

# Echinoids of the Kerguelen Plateau – occurrence data and environmental setting for past, present, and future species distribution modelling

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## Abstract

The present dataset provides a case study for species distribution modelling (SDM) and for model testing in a poorly documented marine region.

The dataset includes spatially-explicit data for echinoid (Echinodermata: Echinoidea) distribution. Echinoids were collected during oceanographic campaigns led around the Kerguelen Plateau (+63°/+81°E; -46°/-56°S) since 1872. In addition to the identification of collection specimens from historical cruises, original data from the recent campaigns POKER II (2010) and PROTEKER 2 to 4 (2013–2015) are also provided. In total, five families, ten genera, and 12 echinoid species are recorded in the region of the Kerguelen Plateau.

The dataset is complemented with environmental descriptors available and relevant for echinoid ecology and SDM. The environmental data was compiled from different sources and was modified to suit the geographic extent of the Kerguelen Plateau, using scripts developed with the R language (R Core Team 2015). Spatial resolution was set at a common 0.1° pixel resolution. Mean seafloor and sea surface temperatures, salinity and their amplitudes, all derived from the World Ocean Database (Boyer et al. 2013) are made available for the six following decades: 1955–1964, 1965–1974, 1975–1984, 1985–1994, 1995–2004, 2005–2012.

Future projections are provided for several parameters: they were modified from the Bio-ORACLE database (Tyberghein et al. 2012). They are based on three IPCC scenarii (B1, AIB, A2) for years 2100 and 2200 (IPCC, 4<sup>th</sup> report).

**Keywords**

Echinoidea, environmental descriptors, future projections, historical overview, Kerguelen Plateau, Southern Ocean

**Project description**

**Project title:** Temporal, spatial, and sampling heterogeneities in species distribution modelling. A case study for the data-poor area of the Kerguelen Plateau.

**Personnel:** Charlène Guillaumot, Alexis Martin, Salomé Fabri-Ruiz, Marc Eléaume, Thomas Saucède

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**Study extent description**

The study area of this dataset includes the Kerguelen Plateau, located at the boundary between the Indian and Southern Oceans, in the flow of the Antarctic Circumpolar Current (Park and Vivier 2011). The plateau is the second largest oceanic igneous province on Earth. It is positioned between 46°S and 62°S latitude, between 63°E and 81°E longitude, and it extends over 500 km from East to West and 2,100 km from North to South for a total surface area of  $2.10^6$  km<sup>2</sup> (Cottin et al. 2011).

The Kerguelen Plateau is subdivided into the Kerguelen Islands shelf in the north and the Heard and McDonalds Islands shelf in the south. The two shelves are separated by a controlling oceanographic barrier: the Polar Front, which position has recurrently been discussed (Park et al. 2014). Topography and currents also strongly control other environmental parameters (temperature, salinity, chlorophyll a concentration) in the vicinity of the Plateau (Graham et al. 2012, Chacko et al. 2014).

The Kerguelen Plateau hosts important economic activities, namely through fishing, generating potential issues for the conservation of marine biodiversity. Exploitation of the marine living resources of the Kerguelen Plateau has been sustainably managed by CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) and by the TAAF (French Southern and Antarctic Lands) in the French EEZ (Exclusive Economic Zone) with scientific support from the Muséum national d'Histoire naturelle of Paris since 1978 (Duhamel and Williams 2011). In the Australian EEZ, in the south, a similar management system was established in 1979 and was followed by the designation in 2002 of the Heard Island and McDonald Islands



(HIMI) Marine Protected Area: one of the world's largest MPA with an area of 65,000 km<sup>2</sup> (Welsford et al. 2011).

The Kerguelen Plateau represents a vast marine area challenged by strong anthropogenic and natural pressures. Relatively few scientific programs have studied marine biodiversity of the Kerguelen Plateau, leaving it poorly documented. In this context, environmental descriptors could prove to be useful proxies to infer species distribution when occurrence data are missing (Hemery et al. 2011).

In addition to the study of collection specimens sampled during historical cruises and identified at species level, the present work also provides original data collected during the recent oceanographic campaign POKER II (2010) and during three field summer campaigns of the IPEV program 1044 PROTEKER (2013-2015) led in nearshore areas of the Kerguelen Islands. The spatial extent of the dataset was based on the bathymetric range of echinoids for species distribution modelling to be performed with limited extrapolations.

