Zorodictyna almae sp. nov.
Raecius asper
Uduba platnicki

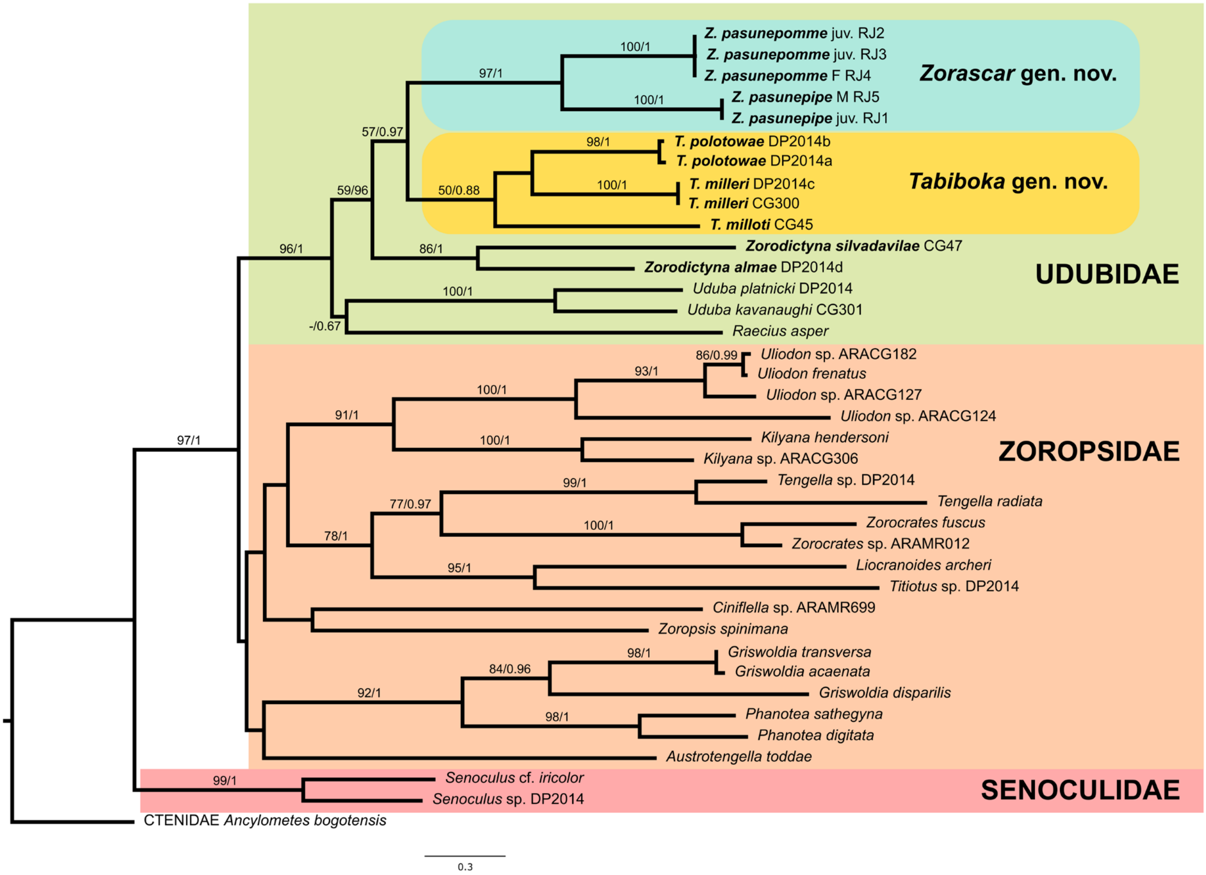


Fig. 2. Phylogenetic reconstruction based on the maximum likelihood (MLi) analysis performed on the COI–16S dataset, showing the relationships between *Zorascar* gen. nov. and other relatives of the family Udubidae Griswold & Polotow, 2015 and Zoropsidae Bertkau,1882. The tree is congruent in its topology (for supported nodes) with the Bayesian analyses of the same dataset. Nodal support values (MLi Bootstraps and posterior probabilities (PPr) are indicated as following = MLi/PPr). Values below 50/0.5 are not shown or indicated by hyphens.

Table 2. Estimates of evolutionary divergence (expressed in %) over sequence pairs between groups. The number of base differences per site from averaging over all sequence pairs between groups is shown for each compared taxon. The rate variation among sites was modeled with a gamma distribution (shape parameter = 4). This analysis involved 15 nucleotide sequences with 1020 positions in the final dataset for COI (lower left corner) and nine sequences with 436 positions in the final dataset for 16S (upper right corner). All ambiguous positions were removed for each sequence pair (pairwise deletion option).

COI (lower part) / 16S (upper part)	*Zorascar* gen. nov.	*Tabiboka* gen. nov.	*Zorodictyna*	*Raecius*	*Uduba*
Zorascar gen. nov.		18.31	18.70	19.08	18.47
Tabiboka gen. nov.	11.78		20.37	21.58	20.00
Zorodictyna	13.64	12.82		18.03	21.38
Raecius	15.53	14.21	14.86		18.59
Uduba	15.50	14.45	14.06	15.31	

Taxonomy

Class Arachnida Cuvier, 1812
Order Araneae Clerck, 1757

Family **Udubidae** Griswold & Polotow, 2015

Udubidae Griswold & Polotow in Polotow *et al.*, 2015: 151.

Type genus

Uduba Simon, 1880: 343 (Type species by monotypy: *Olios madagascariensis* Vinson, 1863 = *Uduba madagascariensis* (Vinson, 1863)).

Diagnosis

Udubidae are entelegyne RTA-clade spiders with three tarsal claws (Fig. 21A–B), multiple rows of tarsal trichobothria of about equal length (Figs 13F, 20E–F), eight eyes in 2 nearly straight rows (Figs 3C, F, 8A–B, 13C–D, 17A, 22A, C, 24A, C), indirect eyes with canoe-shaped tapeta and the cheliceral fang with interior serrula weak to absent. Males may or may not have a subbasal crack or line of autospasy on the leg tibiae (Fig. 24B, arrow; Griswold 1993: figs 3–4). All species have a hyaline conductor (C = the "Sierwald conductor" of Polotow *et al.* 2015), which is relatively small, transverse, hyaline and fan-shaped, prolaterally extending from narrow base to wide flattened tip (Figs 5A–C, 6D–F, 9A–C, 11A–C, 12E, 14D, F, 15D–F). Most have an additional tegular process accompanying the embolus that is a narrow membranous or sclerotized extension inserted between the tegulum and the base of the median apophysis (MA), running backward to MA and ending with fattened fan-shaped tip accompanying the embolus: this is the paraconductor (Pc = the "MTP" and "STP" of Griswold 1993) (Figs 5A–C, 6D–F, 9A–C, 11A–C, 12E, 14D, 15D–F). The paraconductor is found in other members of the Oval Calamistrum (OC) clade (the "TA" in Griswold *et al.* 2005: figs 186B–C, 195B–C), and the Sierwald conductor (C) occurs widely among the OC clade and Dionycha Petrunkevitch, 1928 (Polotow *et al.* 2015: figs. 13E–F, 15A–B, E–F).

Udubidae may be distinguished from most other araneomorph spider families found in Madagascar by the form of their tarsi. The presence of tarsal trichobothria distinguishes udubids from the Filistatidae Ausserer, 1867, Synspermiata Michalik & Ramírez, 2014, Palpimanoidea Forster & Platnick, 1984, Araneoidea Latreille, 1806, Eresidae C.L. Koch, 1845 (in Berendt 1845), Hersiliidae Thorell, 1869 and Oecobiidae Blackwall, 1862, Phyxelididae Lehtinen, 1967 and Titanoecidae Lehtinen, 1967. Multiple rows of tarsal trichobothria distinguish Udubidae from taxa with only a single row of tarsal trichobothria including Agelenidae C.L. Koch, 1837, Dictynidae O. Pickard-Cambridge, 1871, Hahniidae Bertkau, 1878 and most Zodariidae Thorell, 1881 and Thomisidae Sundevall, 1833. Among taxa with multiple rows of tarsal trichobothria udubids may be distinguished from Lycosidae Sundevall, 1833, Pisauridae Simon, 1890 and Oxyopidae Thorell, 1869 in that these latter families have at least one eye row strongly curved, whereas Udubidae have both eye rows nearly straight. Udubids have at least a rudiment of the inferior tarsal claw and lack claw tufts, characters that distinguish them from Sparassidae Bertkau, 1872 and the Dionycha (Cheiracanthiidae Wagner, 1887, Clubionidae Simon, 1878, Corinnidae Karsch, 1880, Gallieniellidae Millot, 1947, Gnaphosidae Banks, 1892, Liocranidae Simon, 1897, Philodromidae Thorell, 1869, Salticidae Blackwall, 1841, Selenopidae Simon, 1897, Trachelidae Simon, 1897, Trochanteriidae Karsch, 1879 and Viridasiidae Lehtinen, 1967). Finally, like Udubidae, the lone genus of Desidae Pocock, 1895 from Madagascar, *Desis* Walckenaer, 1837, has numerous tarsal trichobothria and straight eye rows but the latter is quite distinct in having elongate chelicerae, a dense cover of fine hairs and the posterior tracheal spiracle on the abdomen advanced.

Composition

Campostichomma Karsch, 1892 (Sri Lanka), *Raecius* Simon, 1892 (Africa), and *Tabiboka* gen. nov., *Uduba* Simon 1880, *Zorascar* gen. nov. and *Zorodictyna* Strand, 1907 (Madagascar).

Key to Udubidae of Madagascar

1. Male palp without process between tibia and patella; cymbium with retrobasal extension (CE), short to as long as rest of cymbium (Figs 5B–C, 6A–C, 9B–C, 11B–C, 12B–D, 14A–C, 15A–B, 16A–B, 23B–C, 25C); embolus broad and flat to slender, cylindrical, firmly attached to point of origin on retromargin of tegulum (Figs 5A–B, 6D–E, 8F, 9A–B, 11A–B, 12E, 14E–F, 15B, D–F, 23A–B, 25A–B); tegulum oval apically; conductor hyaline, fan-shaped crest arising from middle to apex of tegulum; female endogyne with spermathecal ducts short, stout, not making loops, at most twisted (Figs 5E, 7C–E, 9E, 11E, 12H, 16D, 18B–D, 19C–F, 23E, 25E) 2

– Male palp with small ventral process at base of tibia between tibia and patella ("UTA" in Griswold *et al.* 2022: figs 27A–B, 39A–C, 40A–C, 41B); cymbium rounded retrobasally; embolus flexibly attached to large, swollen base, embolus elongate and extending behind tegulum and subtegulum to emerge from alveolus near bulb apex (Griswold *et al.* 2022: figs 27A–B, 32C, 41F, 51A); tegulum trilobed apically, with retrolateral (TA1), median (TA2) and prolateral (TA3) processes interacting apically (Griswold *et al.* 2022: figs 27A–B, 29A–I, 51A–C); conductor rectangular hyaline crest arising along apical margin of prolateral tegular lobe near TA3; female endogyne with spermathecal ducts elongate, making at least one (to as many as five) loops (Griswold *et al.* 2022: figs 68B–D, 80B–D, F–G, I–J) ....
.........***Uduba*** Simon, 1880 (the key to *Uduba* species is amply detailed in Griswold *et al.* 2022: 13)

2. With entire cribellum or vestige; PLS and ALS equal in length; strong scopulae beneath leg tarsi and most of length of metatarsi; males with crack-suture on leg tibiae just anteriad of basalmost pair of ventral spines (Fig. 24B) ....3. ***Zorodictyna*** Strand, 1907

– Ecribellate; PLS much smaller than ALS; scopulae absent or only with weak scopulae beneath leg tarsi; most males without crack-suture on leg tibiae 5

3. Male palpal cymbium with rounded retrolateral paracymbial process (PP) (Figs 23B–C, 25B–C); cymbial retrobasal extension (CE) extending at least one-third length of tibia (Figs 23B–C, 25B–C); female epigyne lateral lobes (LL) lacking teeth (Figs 23D, 25D) 4

– Male palpal cymbium evenly convex retrolaterally, without paracymbial process (Griswold 1993: figs 20–21); cymbial retrobasal extension, short, extending only to tibial apex (Griswold 1993: figs 20–21); female epigyne lateral lobes with short teeth (Griswold 1993: fig. 24) ....
....***Zorodictyna oswaldi*** (Lenz, 1891)

4. Male palp with basal embolic process (EBP) nearly triangular, embolus lacking crest, tegulum with retromedian longitudinal ridge that extends for most of tegulum length (Fig. 23A–C); female epigyne lateral lobes (LL) parallel, median sector (MS) rectangular (Fig. 23D); female endogyne with copulatory ducts (CD) larger than spermathecae (Fig. 23E) ....***Zorodictyna almae*** sp. nov.

– Male palp with basal embolic process (EBP) slender, crescentic, embolus with subapical distal crest, and tegulum retromedian longitudinal ridge weak, short, extending for less than one-half tegulum length (Figs 25A–C); female epigyne lateral lobes (LL) converging posteriorly, median sector (MS) triangular (Fig. 25D); female endogyne with copulatory ducts (CD) and spermathecae equal in size (Fig. 25E) ....***Zorodictyna silvadavilae*** sp. nov.

5. Male palp with cymbial retrobasal extension (CE) elongate, extending most of length of tibia, palpal tibia with RTA only, lacking VTA (Figs 14A–B, 15A–B, 16A–B); female epigyne median lobe

(ML) short, concave medially, not extending to posterior margin, copulatory openings (CO) exposed (Figs 16C, E, 18A) .... 6. ***Zorascar*** gen. nov.

– Male palp with cymbial retrobasal extension (CE) shorter, extending to or just past tibial apex, palpal tibia with both VTA and RTA (Figs 5A–C, 6A–C, 9A–C, 11A–C, 12A–D); female epigyne median lobe (ML) extends to posterior margin, separating lateral lobes (LL) and covering copulatory openings (CO) (Figs 4B, 5D, 7A–B, 9D, 11D, 12G) .... 7. ***Tabiboka*** gen. nov.

6. Female epigyne median lobe (ML) broad and shallowly concave medially, copulatory openings (CO) exposed anteromedially (Fig. 16C), spermathecae elongate, curved, eggplant-shaped (Fig. 16D); male palp as in figures (Figs 14A–F, 15A–F, 16A–B) ....***Zorascar pasunepipe*** gen. et sp. nov.

– Female epigyne median lobe (ML) narrow and deeply concave medially, copulatory openings (CO) exposed laterad of median lobe (Figs 16E, 18A, 19A–B), spermathecae stout, rounded, reniform (Figs 18B–D, 19C–F); male unknown ....***Zorascar pasunepomme*** gen. et sp. nov.

7. Male palp with conductor base originating anteriorly, hidden behind embolus or paraconductor (Pc), embolus short, arising retrolaterally near 270° (Figs 5A–C; 6D–F, 8F, 9A–C); female epigyne median lobe (ML) heart-shaped, sides rounded (Figs 4B, 5D, 7A, 9D) 8

– Male palp conductor originating medially, near embolus base, not hidden, embolus elongate, arising retrobasally near 200° (Figs 11A–C, 12A–C, E); female epigyne median lobe (ML) rectangular, narrowest in middle or with sides straight (Figs 11D, 12G) ......***Tabiboka polotowae*** gen. et sp. nov.

8. Male palpal tibia with elongate retrobasal process (RTA), embolus broad, median apophysis (MA) short, apex far proximad of embolus apex (Figs 5A–C, 6D–F); female epigyne median lobe (ML) narrow anteriorly, anterior width less than one-half total width (Figs 4B, 5D, 7A), endogyne with each spermatheca as broad as long (Figs 5E, 7C–E) .... ***Tabiboka milleri*** gen. et sp. nov.

– Male palpal tibia with short, blunt retromedian process (RTA), embolus slender; median apophysis (MA) elongate, cruciform, apex extends to embolus apex (Figs 8C–F, 9A–C); female epigyne median lobe (ML) broad anteriorly, anterior width greater than one-half total width (Fig. 9D), endogyne with each spermatheca narrow, longer than broad (Fig. 9E) ....***Tabiboka milloti*** gen. et sp. nov.

Genus ***Tabiboka*** gen. nov.

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Figs 3–12, 26

Type species

Tabiboka milleri gen. et sp. nov.

Diagnosis

Tabiboka gen. nov. are ecribellate udubids where the male has palps with a short cymbial retrobasal extension (CE) extending to or just past tibial apex, lack a retrolateral paracymbial process, and have the tibia with both VTA and RTA (Figs 5A–C, 6A–C, 9A–C, 11A–C, 12A–D). The female epigyne is provided with a median lobe (ML) that extends to the posterior margin, separating lateral lobes (LL) and covering the copulatory openings (CO) (Figs 4B, 5D, 7A–B, 9D, 11D, 12G). The genus is distinguished from *Uduba* Simon, 1880 males by lacking the threadlike embolus and knob-like process between the palpal patella and tibia and from *Uduba* females by having compact spermathecae rather than multiple loops. Males differ from *Zorascar* gen. nov. by having the cymbial retrobasal extension short, extending to or just past the tibial apex and the palpal tibia with a VTA and RTA. Females differ from the ones of *Zorascar* gen. nov. by having the epigyne with a median lobe that extends to the posterior margin, separating the lateral lobes and covering the copulatory openings. *Tabiboka* is distinguished from *Zorodictyna* Strand, 1907 by lacking an entire cribellum or vestige and lacking an extensive scopulae beneath the leg metatarsi. It is distinguished from all Madagascar udubids, except *Zorascar* by having the posterior spinnerets (PMS and PLS) reduced in size, and the PLS less than half the size of the ALS.

Etymology

The genus name is an arbitrary combination of letters. The gender is feminine.

Description

Body. Medium size spiders (males: 6.90–12.00; females: 8.40–17.00) with smooth teguments of carapace (Figs 3A, C–D, F, 8A–B, 10A–B), sternum and legs. Carapace piriform, longer than wide (L/W: males: 1.21–1.41; females: 1.26–1.46), with sparse cover of short, dark setae; thoracic fovea present, linear; profile higher in ocular and thoracic area and abruptly sloping posteriorly (Fig. 3G–H).

Coloration (Figs 3, 4A, 8A–B, 10). Carapace brownish yellow with darker longitudinal pattern on carapace; chelicerae uniform brownish orange; legs faintly ringed; abdomen brownish yellow with faint complex pale pattern.

Eyes (Figs 3C, F, 8B, 10A–B). In two straight rows: ALE larger than AME, PLE and PME similar to ALE; tapetum of secondary eyes canoe-shaped, shiny. Clypeus with long setae, height 1.14 to 2.86 diameter of AME in male and 1.11 to 2.40 in female.

Prosoma. Chilum double, about three times or more as wide as high. Chelicerae (Figs 3D, F–H): paturon conical, with some long setae medially, three teeth on both margins, with retrolateral thick setae at fang base; fang with serrate texture on proximal edge. Labium (Figs 3B, E, 10C–D) roughly diamond shaped. Endites (Figs 3B, E, 10C–D) roughly rectangular, with retrolateral margins sinuous, distal part slightly wider than proximal part, with subdistal serrula present as simple row. Sternum (Figs 3B, E, 10C–D) oval, slightly longer than wide, with slightly curved margins, not extending between coxae IV.

Legs. Slender (Figs 3A, H, 4A, 8A, 10). Formula 4123. With three tarsal claws; unpaired claw smooth, present on legs I and II, large to small, typically reduced to nubbins on legs III and IV; superior claws with six to eight teeth; without claw tufts or tenent setae; scopulae absent or rarely present (female of *T. polotowae* gen. et sp. nov.). Trichobothria in two or more rows on tarsi, in three or more on metatarsi, starting close to tip, all equal in lengths; distal and proximal plates of bothria well differentiated, proximal plates with transverse ridges. Tarsal organ: tear-drop or keyhole-shaped opening, close to tarsus tip. Spines numerous, with four pairs of ventral spines on tibia I, not overlapping, and with three pairs of ventral spines on metatarsus I. Calamistrum absent. Male tibial crack (autospasy suture) present or absent. Distal borders of leg trochanters with deep (forelegs) or shallow (hind legs) notch (Fig. 4C–D).

Abdomen (Figs 3A–B, D–E, G–H, 8A, 10). Oval, without scuta and without cribellum. Epiandrous glands absent. Colulus: as triangular hairy lobe. Spinnerets: ALS and PLS, conical, biarticulate; PMS one-segmented; ALS large, PMS and PLS small. Females with two ALS major ampullate gland spigots and field of about 20–30 piriform gland spigots and tartipores; PMS with one anterior minor ampullate gland spigot and large tartipore and one to few posterior cylindrical gland spigots and aciniform gland spigots; PLS with one to few cylindrical gland spigots; males lacking cylindrical gland spigots and second of each pair of both major and minor ampullate gland spigots reduced to nubbins.

Male palp (Figs 5A–C, 6, 9A–C, 11A–C). Tibia with large or stout RTA, inserted medially, provided with basal concavity (BC), with short rounded or tapered VTA and with sharp triangular dorso-prolateral process. Cymbium oval with rounded distal extremity, without dorsal patch of short setae, with cymbial retrobasal extension (CE), without retrolateral paracymbial process. Bulbus provided with retrobasal subtegulum locking lobe (SL), and tegulum rounded with well-developed prolateral conical protrusion at base of embolus (corresponding to locking lobe, TL). Embolus (E) with fixed base, originating prolateraly, directed clockwise, long, large and lamellate (Figs 5A–C, 6D–F) or slender and tapered apically (Figs 8C–F, 9A–B, 11A–C, 12A–C, E). Median apophysis (MA) hook-shaped, situated opposite of embolus; conductor (C) hyaline, well developed, fan-shaped, medially extending from narrow base to wide flattened tip. Paraconductor (Pc) as narrow, finger-like membranous extension inserted between tegulum and base of MA.

Genitalia. Epigyne (Figs 4B, 5D, 7A–B, 9D, 11D) single, shield-shaped plate (ML) with convex median and lateral folds, lateral sector (LL) convex or with pocket. Endogyne (Figs 5E, 7C–F, 9E, 11E, 12H): copulatory ducts (CD) very short, twisted; spermatheca (S) two or three lobed, head of spermatheca provided with pores; no evidence of enlarged Bennett's Gland pore through spermathecal base.

Species included

Tabiboka milleri gen. et sp. nov. (type species; ♂♀); *Tabiboka milloti* gen. et sp. nov. (♂♀); *Tabiboka polotowae* gen. et sp. nov. (♂♀).

Affinities

From the molecular analyses (Fig. 2), *Tabiboka* gen. nov. appears closely related to species in the Udubidae that have been identified as *Zorascar* gen. nov.

Distribution

Tabiboka gen. nov. are known only from mid-eastern Madagascar (Fig. 26).

Tabiboka milleri gen. et sp. nov.

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Figs 3–7, 26

Zorocratidae gen. Talatakely sp. Talatakely – Morphbank 2023: images [476092–509952] SpiderAToL, March 3, 2008, https://www.morphbank.net/?id=218853 [accessed 20 Oct. 2023].
Zorodictyna sp. 2 – Polotow *et al.* 2015.
Zorodictyna sp. CG300 – Wheeler *et al.* 2017.

Diagnosis

Males of *Tabiboka milleri* gen. et sp. nov. may be distinguished by the morphology of the palpal tibia with the RTA having an elongate curved spur arising retrobasally and extending distally to the apex of the tibia (Figs 5B–C, 6A–C) (vs *T. milloti* gen. et sp. nov. and *T. polotowae* gen. et sp. nov. have a short and stout RTA, Figs 9B–C, 11B–C), a short, broad embolus (E) and a small, slender paraconductor (Pc) largely hidden behind the embolus (Figs 5A–C, 6D–F) (vs in *T. milloti* and *T. polotowae*, the E is slender and the Pc is situated between the E and the C, Figs 8F, 9B, 11B, 12E). Females of *T. milleri* have the epigyne with a broad, swollen, oval median lobe (ML) that extends posteriorly beyond the epigastric furrow, narrow anteriorly (anterior width less than half the total width, Figs 4B, 5D, 7A) (vs in *T. milloti*, the ML is broad anteriorly, Fig. 9D; and in *T. polotowae*, the ML is medially narrowed, Figs 11D, 12G).

Etymology

The species name is a patronym in honor of Jeremy Miller, who collected widely in Madagascar and led a team that carried out a pioneering study of entelegyne spider phylogeny (Miller *et al.* 2010).

Type material

Holotype

MADAGASCAR – **Fianarantsoa Province** • ♂; Ranomafana National Park, Talatakely; 21°15′ S, 47°25′ E; 900 m a.s.l.; 5–7 Dec. 1993; C. Griswold, N. Scharff, S. Larcher and R. Andriamasamanana leg.; CASENT_9016094; CAS.

Paratypes

MADAGASCAR – **Fianarantsoa Province** • 1 ♀; same collection data as for holotype; [Standard view preparations and images for AToL-Spiders project; SEM preparations Box 79-8, 10, 11, 19, Box 81, 1, 2]; CASENT_9016094; CAS • 1 ♂, 1 ♀; Ranomafana N.P.; 21°12′ S, 47°27′ E; 18 May 1992; V. and B. Roth, S. Kariko leg.; general collecting; [habitus photos, stacked images, H.M. Wood; Apr. 2005]; CASENT_9016098; CAS • 1 ♂, 1 ♀; same data as for preceding; [♂ palp drawn]; CASENT_9016086; CAS • 1 ♂, 1 ♀; Parc National Ranomafana, Talatekely forest, 42.3 km 58° NE of Fianarantsoa; 21°15′28.0″ S, 47°25′21.8″ E; 1050 m a.s.l.; 24 Dec. 2005–14 Jan. 2006; H. Wood, J. Miller, J.J. Rafonomezantsoa, E. Rajeriarison, V. Andriamananony leg.; montane rainforest; general collecting; [AToL DNA Voucher ARACG0300] [HW009/RNAlater: Mad-052]; CASENT_9024004; CAS • 1 ♂; Ranomafana N.P.; 21°12′ S, 47°27′ E; 18 May 1992; V. and B. Roth, S. Kariko leg.; general collecting; [stacked images, HMW, April-2005]; CASENT_9016097; CAS • 1 ♀; Parc National Ranomafana, Vohiparara, 3.6 km W of Ranomafana; 21°14.243′ S, 47°23.842′ E; 1150 m a.s.l.; 13–14 Jan. 2009; D. Andriamalala, C. Griswold, G. Hormiga, A. Saucedo, N. Scharff and H. Wood leg.; primary montane rainforest; general collecting day and night; [NS Photo voucher 893-897; GH photos 5659-5666]; CASENT_9029871; CAS. – **Mahajanga Province** • 1 ♀; Ampijoroa, National Park Ankarafantsika, near Lake Ravelobe; 16°17′48″ S, 46°48′50″ E; 26–28 Jan. 2009; C. Griswold, A. Saucedo, H. Wood leg.; [SEM female epigyne + used for DNA voucher DP-2014c - "Zorodictyna sp. 2"]; CASENT_9035866; CAS.