## **Design description**

Our project aimed at improving the robustness of existing modelling approaches in the case of areas for which only poor and heterogeneous biodiversity data are available, a situation prevailing in the region of the Kerguelen Plateau, and generally in the Southern Ocean (Gutt et al. 2012).

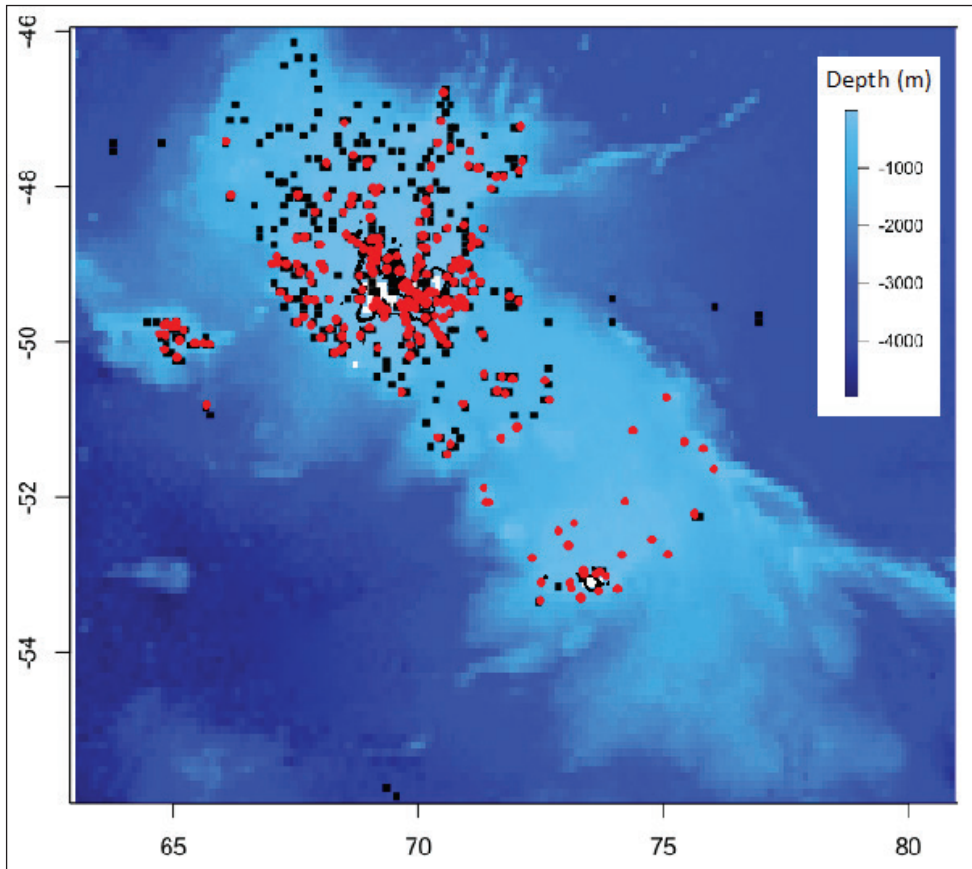
Data compilation from various sources implies temporal heterogeneities that may constitute a critical point when building species distribution models (Aguilar et al. 2015). Spatial and sampling heterogeneities are also likely to introduce biases due to differences in sampling strategies and the gears used during the various cruises. Our objectives were (1) to assess the influence of temporal, spatial, and sampling heterogeneities on species distribution modelling using datasets of echinoid occurrences on the Kerguelen Plateau, (2) to model echinoid distribution on the Kerguelen Plateau for different time periods, and (3) to evaluate potential shifts in species distribution with regards to future projections based on IPCC scenarii (Jueterbock et al. 2013).

## **Data description**

Occurrence data were compiled from many oceanographic campaigns led over a long time-period starting with the Challenger Expedition in 1872 and ending with the recent PROTEKER campaigns that took place between 2013 and 2015 (Table 1). The dataset was modified after Pierrat et al. (2012) and Saucède et al. (2015a). Specimens from recent cruises (POKER II and PROTEKER) were identified at species level and added to the dataset.

**Table 1.** Field campaigns during which echinoids of the dataset were collected. MNHN: Muséum national d'Histoire naturelle.

Campaigns	Year	Occurrence Nb	Research vessels	References	Collections
Challenger Expedition	1872	9	Challenger	A. Agassiz 1879, 1881	National History Museum, London
Gazelle Expedition	1874–76	1	Gazelle	Studer 1876	Museum für Naturkunde, Berlin
Deutsche Tiefsee Expedition	1898–99	3	Valdivia	Döderlein 1906	Museum für Naturkunde, Berlin
Deutsche Südpolar Expedition	1901–03	2	Gauss	Mortensen 1909	Museum für Naturkunde, Berlin
BANZAR Expedition	1929	9	Discovery	Mortensen 1950	National Museum of Australia, Acton
Kerguelen 1962–63	1962–63	8	-	Grua 1963	MNHN, Paris
Eltanin Expedition	1962–72	1	Eltanin	Fell 1976	Smithsonian Institution, Washington
Ker72	1972	5	Japonaise	Guille 1977	MNHN, Paris
MD03	1974	32	Marion Dufresne	De Ridder et al. 1992	MNHN, Paris
MD04	1975	130	Marion Dufresne	De Ridder et al. 1992	MNHN, Paris
SIBEX MD42	1985	13	Marion Dufresne	Pierrat et al. 2012	MNHN, Paris
1985 ANARE Expedition	1985	5	Nella Dan	Burton and Williams 1985	National Museum of Australia, Acton
Benthos/mac	1991	22	Curieuse	Poulin and Féral 1995	Banyuls oceanological observatory
1992 ANARE Expedition	1992	18	Aurora Australis	Green 1993	National Museum of Australia, Acton
Cruise SC26	2003	2	Southern Champion	Pierrat et al. 2012	Australian Antarctic Division, Kingston
POKER II	2010	111	Austral	this study	MNHN, Paris
PROTEKER 2	2013	52	Curieuse	Féral et al. 2013	MNHN, Paris
PROTEKER 3	2014	7	Curieuse	Féral et al. 2014	MNHN, Paris
PROTEKER 4	2015	5	Commerson	Saucède et al. 2015b	MNHN, Paris



**Figure 1.** Sampling effort. Red dots depict echinoid occurrences. Black squares correspond to visited sites at which no echinoid was sampled.

Occurrences are presence-only data for which different sampling tools, protocols, and strategies were used. Moreover, the study area was unevenly investigated, sampling effort being stronger in the northern than in the southern part of the Plateau (Figure 1). Accordingly, campaigns and sampling dates are mentioned in the dataset to take into account spatial and time heterogeneities.

The environmental descriptors provided in the dataset were compiled from different sources (Table 2 – see Annex). They were selected according to their relevance to echinoid ecology.

Environmental data were formatted with R3.3.0 software (R Core Team 2015) to fit the sampling area of where echinoids occur on the Kerguelen Plateau (+63°/+81°E; -46°/-56°S). They were set up to a 0.1° grid-cell spatial resolution with origin fixed at 0 (top left corner). Seafloor temperature, salinity, oxygen and nutrient concentration data were generated by using the provided data of the World Ocean Database (Boyer et al. 2013) and depth data.

In marine nearshore areas, grid-cells with positive depth values above sea level were corrected for accuracy using ArcGis Raster Editor Tool (ESRI 2011) based on geographic charts (IGN: National Geographic Institute, EAN: 3282110102707, scale 1/200 000) and raw depth values measured in the field (Féral et al. 2013, 2014, Saucède et al. 2015b).

Roughness data were computed using the “terrain” function of the raster package R3.3.0 (Hijmans and van Etten 2012).

The time coverage of the environmental data extends from 1955 to 2012. Mean annual surface and seafloor temperatures, salinity and their respective amplitudes (i.e., amplitude between mean summer (January to March) and mean winter (July to September) surface and seafloor temperatures and salinities) are available for the following six decades: 1955 to 1964, 1965 to 1974, 1975 to 1984, 1985 to 1994, 1995 to 2004, and 2005 to 2014.

Future projections of sea surface temperature, salinity, and amplitude were downloaded from the Bio-ORACLE database (Tyberghein et al. 2012). Projections are based on the IPCC A2, A1B, and B1 scenarii published in the 4<sup>th</sup> IPCC report (2007). The modelled data correspond to the extrapolated means for two decades: 2087-2096 (here referred to as 2100) and 2187-2196 (here referred to as 2200) (Jueterbock et al. 2013).

All the environmental descriptors and metadata sources are detailed in the data catalog (Table 2) and data are provided in an ascii raster format. N/A was set as the no data reference for missing data.