Other material examined

MADAGASCAR – **Antananarivo Province** • 1 ♂; Tsinjoarivo Forest, Mahatsinjo; 19°40′47.496″ S, 47°46′22.835″ E; 1654 m a.s.l.; 26–29 Aug. 2014; B.L. Fisher leg.; montane rainforest; BLF35410; CASENT_9065708; CAS • 1 ♂; same data as for preceding; CASENT_9065709; CAS • 1 ♂; same data as for preceding; CASENT_9065678; CAS • 1 ♂; same data as for preceding; CASENT_9065579; CAS • 4 ♂♂, 5 ♀♀; same data as for preceding; CASENT_9017817; CAS • 2 ♀♀; Tsinjoarivo Forest, Ankadivory; 19°43′00″ S, 47°49′18″ E; 1369 m a.s.l.; 28 Apr.–1 May 2014; B.L. Fisher *et al.* leg.; montane rainforest, sifted litter; BLF33370; CASENT_9064661; CAS. – **Fianarantsoa Province** • 1 ♀; Forêt d'Ankazomivady, 28 km SSW of Ambositra, 4.7 km SW of Ambalamanakana; 20°47′ S, 47°10′ E; 1670 m a.s.l.; 7–14 Jan. 1998; S. Goodman, SG0001 leg.; disturbed upper montane forest; pitfall traps #1–3; CASENT_9016064; FMNH • 9 ♀♀; same data as for preceding; CASENT_9016065; FMNH • 1 ♀; same data as for preceding; CASENT_9016066; FMNH • 9 ♀♀; same data as for preceding; CASENT_9016067; FMNH • 1 ♂; same data as for preceding; CASENT_9016068; FMNH • 1 ♂; Ankazomivady, 29 km SSW of Ambositra; 20°47′ S, 47°10′ E; 1700 m a.s.l.; 7 Jan. 1998; B.L. Fisher leg.; forest; EBD10 pitfall trap; BLF1592b; CASENT_9016087; CAS • 1 ♀; Ambatofitorahana, 33 km S of Ambositra; 20°49′00.00″ S, 47°10′59.99″ E; 13 Mar. 1994; A. Pauly leg.; natural forest; BE_RMCA_ARA.Ara.201626; RMCA • 24 ♂♂, 5 ♀♀; Ranomafana National Park, Talatakely; 21°12′ S, 47°27′ E (coordinates approximate); 900 m a.s.l.; 4–16 Jan. 2001; D.H. and K.M. Kavanaugh, R.L. Brett, E. Elsom and F. Vargas leg.; mixed tropical forest; pitfall traps #4–16; COL-DHK-2001-001TN; CASENT_9003432; CAS • 1 ♀; same data as for preceding; CASENT_9003534; CAS • 1 ♀; Parc National Ranomafana, Talatakely; 21°15′ S, 47°26′ E; 13–27 Apr. 1998; C.E. Griswold, D.H. Kavanaugh, N.D. Penny, M.J. Raherilalao, J.S. Ranorianarisoa, J. Schweikert and D. Ubick leg.; pitfall traps; CASENT_9006115; CAS • 1 ♂; same data as for preceding; CASENT_9016084; CAS • 1 ♂; Parc National Ranomafana, Talatakely; 21°15′ S, 47°26′ E; 19–30 Apr. 1998, C.E. Griswold, D.H. Kavanaugh, N.D. Penny, M.J. Raherilalao, J.S. Ranorianarisoa, J. Schweikert, D. Ubick leg.;general collecting; CASENT_9016082; CAS • 2 ♀♀; same data as for preceding; CASENT_9016088; CAS • 6 ♂♂; Parc National Ranomafana, Talatakely, trail F; 21°16′ S, 47°25′ E; 940–985 m a.s.l.; 1–21 Nov. 1998; V.F. Lee and K.J. Ribardo leg.; pitfall trap; CASENT_9016089; CAS • 2 ♂♂; same data as for preceding;

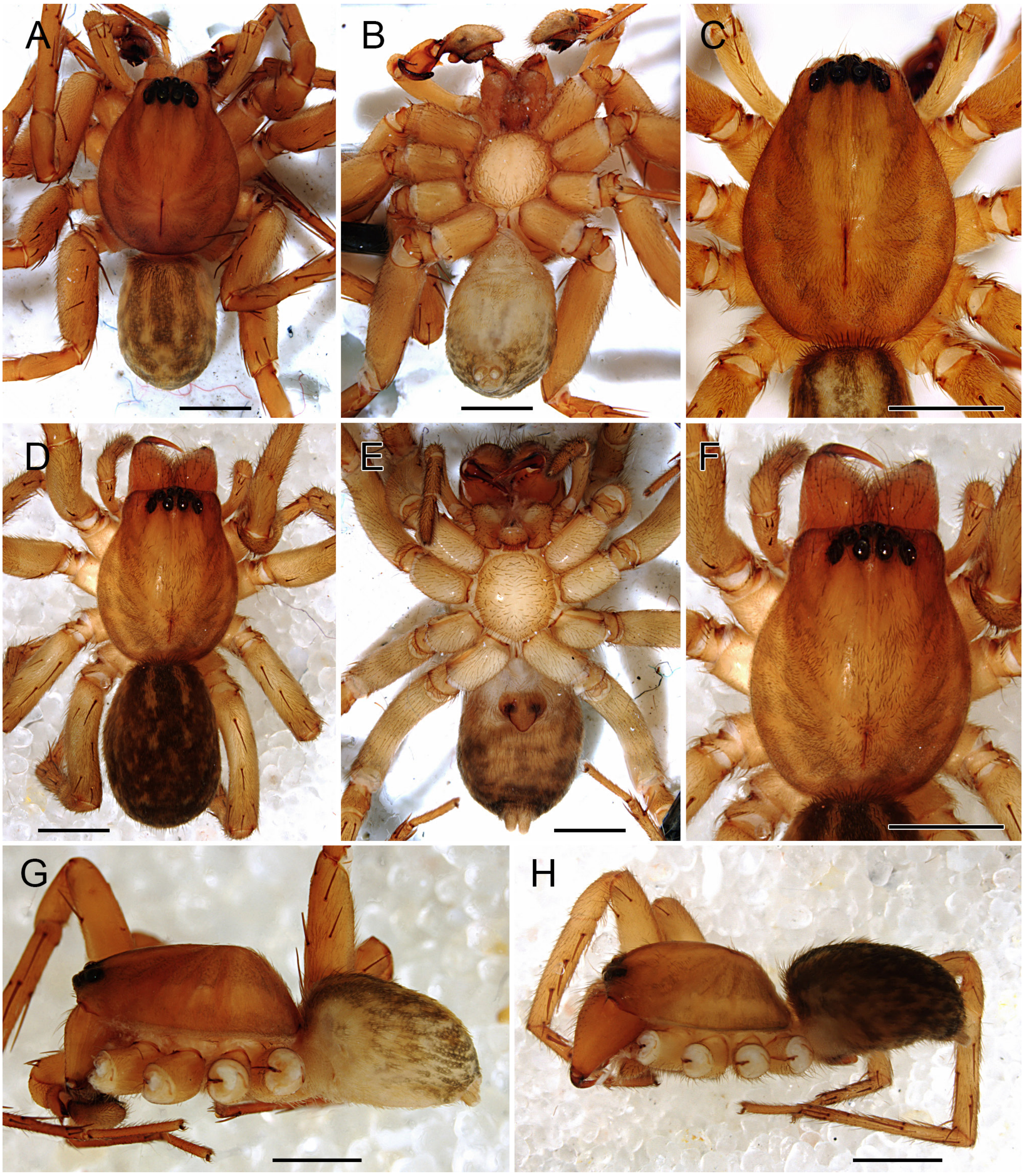

Fig. 3. *Tabiboka milleri* gen. et sp. nov., A–B, G = male paratype (CASENT_9016097; CAS); C = male paratype (CASENT_9016098; CAS); D–F, H = female paratype (CASENT_9016094; CAS). **A, D**. Habitus, dorsal view. **B, E**. Idem, ventral view. **C, F**. Carapace, dorsal view. **G–H**. Habitus, lateral view. Scale bars = 2 mm. Stacked microphotographs by Hannah Wood.

CASENT_9016090; CAS • 1 ♂; same data as for preceding; CASENT_9016093; CAS • 2 ♀♀; Parc National Ranomafana, Vatoharanana; 21°17′ S, 47°26′ E; 1200 m a.s.l.; 15–29 Apr. 1998; C.E. Griswold, D.H. Kavanaugh, N.D. Penny, M.J. Raherilalao, J.S. Ranorianarisoa, J. Schweikert, D. Ubick leg.; primary forest; CEG-MA-1998-03; CASENT_9016080; CAS • 1 ♀; Parc National Ranomafana, Vatoharanana, trail K; 21°17′ S, 47°26′ E; 990 m a.s.l.; 14–19 Nov. 1998; V.F. Lee and K.J. Ribardo leg.; pitfall trap; VFL-KJR-02; CASENT_9016091; CAS • 1 ♀; same data as for preceding; CASENT_9016092; CAS • 1 ♀; Parc National Ranomafana, Vatoharanana River, 4.1 km 231° SW of Ranomafana; 21°17′24″ S, 47°26′00″ E; 1100 m a.s.l.; 27–31 Mar. 2003; Fisher-Griswold Arthropod Team leg.; montane rainforest; general day collecting; BLF8394; CASENT_9017837; CAS • 1 ♀; Parc National Ranomafana, Vohiparara Piste Touristique; 21°14′ S, 47°24′ E; 1000 m a.s.l.; 23 Apr. 1998; C.E. Griswold, D.H. Kavanaugh, N.D. Penny, M.J. Raherilalao, E. Rajeriarison, J.S. Ranorianarisoa, J. Schweikert, D. Ubick leg.; running in litter; general collecting; CEG-MA-1998; CASENT_9016081; CAS • 6 ♂♂; Ranomafana National Park, Vohiparara; 21°12′ S, 47°27′ E (coordinates approximate); 1150 m a.s.l.; 2–22 Jan. 2001; D.H. and K.M. Kavanaugh, R.L. Brett, E. Elsom, F. Vargas leg.; mixed tropical forest; general collecting; COL-DHK-2001-004; CASENT_9003479; CAS • 6 ♀♀; Parc National Ranomafana, 2.3 km N of Vohiparara Village; 21°13′ S, 47°23′ E; 1100 m a.s.l.; 18 Apr. 1998; C.E. Griswold, D.H. Kavanaugh, N.D. Penny, M.J. Raherilalao, E. Rajeriarison, J.S. Ranorianarisoa, J. Schweikert, D. Ubick leg.; CASENT_9016083; CAS • 6♀♀; same data as for preceding; CASENT_9016085; CAS • 2 ♀♀; Ranomafana N.P., Trail F;

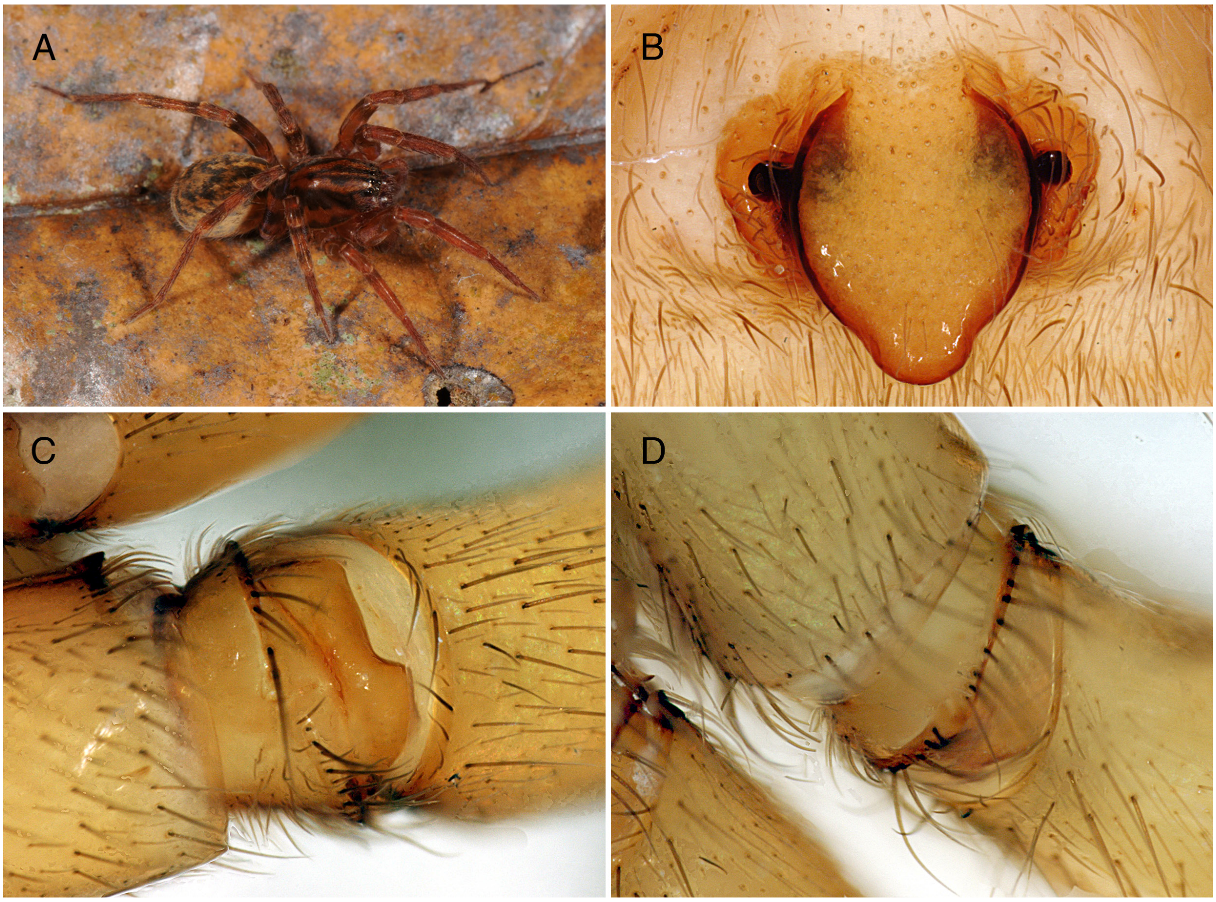

Fig. 4. *Tabiboka milleri* gen. et sp. nov. **A**. Female paratype (CASENT_9029871; CAS) from Ranomafana (Photo © N. Scharff). **B**. Female paratype (CASENT_9016098; CAS), epigyne, ventral view. **C**. Female paratype (CASENT_9016094; CAS), trochanter 1, ventral view. **D**. Idem, trochanter 4. (No scales provided). Stacked microphotographs by Charles Griswold.

21°12′ S, 47°27′ E (coordinates approximate); 18 May 1992; Albert for Kariko, Roth leg.; sifting #1; CASENT_9030889; MCZ • 1 ♀; Ranomafana N.P., Maharira, summit; 21°12′ S, 47°27′ E; 9 Apr. 1992; Albert for Kariko, Roth leg.; cryptic #2; CASENT_9030890; MCZ • 1 ♂; Ranomafana N.P., Trail M; 21°12′ S, 47°27′ E (coordinates approximate); 15 May 1992; Albert for Kariko, Roth leg.; sifting 1hr.

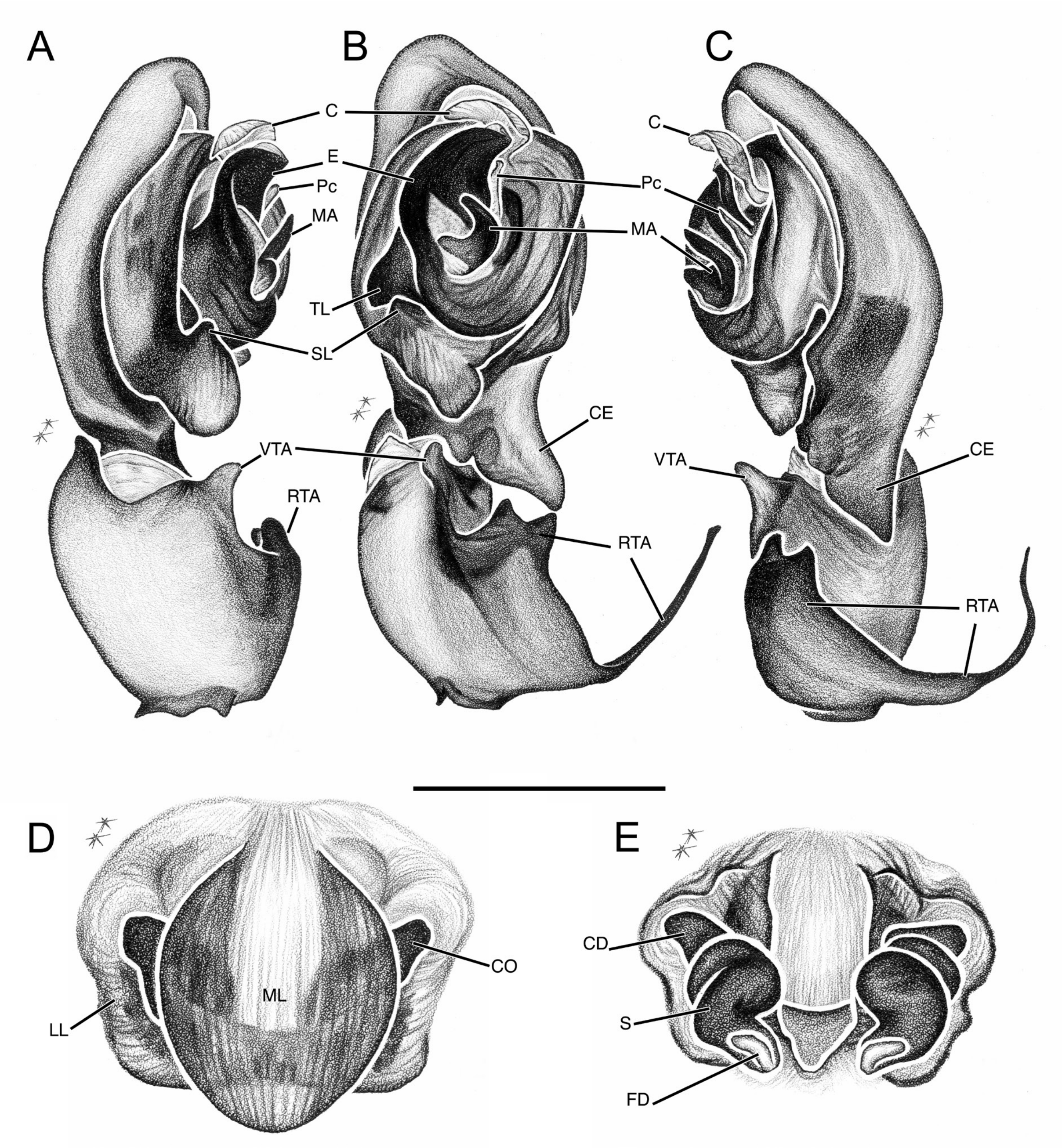

Fig. 5. *Tabiboka milleri* gen. nov. et sp. nov. genitalia drawings of male and female paratypes (CASENT_9016086; CAS). **A**. Male left palp, prolateral view. **B**. Idem, ventral view. **C**. Idem, retrolateral view. **D**. Epigyne, ventral view. **E**. Idem, dorsal view. Abbreviations: C = conductor; CD = copulatory duct; CE = cymbial retrobasal extension; CO = copulatory opening; E = embolus; FD = fertilisation duct; LL = lateral lobe; MA = median apophysis; ML = median lobe; Pc = paraconductor; RTA = retrolateral tibial apophysis; S = spermatheca; SL = subtegular locking lobe; TL = tegular locking lobe; VTA = ventral tibial apophysis. Scale bars = 0.5 mm. Illustrations by Jenny Speckels.

samples #2; CASENT_9030891; MCZ • 1 ♀; Ranomafana N.P., Trail M; 21°12′ S, 47°27′ E (coordinates approximate); 15 May 1992; Albert for Kariko, Roth leg.; sifting; CASENT_9030892; MCZ • 3 ♀♀; Ranomafana N.P., Trail B; 21°12′ S, 47°27′ E (coordinates approximate); 825 m a.s.l.; 19 May 1992; Albert for Kariko, Roth leg.; sifting, #1; CASENT_9030893; MCZ • 1 ♀; Ranomafana N.P., Maharira, summit; 21°12′ S, 47°27′ E (coordinates approximate); 11 Apr 1992; Emile for Kariko, Roth leg.; sifting

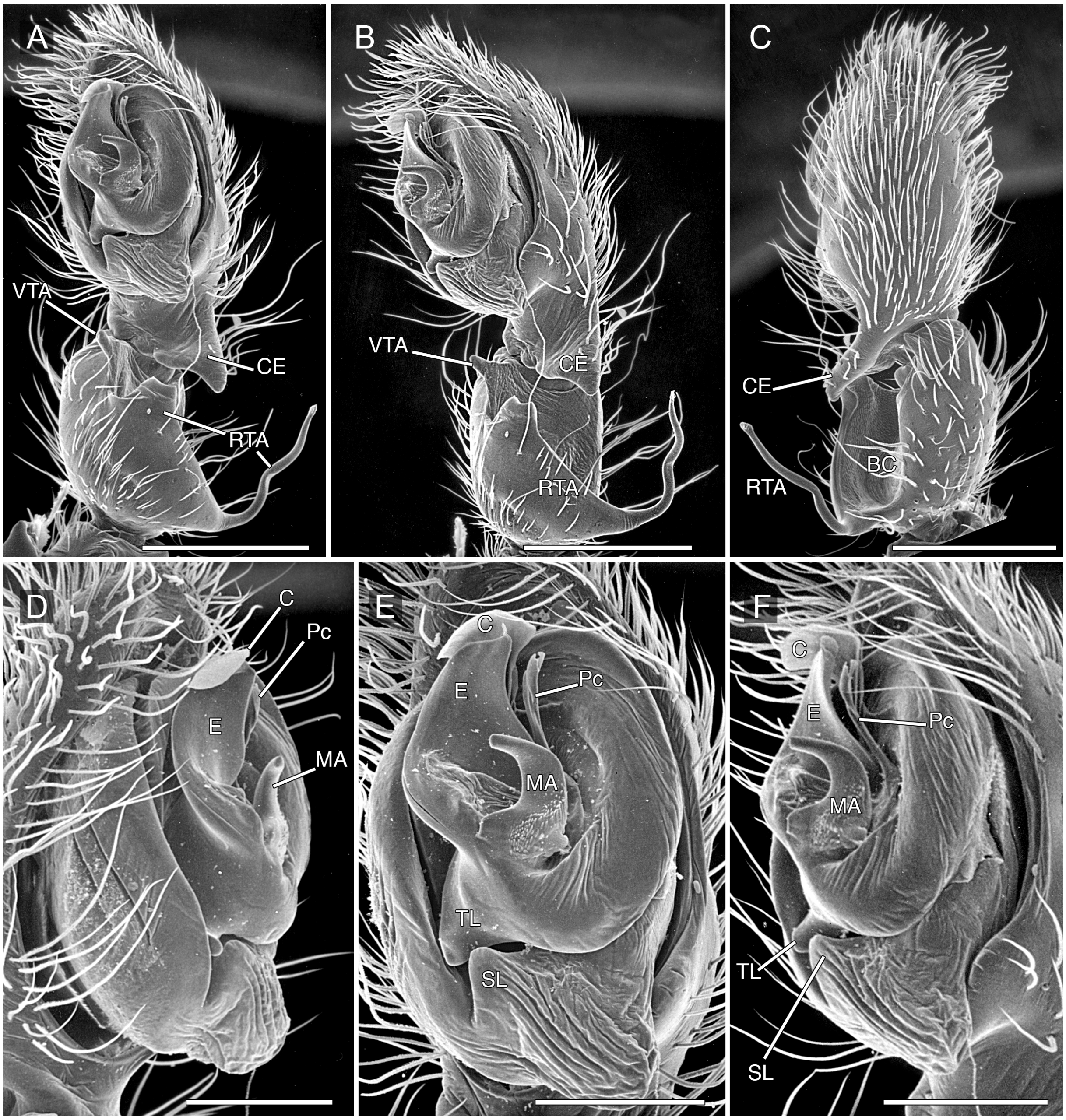

Fig. 6. *Tabiboka milleri* gen. nov. et sp. nov. SEM of male right palp (mirrored), paratype (CASENT_9016094; CAS). **A**. Palp, ventral, slightly retrolateral view. **B**. Idem, retrolateral view. **C**. Idem, dorsal view. **D**. Bulb, prolateral view. **E**. Idem, ventral view. **F**. Idem, retrolateral view. Abbreviations: BC = basal concavity of the RTA; C = conductor; CE = cymbial retrobasal extension; E = embolus; MA = median apophysis; Pc = paraconductor; RTA = retrolateral tibial apophysis; SL = subtegular locking lobe; TL = tegular locking lobe; VTA = ventral tibial apophysis. Scale bars: A–C = 0.43 mm; D–F = 0.2 mm. SEM images by Charles Griswold and Darrell Ubick.

#3; CASENT_9030894; MCZ • 2 ♀♀; Ranomafana N.P.; 21°12′ S, 47°27′ E; Apr. 1992; V. and B. Roth, S. Kariko leg.; forest; general collecting from foliage; Ranomafana-1000-92; CASENT_9016099; CAS • 1 ♂, 1 ♀; Ranomafana N.P., trail F, secondary forest; 21°12′ S, 47°27′ E (coordinates approximate); Apr. 1992; Albert for Kariko, Roth leg.; sifting #3; MCZ-VBR-0116; CASENT_9016100; MCZ • 4 ♂♂,

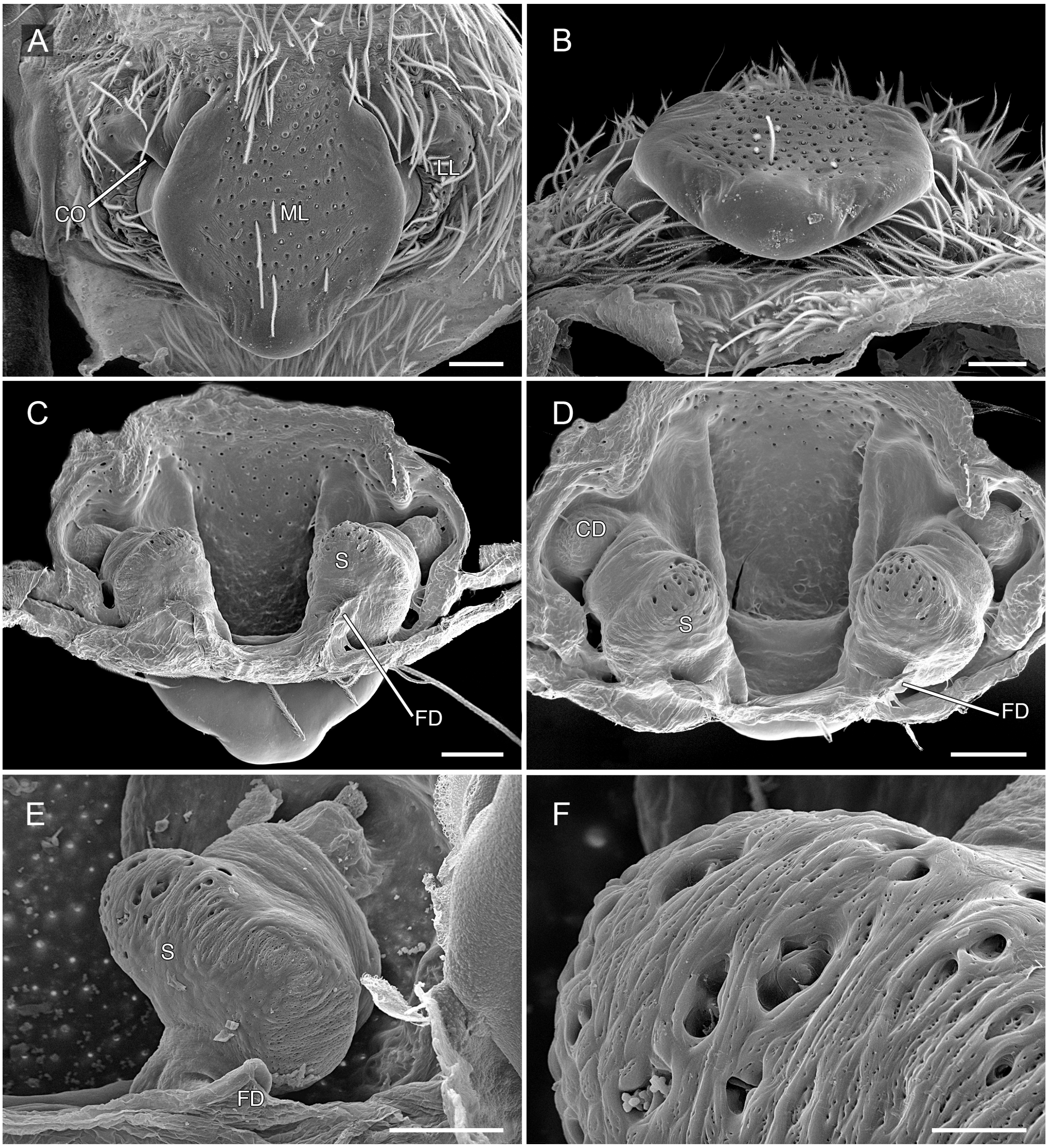

Fig. 7. *Tabiboka milleri* gen. nov. et sp. nov. SEM of female genitalia, A–B, E–F = female paratype (CASENT_9016094; CAS); C–D = female paratype (CASENT_9035866; CAS). **A**. Epigyne, ventral view. **B**. Idem, ventro-posterior view. **C**. Endogyne, dorsal view. **D**. Idem, slightly anterior view. **E**. Spermatheca, right dorsal view. **F**. Idem, detail. Abbreviations: CD = copulatory duct; CO = copulatory opening; FD = fertilisation duct; LL = lateral lobe; ML = median lobe; S = spermatheca. Scale bars: A–E = 0.1 mm; F = 20 µm. SEM images by Diana Silva Dávila.

7 ♀♀; Ranomafana N.P.; 21°12′ S, 47°27′ E (coordinates approximate); 20–31 May 1992; V. and B. Roth leg.; can traps; MCZ-VBR-02; CASENT_9016101; MCZ • 1 ♂; same data as for preceding; CASENT_9016102; CAS.

Description

Male holotype (CASENT_9016094; CAS)
Measurements. Total length: 10.50. Carapace: length 6.10, width 4.40, height 2.20.

Coloration (Fig. 3A–C, G). Carapace brownish yellow, darker along margin, with two faint, longitudinal dark bands along margin of pars cephalica; black on ocular area and surrounding all eyes; chelicerae brownish yellow; sternum yellow, unmarked; legs brownish yellow, unmarked; abdomen brownish yellow with darker cardiac mark and dorsolateral dark bands that break up into chevrons posteriorly, sides brownish yellow mottled with dark marks, venter yellow except darker around spinneret base.

Sternum (Fig. 3B). Oval with slightly sinuous margins; 2.30 wide, 2.60 long.

Chilum. 0.13 high, 0.35 wide.

Eyes. ALE 0.18; AME 0.13; PLE 0.18; PME 0.15; ALE–AME 0.06; AME–AME 0.40; PLE–PME 0.20; PME–PME 0.09; MOQ: AW 0.33, PW 0.48, L 0.35.

Clypeus. 0.25 high, with eight long setae.

Legs. Trochanter I notched, trochanter IV shallowly notched. Unpaired claw smooth, rudimentary on legs III and IV. Scopulae absent.

Leg measurements

	F	P	T	Mt	t	Total
I	4.70	2.00	4.80	4.70	2.80	19.00
II	4.20	1.90	3.80	4.00	2.20	16.10
III	4.30	1.70	3.50	4.10	2.00	15.60
IV	5.20	2.00	4.60	6.50	2.50	20.80

Spination

	F	P	T	Mt
I	pl2d3rl3	–	pl2d2rl2v2-2-2	pl3rl3v2-2-3
II	pl3d3rl4	–	pl3d2rl2v2-2-2-2	pl5rl4v2-1-1
III	pl3d3rl4	pl1rl1	pl2d2rl2v2-2-2	pl4rl4v2-2-2
IV	pl3d3rl2	rl1	pl2d2rl2v2-2-2	pl4rl4v2-2-2

Male palp (Figs 5A–C, 6). Tibia with slender apical VTA, bifid apical RTA continuous with elongate, slender basal RTA; tibia with dorso-retrolateral excavation (BC) bordered dorsad of RTA, accommodating conical retrobasal cymbial extension; cymbium oval with rounded apical extremity, without dorsal patch of chemosensitive setae, with sinuous retrolateral margin, with conical retrobasal cymbial extension (CE) that extends ⅓ of tibial length from tibial apex; subtegulum large, filling most of cymbial concavity, with rounded lobe extending proximad and small, conical lobe (SL) that interacts with the tegulum; tegulum oval with large, rounded retrodistal protuberance and conical promedian lobe (TL) that locks with subtegulum; embolus (E) arises from center of tegulum, short, broad; strongly sclerotized MA forms short hook curved prolaterad; conductor (C) hyaline, translucent, flattened, fan-shaped, narrow at base and strongly widened at extremity; paraconductor (Pc) as finger-like membranous structure originating at base of MA and extending to anterior half of E.

Female paratype (CASENT_9016094; CAS)
Measurements. Total length: 14.00. Carapace: length 6.80, width 5.20, height 2.70.

Colour (Figs 3D–F, H, 4A). As in male except abdomen much darker, mostly brown with lighter paracardiac marks and faint posterodorsal chevrons, sides dark, venter yellow brown with transverse dark mottling.

Sternum (Fig. 3E). Oval with slightly sinuous margins; 2.60 wide, 3.00 long.

Chilum. 0.13 high, 0.50 wide.

Eyes. ALE 0.18; AME 0.13; PLE 0.18; PME 0.15; ALE–AME 0.06; AME–AME 0.40; PLE–PME 0.25; PME–PME 0.11; MOQ: AW 0.40, PW 0.55, L 0.48.

Clypeus. 0.30 high, with eight long setae.

Legs. Trochanter I notched (Fig. 4C), trochanter IV shallowly notched (Fig. 4D). Unpaired claw smooth, rudimentary on legs III and IV. Scopulae absent.

Leg measurements

	F	P	T	Mt	t	Total
I	5.10	2.40	4.20	3.60	1.90	17.20
II	4.80	2.40	3.60	3.30	1.80	15.90
III	4.00	1.90	2.90	4.00	1.80	14.60
IV	5.20	2.20	4.40	6.10	2.30	20.20

Spination

	F	P	T	Mt
I	pl1d2	–	v2-2-2-2	v2-2-2
II	pl1d1	–	v2-2-2-2	v2-2-2
III	pl2d3rl1	pl1rl1	pl2d2rl2v2-2-2	pl5rl3v2-2-1-2
IV	pl1d3rl1	pl1rl1	pl2d2rl2v2-2-2	pl5rl3v2-2-1-2

Genitalia. Epigyne (Figs 5D, 7A–B) with broad, oval median lobe (ML) that extends posteriad of epigastric furrow; lateral lobes (LL) convex, lacking teeth or concavities; copulatory openings (CO) located beneath anteromedian margin of median lobe and, in many specimens, containing simple plugs. Endogyne (Figs 5E, 7C–F) with spermathecae (S) dark, smoothly convex, simple or with slight transverse indentations; sperm ducts (CD) anteromedian, short, joining seamlessly with spermathecae; spermathecal heads with 20–30 small pores; fertilization ducts (FD) short, flattened and slightly curved (Figs 5E, 7E).

Variation

Males (n = 5)
Male genitalia display slight geographic variation. Males from Ranomafana have very slender retrobasal tibial processes, with length greater than 20 times width, whereas in males from Ankazomivay and Tsinjoarivo these are thick, with length less than 15 times width. The distal RTA may be deeply cleft in males from Ranomafana or only slightly cleft as in males from Ankazomivady. Most individuals have a

crack across the subbasal part of the leg tibia just distad of the basalmost ventral spines, but this varies. Within the Ranomafana population some have the tibial leg crack clearly marked whereas in others the crack cannot be distinguished. Total length = 9.60–12.00, carapace length/width = 1.28–1.41, carapace height/width = 0.44–0.59, PER/carapace width = 0.24–0.26, PER/OAL = 2.33–2.65, PER/AER = 1.38–1.46, OAL/OQL = 1.24–1.42, OQP/OQA = 1.46–1.57. Clypeus height/AME = 1.20–2.86, cheliceral length/clypeus height = 8.00–13.33, sternum length/width = 1.11–1.19, palpal coxa length/width = 2.14–2.50, femur I length/carapace width = 1.04–1.22, metatarsus I length/carapace width = 1.02–1.11, femur IV length/carapace width = 1.09–1.30, cymbium length/carapace width = 0.36–0.42, cymbium length/palpal patella length = 1.45–2.43, cymbium length/palpal tibia length = 1.23–1.90, cymbium length/palpal femur length = 0.76–0.92, palpal tibia length/palpal patella length 1.00–1.57.

Females (n = 5)
Total length = 11.50–14.00, carapace length/width = 1.26–1.31, carapace height/width = 0.45–0.65, PER/carapace width = 0.25–0.33, PER/OAL = 2.44–2.95, PER/AER = 1.35–1.70, OAL/OQL = 1.13–1.38, OQP/OQA = 1.33–1.71, clypeus height/AME = 1.60–2.40, cheliceral length/clypeus height = 7.67–12.50, sternum length/width = 1.14–1.30, palpal coxa length/width = 1.94–2.57, femur I length/carapace width = 0.92–1.10, metatarsus I length/carapace width = 0.62–0.71, femur IV length/ carapace width = 0.92–1.10, palpal tarsus length/carapace width = 0.32–0.37, palpal tarsus length/palpal tibia length = 1.15–1.31, palpal tarsus length/palpal femur length = 0.74–0.86, palpal tibia length/palpal patella length = 1.08–1.37. The oval epigynal median lobe may be evenly curved in lateral outline (Fig. 5D) or be attenuated posteriorly (Fig. 4B). Median lobe length 0.93–1.38 times width, with median lobe extending posteriad of epigastric furrow by 0.11–0.29 of lobe length. Spermathecae may be evenly rounded or have as many as two shallow dorsal constrictions. Spermathecae separated by 0.27–0.35 the total width of the spermathecae.

Note on synonyms

Specimens of this species have been used as exemplars in previous studies including morphological documentation and in published molecular phylogenies. The morphology of the species was documented for the Spiders Assembling the Tree of Life (AToL) study (2001–2009) as the exemplar "Zorocratidae gen. Talatakely sp. Talatakely", Images [476092–509952] SpiderAToL, March 3, 2008, https://www.morphbank.net/?id=218853 (Morphbank 2023): CASENT_9016094. Specimens were used as the exemplars "*Zorodictyna* sp. 2" by Polotow *et al.* (2015) (CASENT_9035866) and as "*Zorodictyna* sp. CG300" by Wheeler *et al.* (2017) (CASENT_9024004).

Natural history

This species is commonly found running on leaf litter in closed-canopy montane rainforest. Individuals were also collected in pitfall traps or under objects.

Distribution

Tabiboka milleri gen. et sp. nov. are known only from rainforests in Antananarivo and Fianarantsoa Provinces in southeastern Madagascar (Fig. 26).

Tabiboka milloti gen. et sp. nov.

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Figs 8–9, 26

Zorodictyna sp. CG45 – Wheeler *et al.* 2017.

Diagnosis

The males of *Tabiboka milloti* gen. et sp. nov. may be distinguished by the palpal tibia with a short, blunt retromedian process (RTA) and broad, thumb-like ventral apical process (VTA) (Figs 8E, G, 9B–C), the slender embolus (E) and the elongate, cruciform median apophysis (MA) with the apex extending to embolus tip (Figs 8F, 9A–B) (vs in *T. milleri* gen. et sp. nov., the the VTA is smaller and the RTA is greatly elongated, Fig. 5A–C, and the E and the MA are shorted and broader; and in *T. polotowae* gen. et sp. nov., the VTA is finger-like and the MA is shorter, Fig. 11A–C). Females of *T. milloti* have the epigyne with a heart-shaped median lobe (ML), broad anteriorly (anterior width greater than one-half total width, Fig. 9D) (vs in *T. milleri*, the ML is narrow anteriorly, anterior width less than one-half total width, Fig. 5D; and in *T. polotowae*, the ML is rectangular, narrowest in middle or with sides straight, Fig. 11D).

Etymology

The species name is a patronym in honor of Jacques Millot, who collected the holotype of this species and many other interesting arthropods in Madagascar during his missions in the mid-20th century.

Type material

Holotype

MADAGASCAR – **Toamasina Province** • ♂; Périnet (= Andasibe), Res. Analamazaotra, Parc National Andasibe; Aug. 1946; J. Millot leg.; CASENT_9016063; MNHN.

Paratypes

MADAGASCAR– **Toamasina Province** • 1 ♀; Res. Analamazaotra, Parc National Andasibe, road 23 km E of Moramanga; 960 m a.s.l.; 18°56′38″ S, 48°25′03″ E; 16–18 Jan. 2003; C. Griswold, D. Silva and D. Andriamalala leg.; general collecting in rainforest; BLF7993; CASENT_9018308; CAS • 1 ♂; same data as for preceding; general collecting at night in rainforest; AToL DNA voucher: ARACG045; BLF7994; CASENT_9005657; CAS • 1 ♂; same data as for preceding; CASENT_9005261; CAS.

Other material examined

MADAGASCAR – **Antananarivo Province** • 2 ♂♂; Tsinjoarivo forest, Ankadivory; 19°42′56.592″ S, 47°49′15.0234″ E; 1385 m a.s.l.; 11–14 Jan. 2015; B.L. Fisher *et al.* leg.; pitfall traps in montane rainforest; BLF35447-5; CASENT_9065578; CAS • 1 ♂; same data as for preceding; BLF35447-20; CASENT_9065583; CAS • 1 ♂; same data as for preceding; CASENT_906558; CAS.

Description

Male holotype (CASENT_9016063; MNHN)

Measurements. Total length: 7.50. Carapace: length 4.60, width 3.70, height 1.80.

Coloration (Fig. 8A–B). Carapace pale brownish yellow, darker along margin, with two faint, longitudinal dark bands along margin of pars cephalica; black surrounding all eyes; chelicerae brownish yellow; sternum yellow-white, unmarked; legs brownish yellow, femora, tibiae and metatarsi with faint median and subapical dusky annuli; abdomen pale yellow with darker cardiac mark and dorsolateral dark bands that break up into chevrons posteriorly, sides mottled with dark marks, venter yellow except with darker mottling around spinneret base.

Sternum. Oval with slightly sinuous margins; 2.00 wide, 2.50 long.

Chilum. 0.13 high, 0.35 wide.

Eyes. ALE 0.33; AME 0.13; PLE 0.15; PME 0.14; ALE–AME 0.05; AME–AME 0.20; PLE–PME 0.13; PME–PME 0.06; MOQ: AW 0.26, PW 0.38, L 0.30.

Clypeus. 0.10 high, with six long setae.

Legs. Trochanters deeply notched. Unpaired claw smooth, rudimentary on legs III and IV. Metatarsi lacking subbasal crack. Scopulae absent.

Leg measurements

	F	P	T	Mt	t	Total
I	4.30	1.80	3.90	3.50	2.20	15.50
II	3.80	1.80	3.10	3.00	1.90	13.60
III	3.50	1.50	2.60	3.30	1.80	12.70
IV	5.30	1.80	4.00	5.40	2.40	18.90

Spination

	F	P	T	Mt
I	pl1d3rl1	–	pl2rl1v2-2-2-2	pl1-2v2-2-2
II	pl2d3rl2	–	pl2rl2v2-2-2-2	pl1-2v2-2-2
III	pl3d3rl2	pl1rl1	pl2rl2v2-2-2	pl2rl2v2-2-2
IV	pl3d3rl2	rl1	pl2d1rl2v2-2-2	pl4d3rl2v1-2-1-2-2

Male palp (Figs 8C–G, 9A–C). Tibia with VTA thumb-shaped, RTA broad, median with sharp, ventroapical point (vRTA), blunt retrodorsal projection (dRTA); cymbium oval with rounded apical extremity, without dorsal patch of chemosensitive setae, with small, sharp, conical retrobasal cymbial extension (CE) extending to tibial apex; subtegulum large, filling most of cymbial concavity, with transverse ridge (SL) that interacts with tegulum; tegulum oval with large, with rounded retrodistal protuberance and conical promedian lobe (TL) that locks with subtegulum; embolus (E) arises from retromargin of tegulum, short, simple, narrow; median apophysis (MA) strongly sclerotized elongate hook curved 270° prolaterad; conductor (C) hyaline, translucent, flattened, fan-shaped, widened at extremity; paraconductor (Pc) finger-like membranous, originating at base of MA and extending two-thirds length of E.

Female paratype (CASENT_9018308; CAS)
Measurements. Total length: 10.20. Carapace: length 5.00, width 3.60, height 1.80.

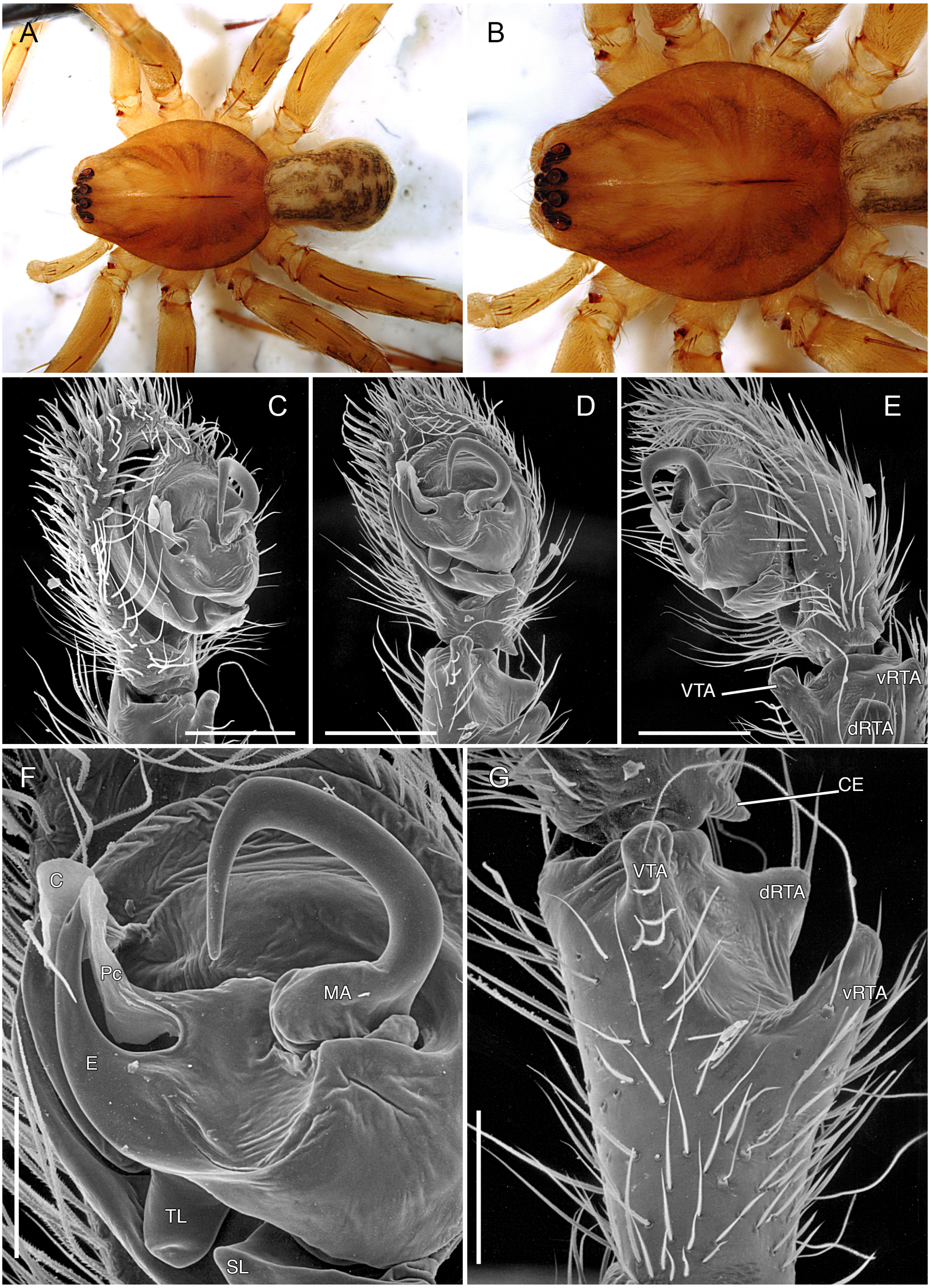
Colour. As in male except contrast between yellow-white background and dusky markings much bolder, especially annuli on posterior femora, tibiae and metatarsi.

Sternum. Oval with slightly sinuous sides; 2.20 wide, 2.40 long.

Chilum. 0.13 high, 0.35 wide.

Eyes. ALE 0.18; AME 0.13; PLE 0.18; PME 0.18; ALE–AME 0.08; AME–AME 0.15; PLE–PME 0.18; PME–PME 0.16; MOQ: AW 0.25, PW 0.38, L 0.38.

Fig. 8 (on next page). *Tabiboka milloti* gen. nov. et sp. nov. male holotype (CASENT_9016063; MNHN). **A**. Habitus, dorsal view. **B**. Carapace, dorsal view. **C**. SEM of right male palp (mirrored), prolateral view. **D**. Idem, ventral view. **E**. Idem, retrolateral view. **F**. Idem, detail of bulb, ventral view. **G**. Idem, detail of the RTA. Abbreviations: C = conductor; CE = cymbial retrobasal extension; dRTA = retrodorsal tibial apophysis**;** E = embolus; MA = median apophysis; Pc = paraconductor; dRTA = retrodorsal tibial apophysis; SL = subtegular locking lobe; TL = tegular locking lobe; vRTA = retroventral tibial apophysis; VTA = ventral tibial apophysis. Scale bars: A–B = no scales provided (note: carapace length = 4.6 mm); C–E = 0.5 mm; F–G = 0.1 mm. Stacked microphotographs by Hannah Wood; SEM images by Charles Griswold and Darrell Ubick.


A
B
C
D
E
VTA
vRTA
dRTA
F
C
Pc
MA
E
TL
SL
G
CE
VTA
dRTA
vRTA

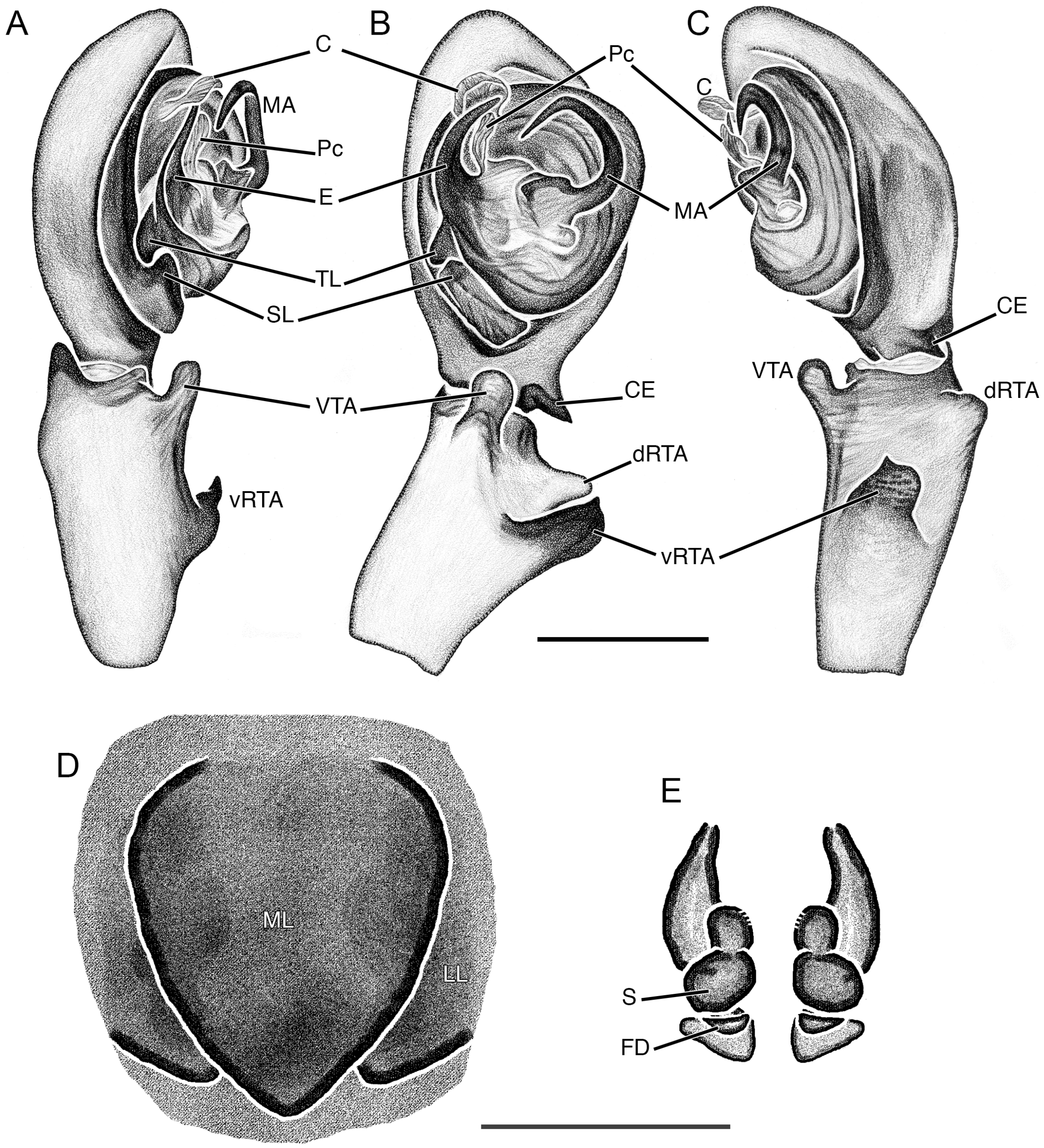


Fig. 9. *Tabiboka milloti* gen. nov. et sp. nov. genitalia drawings. **A–C** = male holotype (CASENT_9016063; MNHN). **D–E** = female paratype (CASENT_9018308; CAS). **A**. Left palp, prolateral view. **B**. Idem, ventral view. **C**. Idem, retrolateral view. **D**. Epigyne, ventral view. **E**. Endogyne, dorsal view. Abbreviations: C = conductor; CE = cymbial retrobasal extension; dRTA = retrodorsal tibial apophysis; E = embolus; FD = fertilisation duct; LL = lateral lobe; MA = median apophysis; ML = median lobe; Pc = paraconductor; S = spermatheca; SL = subtegular locking lobe; TL = tegular locking lobe; vRTA = retroventral tibial apophysis; VTA = ventral tibial apophysis. Scale bars = 0.25 mm. Illustrations A–C by Jenny Speckels; D–E by Charles Griswold.

Clypeus. 0.20 high, with five long setae.

Legs. Scopulae absent.

Leg measurements

	F	P	T	Mt	t	Total
I	3.50	1.70	3.00	2.50	1.40	12.10
II	3.20	1.70	2.50	2.30	1.50	11.20
III	3.20	1.30	2.20	2.70	1.40	10.80
IV	4.50	1.60	3.40	4.50	1.90	15.90

Spination

	F	P	T	Mt
I	pl1d1	–	v2-2-2-2	v2-2-2
II	pl1d1	–	v2-2-2-2	v2-2-2
III	pl1d3rl1	–	pl2d2rl2v2-2-2	pl4d2rl3v2-2-2
IV	pl1d3rl1	–	pl2d2rl2v2-2-2	pl2d5rl3v2-1-2-2

Genitalia. Epigyne (Fig. 9D) median lobe (ML) heart-shaped, sides rounded, broad anteriorly, anterior width greater than one-half total width. Endogyne (Fig. 9E) with each spermatheca narrow, longer than broad.

Variation

Male (n = 3)

Total length = 6.90–7.50, carapace length/width = 1.21–1.29, carapace height/width = 0.43–0.59, PER/carapace width = 0.23–0.24, PER/OAL = 2.38–2.44, PER/AER = 1.38–1.39, OAL/OQL = 1.13–1.23, OQP/OQA = 1.38–1.43, clypeus height/AME = 1.14–1.56, cheliceral length/clypeus height = 9.14–18.00, sternum length/width = 1.05–1.25, palpal coxa length/width = 2.00–2.80, femur I length/carapace width = 1.11–1.12, metatarsus I length/carapace width = 0.95–1.00, femur IV length/carapace width = 1.23–1.43, cymbium length/carapace width = 0.32–0.35, cymbium length/palpal patella length = 1.20–1.50, cymbium length/palpal tibia length = 1.09–1.26, cymbium length/palpal femur length = 0.63–0.75, palpal tibia length/palpal patella length 1.10–1.38. Males from Tsinjoarivo and Analamazaotra are marked like the holotype but the contrast between the yellow-white background and dusky markings on the cephalothorax, legs and abdomen is much greater.

Female

Variation unknown; only one female has been discovered.

Note on synonym

A specimen of this species (CASENT_9005657) was used as an exemplar in a previously published molecular phylogeny: it was listed as “*Zorodictyna* sp. CG45” by Wheeler *et al.* (2017).

Natural history

The species *Tabiboka milloti* gen. et sp. nov. is only known from rainforest.

Distribution

Tabiboka milloti gen. et sp. nov. is known only from mountains in east-central Madagascar (Fig. 26).

Tabiboka polotowae gen. et sp. nov.
urn:lsid:zoobank.org:act:5FF0F818-0EC8-428C-86F4-36FF94F62ED7
Figs 10–12, 26

Zorodictyna spp. 3 and 4 – Polotow *et al.* 2015.

Diagnosis

The males of *Tabiboka polotowae* gen. et sp. nov. may be distinguished by an elongate embolus (E) arising retrobasally near 200°, the paraconductor (Pc) visible between embolus and the conductor (C) base, the palpal tibia having blunt retromedian process (RTA) arising near basally and narrow, finger-like ventral apical process (VTA) (Figs 11A–C, 12A–F) (vs in *T. milleri* gen. et sp. nov., males have shorter and broader E and MA, a small VTA and greatly elongated RTA, Fig. 5A–C; and in *T. milloti* gen. et sp. nov., the MA is elongate, cruciform, and the VTA is thumb-like, Fig. 9A–C). Females of *T. polotowae* have epigyne median lobe (ML) rectangular, narrowest in middle or with sides straight (Figs 11D, 12G) (vs heart-shaped ML in *T. milleri*, Figs 4B, 5D, 7A and *T. milloti*, Fig. 9D).

Etymology

The species name is a matronym in honor of Dr Daniele Polotow, who studies the phylogenetics and taxonomy of spiders of the OC clade including Lycosoidea. She led the research that in 2015 led to the proposal and diagnosis of the Udubidae and the current phylogenetic framework for Lycosoidea interrelationships, and she collected many of the data used in this paper.

Type material

Holotype

MADAGASCAR – **Antananarivo Province** • ♂; NE outskirts of Antananarivo, Ambohimanga Village; 18°44′ S, 47°34′ E (coordinates approximate); 27 Jul. 1992; V. and B. Roth leg.; VBRoth002; [palp & endogyne drawn; SEM palp]; CASENT_9016117; CAS.

Paratypes

MADAGASCAR – **Antananarivo Province** • 1 ♀; same data as for holotype; CASENT_9016117; CAS • 1 ♀; same data as for preceding; 1 Nov. 1993; J. Coddington, N. Scharff, S. Larcher, C. Griswold, R. Andriamasimanana leg.; Berlese of fine leaf litter; CEG010; CASENT_9016116; CAS • 1 ♂; 10 km NE of Tana; 18°45′32″ S, 48°33′45″ E; 1300 m a.s.l.; 5 August 1992; V. Roth, leg.; [habitus photos of male]; Roth001; CASENT_9016118; CAS. – **Fianarantsoa Province** • 1 ♀; Parc National Andringitra, 34 km S of Ambalavao; 22°08′48.9″ S, 45°57′03.4″ E; 1580 m a.s.l.; 7 Jan. 2009; H. Wood leg.; sifting litter in the day; primary montane rainforest; [SEM stubs 221, 9, 10, 222, 4] [Voucher DP-2014b -“Zorodictynidae sp. 3”, D. Polotow Lycosoidea Total Evidence Phylogeny]; HW0813; CASENT_9029890; CAS • 1 ♀; same data as for preceding; [Voucher DP-2014a -“Zorodictynidae sp. 4”, D. Polotow Lycosoidea Total Evidence Phylogeny]; CASENT_9029889; CAS.

Other material examined

MADAGASCAR – **Antananarivo Province** • 1 ♀; Station Forestière Angavokely, 22 km E of Antananarivo; 18°56′ S, 47°45′ E; 1300 m a.s.l.; low canopy remnant forest, general collecting; 8 Sep. 2001; D. Ubick, D. Andriamalala, T. Andriambinintsoa, J.J. Rafanomezantsoa leg.; DU-01-2; CASENT_901371; CAS • 1 ♂, 1 ♀; same data as for preceding; CASENT_901317; CAS • 1 ♂; Ambohimanga; 18°44′ S, 47°34′ E; 1400 m a.s.l.; 2 Nov. 1993; C. Griswold, S. Larcher, N. Scharff leg.; night collecting; CEG009; CASENT_9016115; USNM • 1 ♂; 10 km NE of Tana; 18°45′32″ S, 48°33′45″ E; 1300 m a.s.l.; 5 Aug. 1992; V. Roth, leg.; [habitus photos of male]; Roth001; CASENT_9016118; CAS.

Description

Male holotype (CASENT_9016117; CAS)

Measurements. Total length: 8.10. Carapace: length 4.50, width 3.40, height 1.90.

Coloration (Fig. 10A, C). Carapace brownish yellow, darker along margin, with two faint, longitudinal dark bands along margin of pars cephalica; black on ocular area and surrounding all eyes; chelicerae

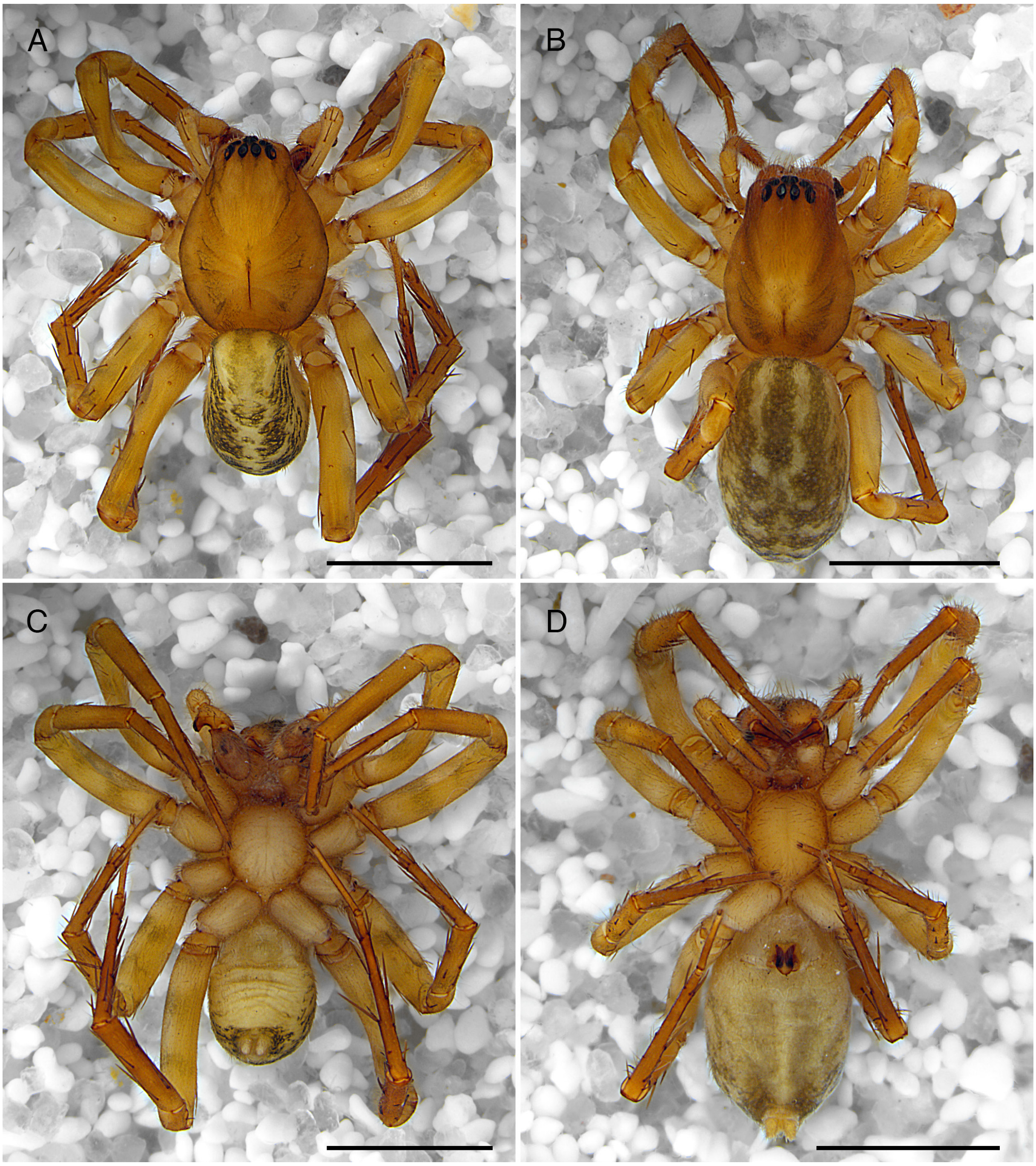


Fig. 10. *Tabiboka polotowae* gen. et sp. nov., male and female habitus; A, C = male paratype (CASENT_9016118; CAS); B, D = female paratype (CASENT_9016116; CAS). **A–B**. Dorsal view. **C–D**. Ventral view. Scale bars = 2.5 mm. Stacked microphotographs by Franklyn Cala Riquelme.

brownish yellow; sternum yellow, unmarked; legs brownish yellow, with subbasal and subapical dusky annuli on all femora, other segments unmarked; abdomen brownish yellow with darker cardiac mark and dorsolateral dark bands that break up into chevrons posteriorly, sides brownish yellow mottled with dark marks, venter yellow except darker around spinneret base.