## Quality control description

Specimens sampled during POKER II and PROTEKER 2, 3 and 4 campaigns were all identified by T. Saucède at the species level. Identifications and taxonomic accuracies are based on Anderson (2009), Anderson (2012), David et al. (2005), Kroh and Smith (2010), Pierrat et al. (2012), and Saucède et al. (2015a).

The final compiled dataset was checked for consistency using the WoRMS database (WoRMS Editorial Board 2016) in order to match our data with the most up-to-date taxonomy. The dataset was checked for duplicates and errors due to overlapping origins, georeferencing mistakes, and species synonymy or mis-spelling. Only occurrence data identified at the species level were included.

Environmental data relies on different sources as reported in Table 2. The range of data was studied to check for variables consistencies. Data were not interpolated to limit interpolation biases and missing data were reported as N/A values.

## Taxonomic coverage

### General taxonomic coverage description:

The present dataset focuses on all species of the class Echinoidea (Echinodermata) occurring on the Kerguelen Plateau.

**Table 2.** Environmental variables provided in the present data paper. Salinity data are reported in the Practical Salinity Scale (PSS) format.

Environmental layer name	Spatial cover	Unit	Source	URL
seafloor_salinity_amplitude_1955_1964	46_56°S/63_81°E	PSS	This study: Derived from World Ocean Database (Boyer et al. 2013) surface salinity layers	<a href="https://www.node.noaa.gov/OC5/woa13/woa13data.html">https://www.node.noaa.gov/OC5/woa13/woa13data.html</a>
seafloor_salinity_amplitude_1965_1974	46_56°S/63_81°E	PSS		
seafloor_salinity_amplitude_1975_1984	46_56°S/63_81°E	PSS		
seafloor_salinity_amplitude_1985_1994	46_56°S/63_81°E	PSS		
seafloor_salinity_amplitude_1995_2004	46_56°S/63_81°E	PSS		
seafloor_salinity_amplitude_2005_2012	46_56°S/63_81°E	PSS		
seafloor_salinity_amplitude_1955_2012	46_56°S/63_81°E	PSS		
seasurface_salinity_amplitude_1955_1964	46_56°S/63_81°E	PSS		
seasurface_salinity_amplitude_1965_1974	46_56°S/63_81°E	PSS		
seasurface_salinity_amplitude_1975_1984	46_56°S/63_81°E	PSS		
seasurface_salinity_amplitude_1985_1994	46_56°S/63_81°E	PSS	World Ocean Database (Boyer et al. 2013)	
seasurface_salinity_amplitude_1995_2004	46_56°S/63_81°E	PSS		
seasurface_salinity_amplitude_2005_2012	46_56°S/63_81°E	PSS		
seasurface_salinity_amplitude_1955_2012	46_56°S/63_81°E	PSS		
seasurface_temperature_amplitude_2100_A1B	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_amplitude_2100_A2	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_amplitude_2100_B1	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_amplitude_2200_A1B	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_amplitude_2200_B1	46_56°S/63_81°E	°Celsius degrees		
seafloor_temperature_amplitude_1955_1964	46_56°S/63_81°E	°Celsius degrees		
seafloor_temperature_amplitude_1965_1974	46_56°S/63_81°E	°Celsius degrees	This study: Derived from World Ocean Database (Boyer et al. 2013) sea surface temperature layers	<a href="https://www.node.noaa.gov/OC5/woa13/woa13data.html">https://www.node.noaa.gov/OC5/woa13/woa13data.html</a>
seafloor_temperature_amplitude_1975_1984	46_56°S/63_81°E	°Celsius degrees		
seafloor_temperature_amplitude_1985_1994	46_56°S/63_81°E	°Celsius degrees		
seafloor_temperature_amplitude_1995_2004	46_56°S/63_81°E	°Celsius degrees		
seafloor_temperature_amplitude_2005_2012	46_56°S/63_81°E	°Celsius degrees		
seafloor_temperature_amplitude_1955_2012	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_amplitude_1955_1964	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_amplitude_1965_1974	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_amplitude_1975_1984	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_amplitude_1995_2004	46_56°S/63_81°E	°Celsius degrees		