Sternum (Fig. 10C). Oval with gently curved margins; 1.70 wide, 2.20 long.

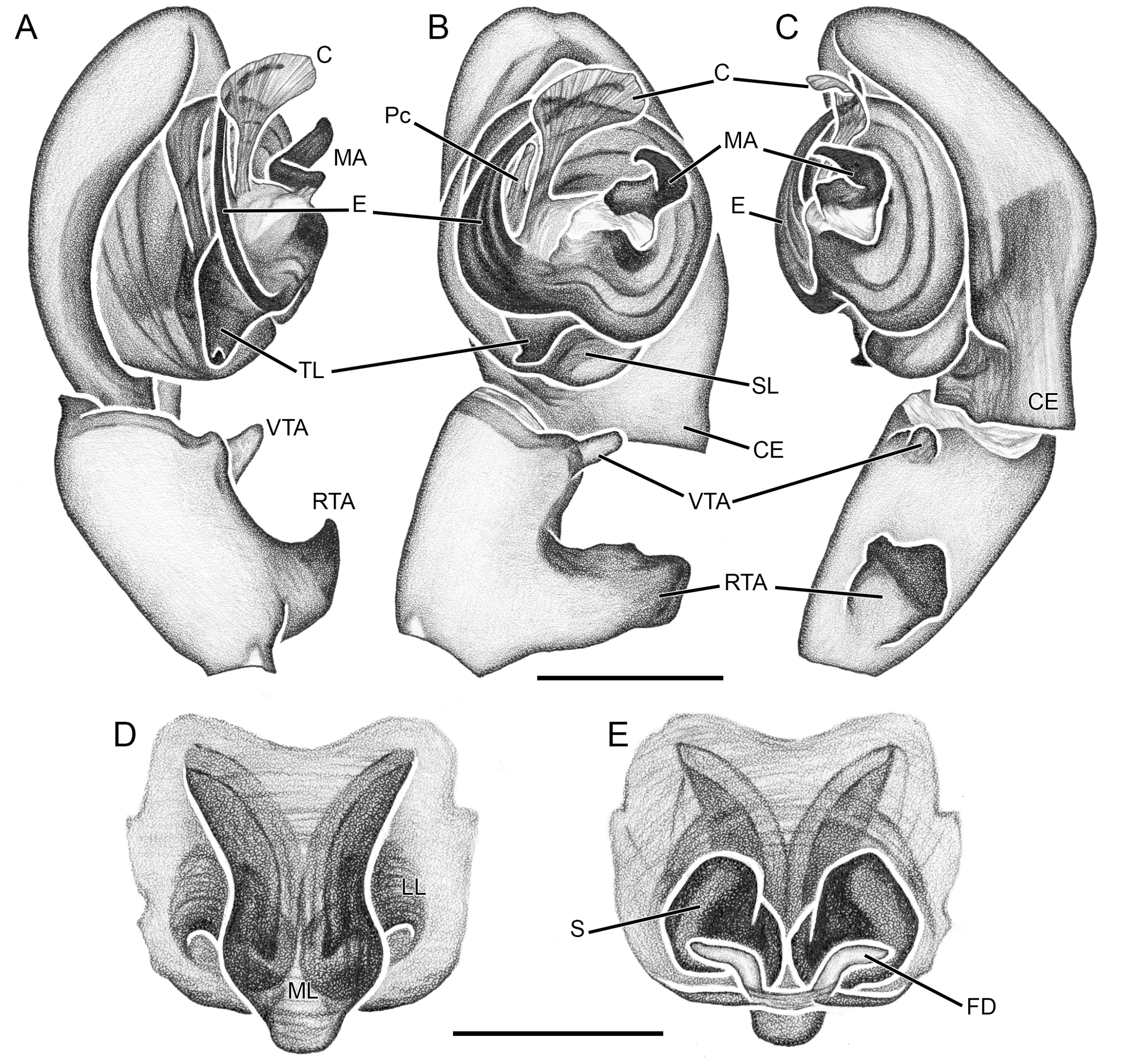


Fig. 11. *Tabiboka polotowae* gen. et sp. nov., genitalia drawings; A–C = male holotype (CASENT_9016117; CAS); D–E = female paratype (CASENT_9016117; CAS). **A**. Left palp, prolateral view. **B**. Idem, ventral view. **C**. Idem, retrolateral view. **D**. Epigyne, ventral view. **E**. Endogyne, dorsal view. Abbreviations: C = conductor; CE = cymbial retrobasal extension; E = embolus; FD = fertilisation duct; LL = lateral lobe; MA = median apophysis; ML = median lobe; Pc = paraconductor; RTA = retrolateral tibial apophysis; S = spermatheca; SL = subtegular locking lobe; TL = tegular locking lobe; VTA = ventral tibial apophysis. Scale bars = 0.25 mm. Illustrations by Jenny Speckels.

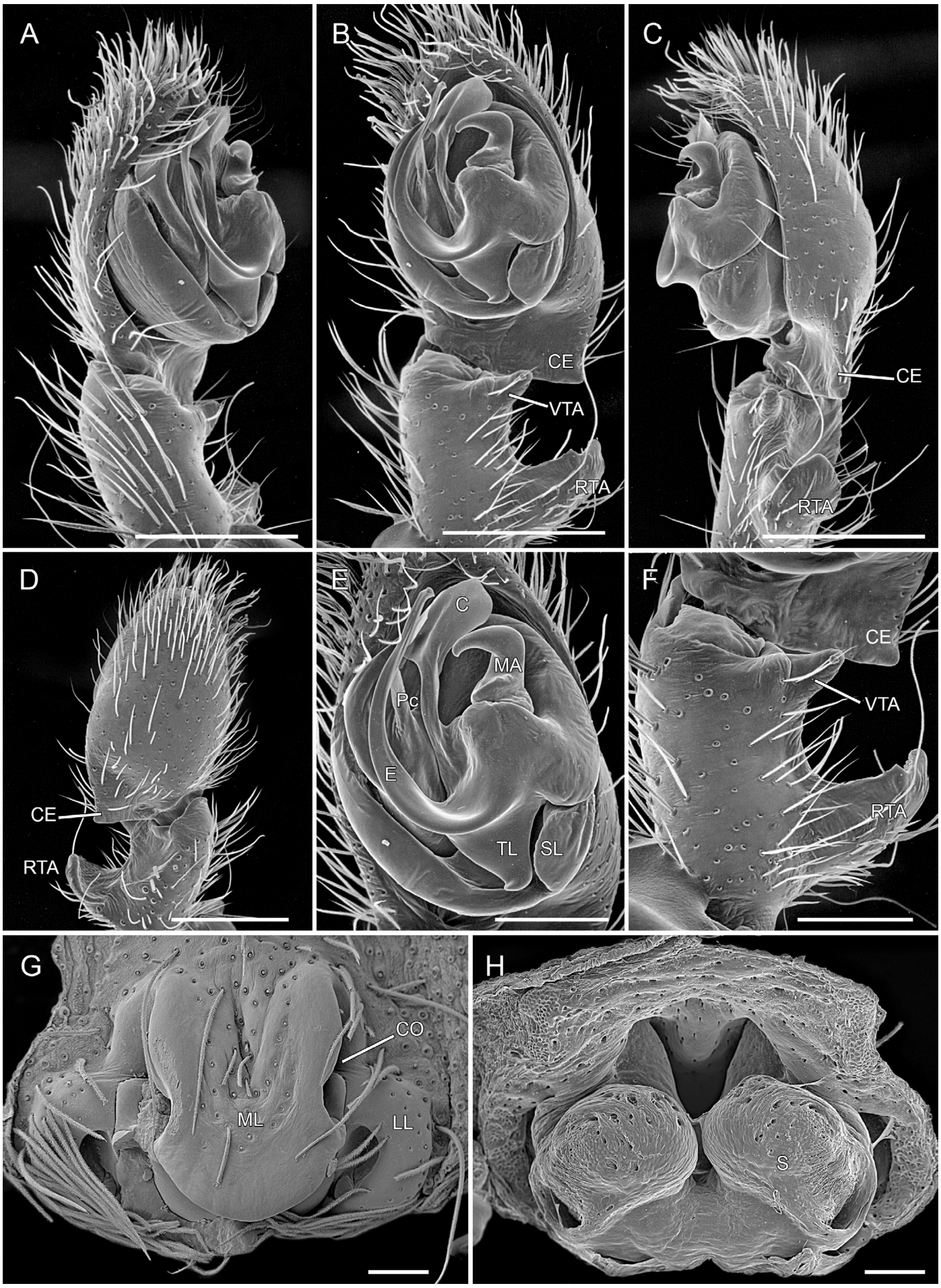


Fig. 12. *Tabiboka polotowae* gen. et sp. nov., SEM of male and female genitalia; A–F = male holotype (CASENT_9016117; CAS); G–H = female paratype (CASENT_9029889; CAS). **A**. Right palp (mirrored), prolateral, slightly ventral view. **B**. Idem, ventral view. **C**. Idem, retrolateral view. **D**. Idem, dorsal view. **E**. Bulb, ventral view. **F**. RTA, ventral view. **G**. Epigyne, ventral view. **H**. Endogyne, dorsal, slightly anterior view. Abbreviations: C = conductor; CE = cymbial retrobasal extension; CO = copulatory opening; E = embolus; LL = lateral lobe; MA = median apophysis; ML = median lobe; Pc = paraconductor; RTA = retrolateral tibial apophysis; S = spermatheca; SL = subtegular locking lobe; TL = tegular locking lobe; VTA = ventral tibial apophysis. Scale bars: A–D = 0.5 mm; E–F = 0.15 mm; G–H = 0.1 mm. SEM images A–F by Charles Griswold and Darrell Ubick, G–H by Daniele Polotow.

Chilum. 0.08 high, 0.28 wide.

Eyes. ALE 0.11; AME 0.09; PLE 0.13; PME 0.13; ALE–AME 0.05; AME–AME 0.20; PLE–PME 0.33; PME–PME 0.13; MOQ: AW 0.23, PW 0.33, L 0.28.

Clypeus. 0.18 high, with four long setae.

Legs. Trochanters shallowly notched. Unpaired claw smooth, well developed on all legs. Metatarsi lacking subbasal crack. Scopulae absent.

Leg measurements

	F	P	T	Mt	t	Total
I	3.05	1.50	3.20	2.80	1.80	12.35
II	3.20	1.50	2.50	2.30	1.60	11.10
III	3.00	1.30	2.10	2.60	1.50	10.50
IV	3.90	1.40	2.30	4.30	2.00	13.90

Spination

	F	P	T	Mt
I	pl1d3	–	pl2d1v2-2-2-2	pl2rl2v2-2-2
II	pl1d3rl1	–	pl2v2-2-2-2	pl3d1rl2v2-2-2
III	pl2d2rl3	pl1rl1	pl2d2rl2v2-2-2	pl4rl3v2-2-2
IV	pl2d3rl1	rl1	pl2d2rl2v2-2-2	pl3rl4v1-1-2-2-2

Male palp (Figs 11A–C, 12A–F). Tibia with narrow finger-shaped VTA at retroapical margin and broad, median RTA arising near tibia base; cymbium oval, without dorsal patch of chemosensitive setae, with broad, sharp, conical retrobasal cymbial extension (CE) that extends to tibial apex; subtegulum large, filling most of cymbial concavity, with basal ridge (SL) at 180° that interacts with tegulum; tegulum oval with broad, basal notch, beneath this, conical lobe (TL) at 180° that locks with subtegulum; embolus (E) arises from retromargin of tegulum, simple, narrow, elongate, extending past apex of tegulum; median apophysis (MA) as sclerotized hook arising from soft base; conductor (C) hyaline, translucent, with narrow base arising near E base and greatly widened at extremity; paraconductor (Pc) as finger-like membranous structure originating between bases of E and C and extending less than half length of E.

Female paratype (CASENT_9016116; CAS)

Measurements. Total length: 11.50. Carapace: length 5.20, width 3.60, height 2.00.

Colour (Fig. 10B, D). As in male except ocular area not all black and legs only faintly marked.

Sternum (Fig. 10D). Oval with slightly sinuous margins; 2.10 wide, 2.40 long.

Chilum. 0.09 high, 0.33 wide.

Eyes. ALE 0.14; AME 0.08; PLE 0.15; PME 0.13; ALE–AME 0.06; AME–AME 0.25; PLE–PME 0.20; PME–PME 0.09; MOQ: AW 0.28, PW 0.38, L 0.28.

Clypeus. 0.10 high, with four long setae.

Legs. Very weak scopula beneath tarsus I, scopulae otherwise absent.

Leg measurements

	F	P	T	Mt	t	Total
I	3.30	1.60	2.70	2.20	1.60	11.40
II	3.05	1.70	2.30	2.25	1.40	10.70
III	2.80	1.30	2.00	2.30	1.50	9.90
IV	3.90	1.60	3.00	4.00	2.00	14.50

Spination

	F	P	T	Mt
I	pl1d1	–	v2-2-2-2	v2-2-2
II	pl1d1	–	v2-2-2	v2-2-2
III	pl2d3rl1	–	pl2d1rl2v2-2-2	pl5rl3v2-2-3
IV	pl1d2rl1	–	pl1d2v1-2-2	pl4d2rl1v1-1-2-2-3

Genitalia. Epigyne (Figs 11D, 12G) median lobe (ML) rectangular, elongate, narrowest in middle with apex of ML extending beyond epigastric furrow; lateral lobe (LL) convex, with transverse curved concavity posteriorly, narrow, only 0.25 maximum width of ML, copulatory openings (CO) hidden beneath anterolateral margins of ML. Endogyne (Figs 11E, 12H): spermathecae (S) simple, oval, length 1.06 times width, with scattered pores anteriorly on spermathecal head.

Variation

Male (n = 2)

Total length = 8.10–8.50, carapace length/width = 1.32–1.34, carapace height/width = 0.40–0.56, PER/OAL = 2.21–2.22, PER/AER = 1.33–1.38, OAL/OQL = 1.22–1.23, OQP/OQA = 1.44–2.00, clypeus height/AME = 1.00–2.33, cheliceral length/clypeus height = 8.57–17.00, sternum length/width = 1.05–1.29, palpal coxa length/width = 2.08–2.17, femur I length/carapace width = 0.90–1.06, metatarsus I length/carapace width = 0.82–0.86, cymbium length/carapace width = 0.37–0.40, cymbium length/palpal patella length = 2.15–2.27, cymbium length/palpal tibia length = 1.75–2.27, cymbium length/palpal femur length = 0.78–1.00, palpal tibia length/palpal patella length = 1.00–1.23.

Female (n = 3)

Total length = 8.40–17.00, carapace length/width = 1.31–1.46, carapace height/width = 0.44–0.75, PER/carapace width = 0.25–0.27, PER/OAL = 2.40–2.88, PER/AER = 1.31–1.45, OAL/OQL = 1.20–1.36, OQP/OQA = 1.36–1.56, clypeus height/AME = 1.33–2.33, cheliceral length/clypeus height = 10.67–20.00, sternum length/width = 1.14–1.22, palpal coxa length/width = 1.57–2.26, femur I length/carapace width = 0.89–1.32, metatarsus I length/carapace width = 0.61–0.64, femur IV length/carapace width = 1.00–1.18, palpal tarsus length/carapace width = 0.33–0.38, palpal tarsus length/palpal tibia length = 1.91–2.15, palpal tarsus length/palpal tibia length = 1.33–1.75, palpal tarsus length/palpal femur length = 0.88–0.89, palpal tibia length/palpal patella length = 1.09–1.23. Epigyne with median lobe length 1.29–1.38 times width; median lobe maximum width 1.34–2.10 times minimum width; median lobe width 2.00–5.00 times lateral lobe width; median lobe extends to (Fig. 12G) or beyond (Fig. 11D) epigastric furrow. Spermatheca (each) length 1.06 times width.

Note on synonyms

Specimens of this species have been used as exemplars in a previously published molecular phylogeny: they were listed by Polotow *et al.* (2015) as "*Zorodictyna* sp. 3" (CASENT_9029890; CAS) and "*Zorodictyna* sp. 4" (CASENT_9029889; CAS).

Natural history

The species *Tabiboka polotowae* gen. et sp. nov. is recorded from both highly disturbed and intact forest habitats. Many specimens have been collected while concealed in leaf litter.

Distribution

Tabiboka polotowae gen. et sp. nov. occurs in the eastern uplands of Madagascar from the south to the center (Fig. 26).

Genus ***Zorascar*** gen. nov.

urn:lsid:zoobank.org:act:F5981AD2-4EC8-412D-B90A-0F6A51FEF784

Figs 13–21, 26

Type species

Zorascar pasunepipe gen. et sp. nov.

Diagnosis

Zorascar gen. nov. are ecribellate udubids distinguished from all Madagascar udubids (except *Tabiboka* gen. nov.) by having the posterior spinnerets (PMS and PLS) reduced in size, with the PLS less than one half the size of ALS; the male palp (Figs 14A–C; 15A–C, 16A–B) with an RTA only, lacking the VTA, the cymbial retrobasal extension (CE) elongate, extending most of length of tibia, without retrolateral paracymbial process; the female epigyne with short median lobe (ML), concave medially and not extending to posterior margin of epigyne, with copulatory openings (CO) exposed (Fig. 16C, E). *Zorascar* is further distinguished from *Uduba* Simon, 1880 males by lacking a threadlike embolus and a knob-like process between palpal patella and tibia and from *Uduba* females by having compact spermathecae rather than multiple loops. It is distinguished from *Zorodictyna* by lacking an entire cribellum or vestige and in lacking extensive scopulae beneath leg metatarsi. *Zorascar* may be distinguished from *Tabiboka* gen. nov. by having the male palp with cymbial retrobasal extension (CE) elongate (*Tabiboka* shorter), palpal lacking a VTA (Figs 14A–B, 15A–B, 16A–B) (*Tabiboka* with a VTA); female epigyne median lobe (ML) short, concave medially, not extending to posterior margin, copulatory openings (CO) covered (Figs 16C, E, 18A).

Etymology

The genus name is derived from the name '*Zorodictyna*', in combination with the ending of Madagascar. The gender is masculine.

Description

Body. Medium size spiders (males: 7.81–8.60; females: 8.50–10.10) with smooth teguments of carapace (Figs 13A–D, 17A, C), sternum and legs. Carapace longer than wide (L/W: males; 1.21–1.34; females: 1.33–1.34) with sparse cover of dark setae; widest at level of coxae II, narrowed to 0.56 times maximum width in male and 0.70 times maximum width in female (cephalic width measured on posterior tangent of PME); profile convex, highest point located at well-developed fovea.

Coloration (Figs 13A–E, 17A–C). Sclerites brownish yellow with darker longitudinal pattern on carapace and chelicerae; legs ringed; abdomen brownish yellow with faint complex pattern.

Eyes (Figs 13C–D, 17A). In two straight rows: ALE larger than AME, PLE and PME similar to ALE; tapetum of secondary eyes canoe shaped. Clypeus straight, narrow, with long setae.

PROSOMA. Chilum double, about twice as wide as high, lateral margin faintly delimited. Chelicerae (Figs 13A–E, 17A–B): paturon conical with some long setae in center and two faint longitudinal stripes; three teeth on both margins; fangs smooth. Labium (Figs 13E, 17B) roughly rectangular. Endites (Figs 13E, 17B, 20D) roughly rectangular, with retrolateral margins sinuous, distal part slightly wider than proximal part, with distal serrula present, as simple row (Fig. 20D). Sternum (Figs 13E, 17B) oval, slightly longer than wide, with slightly sinuous margins, and with tiny triangular extensions or precoxal sclerites, not extending between coxae IV.

LEGS (Figs 13A–B, E, 17A–C, 20E–F). Slender. Formula 4123 or 4132. With three tarsal claws, unpaired claw smooth, rudimentary on legs III and IV, superior claws with six to eight teeth (Figs 21A–B). Without claw tufts, tenent setae or scopulae. Numerous spines, pairs of ventral spines on metatarsus overlapping. Trichobothria on tarsi in three rows, starting close to tip, length variable but not increasing (Figs 13F, 20E–F); proximal plate of bothria with six ridges (Figs 21D–E). Tarsal organ with circular opening provided with two to three anterior slits, in distal half of tarsus (Figs 20E, 21C–D).

ABDOMEN (Figs 13A–B, E, 17A–C). Oval, without scuta and cribellum. Colulus: as hairy field. Spinnerets (Figs 20A–C): ALS large, conical, biarticulate, in juvenile provided with two major ampullate and four piriform gland spigots (Fig. 20A); PLS smaller, with three spigots (Fig. 20B); PMS reduced, with three spigots (Fig. 20C). Adult spinnerets much as in *Tabiboka* gen. nov. ALS and PLS, conical, biarticulate; PMS one-segmented; ALS large, PMS and PLS small. Females with two ALS major ampullate gland spigots and field of piriform gland spigots and tartipores; PMS with at least one anterior minor ampullate gland spigot and one to few posterior cylindrical gland spigots and aciniform gland spigots; PLS with one to few cylindrical gland spigots; males lack cylindrical gland spigots and have second major ampullate gland spigot reduced to nubbin.

MALE PALP (Figs 14–15, 16A–B). Tibia with short RTA inserted medially and sharp triangular prolateral process (Figs 14C, 15C), without VTA at retroapical margin; cymbium oval with rounded distal extremity, without dorsal patch of short setae, with large pipe shaped posterior extension (CE); bulbus provided with very large retrobasal subtegulum lobe (SL), visible over one third of bulbus, and tegulum rounded with well developed prolateral conical protrusion (corresponding locking lobe, TL) (Figs 14E–F, 15B–C, 16A); embolus (E) with large base inserted in center of tegulum, short, conical and folded (Figs 14D–F, 15E–F); median apophysis (MA) situated at base of E, short, sclerotized with membranous base; conductor (C) relatively small, transverse, hyaline fan-shaped, prolaterally extending from narrow base to wide flattened tip (Figs 14D, F, 15D–F); paraconductor (Pc) as narrow membranous extension inserted between tegulum and base of MA, running backward to MA and ending with fattened fan-shaped tip accompanying E (Figs 14D, 15D–E, 16A–B).

GENITALIA. Epigyne (Figs 16C, E, 18A, 19A–B) with median lobe (ML) as single plate with central roughly triangular depression, delimited by margins forming narrow, elongate arch, lateral lobe (LL) basally with two short but stout, conical and blunt projections (LP). Endogyne (Figs 16D, 18B–D, 19C–F) with copulatory ducts (CD) very short, twisted; spermathecae (S) with narrow base and broad roughly reniform dorsal part; no evidence of large Bennett's Gland pore; fertilization ducts (FD) short, median.

Species included

Zorascar pasunepipe gen. et sp. nov. (type species; ♂♀); *Zorascar pasunepomme* gen. et sp. nov. (♀).

Affinities

From the molecular analyses (Fig. 2), *Zorascar* nov. gen. appears closely related to species in the Udubidae that have been identified as *Tabiboka* gen. nov.

Distribution

Zorascar gen. nov. is known only from highland forest in northwestern Madagascar (Fig. 26).

Zorascar pasunepipe gen. et sp. nov.

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Figs 13–15, 16A–D, 26

Diagnosis

The male of *Zorascar pasunepipe* gen. et sp. nov. is easily recognized by the presence of an enormous and tortuous cymbial retrobasal extension (CE), extending most of the tibial length (Figs 14A–C, 15A–B, 16A–B). The female is provided with an epigyne (Fig. 16C) with the median lobe (ML) that is broad and shallowly concave medially, copulatory openings (CO) exposed anteromedially (vs the female epigyne of *Z. pasunepomme* gen. et sp. nov. has a ML that is narrow and deeply concave medially, and with CO exposed laterad of the ML, Fig. 16E).

Etymology

The species name, a noun in apposition, refers to the famous painting of René Magritte depicting a pipe, named 'Ceci n'est pas une pipe', to which the cymbial extension is reminiscent, at least according the artist who made the drawings of *Zorascar* gen. nov. for the present paper.

Type material

Holotype

MADAGASCAR – **Antsiranana Province** • ♂; Bamevika, Andriakanala Forest; 14°18′58.932″ S, 48°43′22.886″ E; 1586 m a.s.l.; 6–11 Feb. 2019; M. Jocque leg.; hand collected around camp; DNA RJ5; BINCO_MAD_19_0079_2; BE_RMCA_ARA.Ara.247343; RMCA.

Paratypes

MADAGASCAR – **Antsiranana Province** • 1 juv.; same data as for holotype; DNA RJ1; BINCO_MAD_19_0079_2; BE_RMCA_ARA.Ara.247344; RMCA • 1 ♂, 1 ♀; Réserve Spéciale Manongarivo, 10.8 km 229° SW of Antanambao; 13°58′ S, 48°26′ E; 400 m a.s.l.; 8 Nov. 1998; B.L. Fisher leg.; rainforest; EC19 sifted litter; [SEM stub 30:4]; CASENT_9016138; CAS.

Other material examined

MADAGASCAR – **Antsiranana Province** • 1 ♂; Réserve Spéciale Manongarivo, 10.8 km 229° SW of Antanambao, 13°58′ S, 48°26′ E; 400 m a.s.l.; 8 Nov. 1998; B.L. Fisher leg.; rainforest; EC19 sifted litter; [male palp drawn; male stacked images]; CASENT_9016135; CAS • 1 ♂; same data as for preceding; CASENT_9016136; CAS • 1 ♂; same data as for preceding; CASENT_9016137; CAS • 1 ♀; Réserve Spéciale Manongarivo, 14.5 km 220° SW of Antanambao; 13°60′ S, 48°26′ E; 1175 m a.s.l.; 20 Oct. 1998; B.L. Fisher leg.; rainforest; EB09 sifted litter; BLF1938; CASENT_9016139; CAS • 1 ♀; same data as for preceding; CASENT_9016141; CAS.

Description

Male holotype (BE_RMCA_ARA.Ara.247343; RMCA)

Measurements. Total length: 7.81. Carapace: length 3.91, width 2.91, height 1.85.

Coloration (Figs 13A, C, E). Carapace brownish yellow, with two faint, longitudinal dark bands along margin and between PME and fovea; chelicerae brownish with two faint longitudinal darker stripes; sternum brownish yellow, with faint radiating stripes; legs brownish yellow with three faint darker rings

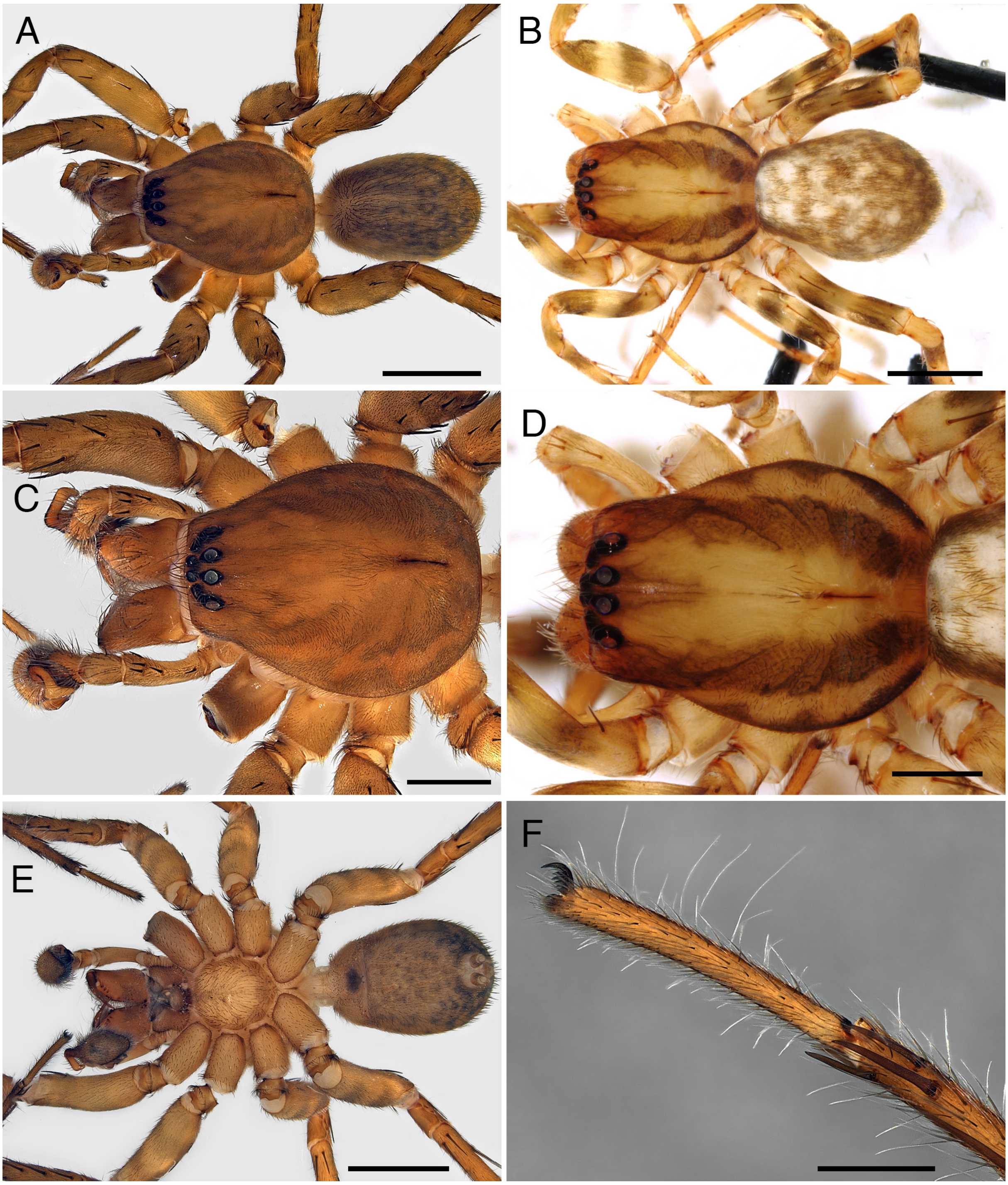

Fig. 13. *Zorascar pasunepipe* gen. et sp. nov.; A, C, E–F = holotype male (BE_RMCA_ARA.Ara.247343; RMCA); B, D = paratype female (CASENT_9016138; CAS). **A–B**. Habitus, dorsal view. **C–D**. Prosoma, dorsal view. **E**. Habitus, ventral view. **F**. Tarsus of leg I, retrolateral view. Scale bars: A–B, E = 2 mm; C–D = 1 mm; F = 0.5 mm. Stacked microphotographs A, C, E–F by Arnaud Henrard and Rudy Jocqué; B, D by Hannah Wood.

on femora and two on tibias, distally and proximally; abdomen brownish yellow with ill-defined pattern on dorsum and sides; spinnerets pale yellow.

Sternum (Fig. 13E) oval with slightly sinuous margins; 1.49 wide, 1.70 long.

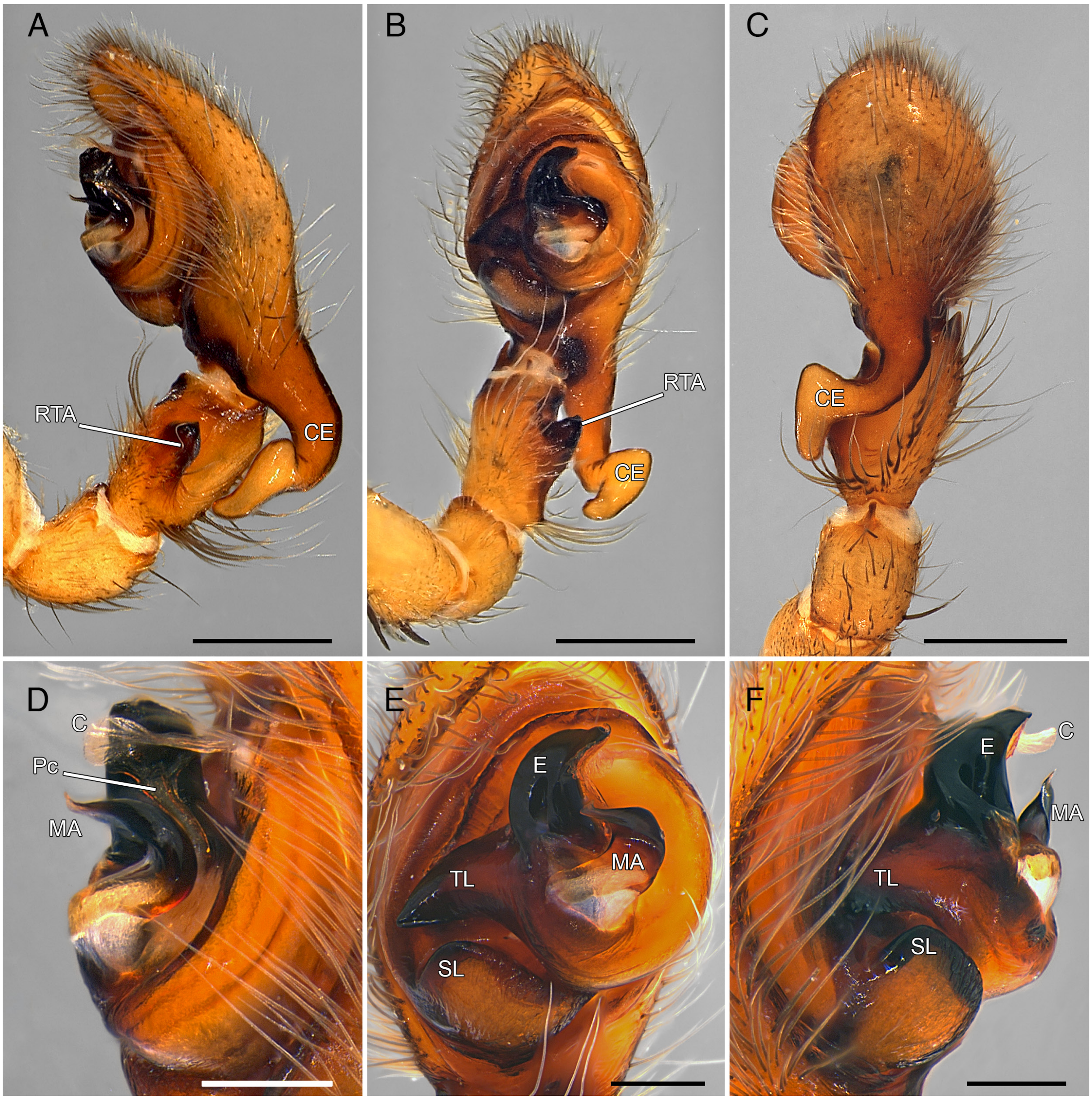

Fig. 14. *Zorascar pasunepipe* gen. et sp. nov., holotype male (BE_RMCA_ARA.Ara.247343; RMCA). **A**. Male right palp (mirrored), retrolateral view. **B**. Idem, ventral view. **C**. Idem, dorsal view. **D**. Idem, bulbus, retrolateral view. **E**. Idem, ventral view. **F**. Idem, prolateral view. Abbreviations: C = conductor; CE = cymbial retrobasal extension; E = embolus; MA = median apophysis; Pc = paraconductor; RTA = retrolateral tibial apophysis; SL = subtegular locking lobe; TL = tegular locking lobe. Scale bars: A–C = 0.5mm; D–F = 0.2 mm. Stacked microphotographs by Arnaud Henrard and Rudy Jocqué.

Chilum. 0.12 high, 0.20 wide.

Eyes. ALE 0.18; AME 0.15; PLE 0.18; PME 0.16; ALE–AME 0.05; AME–AME 0.08; PLE–PME 0.18; PME–PME 0.10; MOQ: AW 0.33, PW 0.44, L 0.44.

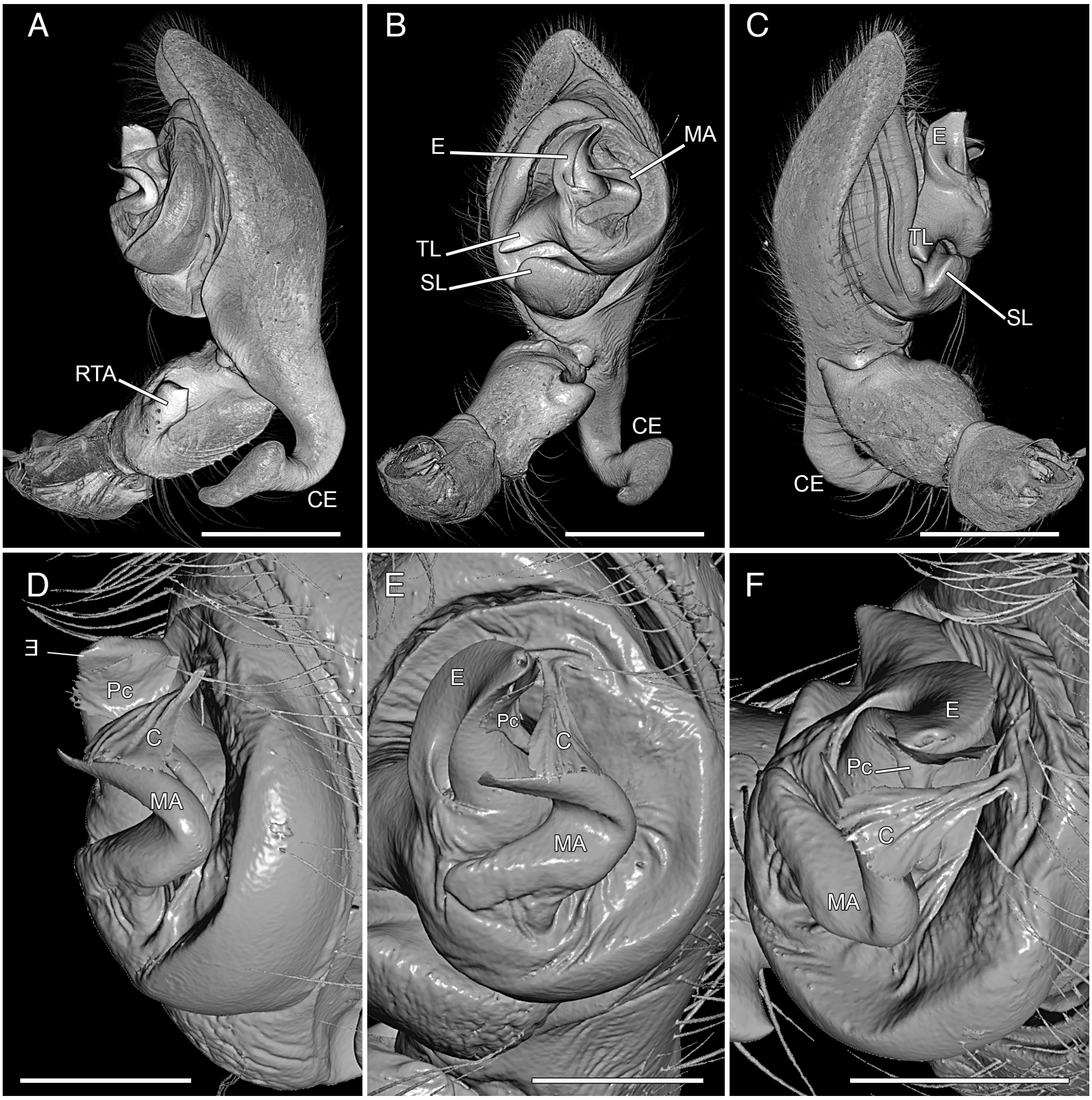

Fig. 15. *Zorascar pasunepipe* gen. et sp. nov., holotype (BE_RMCA_ARA.Ara.247343; RMCA), micro-CT scans of right male palp (mirrored). **A**. Retrolateral view. **B**. Ventral view. **C**. Prolateral view. **D**. Bulbus, retrolateral view. **E**. Bulbus, ventral view. **F**. Bulbus, apical view. Abbreviations: C = conductor; CE = cymbial retrobasal extension; E = embolus; MA = median apophysis; Pc = paraconductor; RTA = retrolateral tibial apophysis; SL = subtegular locking lobe; TL = tegular locking lobe. Scale bars: A–C = 0.5 mm; D–F = 0.2 mm. 3D micro-CT scans by Arnaud Henrard.

Clypeus. With 14 long setae.

Legs. Trochanters shallowly notched. Unpaired claws smooth, rudimentary on legs III and IV.

Leg measurements

	F	P	T	Mt	t	Total
I	3.36	1.33	3.15	2.73	1.05	11.62
II	3.15	1.26	2.10	2.73	1.33	10.57
III	2.45	0.84	1.96	2.73	1.05	9.03
IV	3.50	1.26	3.08	4.27	1.40	13.51

Spination

	F	P	T	Mt
I	pl2d3rl3	pl1	pl2d2rl2v2-2-2-2	pl2rl2v2-2
II	pl3d3rl4	pl1	pl2d3rl3v2-2-2-2	pl2rl2v2-2-1
III	pl3d3rl4	pl1rl1	pl2d2rl2v2-2-2	pl3d1rl3v2-2-2
IV	pl4d3rl1	pl1rl1	pl2d2rl2v2-2-2	disp14

Male palp (Figs 14–15, 16A–B). RTA short, emerging in center of tibia, with cylindrical base and sharp triangular apex; tibia with dorso-retrolateral excavation bordered by median row of long setae and dorsal margin of RTA, accommodating very large, pipe-shaped retrobasal cymbial extension (CE); cymbium oval with rounded apical extremity, without dorsal patch of chemosensitive setaeor retrobasal paracymbial process; subtegulum large, filling posterior third of cymbial concavity, with basal ridge (SL) interacting with the tegulum; tegulum rounded with massive, pointed, prolateral protuberance (TL); embolus (E) inserted on center of tegulum, short, stout at base, with medial groove, lamellar apically and curved retrolaterad; median apophysis (MA) strongly sclerotized, short, hooked, curved prolaterad; conductor (C) translucent, flattened, fan shaped, narrow at base and strongly widened at extremity; paraconductor (Pc) pedicel-like membranous extension originating at base of MA, running backward along MA and ending with flattened fan-shaped tip embracing E.

Female (CASENT_9016138; CAS)
Measurements. Total length: 8.50. Carapace: length 4.80, width 3.60, height 1.70.

Colour (Figs 13B, D). Carapace brownish yellow, dark along margin and with two contrasting dark bands along margin of pars cephalica, short longitudinal line behind each PME and longer faint median band between PME and fovea; chelicerae brownish-yellow, anteriorly with two thin longitudinal darker stripes; sternum yellowish white with faint median dusky oval mark; legs brownish yellow with three darker rings basally, medially and apically on femur and two basally and apically on tibia; abdomen yellow-white with spotted pattern on dorsum and sides, venter with two broken dusky longitudinal bands and dark surrounding spinnerets, spinnerets pale yellow.

Sternum. Oval with slightly sinuous sides; 2.10 wide, 2.20 long.

Chilum. 0.15 high, 0.20 wide.

Eyes. ALE 0.13; AME 0.09; PLE 0.16; PME 0.15; ALE–AME 0.08; AME–AME 0.25; PLE–PME 0.18; PME–PME 0.10; MOQ: AW 0.26, PW 0.43, L 0.35.

Clypeus. With eight long setae.

Leg measurements

	F	P	T	Mt	t	Total
I	3.40	1.60	3.30	2.60	1.80	12.70
II	3.10	1.40	2.60	2.50	1.60	11.20
III	3.00	1.30	2.10	2.70	1.60	10.70
IV	4.00	1.40	3.60	2.90	1.60	13.50

Spination

	F	P	T	Mt
I	pl1d12	–	v2-2-2-2	v2-2-2
II	d1	–	v2-2-2-2	v2-2-2
III	pl1d2rl1	–	pl2d2rl2v2-2-2	pl4rl4v2-2-2
IV	pl1d2	–	pl2d2rl2v2-2-2	pl4rl4v2-1-2-2

Genitalia. Epigyne (Fig. 16C) with median lobe (ML) broad and shallowly concave medially, copulatory openings (CO) exposed anteromedially; lateral lobes (LL) rounded and becoming narrowed to a blunt point medially over median sector (MS); lateral processes (LP) small, blunt. Endogyne (Fig. 16D) with narrow, curved copulatory ducts (CD), these hidden beneath the spermathecal heads (S); fertilization ducts (FD) posterior.

Variation

Male (n = 5)

Total length = 7.81–8.60, carapace length/width = 1.21–1.34, carapace height/width = 0.46–0.56, PER/carapace width = 0.23–0.24, PER/OAL = 2.28–2.44, PER/AER = 1.40–1.44, OAL/OQL = 1.14–1.25, OQP/OQA = 1.00–1.52, sternum length/width = 1.07–1.16, palpal coxa length/width = 2.00–2.50, femur I length/carapace width = 1.05–1.13, metatarsus I length/carapace width = 0.87–1.12, femur IV length/carapace width = 1.17–1.24, cymbium length/carapace width = 0.39–0.46, cymbium length/palpal patella length = 2.00–2.57, cymbium length/palpal tibia length = 1.60–2.29, cymbium length/palpal femur length = 0.84–1.00, palpal tibia length/palpal patella length 1.00–1.43. Male palp of the holotype from Andriakanala Forest and of specimens from Manongarivo. i.e.; CASENT_9016135–138 and CASENT_9016141 are very similar but differ in a few characteristics. The the holotype has the RTA more narrowly pointed, the cymbial retrobasal extension longer and more twisted, the tegular prolateral locking process more narrowly triangular and the apex of the MA sharper than those features in males from Manongarivo.

Female (n = 2)

Total length = 8.50–10.10, carapace length/width = 1.33–1.34, carapace height/width = 0.47–0.58, PER/AER = 1.37–1.39, OQP/OQA = 1.48–1.62, sternum length/width = 1.05–1.12, palpal coxa length/width = 2.50–2.55, femur I length/carapace width = 0.94–0.97, metatarsus I length/carapace width = 0.72–0.76, palpal tarsus length/carapace width = 0.34–0.36, palpal tarsus length/palpal tibia length = 1.44–2.17, palpal tarsus length/palpal tibia length = 1.30–1.44, palpal tibia length/palpal patella length = 1.11–1.50. Epigyne with median lobe length 1.80–3.33 times width; distance from atrium base to epigastric fold 0.19–0.26 times epigyne length.

Natural history

This species has been collected in forest from 400 m to 1600 m a.s.l. The function of the remarkable retrobasal cymbial extension on the male palp is unknown.

Distribution

Zorascar pasunepipe gen. et sp. nov. is known only from Antsiranana Province in northwestern Madagascar (Fig. 26).

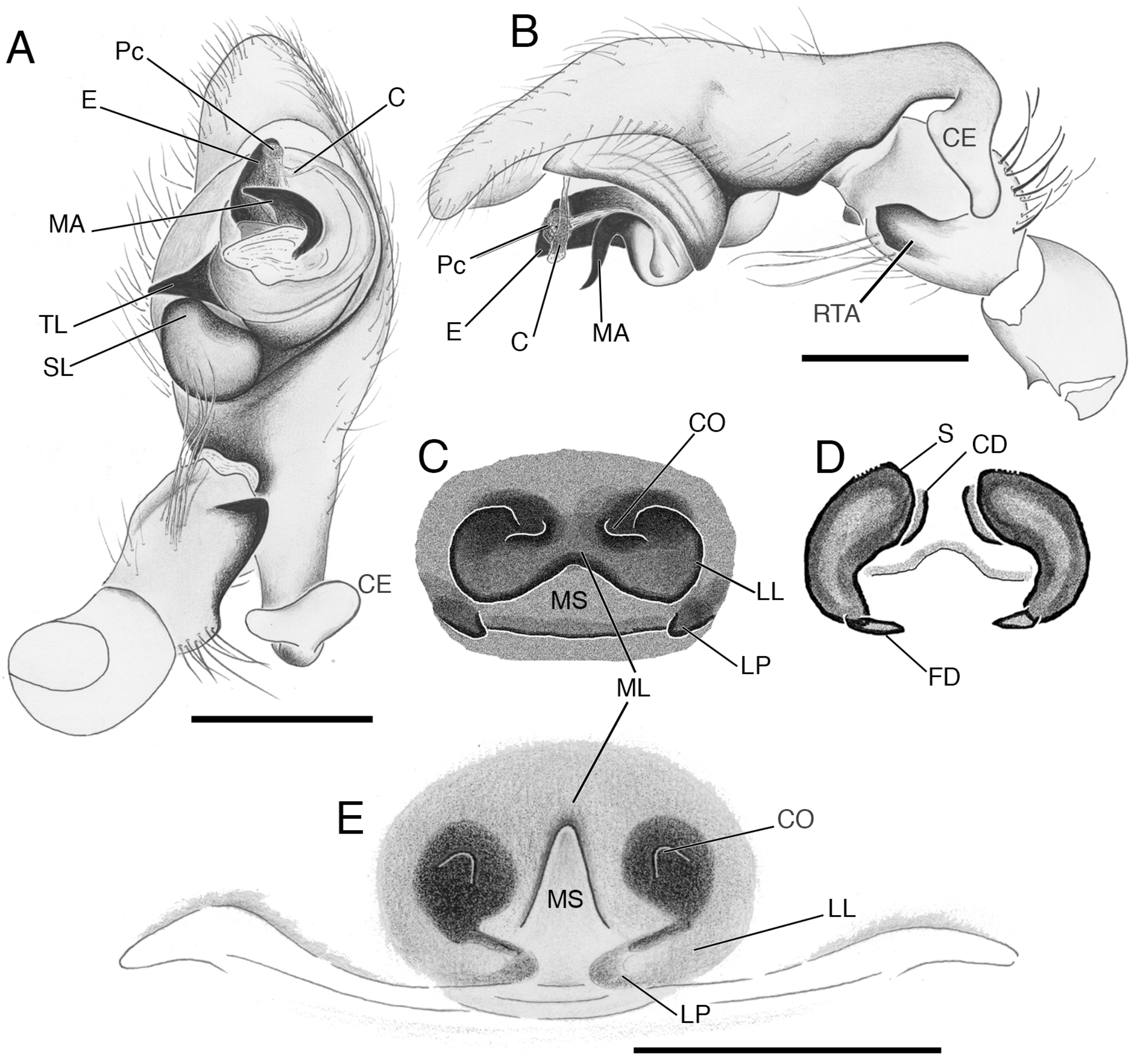

Fig. 16. Drawings of genitalia; A–B **=** *Zorascar pasunepipe* gen. et sp. nov., holotype male (BE_RMCA_ARA.Ara.247343; RMCA); C–D = *Z. pasunepipe,* paratype female (CASENT_9016138; CAS); E = *Zorascar pasunepomme* gen. et sp. nov., holotype female (BE_RMCA_ARA.Ara.247346; RMCA). **A**. Male right palp (mirrored), ventral view. **B**. Idem, retrolateral view. **C, E**. Epigyne, ventral view. **D**. Endogyne, dorsal view. Abbreviations: C = conductor; CD = copulatory duct; CE = cymbial retrobasal extension; CO = copulatory opening; E = embolus; FD = fertilisation duct; LL = lateral lobe; LP = lateral process; MA = median apophysis; ML = median lobe; MS = median sector; Pc = paraconductor; RTA = retrolateral tibial apophysis; S = spermatheca; SL = subtegular locking lobe; TL = tegular locking lobe. Scale bars: A–B = 2 mm; C–E = 0.5 mm. Illustrations A–B, E by Alain Reygel; C–D by Charles Griswold.

Zorascar pasunepomme gen. et sp. nov.
urn:lsid:zoobank.org:act:CC2504B1-3B59-4DE9-9C27-0457AAE53102
Figs 16E, 17–21, 26

Diagnosis

The female of *Zorascar pasunepomme* gen. et sp. nov. is characterized by the epigyne with a median lobe (ML) that is narrow and deeply concave medially and copulatory openings (CO) exposed laterad of median lobe (Figs 16E, 18A, 19A).

Etymology

The species name, a noun in apposition, refers to the famous painting of René Magritte depicting an apple, named 'Ceci n'est pas une pomme', to which the genitalia appear to be reminiscent.

Type material

Holotype

MADAGASCAR – **Antsiranana Province** • ♀; Bamevika; 14°18′57.312″ S, 48°43′26.180″ E; 1581 m a.s.l.; 2 May 2019; L. Kemp leg.; hand collected, grassland; DNA RJ4; BINCO_MAD_19_0079_2; BE_RMCA_ARA.Ara.247346; RMCA.

Paratypes

MADAGASCAR – **Antsiranana Province** • 1 juv.; same data as for holotype; [SEM imaged]; BINCO_MAD_19_0079_2; BE_RMCA_ARA.Ara.247347; RMCA • 1 juv.; Bamevika; 14°18′58.9″ S, 48°43′22.9″ E; 1557 m a.s.l.; M. Jocque leg.; hand collected, forest leaf litter; DNA RJ2; BINCO_MAD_19_0079_2; BE_RMCA_ARA.Ara.247349; RMCA • 1 juv.; same data as for preceding; DNA RJ3; BINCO_MAD_19_0079_2; BE_RMCA_ARA.Ara.247348; RMCA.

Description

Female holotype (BE_RMCA_ARA.Ara.247346; RMCA)

Measurements. Total length: 6.82. Carapace: length 2.91, width 2.30, height 1.42.

Colour (Figs 17). Carapace brownish yellow, with two contrasting dark bands of short setae along margin and faint median band between PME and fovea; chelicerae brownish, anteriorly with two thin longitudinal darker stripes; sternum yellowish brown; legs brownish yellow with three darker rings on femora, two on tibiae, distally and proximally; abdomen brownish yellow with spotted pattern on dorsum and sides; spinnerets pale yellow.

Sternum (Fig. 17B). Oval with slightly sinuous sides; 1.21 wide, 1.42 long.

Chilum. 0.12 high, 0.20 wide.

Eyes. ALE 0.16; AME 0.12; PLE 0.16; PME 0.16; ALE–AME 0.05; AME–AME 0.07; PLE–PME 0.16; PME–PME 0.10; MOQ: AW 0.28, PW 0.39, L 0.36.

Clypeus. With five long setae.

Leg measurements

	F	P	T	Mt	t	Total
I	2.10	1.05	1.82	1.61	1.00	7.58
II	1.68	0.91	1.47	1.40	0.80	6.26
III	1.75	0.84	1.33	1.61	0.70	6.23
IV	2.31	0.91	2.03	2.66	1.20	9.11

Fig. 17. *Zorascar pasunepomme* gen. et sp. nov., holotype female (BE_RMCA_ARA.Ara.247346; RMCA), habitus. **A**. Dorsal view. **B**. Ventral view. **C**. Lateral view. Scale bars = 1 mm. Stacked microphotographs by Arnaud Henrard and Rudy Jocqué.

Spination

	F	P	T	Mt
I	pl1d1v1	–	v2-2-2-2	v2-2-2
II	pl2d1	–	pl3v2-2-2-2	v2-2-2
III	pl3d3rl2	pl1rl1	pl2d2rl2v2-2-2	pl3d1rl3v2-2-2
IV	pl3d2rl1	pl1rl1	pl2d2rl2v2-2-2	disp14

Genitalia. Epigyne (Figs 16E, 18A, 19A–B) with median lobe (ML) narrow and deeply concave medially (MS), copulatory openings (CO) exposed laterad of ML; lateral lobe (LL) with pair of stout basal, blunt, conical projections (LP); spermathecae dark, comma shaped as in transparency. Endogyne (Figs 18B–D, 19C–F): sperm ducts (CD) short, cylindrical, with three twists; spermathecae (S) reniform, with fairly narrow ventral base, and dorsal, roughly semicircular part, provided with few pores; fertilization ducts (FD) short, flattened and slightly curved.

Male

Unknown.

Distribution

Known only from the type locality in northern Madagascar at an altitude of around 1500 m (Fig. 26).

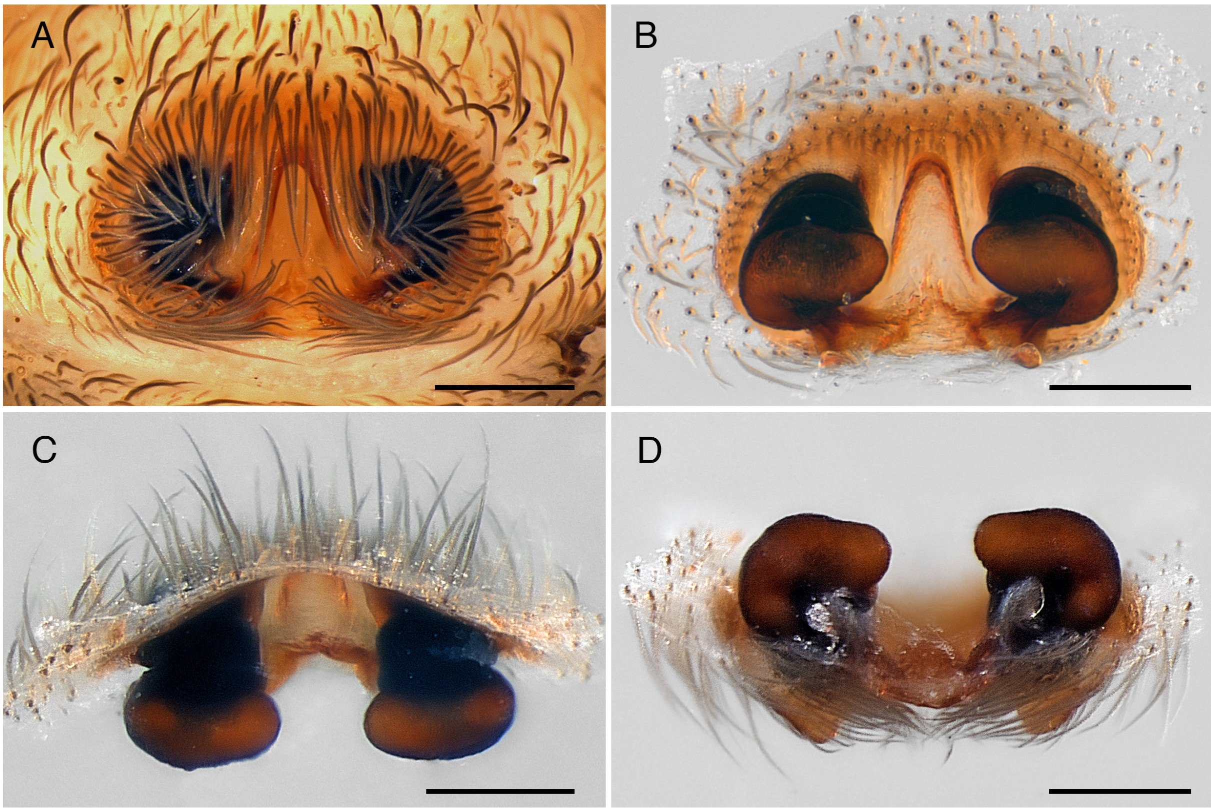

Fig. 18. *Zorascar pasunepomme* gen. et sp. nov. holotype female (BE_RMCA_ARA.Ara.247346; RMCA), genitalia. **A**. Epigyne, ventral view. **B**. Endogyne, cleared, dorsal view. **C**. Idem, dorso-anterior view. **D**. Idem, dorso-posterior view. Scale bars = 0.2 mm. Stacked microphotographs by Arnaud Henrard and Rudy Jocqué.

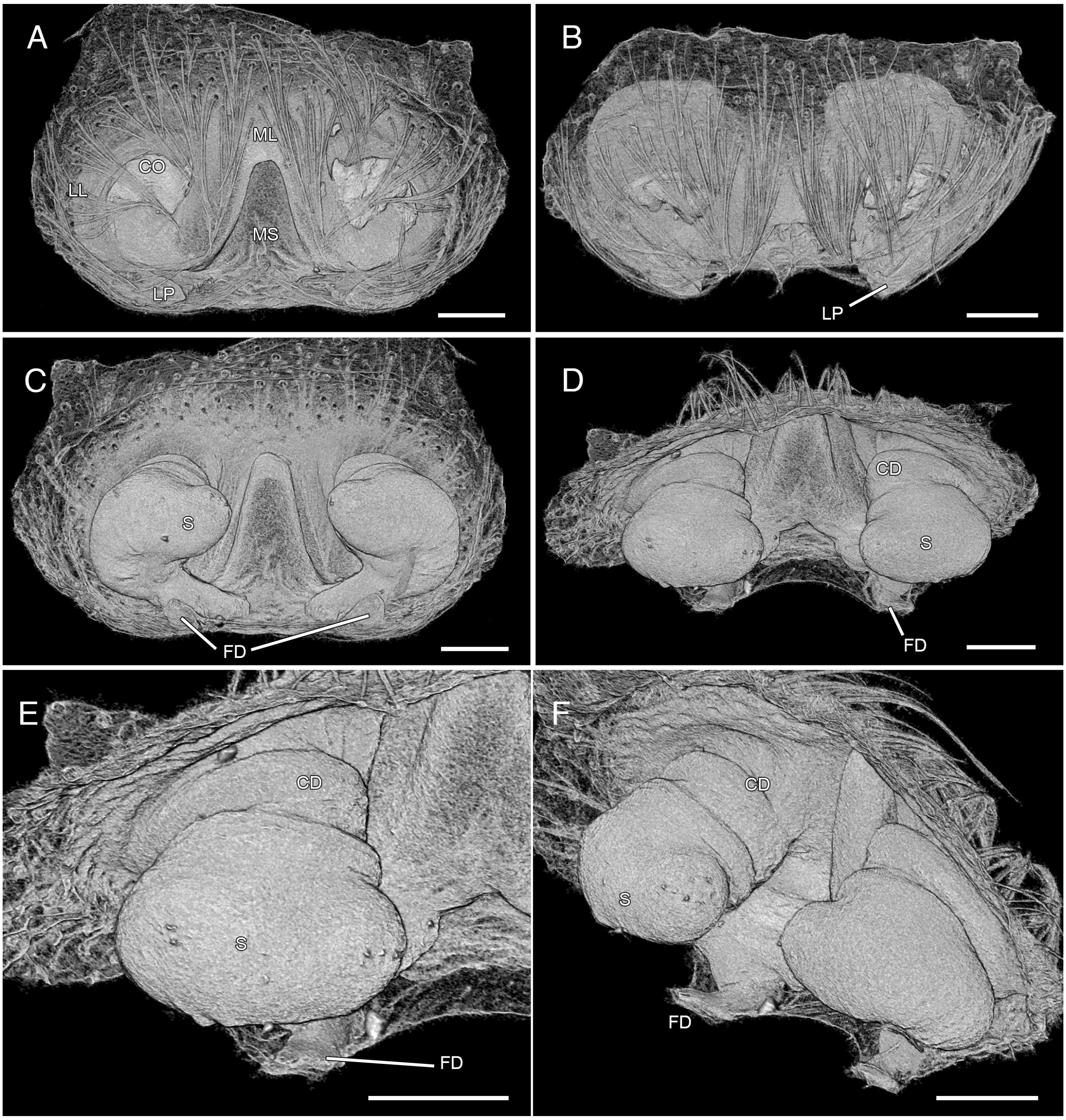

Fig. 19. *Zorascar pasunepomme* gen. et sp. nov., holotype (BE_RMCA_ARA.Ara.247346; RMCA), epigyne, CT-scan images. **A**. ventral view. **B**. ventro-anterior view. **C**. dorsal view. **D**. dorso-anterior view. **E**. idem, detail. **F**. Idem, dorso-lateral view. Abbreviations: CD = copulatory duct; CO = copulatory opening; FD = fertilisation duct; LL = lateral lobe; LP = lateral process; ML = median lobe; MS = median sector; S = spermatheca. Scale bars = 0.2 mm. 3D micro-CT scans by Arnaud Henrard.

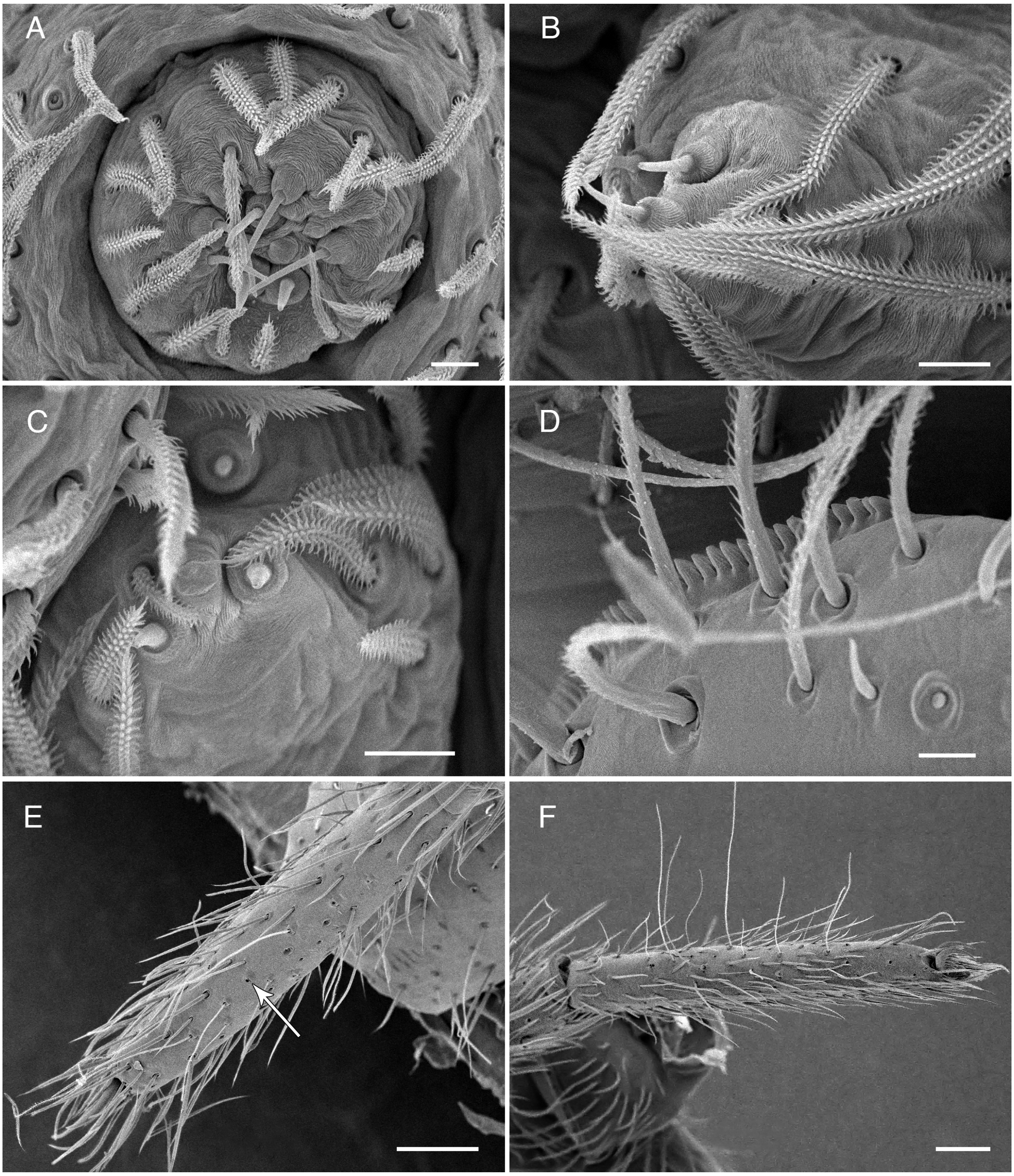

Fig. 20. *Zorascar pasunepomme* gen. et sp. nov., paratype juvenile (BE_RMCA_ARA.Ara.247347; RMCA), SEM pictures. **A**. ALS, caudal view. **B**. PLS, posterior view. **C**. PMS, posterior view. **D**. Right serrula, ventral view. **E**. Tarsus of leg 1, arrow pointing to the tarsal organ. **F**. Tarsus of leg 4. Scale bars: A–D = 10 µm; E–F = 100 µm. SEM images by Rudy Jocqué.

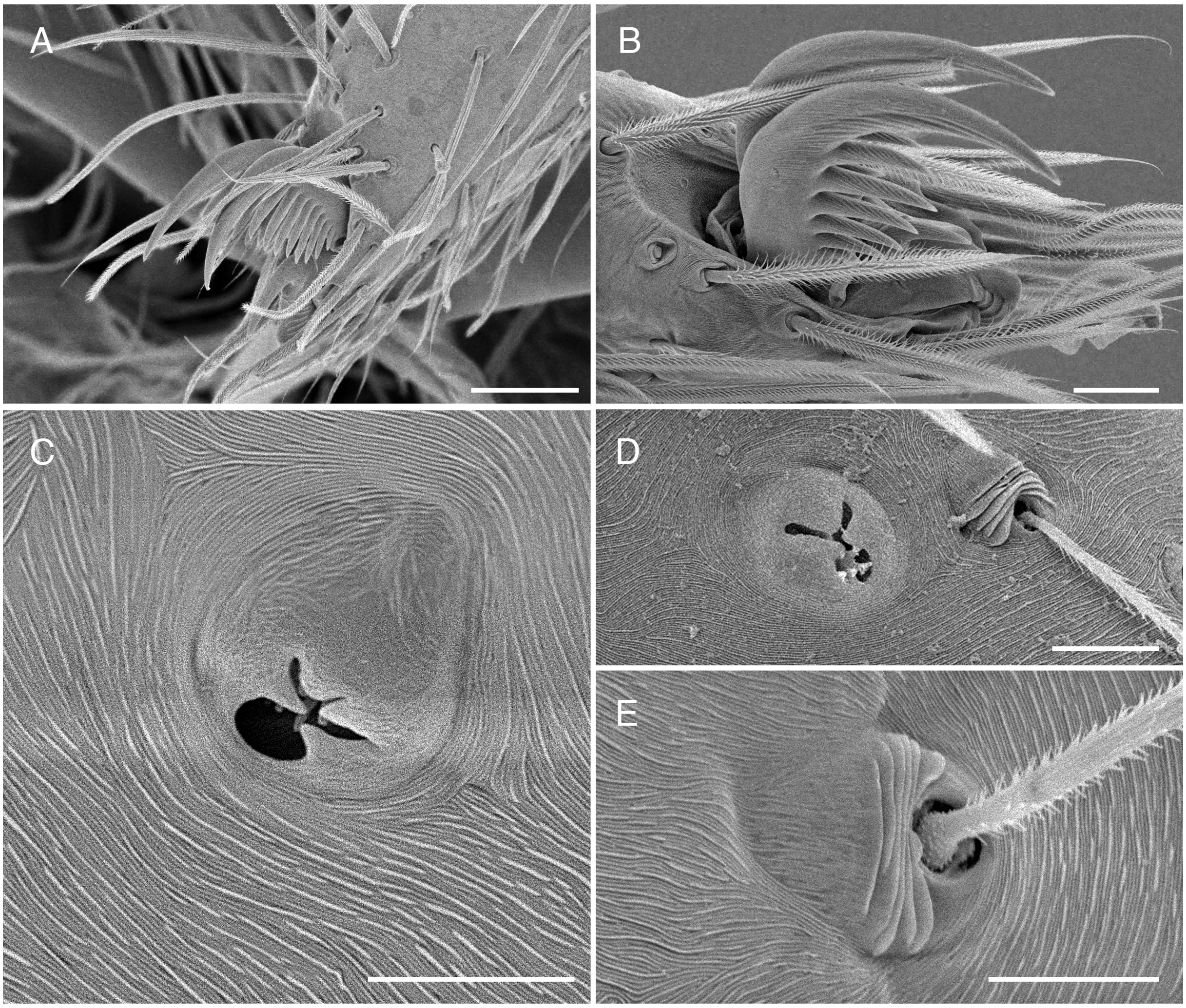

Fig. 21. *Zorascar pasunepomme* gen. et sp. nov., paratype juvenile (BE_RMCA_ARA.Ara.247347; RMCA). **A**. Tarsal claws of leg 1. **B**. Tarsal claws of leg 4. **C**. Tarsal organ of leg 2. **D**. Tarsal organ and trichobothrium of leg 4. **E**. Trichobothrium, tarsus 1. Scale bars: A = 50 µm; B = 20 µm; C, E = 5 µm; D = 10 µm. SEM images by Rudy Jocqué.

Genus ***Zorodictyna*** Strand, 1907
Figs 22–26

Type species

Zorodictyna intermedia Strand, 1907 (= junior synonym of *Zorodictyna oswaldi* (Lenz, 1891), see below), by monotypy.

Diagnosis

Cribellate udubids having an entire or vestigial cribellum and a strong scopulae beneath leg tarsi and most of length of metatarsi. The male palp (Figs 23C, 25C) is provided with a short paracymbium retrolateral process (PP) (absent in *Zorodictyna oswaldi* (Lenz, 1891)) and the female epigyne has a median lobe (ML) broad, nearly rectangular, not extending to posterior margin of epigyne (Figs 23D, 25D). The genus is distinguished from *Uduba* males in lacking a threadlike embolus and a knob-like process between palpal patella and tibia and from *Uduba* females by having compact spermathecae rather than multiple loops. It is distinguished from *Tabiboka* gen. nov. and *Zorascar* gen. nov. by having a strong tarsal and metatarsal scopulae and having a cribellum rather than a colulus.

Description

Body. Large spiders (males: 13.00–24.00; females: 19.00–31.00) with smooth teguments of carapace, sternum and legs (Figs 22, 24). Carapace piriform, longer than wide (L/W: males: 1.12–1.50; females: 1.24–1.41), with thoracic fovea linear; with sparse cover of short, dark setae; profile higher in ocular and thoracic area and abruptly sloping posteriorly.

Coloration (Figs 22, 24). Cephalothorax brown dorsally, yellow-brown ventrally; abdomen dark with obscure pattern (*Z. almae* sp. nov., *Z. silvadavilae* sp. nov.) or with bold markings (*Z. oswaldi* (Lenz, 1891)).

Eyes (Figs 22A, C, 24A, C). In two nearly straight rows: ALE larger than AME, PLE and PME similar to ALE; tapetum of secondary eyes canoe shaped, shiny. Clypeus with long setae.

Prosoma. Chilum double, about three times or more as wide as high. Chelicerae: paturon conical, with some long setae medially, three teeth on both margins, with retrolateral thick setae at fang base; fang with serrate texture on proximal edge. Labium (Figs 22B, D, 24B, D) rectangular. Endites (Figs 22B, D, 24B, D) roughly rectangular, with retrolateral margins sinuous, distal part slightly wider than proximal part, with subdistal serrula present as simple row. Sternum (Figs 22B, D, 24B, D) oval, slightly longer than wide, length 1.22–1.33 times width, with slightly curved margins, not extending between coxae IV.

Legs (Figs 22, 24). Slender. Formula 4123 or 1423. Three tarsal claws, unpaired claw smooth, small to absent, superior claws with six to eight teeth; without claw tufts or tenent setae; scopulae present beneath all tarsi and distal parts of metatarsi. Trichobothria in two or more rows on tarsi, in three or more on metatarsi, all equal in length; distal and proximal plates of bothria well differentiated, proximal plates with transverse ridges (Griswold 1993: fig. 62). Tarsal organ with tear-drop or keyhole-shaped opening (Griswold 1993: fig. 63), close to tip of tarsus. Spines numerous, with four pairs of ventral spines on tibia I, not overlapping, and three pairs of ventral spines on metatarsus. Calamistrum present, oval in basal third of metatarsus. Male tibial crack (autospasy suture) present in males as a suture through the bases of leg tibia just distad to the basalmost pair of ventral spines (Fig. 24B, arrow). Trochanters distally notched to entire.

Abdomen (Figs 22, 24). Oval, without scuta. Epiandrous glands absent. Cribellum entire. Spinnerets: ALS and PLS large, conical, biarticulate; PMS one-segmented, small. Females with two ALS major ampullate gland spigots and field of about 10–20 piriform gland spigots and tartipores; PMS with two anterior minor ampullate gland spigots and posterior cylindrical gland spigots and aciniform gland spigots; PLS with few cylindrical gland spigots and aciniform gland spigots, apically with unique spigot, probably “modified” or “pseudoflagelliform” gland spigot; males lack cylindrical gland spigots and have “modified” gland spigot and second of each pair of major ampullate gland and minor ampullate gland spigots spigot reduced to nubbins.

Male palp (Figs 23A–C, 25A–C; Lenz 1891: fig. 6b–c; Lehtinen 1967: fig. 78; Griswold 1993: figs 19–21). Tibia with large or stout RTA, inserted medially, provided with basal concavity, with short rounded or tapered VTA; cymbium oval with rounded distal extremity, without dorsal patch of short setae, with rounded paracymbial retrolateral process (PP) (absent in *Zorodictyna oswaldi*) and conical retrobasal extension (CE); bulbus provided with retrobasal subtegulum lobe (locking lobe, SL), and tegulum rounded with well-developed prolateral conical protrusion at base of embolus (corresponding locking lobe, TL);

embolus (E) with fixed base, originating prolateraly, directed clockwise, short and lamellate (Figs 23A–B, 25A–B); median apophysis (MA) hook-shaped, situated opposite to E; conductor (C) hyaline, well developed, fan-shaped, medially extending from narrow base to wide flattened tip; paraconductor (Pc) as narrow, finger-like membranous extension inserted between tegulum and base of MA with sharp triangular dorso-prolateral process (EBP) arising near bases of embolus and paraconductor.

Genitalia. Epigyne (Figs 23D, 25D; Lenz 1891: fig. 8b; Lehtinen 1967: figs 72, 76; Griswold 1993: figs 22–24) as single, shield-shaped plate (ML) with convex median and lateral folds; lateral sector convex or with tooth. Endogyne (Figs 23E, 25E): copulatory ducts (CD) very short, twisted; spermatheca (S) one or two lobate, head of spermatheca provided with one or more pores; no evidence of enlarged Bennett's Gland pore through spermathecal base.

Species included

Zorodictyna oswaldi (type species, ♂♀); *Zorodictyna almae* sp. nov. (♂♀); *Zorodictyna silvadavilae* sp. nov. (♂♀).

Note on the type species

The first species name used in *Zorodictyna* was *Zorodictyna intermedia* Strand, 1907, which is the type species by monotypy. However, there is good reason to consider Z. *intermedia* Strand, 1907 a junior synonym of *Uduba inhonesta* Simon, 1906 (now Z. *inhonesta*), which was already recognized by Lehtinen (1967). Furthermore, we have carefully examined the type specimens of *Agroeca oswaldi* Lenz, 1891 (now *Z. oswaldi*) and *Z. inhonesta*: the distinction observed by Lehtinen 1967 was artifactual, resulting from a mating plug lodged in the epigyne of the type of Z. *oswaldi* in contrast with the clean epigyne of the type of *Uduba inhonesta* Simon, 1906. We have established that *Z. inhonesta* (Simon, 1906) is itself a junior synonym of *Z. oswaldi*. Therefore, the type species of *Zorodictyna* Strand, 1907 is also a junior synonym of *Z. oswaldi*. For more complete details concerning the synonymy, see the description of *Zorodictyna oswaldi* (Lenz, 1891) below.

Affinities

From the molecular analyses (Fig. 2), *Zorodictyna* appears closely related to species in the Udubidae that have been identified as *Tabiboka* gen. nov. and *Zorascar* nov. gen.

Distribution

Species of the genus *Zorodictyna* occur in Madagascar (Fig. 26).

Zorodictyna oswaldi (Lenz, 1891)
Fig. 26

Agroeca oswaldi Lenz, 1891: 169, plate 1, figs 6a–c, 8a–b. Syntype male and female from Nossi Be, Madagascar, syntypes, ZMH [examined].
Uduba inhonesta Simon, 1906: 294. Type female from Nosi Be, Madagascar, in MNHN [examined]. **Syn**. **nov**.
Zorodictyna intermedia Strand, 1907: 725 (type destroyed, but the type locality on Nosi Be suggests that this is the same species as *Zorodictyna oswaldi* (Lenz, 1891).

Uliodon oswaldi – Strand 1908: 118. — Roewer 1955: 659. — Bonnet 1959: 4754.
Zorodictyna intermedia – Petrunkevitch 1928: 146. — Roewer 1955: 1284. — Bonnet 1959: 4991.
Uduba inhonesta – Roewer 1955: 1283. — Bonnet 1959: 4754.
Uduba oswaldi – Bonnet 1959: 4750.

Zorodictyna inhonesta – Lehtinen 1967: 276, fig. 76 (transferred to *Zorodictyna* from *Uduba*, and declared a senior synonym of *Zorodictyna intermedia* Strand, 1907).
Zorodictyna oswaldi – Lehtinen 1967: 276, figs 72, 76, 78 (transfer to *Zorodictyna* from *Uliodon*). — Griswold 1993: 8, figs 19–24, 62–63.

Diagnosis

Zorodictyna oswaldi is distinguished from other *Zorodictyna* by having the male palpal cymbium narrow (Griswold: 1993: figs 19–21), with length 2.25 times width, with a short cymbial retrobasal extension (CE), extending only to tibial apex, and without a paracymbial process (PP) (vs in *Z. almae* sp. nov. and *Z. silvadavilae* sp. nov., males have the cymbium length less than 2 times width, and well-developed paracymbial processes (CE and PP), Figs 23B–C, 25B–C). *Zorodictyna oswaldi* females have the lateral lobes (LL) of epigyne with short teeth, which are absent in *Z. almae* (Fig. 23D) and *Z. silvadavilae* (Fig. 25D). *Zorodictyna oswaldi* also has abdomen boldly marked (Lenz 1891: fig. 8a) with strongly marked, contrasting ventral black and white stripes, whereas abdomens of *Z. almae* (Fig. 22A–D) and *Z. silvadavilae* (Fig. 24A–D) have obscure markings.

Type material examined

Syntypes of *Agroeca oswaldi* Lenz, 1891
MADAGASCAR • 1 ♂, 1 ♀; Nosi Be Island; 2 Jul. 1888; ZMH.

Type of *Uduba inhonesta* Simon, 1906
MADAGASCAR • 1 ♀; Nosi Be Island; MNHN.

Description (abbreviated)

Male syntype (ZMH)
Measurements. Total length: 13.00. Carapace: length 7.00, width 5.00.

Coloration (Lenz 1891: fig. 6a). Cephalothorax yellow-brown, with narrow dark mark along pars cephalica and broad dark bands near edges of pars thoracica, venter of sternum, mouthparts, coxae and trochanters yellow brown; abdomen and legs grey-brown, dorsum of abdomen dark with anterior light cardiac mark and four pairs of dark spots posteriorly (Lenz 1891: fig. 6a), sides dark, venter yellow-white with broad median longitudinal dark band.

Ratios. Carapace length/width = 1.50, PER/carapace width = 0.38, PER/OAL = 2.71, PER/AER = 1.27, OQP/OQA = 1.16, sternum length/width = 1.22, palpal coxa length/width = 1.73, cymbium length/palpal tibia length = 1.60, cymbial retrobasal extension = 0.16 of cymbial length.

Spination

	F	P	T	Mt
I	Pl2d3rl4	Pl1rl1	Pl3d3rl3v2222	Pl3rl3v221
II	Pl4d3rl4	Pl1rl1	Pl3d3rl3v2222	Pl12r1l2v221
III	Pl4d3rl4	Pl1rl1	Pl2d2rl2v222	Pl12rl12v222
IV	Pl4d3rl3	Pl1rl1	pl2d2rl2v222	Pl4rl4v11122

Male palp. Cymbium narrow, length 2.25 times width, evenly convex retrolaterally, without paracymbial process, cymbial retrodorsal extension short, extending only to tibial apex; median apophysis more than twice longer than wide (Lenz 1891: fig. 6b–c; Lehtinen 1967: fig. 78; Griswold 1993: figs 19–21).

Female syntype (ZMH)
Measurements. Total length: 19.00. Carapace: length 79.60, width 7.00, height 4.60.

Coloration (Lenz 1891: fig. 8a). Cephalothorax yellow-brown, with narrow dark mark along pars cephalica and broad dark bands near edges of pars thoracica, venter of sternum, mouthparts, coxae and trochanters yellow-brown; abdomen and legs grey-brown, abdomen dorsum dark with anterior light cardiac mark and four pairs of dark spots posteriorly (Lenz 1891: fig. 8a), sides dark, venter yellow-white with broad median longitudinal dark band.

Ratios. Carapace length/width = 1.37, carapace height/width = 0.66, PER/carapace width = 0.52, PER/OAL = 4.00, PER/AER = 1.24, OQP/OQA = 1.20, sternum length/width = 1.26, palpal coxa length/width = 2.00.

Spination

	F	P	T	Mt
I	Pl2	–	v2222	v222
II	Pl2d1	–	v2222	v222
III	Pl4d3rl4	Pl1rl1	Pl2d2rl2v222	Pl122rl122v222
IV	Pl2d3rl1	Pl1rl1	pl2d2rl2	Pl112rl112v1112

Genitalia. Epigyne with short, broad teeth on lateral lobes (Griswold 1993: fig. 24), median lobe length 0.47 times width, length from median lobe base to epigastric furrow 0.44 of median lobe length. Endogyne (Griswold 1993: figs 22–23) with spermatheca as single, large chamber, spermathecal head with single anterior pore.

Synonymy

We have examined the male and female syntypes of *Agroeca oswaldi* Lenz, 1891 (ZMH) and the female type of *Uduba inhonesta* Simon, 1906 (MNHN, Paris), both of which were collected on the island of Nosi Be, northwest of Madagascar. The females of each are identical, and are as illustrated by Griswold (1993: 8, figs 22–24) and Lenz (1891: 169, plate 1, figs 6, 8). We hereby declare *U. inhonesta* Simon, 1906 to be a junior synonym of *A. oswaldi* Lenz, 1891 (new synonymy).

Notes

Some confusion over the identity of the female types of *Agroeca oswaldi* Lenz, 1891 and *Uduba inhonesta* Simon, 1906 may have arisen from the condition of the epigyne in the *Agroeca oswaldi* type. The specimen had a mating plug in the epigyne, which superficially changed the appearance from that of the *Uduba inhonesta* type. Lehtinen (1967) illustrated both types, *Agroeca oswaldi* with the plug (fig. 72) and *Uduba inhonesta* lacking a plug (fig. 76). Griswold (1993: figs 22–24) removed the plug before illustrating the *Agroeca oswaldi* type, which then is virtually identical to the type of *Uduba inhonesta*.

Benoit illustrated a species of Udubidae from the collection in Tervuren (BE_RMCA_ARA.Ara.136920), for which he provides the new combination *Uduba inhonesta* (Benoit 1972: 180, fig. 3). The illustrated male is an *Uduba*. Although Benoit declares "Le mâle est identique au type [female], originaire de Nossi Be present dans la collection SIMON au Muséum de Paris", this statement is incorrect. After examination and analyses of the palp with micro-CT 3D scans (see Appendix 5), this male specimen is now correctly identified as *Uduba madagascariensis* (Vinson, 1863) (see Griswold *et al.* 2022 for a complete description of that species).

Distribution

Known only from Nosi Be Island off of northwestern Madagascar (Fig. 26).

Zorodictyna almae sp. nov.

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Figs 22–23, 26

Zorodictyna sp. 1 – Polotow *et al.* 2015.

Diagnosis

Males of *Zorodictyna almae* sp. nov. are distinguished from *Z. oswaldi* (Lenz, 1891) by having a retrobasal cymbial extension (CE) that extends at least ¼ the length of the papal tibia and a thick retrobasal paracymbial process (PP) (Fig. 23B–C) (vs *Z. oswaldi* lacks the PP and has a very short CE; Griswold 1993: 19–21). It is distinguished from *Z. silvadavilae* sp. nov. in having the male palp with a nearly triangular basal embolic hook, the embolus lacking a crest, and a retromedian longitudinal ridge that extends for most of the tegulum length (Fig. 23A–C) (vs *Z. silvadavilae* has slender, crescentic basal embolic hook, the embolus with subapical distal crest, and the tegular retromedian longitudinal ridge that is weak, short, extending for less than one-half tegulum length, Fig. 25A–C). Females of *Z. almae* are distinguished from *Z. oswaldi* by lacking teeth on the lateral lobes (LL) of the epigyne (Fig. 23D) (vs *Z. oswaldi* has the LL with teeth; Griswold 1993: fig. 24); females of *Z. almae* are distinguished from *Z. silvadavilae* by having the lateral lobes of epigyne parallel and the median sector (MS) rectangular (Fig. 23D). The female endogyne has copulatory ducts (CD) larger than spermathecae (Fig. 23E) (vs in *Z. silvadavilae*, the LL are converging posteriorly, and the MS is triangular, Fig. 25D, and the endogyne has CD and spermathecae equal in size, Fig. 25E).

Etymology

The species name is a matronym in honor of Alma Saucedo Mejia, participant in the 2011 expedition that produced the female paratype (CASENT_9031271) that was a DNA voucher in Polotow *et al.* (2015) [DNA-DP-Lyc-voucher, Z-1, DP2014d]. She is also the discoverer of many Madagascar goblin spiders.

Type material

Holotype

MADAGASCAR – **Mahajunga Province** • ♂; R. F. l'Ankarafantsika, 5 km SSW of Ampijaroa; 16°20.3′ S, 46°47.6′ E; 160 m a.s.l.; 4–7 Feb. 1997; S. Goodman leg.; CASENT_9082245; FMNH.

Paratypes

MADAGASCAR – **Mahajunga Province** • 1 ♀; same data as for holotype; CASENT_9082245; FMNH • 1 ♀; Ampijoroa, National Park Ankarafantsika, near Lake Ravelobe; 16°17.48′7″ S, 46°48.50′7″ E; 26–28 Jan. 2009; C. Griswold, A. Saucedo and H. Wood leg.; DNA-DP-Lyc-voucher, *Zorodictyna* sp. 1, in Polotow D., Carmichael A. & Griswold C.E. 2015; Z-1; DP2014d; CASENT_9031271; CAS • 1 ♀; Parc National d'Ankarafantsika, Forêt de Tsimaloto, 18.3 km 46° NE of Tsaramandroso; 16°3′41″ S, 46°8′37″ E; 135 m a.s.l.; 2–8 Apr. 2001; J.J. Rafanomezantsoa *et al.* leg.; general collecting, day, tropical dry forest; [epigyne illustrated by CEG]; CASENT_9002829; CAS.

Other material examined

MADAGASCAR – **Mahajanga Province** • 1 ♀; Ampijoroa, National Park Ankarafantsika, near Lake Ravelobe; 16°17.487′ S, 46°48.507′ E; 26–28 Jan. 2009; C. Griswold, A. Saucedo and H. Wood leg.; CASENT_9031270; CAS.

Description

Male holotype (CASENT_9082245; FMNH)

MEASUREMENTS. Total length: 21.00. Carapace: length 12.00, width 9.80, height 5.70.

Coloration (Fig. 22A–B). Dorsal and lateral sides of cephalothorax, abdomen and legs unicolorous grey-brown, venter of sternum, mouthparts, coxae and trochanters yellow white.

Sternum (Fig. 22B). Oval with slightly sinuous margins; 4.50 wide, 5.60 long.

Chilum. 0.25 high, 0.85 wide.

Eyes. ALE 0.28; AME 0.28; PLE 0.35; PME 0.30; ALE–AME 0.13; AME–AME 0.70; PLE–PME 0.45; PME–PME 0.28; MOQ: AW 0.73, PW 0.83, L 0.80.

Clypeus. With 18 long setae.

Legs. Trochanters deeply notched. Unpaired claws smooth, rudimentary on legs III and IV. Strong scopulae beneath all tarsi, apices of metatarsi III and IV, and apical halves of metatarsi I and II.

Leg measurements

	F	P	T	Mt	t	Total
I	10.20	5.10	11.50	11.10	6.30	44.20
II	11.00	5.00	9.70	9.80	5.00	40.50
III	9.30	4.10	7.60	9.40	4.60	35.00
IV	11.90	4.70	10.90	15.20	6.00	48.70

Spination

	F	P	T	Mt
I	pl3d3rl2	pl1rl1	pl3d3rl3v2-2-2-2	pl4rl4v2-2-3
II	pl3d3rl3	–	pl2d3rl2v2-2-2-2	pl3rl3v2-2-3
III	pl3d3rl3	pl1rl1	pl2d2rl2v2-2-2	pl4d1rl4v2-2-2
IV	pl3d3rl3	pl1rl1	pl2d2rl2v2-2-2	pl4rl4v1-1-1-2-3

Male palp (Fig. 23 A–C). Tibia VTA apical, curved and blunt-tipped, RTA triangular, sharply pointed, located behind this dorso-retrolateral excavation to accommodate retrobasal cymbial extension (CE); cymbium oval, apical extremity narrowly rounded, without dorsal patch of chemosensitive setae, with protruding retrolateral paracymbial process (PP), retrobasal cymbial extension (CE) conical, extending at least ¼ the length of papal tibia; subtegulum large, filling most of cymbial concavity and extending to prolateral cymbial margin, with probasal broad ridge (SL) that interlocks with tegulum; tegulum rounded with rectangular process on prolateral margin (TL), which interlocks with subtegular ridge; embolus (E) proapical, broad and thick, with pointed apex, inner margin with twisted longitudinal ridge and triangular basomedian process (EBP) arising from embolus base; median apophysis (MA) strongly sclerotized, short, hooked, curved prolaterad; conductor (C) hyaline, fan shaped, narrow at base; paraconductor (Pc) large, cradling inner margin of E and extending past E apex; retroventral surface of tegulum with deep longitudinal groove that extends for two thirds of tegulum length.

Female paratype (CASENT_9082245; FMNH; except as otherwise indicated)
Measurements. Total length: 30.00. Carapace: length 14.00, width 11.30, height 4.40.

Colour (Fig. 22C–D). As in male: dorsal and lateral surfaces of cephalothorax, abdomen and legs unicolorous grey-brown; venter of sternum, mouthparts, coxae and trochanters yellow white.

Sternum (Fig. 22D). Oval with slightly sinuous sides; 4.90 wide, 6.40 long.

Chilum. 0.25 high, 1.08 wide.

Eyes. ALE 0.33; AME 0.33; PLE 0.31; PME 0.29; ALE–AME 0.20; AME–AME 0.75; PLE–PME 0.55; PME–PME 0.35; MOQ: AW 0.78, PW 0.93, L 0.78.

Clypeus. With ten long setae.

Legs. Trochanters deeply notched. Unpaired claws smooth, rudimentary on legs III and IV. Strong scopulae beneath all tarsi, apex of metatarsus III, apical half of metatarsus II and all of metatarsus I.

Leg measurements

	F	P	T	Mt	t	Total
I	10.30	5.20	11.50	11.10	6.30	44.20
II	9.50	4.90	7.20	6.80	3.80	32.30
III	8.20	4.20	5.80	7.20	3.80	29.20
IV	10.90	4.70	9.00	12.60	4.80	42.00

Spination

	F	P	T	Mt
I	pl1d2	–	v2-2-2-2	v2-2-2
II	pl2d2	–	v2-2-2-2	v2-2-2
III	pl3d3rl4	pl1rl1	pl2d2rl2v2-2-2	pl4d1rl4v2-2-2
IV	pl1d3rl3	pl1rl1	pl2d2rl2v2-2-2	pl5rl4v2-1-2-2

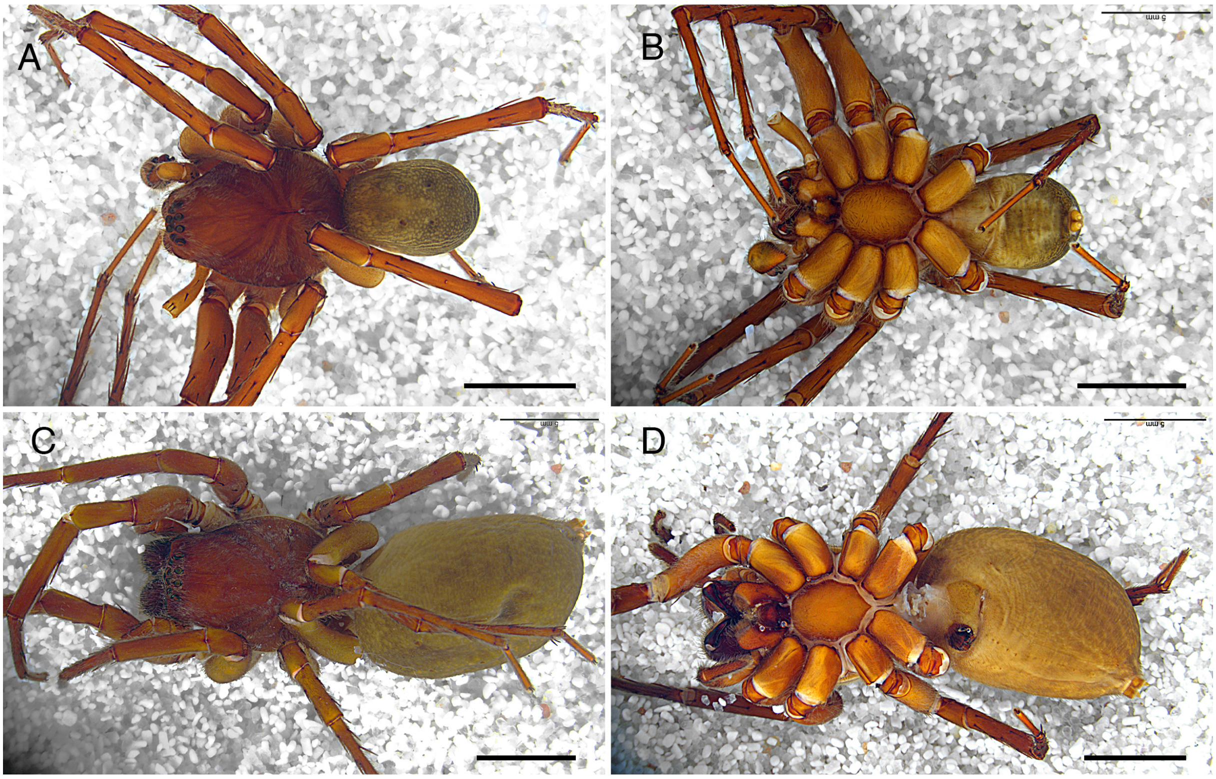

Fig. 22. *Zorodictyna almae* sp. nov., male and female habitus; A–B = male holotype (CASENT_9082245; FMNH); C–D = female paratype (CASENT_9082245; FMNH). **A, C**. Dorsal view. **B, D**. Ventral view. Scale bars = 5 mm. Stacked microphotographs by Franklyn Cala Riquelme.

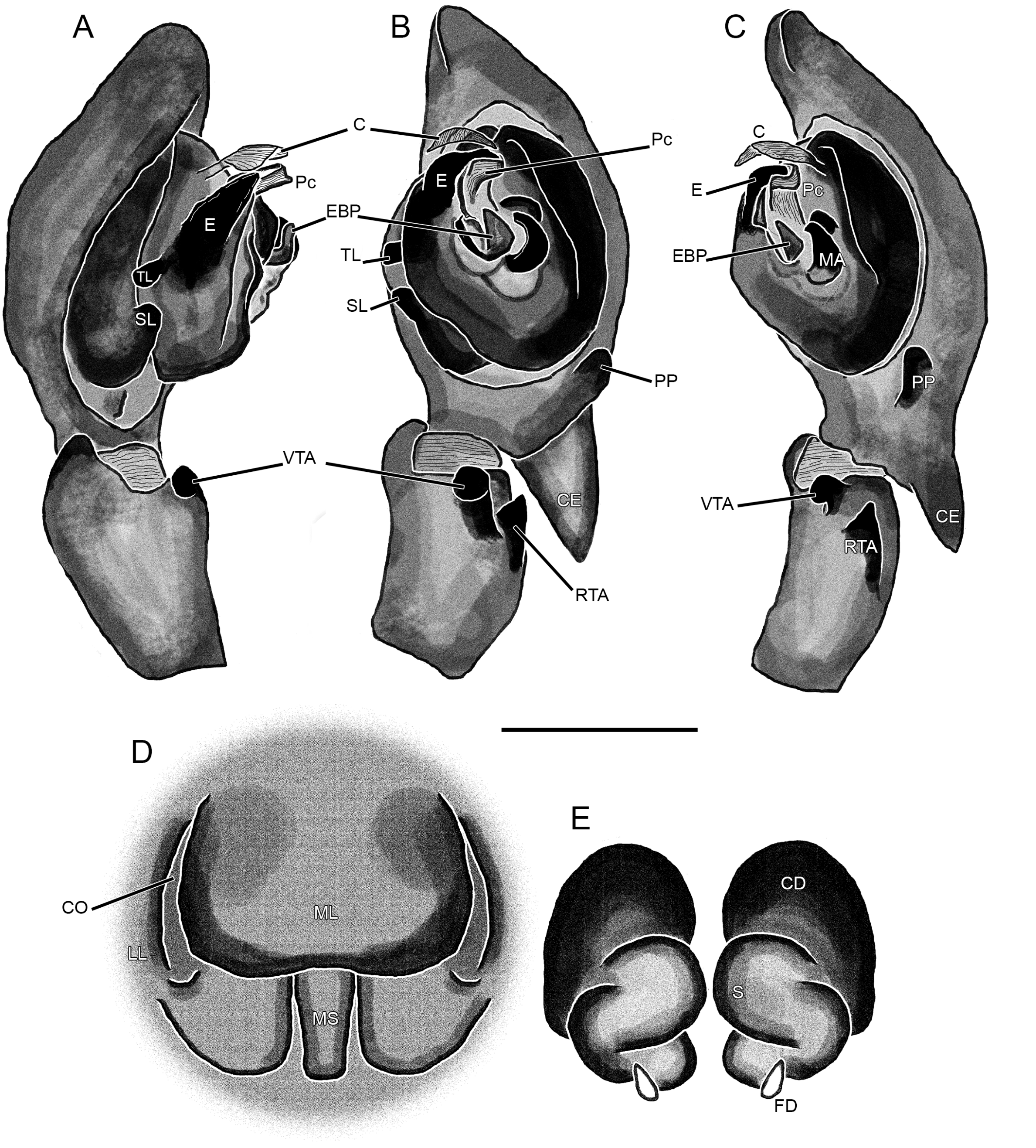

Fig. 23. *Zorodictyna almae* sp. nov., genitalia drawings; A–C = male holotype (CASENT_9082245; FMNH); D–E = female paratype (CASENT_9002829; CAS). **A**. Left palp, prolateral view. **B**. Idem, ventral view. **C**. Idem, retrolateral view. **D**. Epigyne, ventral view. **E**. Endogyne, dorsal view. Abbreviations: C = conductor; CD = copulatory duct; CE = cymbial retrobasal extension; CO = copulatory opening; E = embolus; EBP = embolus basal process; FD = fertilisation duct; LL = lateral lobe; MA = median apophysis; ML = median lobe; MS = median sector; Pc = paraconductor; PP = paracymbial process; RTA = retrolateral tibial apophysis; S = spermatheca; SL = subtegular locking lobe; TL = tegular locking lobe; VTA = ventral tibial apophysis. Scale bars = 0.25 mm. Illustrations by Charles Griswold.

GENITALIA. Epigyne (paratype CASENT_9002829; CAS) (Fig. 23D) transverse quadrangular median lobe (ML) plate with smooth margin; copulatory openings (CO) hidden beneath anterolateral corners of ML; lateral lobes (LL) convex, without lateral teeth or projections but with concavities along lateral margins of ML, LL straight and parallel medially, exposing rectangular area of median sector (MS). Endogyne (Fig. 23E) with broad, simple, dark copulatory ducts (CD) larger than spermathecae (S), spermathecae with one half twist; fertilization ducts (FD) short and straight.

Variation

Male

Variation unknown: only the single holotype has been studied.

Female (n = 3)

[Female variation from CASENT_9082245, CASENT_9031270 and CASENT_9031271]. Total length = 20.00–30.00, carapace length/width = 1.24–1.30, carapace height/width = 0.39–0.48, PER/carapace width = 0.21–0.24, PER/OAL = 2.90–3.13, PER/AER = 1.35–1.36, OQP/OQA = 1.18–1.23, sternum length/width = 1.20–1.31, palpal coxa length/width = 2.24–2.44, femur I length/carapace width = 0.87–1.00, metatarsus I length/carapace width = 0.64–0.74, femur IV length/carapace width = 0.96–1.06, palpal tarsus length/carapace width = 0.34–0.41, palpal tarsus length/palpal patella length = 1.46–2.00, palpal tarsus length/palpal tibia length = 1.09–1.57, palpal tarsus length/palpal femur length = 0.76–0.95, palpal tibia length/palpal patella length = 1.08–1.40.

Note on synonym

A specimen of this species (CASENT_9031271) was used as an exemplar in a previously published molecular phylogeny, listed as "*Zorodictyna* sp. 1" by Polotow *et al.* (2015).

Natural history

The species *Zorodictyna almae* sp. nov. is recorded from tropical dry forest. Although they have an entire cribellum we know nothing of their use of cribellate silk.

Distribution

Zorodictyna almae sp. nov. is known from National Park Ankarafantsika in Mahajunga Province in northwestern Madagascar (Fig. 26).

Zorodictyna silvadavilae sp. nov.

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Figs 24–26

Zorodictyna sp. CG47 – Wheeler *et al.* 2017.

Diagnosis

Males of *Zorodictyna silvadavilae* sp. nov. are distinguished from those of *Z. oswaldi* (Lenz, 1891) by the retrobasal cymbial extension (CE) that extends at least ¼ the length of papal tibia and thick retrolateral paracymbial process (PP) (vs *Z. oswaldi* lacks the PP and has very short CE; Griswold 1993: figs 19–21); males are distinguished from *Z. almae* sp. nov. by having only a small or no crest on embolus, and the retrolateral branch of RTA simple (Fig. 25A–C) (vs *Z. almae* has a large crest on the E and the retrolateral branch of RTA is forked apically, Fig. 23A–C). Females of *Z. silvadavilae* are distinguished from *Z. oswaldi* by lacking teeth on lateral lobes (LL) (Fig. 25D) (vs *Z. oswaldi* have teeth on LL; Griswold 1993: fig. 24). The females are distinguished from *Z. almae* by having an endogyne with copulatory ducts (CD) equal to spermathecae (S) (Fig. 25E) (vs in *Z. almae*, the CD are much larger than S, Fig. 23E).

Etymology

The species name is a matronym in honor of Dr Diana Silva Dávila, who made an extensive expedition to Madagascar in 2003, collecting specimens and tissues for the Spiders–AToL (Assembling the Tree of Life) project.

Type material

Holotype

MADAGASCAR – **Antsiranana Province** • ♂; Marojejy Reserve, 8.4 km NNW of Manantenina; 14°26′ S, 49°45′ E; 700 m a.s.l.; 10–16 Nov. 1993; C. Griswold, J. Coddington, N. Scharff, S. Larcher, R. Andriamasimanana leg.; general collecting; CEG008; [habitus and male palp illustrated]; CASENT_9006231; CAS.

Paratypes

MADAGASCAR – **Antsiranana Province** • 1 ♂; same data as for holotype; CASENT_9006231; CAS • 1 ♂; same data as for preceding; CASENT_9082258; USNM • 1 ♀; same data as for preceding; S. Larcher leg.; [endogyne drawn]; CASENT_9006230; USNM. – **Toamasina Province** • 1 ♂; Parc National Masoala, Ambohitsitondroina Mt., Ambanizana; 15°34′20″ S, 50°00′25″ E; 900–1010 m a.s.l.; 5 Mar.

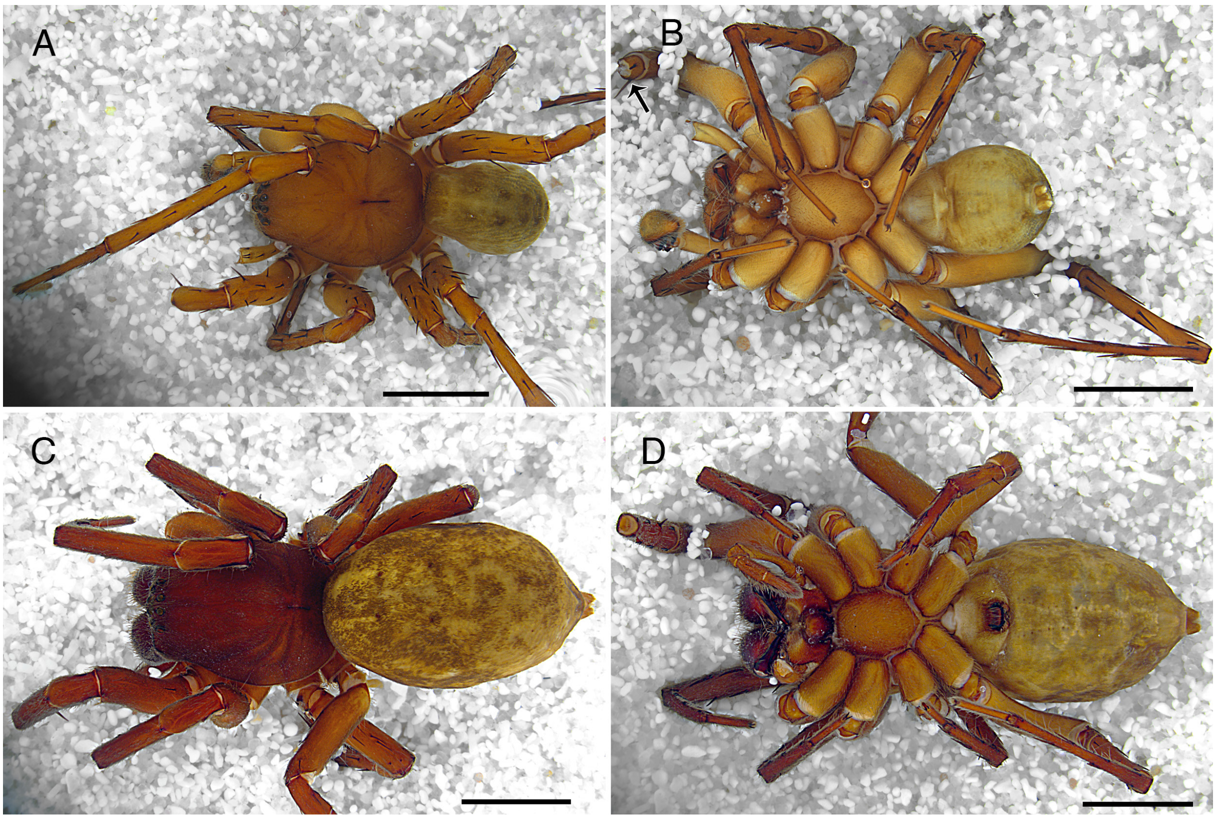

Fig. 24. *Zorodictyna silvadavilae* sp. nov., male and female habitus; A–B = male holotype (CASENT_9006231; CAS); C–D = female paratype (FMNH-0000-056-622; FMNH). **A, C**. Dorsal view. **B, D**. Ventral view, the arrow in B points to the tibial crack. Scale bars = 5 mm. Stacked microphotographs by Franklyn Cala Riquelme.

2003; Diana Silva Dávila leg.; raking tree trunks; montane rainforest; DNA vouchers ARACG000047; DSD0024; CASENT_9014998; CAS • 1 ♀; same data as for preceding; CASENT_9015400; CAS • 2 ♀♀; Parc National de Marojejy, NW; 810 m a.s.l.; Feb. 2002; S. Goodman leg.; pitfall; [habitus illustrated]; FMNH-INS 0000-056-622; FMNH • 1 ♀; Mt. Ambanizana; 15°34′29.9″ S, 050°00′12.3″ E; 750–800 m a.s.l.; 1 Mar. 2003; D. Andriamalala, D. Silva Dávila *et al.* leg.; rainforest; DSD0017; CASENT_9015400; CAS.

Other material examined

MADAGASCAR • 1 ♂; R.N.I. Marojejy, 11 km NW of Manantenina, Antranohofa; 1225 m a.s.l.; 14°26.2′ S, 49°44.5′ E; 24 Oct.–2 Nov. 1996; S. Goodman leg.; undisturbed mossy forest; pitfalls at camp #3; Mad1996#7; FMNH.

Description

Male holotype (CASENT_9006231; CAS; except as otherwise indicated)
Measurements. Total length: 17.60. Carapace: length 10.50, width 8.30, height 4.50.

Coloration (Fig. 24A–B). Dorsal and lateral of cephalothorax, abdomen and legs unicolorous grey-brown, venter of sternum, mouthparts, coxae and trochanters yellow white.

Sternum (Fig. 24B). Oval with slightly sinuous margins; 3.70 wide, 4.50 long.

Chilum. 0.18 high, 0.63 wide.

Eyes. ALE 0.28; AME 0.23; PLE 0.28; PME 0.25; ALE–AME 0.30; AME–AME 0.40; PLE–PME 0.35; PME–PME 0.15; MOQ: AW 0.58, PW 0.73, L 0.65.

Clypeus. With ten long setae.

Legs. Trochanters I–III shallowly notched, IV entire. Unpaired claws smooth, rudimentary on legs III and IV. Scopulae beneath all tarsi, apical half of metatarsus I and apical third of metatarsus II.

Leg measurements (paratype CASENT_9014998; CAS)

	F	P	T	Mt	t	Total
I	9.70	3.80	–	–	–	–
II	8.50	3.70	7.90	8.00	3.90	32.00
III	7.50	3.40	6.00	7.70	3.60	28.20
IV	10.00	3.20	8.50	12.60	4.70	39.00

Spination (paratype CASENT_9014998; CAS)

	F	P	T	Mt
I	pl2d3rl4	pl1rl1	–	–
II	pl3d3rl4	pl1rl1	pl2d2rl3v2-2-2-2	pl4rl3v2-3-2
III	pl3d3rl4	pl1rl1	pl2d2rl2v2-2-2	pl5rl5v2-1-2-2
IV	pl4d3rl3	pl1rl1	pl2d2rl2v2-2-2	pl5rl5v2-1-2-2

Male palp (Fig. 25A–C). Tibia with apical, short pronged VTA connected to conical RTA, behind which dorso-retrolateral excavation accommodates retrobasal cymbial extension; cymbium oval with narrowly-rounded apical extremity, without dorsal patch of chemosensitive setae, having stout retrolateral paracymbial process (PP) and retrobasal cymbial extension (CE) extending at least ¼ length of papal tibia; subtegulum large, filling most of cymbial concavity and extending to prolateral cymbial margin, and with probasal broad ridge (SL) that interlocks with tegulum; tegulum rounded with conical process (TL) on prolateral margin, this process interlocking with subtegular ridge; embolus (E) broad and thick, arising proapically, with pointed apex, small crest subapically and curved basomediam process (EBP) arising from embolus base; median apophysis (MA) strongly sclerotized, short, hooked, curved prolaterad; conductor (C) hyaline fan-shaped, narrow at base; paraconductor (Pc) small, cradling inner margin of E.

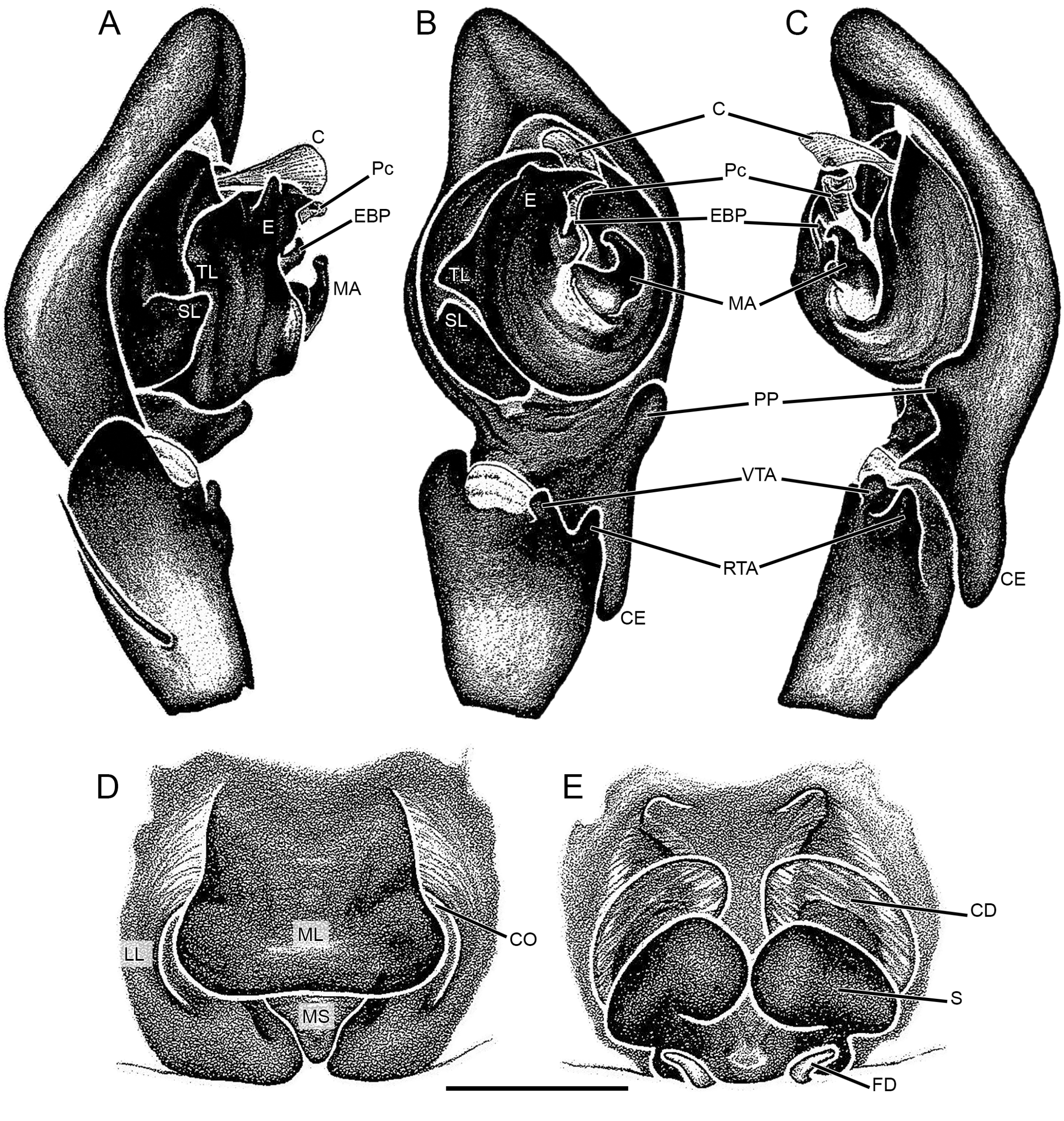

Fig. 25. *Zorodictyna silvadavilae* sp. nov., genitalia drawings; A–C = male holotype (CASENT_9006231; CAS); D–E = female paratype (CASENT_9006230; USNM). **A**. Left palp, prolateral view. **B**. Idem, ventral view. **C**. Idem, retrolateral view. **D**. Epigyne, ventral view. **E**. Endogyne, dorsal view. Abbreviations: C = conductor; CD = copulatory duct; CE = cymbial retrobasal extension; CO = copulatory opening; E = embolus; EBP = embolus basal process; FD = fertilisation duct; LL = lateral lobe; MA = median apophysis; ML = median lobe; MS = median sector; Pc = paraconductor; PP = paracymbial process; RTA = retrolateral tibial apophysis; S = spermatheca; SL = subtegular locking lobe; TL = tegular locking lobe; VTA = ventral tibial apophysis. Scale bars = 0.25 mm. Illustrations by Jenny Speckels.

Female paratype (CASENT_9015400; CAS; except as otherwise indicated)
MEASUREMENTS. Total length: 23.00. Carapace: length 11.20, width 8.30, height 5.00.

COLOUR (Fig. 24C–D). As in male: dorsal and lateral of cephalothorax, abdomen and legs unicolorous grey-brown, venter of sternum, mouthparts, coxae and trochanters yellow white.

STERNUM (Fig. 24D). Oval with sides straight next to leg coxae; 4.10 wide, 4.90 long.

CHILUM. 0.25 high, 0.75 wide.

EYES. ALE 0.30; AME 0.29; PLE 0.31; PME 0.28; ALE–AME 0.18; AME–AME 0.50; PLE–PME 0.48; PME–PME 0.23; MOQ: AW 0.73, PW 0.83, L 0.23.

CLYPEUS. With 14 long setae.

LEG. Scopulae beneath all tarsi, apical half of metatarsus I and apical third of metatarsus II.

Leg measurements

	F	P	T	Mt	t	Total
I	8.30	4.30	7.00	6.20	3.10	28.90
II	7.50	4.00	5.60	5.80	2.90	25.80
III	6.20	3.20	4.60	5.00	3.00	22.00
IV	8.80	3.60	7.00	12.40	3.50	33.30

Spination

	F	P	T	Mt
I	pl2d1	–	v2-2-2-2	v2-2-2
II	pl2d1	–	v2-2-2-2	v2-2-2
III	pl2d3rl3	pl1rl1	pl2d2rl2v2-2-2	pl4rl4v2-2-1-2
IV	pl3d3rl1	pl1rl1	pl2d2rl2v2-2-2	pl4d2rl3v2-2-1-2

GENITALIA. Epigyne (paratype CASENT_9006230; USNM), (Fig. 25D) with quadrangular median lobe (ML) plate transverse with smooth margin; copulatory openings (CO) hidden beneath anterolateral corners of ML; lateral lobes (LL) convex, without lateral teeth or projections but with faint concavities along margin of ML, converging posteriorly and exposing triangular area of median sector (MS). Endogyne (Fig. 25E) with broad, semitransparent copulatory ducts (CD) extending from beneath ML to simple, convex, bean-shaped spermathecae (S), spermathecal head with several small pores; spermathecal bases meeting in center; fertilization ducts (FD) short and slightly curved.

Variation

Males (n = 4)
Total length = 17.60–24.00, carapace length/width = 1.12–1.28, carapace height/width = 0.44–0.54, PER/carapace width = 0.20–0.22, PER/OAL = 2.50–2.80, PER/AER = 1.35–1.56, OAL/OQL = 1.00–1.13, OQP/OQA = 1.22–1.46, sternum length/width = 1.22–1.33, palpal coxa length/width = 1.92–2.90, femur I length/carapace width = 1.04–1.23, metatarsus I length/carapace width = 0.98–1.16, femur IV length/carapace width = 1.10–1.31. Male palp with apical RTA tips acute (Marojejy) to blunt (Masoala), EBP hook at embolic base triangular (Marojejy) to crescentic (Masoala), retromedian tegular lock (TL) blunt (Marojejy) to sharply triangular (Masoala). Males from Marojejy have a small subterminal crest on the embolus, which is absent from the male from Masoala.

Females (n = 4)
Total length = 23.00–32.50, carapace length/width = 1.26–1.41, carapace height/width = 0.46–0.60, PER/carapace width = 0.23–0.26, PER/OAL = 2.87–3.41, PER/AER = 1.30–1.43, OAL/OQL = 1.03–1.06, OQP/OQA = 1.14–1.23, sternum length/width = 1.18–1.24, palpal coxa length/width = 2.32–3.45, femur I length/carapace width = 0.92–1.00, metatarsus I length/carapace width = 0.66–0.75, femur IV length/carapace width = 1.02–1.07. Epigyne with median lobe length 0.70–0.78 times width; distance from median lobe base to epigastric fold 0.29–0.40 times median lobe length.

Note on synonym

A specimen of this species (CASENT_9014998) was used as an exemplar in a previously published molecular phylogeny: it was listed as "*Zorodictyna* sp. CG47" by Wheeler *et al.* (2017).

Natural history

This species has been collected when running on leaf litter in closed canopy montane rainforest. Individuals have an entire cribellum but we have yet to learn details of their use of silk.

Distribution

Individuals of this species are known only from the montane rainforests on the Marojejy Massif and the Masoala Peninsula in northeastern Madagascar (Fig. 26).

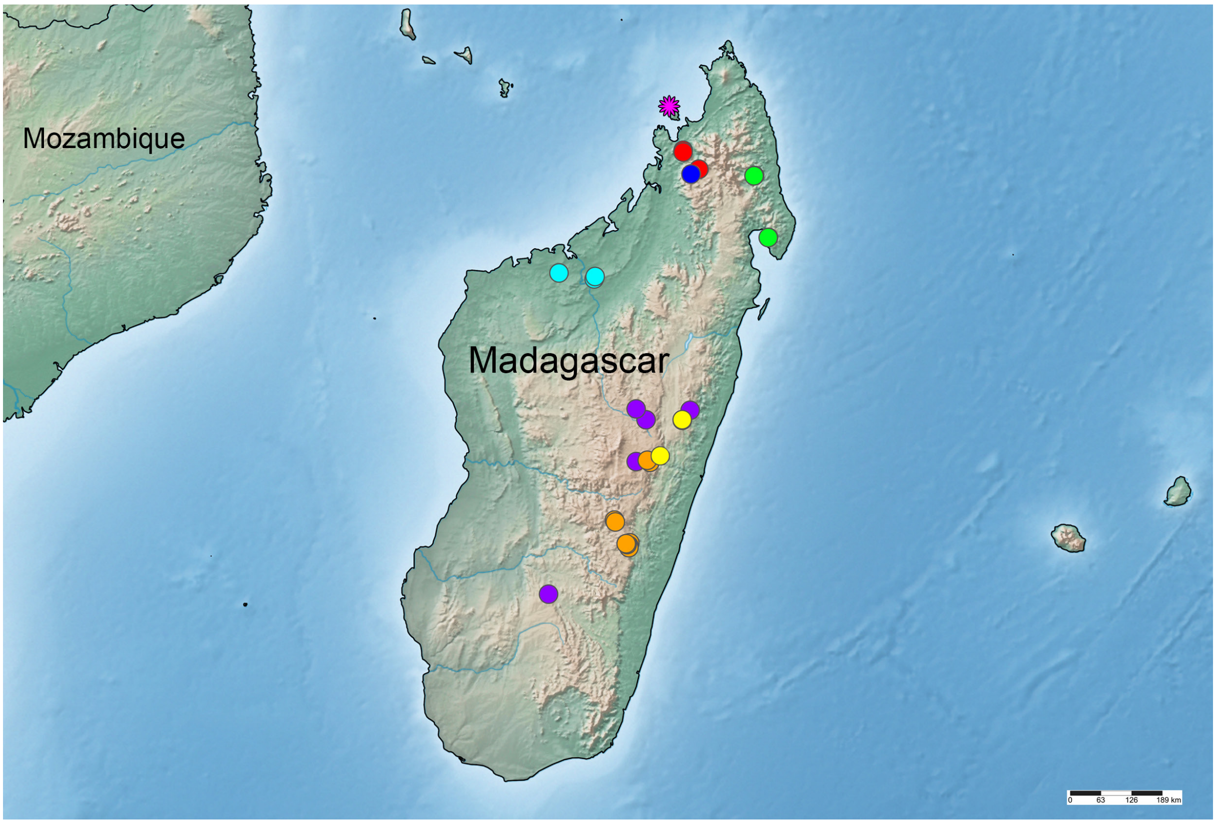

Fig. 26. Distribution map of species, and samples localities in the northern and eastern part of Madagascar. *Tabiboka milleri* gen. et sp. nov. (orange), *Tabiboka milloti* gen. et sp. nov. (yellow), *Tabiboka polotowae* gen. et sp. nov. (purple), *Zorascar pasunepipe* gen. et sp. nov. (red), *Zorascar pasunepomme* gen. et sp. nov. (dark blue), *Zorodictyna almae* sp. nov. (pale blue), *Zorodictyna silvadavilae* sp. nov. (green), *Zorodictyna oswaldi* (Lenz, 1891) (pink star).

Discussion

The study of the families in the Oval-Calamistrum clade has made significant progress since beginning in the last century (Griswold 1993) but the monophyly and limits of many taxa remain poorly supported, and relationships of other taxa, e.g., *Campostichomma* Karsch, 1892, remain untested. Notably, the scope and placement of Zoropsidae is still unsettled (Wheeler *et al.* 2017; Kulkarni *et al.* 2023). Polotow *et al.* (2015) made a significant step to construct a more comprehensive phylogeny of these spiders based on a "total evidence" approach (combining both morphological and molecular data). Their work led to the establishment of a well-supported Udubidae family, which included the genera *Uduba*, *Campostichomma* Karsch, 1892, *Raecius*, and *Zorodictyna*. Amidst this taxonomic instability, the monophyly of Udubidae appears to stand on solid ground (Griswold & Ramírez 2017).

The attribution of the genera to the different families remains a difficult undertaking, certainly when it is based on morphological characters alone. Sometimes, DNA analyses are needed to provide sufficient resolution and algorithmic support to place taxa. It is worth noting that at the beginning of the present research, the "*Zorodictyna*" samples used in Polotow *et al.* (2015), Wheeler *et al.* (2017) and Kulkarni *et al.* (2023) in a much larger molecular dataset, were represented by then undescribed "*Zorodictyna*" species from Madagascar. These sequences were then compared here with those of our recently collected representatives (i.e., *Zorascar* gen. nov.). According to our analysis, including the morphological data of Polotow *et al.* (2015), our species of *Zorascar* form a monophyletic entity, sister to Udubidae. According to our molecular study, they group close to *Zorodictyna*, which places them in the Udubidae. Finally, our analysis of these data revealed at least two species-groups, which means that apart from *Zorodictyna* other genera need to be created to accommodate these unidentified GenBank taxa. The erection of *Tabiboka* gen. nov. and *Zorascar* is the first step for this process. In this work, we have described these unknown udubids, including two new genera and five new species in the family.

Madagascar is known for its remarkable flora and fauna, making it a hotspot for biodiversity (Myers *et al.* 2000; Goodman 2022). This remarkably rich diversity extends to spiders as well (Griswold 2002; Henrard & Jocqué 2017; Griswold *et al.* 2022; Wood & Griswold 2022). Recently, Griswold *et al.* (2022) highlighted the rich fauna of Udubidae in Madagascar with the description of 35 new species in the genus *Uduba* (from four previously known). This pattern is likely to continue as research on other udubid groups progresses. Certainly, with the contribution of molecular data, future studies will illuminate the phylogeny of the many species in this larger "*Zorodictyna*" group (more than 50 expected, CEG, pers. obs. 2023). It remains to be seen whether these generic diagnoses will hold up when another fifty or more species are taken into account. However, the current efforts to unveil the hidden facets of this biodiversity promise to be an exciting journey in the study of this group of spiders.

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Appendices

Appendix 1. Information on the primers (names. strand direction - forward (F) or reverse (R) - sequences and sources) used in this study for the amplification and sequencing of the studied markers

Marker	Primer name	Direction	Primer sequence	References
COI	C1-J-1718-spider	F	5'-GGNGGATTTGGAAATTGRTTRGTTCC-3'	Vink *et al.* (2005)
	C1-N-2568	R	5'-GCTACAACATAATAAGTATCATG-3'	Hedin & Maddison (2001)
	LCO1-1490	F	5'-GGTCAACAAATCATAAAGATATTG-3'	Folmer *et al.* (1994)
16S rRNA	LR-N-13398 (16Sar)	F	5'-CGCCTGTTTAACAAAAACAT-3'	Simon *et al.* (1994)
	LR-J-12887 (16Sbr)	R	5'-CCGGTCTGAACTCAGATCACGT-3'	Simon *et al.* (1994)

Appendix 2 (continued on next page). GenBank sequences included in the phylogenetic analyses. In **blod** specimens belonging to species newly described in this work.

Familly	***Species***	**isolate**	**Reference**	**Collection reference**	**Locality**	**COI**	**16S**
Ctenidae	*Ancylometes bogotensis*	ARACG256	Wheeler *et al.*2017	CASENT 9021737	French Guiana	KY017632	KY015784
Senoculidae	*Senoculus cf. iricolor*	ARAMR700	Wheeler *et al.*2017	MACN-Ar 11315	Argentina	KY017912	KY016110
Senoculidae	*Senoculus* sp.	DP-2014	Polotow *et al.* 2015	UFMG 3250	Brazil	KM225122	/
Udubidae	*Raecius asper*	496-ARAMR496	Polotow *et al.* 2015, Wheeler *et al.*2017	AMNH	Cameroon	KM225121-KY018035	KY016220
Udubidae	*Uduba platnicki*	DP-2014	Polotow *et al.* 2015	CASENT 9030253	Madagascar	KM225129	/
Udubidae	*Uduba kavanaughi*	ARACG301	Wheeler *et al.*2017	CASENT 9024063	Madagascar	KY018036	KY016221
Udubidae	***Tabiboka milleri*** gen. et sp. nov.	ARACG300	Wheeler *et al.*2017	CASENT 9024004	Madagascar	KY018037	/
Udubidae	***Tabiboka milloti*** gen. et sp. nov.	ARACG045	Wheeler *et al.*2017	CASENT 9005657	Madagascar	KY018038	KY016222
Udubidae	***Zorodictyna silvadavilae*** sp. nov.	ARACG047	Wheeler *et al.*2017	CASENT 9014998	Madagascar	KY018039	KY016223
Udubidae	***Zorodictyna almae*** sp. nov.	DP-2014d	Polotow *et al.* 2015	CASENT 9031271	Madagascar	KM225137	/
Udubidae	***Tabiboka milleri*** gen. et sp. nov.	DP-2014c	Polotow *et al.* 2015	CASENT 9035866	Madagascar	KM225136	/
Udubidae	***Tabiboka polotowae*** gen. et sp. nov.	DP-2014b	Polotow *et al.* 2015	CASENT 9029890	Madagascar	KM225135	/
Udubidae	***Tabiboka polotowae*** gen. et sp. nov.	DP-2014a	Polotow *et al.* 2015	CASENT 9029889	Madagascar	KM225134	/
Zoropsidae	*Australotengella toddae*	9023720	Polotow *et al.* 2015	CASENT 9023720	Australia	KM225097	/
Zoropsidae	*Ciniflella* sp. '*Iguazu*'	ARAMR699	Wheeler *et al.*2017	MACN-Ar 11314	Argentina	KY018070	KY016252
Zoropsidae	*Griswoldia acaenata*	90423202	Polotow *et al.* 2015	CASENT 9043202	South Africa	KM225109	/
Zoropsidae	*Griswoldia disparilis*	9024917	Polotow *et al.* 2015	CASENT 9024917	South Africa	KM225110	/
Zoropsidae	*Griswoldia transversa*	ARACG304	Wheeler *et al.*2017	CASENT 9023631	South Africa	KY018071	/
Zoropsidae	*Kilyana hendersoni*	9023591 - ARACG307	Polotow *et al.* 2015, Wheeler *et al.*2017	CASENT 9023591 - CASENT 9023718	Australia	KM225112-KY018072	KY016253
Zoropsidae	*Kilyana* sp.	ARACG306	Wheeler *et al.*2017	CASENT 9023680	Australia	KY018073	KY016254
Zoropsidae	*Liocranoides archeri*	ARAMH011	Wheeler *et al.*2017	MACN_MCH 05_057	USA	KY018074	KY016255
Zoropsidae	*Phanotea digitata*	9043274	Polotow *et al.* 2015	CASENT 9043274	South Africa	KM225119	/
Zoropsidae	*Phanotea sathegyna*	ARACG309	Wheeler *et al.*2017	CASENT 9023618	South Africa	KY018075	KY016256
Zoropsidae	*Tengella radiata*	ARASP070	Wheeler *et al.*2017	AMNH-USNM	Costa-Rica	KY018076	KY016257
Zoropsidae	*Tengella* sp.	DP-2014	Polotow *et al.* 2015	CAS 9047627	Panama	KM225123	/

Appendix 2 (continued). GenBank sequences included in the phylogenetic analyses. In **blod** specimens belonging to species newly described in this work.

Familly	***Species***	**isolate**	**Reference**	**Collection reference**	**Locality**	**COI**	**16S**
Zoropsidae	*Titiotus* sp.	DP-2014	Polotow *et al.* 2015	CASENT 9047630	USA	KM225126	/
Zoropsidae	*Uliodon frenatus*	9047620	Polotow *et al.* 2015	CASENT 9047620	New Zealand	KM225130	/
Zoropsidae	*Uliodon* sp.	ARACG127	Wheeler *et al.*2017	CASENT 9021454	New Zealand	KY018078	KY016259
Zoropsidae	*Uliodon* sp.	ARACG124	Wheeler *et al.*2017	CASENT 9021450	New Zealand	KY018077	KY016258
Zoropsidae	*Uliodon* sp.	ARACG182	Wheeler *et al.*2017	CASENT 9021453	New Zealand	KY018079	KY016260
Zoropsidae	*Zorocrates fuscus*	/	Blackledge *et al.* 2009	AMNH	Mexico	FJ607588	FJ607475
Zoropsidae	*Zorocrates* sp.	ARAMR012	Wheeler *et al.*2017	AMNH	Mexico	KY018080	KY016261
Zoropsidae	*Zoropsis spinimana*	ARACG048	Wheeler *et al.*2017	CASENT 9019845	USA	KY018081	KY016262

Appendix 3. Selection model estimated using PartitionFinder 2 (Lanfear *et al.* 2016) and based on one partition for 16S and three for COI (partitioned into single codon positions).

Settings used

alignment :\./Zorascar_COI-16S.phy

branchlengths : linked

models : JC, K80, SYM, F81, HKY, GTR, JC+G, K80+G, SYM+G, F81+G, HKY+G, GTR+G, JC+I, K80+I, SYM+I, F81+I, HKY+I, GTR+I, JC+I+G, K80+I+G, SYM+I+G, F81+I+G, HKY+I+G, GTR+I+G

model_selection : bic

search : greedy

Best partitioning scheme

Scheme Name : start_scheme

Scheme lnL : -13427.333252

Scheme BIC : 27663.737478

Number of params : 111

Number of sites : 1464

Number of subsets : 4

Subset	Best Model	# sites	Partition names
1	GTR+I+G	343	COI_1
2	GTR+I+G	343	COI_2
3	HKY+G	343	COI_3
4	GTR+I+G	435	16S

Nexus formatted character sets used for GARLI

begin sets;

charset Subset1 = 1-1029\3;

charset Subset2 = 2-1029\3;

charset Subset3 = 3-1029\3;

charset Subset4 = 1030-1464;

```
charpartition PartitionFinder = Group1:Subset1, Group2:Subset2, Group3:Subset3, Group4:Subset4;

end;
```

MrBayes block for partition definitions

```
begin mrbayes;

	charset Subset1 = 1-1029\3;

	charset Subset2 = 2-1029\3;

	charset Subset3 = 3-1029\3;

	charset Subset4 = 1030-1464;

	partition PartitionFinder = 4:Subset1, Subset2, Subset3, Subset4;

	set partition=PartitionFinder;

	lset applyto=(1) nst=6 rates=invgamma;

	lset applyto=(2) nst=6 rates=invgamma;

	lset applyto=(3) nst=2 rates=gamma;

	lset applyto=(4) nst=6 rates=invgamma;

	prset applyto=(all) ratepr=variable;

	unlink statefreq=(all) revmat=(all) shape=(all) pinvar=(all) tratio=(all);

end;
```

Appendix 4. Estimates of evolutionary divergence (expressed in %) between sequences of *Zorascar* gen. nov. and the Udubidae representatives used in the study. The number of base differences per site from between sequences is shown for each compared taxa. The rate variation among sites was modeled with a gamma distribution (shape parameter = 4). This analysis involved 15 nucleotide sequences with 1020 positions in the final dataset for COI (lower left corner) and nine sequences with 436 positions in the final dataset for 16S (upper right corner). All ambiguous positions were removed for each sequence pair (pairwise deletion option). Evolutionary analyses were conducted in MEGA X (Kumar *et al.* 2018; Stecher *et al.* 2020). In **blod** specimens belonging to species newly described in this work.

COI (lower part)/16S upper part)	RJ5	RJ1	RJ4	RJ2	RJ3	R. asper	CG301	DP2014	CG300	CG45	CG47	DP2014d	DP2014c	DP2014b
RJ5 *Zorascar pasunepipe* gen. et sp. nov. M		0	10.21	10.21	10.21	18.18	17.54			18.69	17.45			
RJ1 *Zorascar pasunepipe* gen. et sp. nov. juv.	0		10.07	10.07	10.07	18.31	17.89			18.12	17.32			
RJ4 *Zorascar pasunepomme* gen. et sp. nov. F	10.56	10.55		0	0	19.63	18.97			18.24	19.58			
RJ2 *Zorascar pasunepomme* gen. et sp. nov. juv.	10.52	10.55	0		0	19.63	18.97			18.24	19.58			
RJ3 *Zorascar pasunepomme* gen. et sp. nov. juv.	10.91	10.91	1.07	1.07		19.63	18.97			18.24	19.58			
Raecius asper	15.64	16.13	15.06	15.01	15.82		18.59			21.58	18.03			
Uduba kavanaughi CG301	14.92	15.95	13.76	13.71	14.12	15.75				20	21.38			
Uduba platnicki DP2014	15.5	17.12	16.44	16.33	17.12	14.86	9.5				20.37			
***Tabiboka milleri* gen. et sp. nov. CG300**	12.15	12.35	12.46	12.41	13.05	13.89	15	15.3						
***Tabiboka milloti* gen. et sp. nov. CG45**	13.99	14.26	11.8	11.75	12.3	15.98	13.47	13.69	10.17					
***Zorodictyna silvadavilae* sp. nov. CG47**	16.11	17.51	15.18	15.13	15.3	16.48	15	15.3	13.43	14.61				
***Zorodictyna almae* sp. nov. (sp1) DP2014d**	11.09	12.16	11.26	11.19	11.49	13.25	12.56	13.37	12.4	13.2	12.08			
***Tabiboka milleri* gen. et sp. nov. (sp2) DP2014c**	12.07	12.16	11.71	11.63	11.71	14.22	15.3	15.3	0.32	10.31	13.04	12.4		
***Tabiboka polotowae* gen. et sp. nov. (sp3) DP2014b**	10.6	11.26	10.36	10.29	10.59	13.7	13.05	15.01	10.77	12.4	13.05	11.58	10.77	
***Tabiboka polotowae* gen. et sp. nov. (sp4) DP2014a**	10.6	11.94	10.81	10.74	11.49	13.25	13.2	15.14	11.59	11.59	12.88	11.59	11.59	2.45

Appendix 5. Illustrations of the male specimen BE_RMCA_ARA.Ara.136920, re-identified as *Uduba madagascariensis* (Vinson, 1863).

Benoit (1972: 180, fig. 3) misidentified the male specimen BE_RMCA_ARA.Ara.136920, which he believed to be conspecific with the female *Zorodictyna inhonesta* (Simon, 1906). The examination and analyses of the palp with micro-CT 3D scans (see Figs A.5-1–2), revealed that this male specimen belongs to the species *Uduba madagascariensis* (Vinson, 1863) (see Griswold *et al.* 2022 for a complete description of that species). Images and 3D model of the palp are also visible on the RMCA Virtual Collection (https://virtualcol.africamuseum.be/providence/pawtucket/index.php, accessed in October 2023).

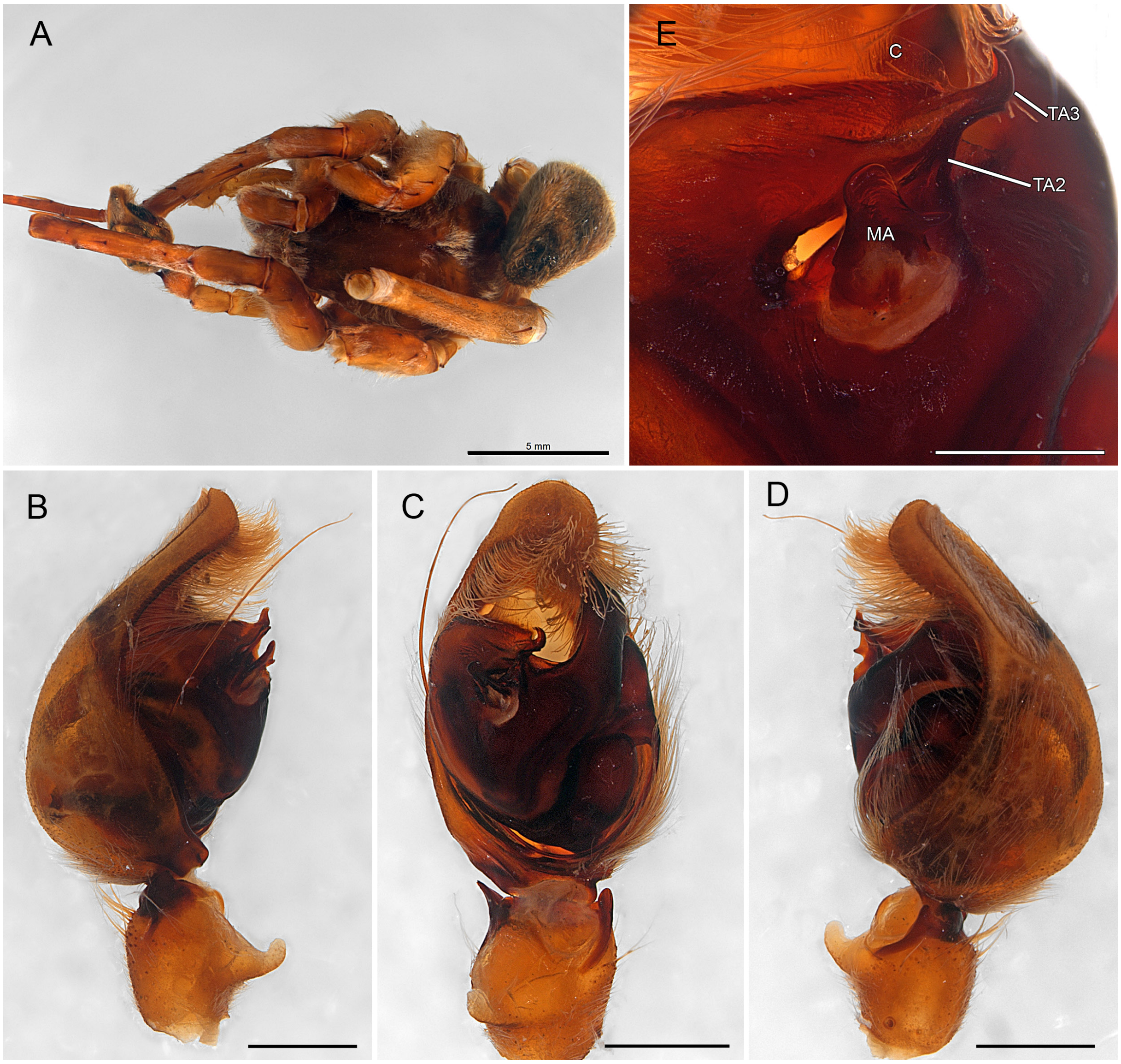

Fig. A.5-1. *Uduba madagascariensis* (Vinson, 1863), male wrongly identified by P.L.G. Benoit as *Uduba inhonesta* Simon, 1906 (Benoit 1972: 180, fig. 3) (BE_RMCA_ARA.Ara.136920; RMCA). **A**. Habitus dorsal view. **B**. Right palp, retrolateral view. **C**. Idem, ventral view. **D**. Idem, prolateral view. **E**. Bulbus, with detail on tegular apophyses, retroventral view. Abbreviations: C = conductor; MA = median apophyis; TA1 = proapical tegular apophysis; TA2 = proapical tegular apophysis, arising just prolaterad of distal notch; TA3 = retroapical tegular apophysis, with apex extending in prolateral direction. Scale bars: A = 5 mm, B–D = 1mm, E = 0.5 mm.

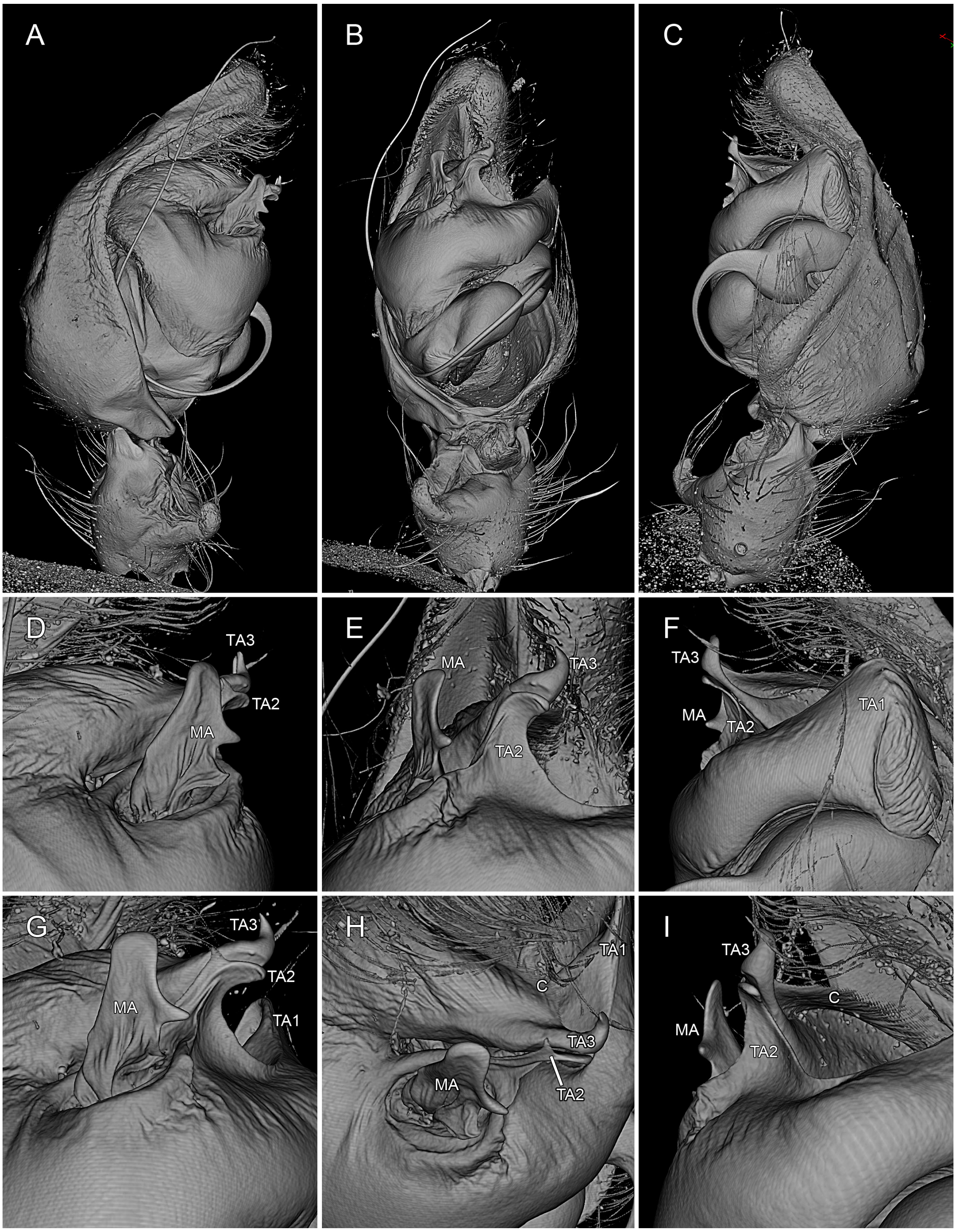

Fig. A.5-2. *Uduba madagascariensis* (Vinson, 1863), micro-CT 3D scans of the palp of male wrongly identified by P.L.G. Benoit as *Uduba inhonesta* Simon, 1906 (Benoit 1972: 180, fig. 3) (BE_RMCA_ARA.Ara.136920; RMCA). **A**. Right palp, retrolateral view. **B**. Idem, ventral view. **C**. Idem, prolateral view. **D**. Detail of tegular apophyses, retrolateral view. **E**. Idem, ventral view. **F**. Idem, proventral view. **G**. Idem, retroventral view. **H**. Idem, anterior view. **I**. Idem, prolateral view. Abbreviations: C = conductor; MA = median apophyis; TA1 = proapical tegular apophysis; TA2 = proapical tegular apophysis, arising just prolaterad of distal notch; TA3 = retroapical tegular apophysis, with apex extending in prolateral direction. No scale provided.