Environmental layer name	Spatial cover	Unit	Source	URL
seasurface_temperature_amplitude_1985_1994	46_56°S/63_81°E	°Celsius degrees	World Ocean Database (Boyer et al. 2013)	<a href="https://www.nodc.noaa.gov/OC5/woa13/woa13data.html">https://www.nodc.noaa.gov/OC5/woa13/woa13data.html</a>
seasurface_temperature_amplitude_1995_2004	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_amplitude_2005_2012	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_amplitude_1955_2012	46_56°S/63_81°E	°Celsius degrees		
chlorophylla_summer_mean_2002_2009	46_56°S/63_81°E	mg/m³	MODIS AQUA (NASA) 2010	<a href="http://gdal1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_8day">http://gdal1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_8day</a>
geomorphology	46_56°S/63_81°E	categorical	ATLAS ETOPO2 2014 (Douglass et al. 2014)	<a href="http://ropex.ucsd.edu/WWW_mar_topo.html">http://ropex.ucsd.edu/WWW_mar_topo.html</a>
depth	46_56°S/63_81°E	meter	This study. Derived from Smith & Sandwell 1997	
seafloor_nitrate_mean_1955_2012	46_56°S/63_81°E	µmol/L	This study. Derived from World Ocean Database (Boyer et al. 2013) sea surface nitrate concentration layers	<a href="https://www.nodc.noaa.gov/OC5/woa13/woa13data.html">https://www.nodc.noaa.gov/OC5/woa13/woa13data.html</a>
seasurface_nitrate_mean_1955_2012	46_56°S/63_81°E	µmol/L	World Ocean Circulation Experiment 2013	
seafloor_oxygen_mean_1955_2012	46_56°S/63_81°E	mL/L	This study. Derived from World Ocean Database (Boyer et al. 2013) sea surface oxygen concentration layers	
seasurface_oxygen_mean_1955_2012	46_56°S/63_81°E	mL/L	World Ocean Circulation Experiment 2013	
seafloor_phosphate_mean_1955_2012	46_56°S/63_81°E	µmol/L	This study. Derived from World Ocean Database (Boyer et al. 2013) sea surface phosphate concentration layers	
seasurface_phosphate_mean_1955_2012	46_56°S/63_81°E	µmol/L	World Ocean Circulation Experiment 2013	
roughness	46_56°S/63_81°E	meter	This study. Derived from bathymetric layer	<a href="https://www.nodc.noaa.gov/OC5/woa13/woa13data.html">https://www.nodc.noaa.gov/OC5/woa13/woa13data.html</a>
seafloor_salinity_mean_1955_1964	46_56°S/63_81°E	PSS	This study. Derived from World Ocean Database (Boyer et al. 2013) sea surface salinity layers	
seafloor_salinity_mean_1965_1974	46_56°S/63_81°E	PSS		
seafloor_salinity_mean_1975_1984	46_56°S/63_81°E	PSS		
seafloor_salinity_mean_1985_1994	46_56°S/63_81°E	PSS		
seafloor_salinity_mean_1995_2004	46_56°S/63_81°E	PSS		
seafloor_salinity_mean_2005_2012	46_56°S/63_81°E	PSS		
seafloor_salinity_mean_1955_2012	46_56°S/63_81°E	PSS		
seasurface_salinity_mean_1955_1964	46_56°S/63_81°E	PSS		
seasurface_salinity_mean_1965_1974	46_56°S/63_81°E	PSS	World Ocean Database (Boyer et al. 2013)	
seasurface_salinity_mean_1975_1984	46_56°S/63_81°E	PSS		
seasurface_salinity_mean_1985_1994	46_56°S/63_81°E	PSS		
seasurface_salinity_mean_1995_2004	46_56°S/63_81°E	PSS		
seasurface_salinity_mean_1995_2004	46_56°S/63_81°E	PSS		

Environmental layer name	Spatial cover	Unit	Source	URL
seasurface_salinity_mean_2005_2012	46_56°S/63_81°E	PSS	World Ocean Database (Boyer et al. 2013)	<a href="https://www.node.noaa.gov/OC5/woa13/woa13data.html">https://www.node.noaa.gov/OC5/woa13/woa13data.html</a>
seasurface_salinity_mean_1955_2012	46_56°S/63_81°E	PSS		
seasurface_salinity_mean_2100_A1B	46_56°S/63_81°E	PSS		
seasurface_salinity_mean_2100_A2	46_56°S/63_81°E	PSS	BIO-ORACLE (Tyberghein et al. 2012)	<a href="http://www.oracle.ugent.be/">http://www.oracle.ugent.be/</a>
seasurface_salinity_mean_2100_B1	46_56°S/63_81°E	PSS		
seasurface_salinity_mean_2200_A1B	46_56°S/63_81°E	PSS		
seasurface_salinity_mean_2200_B1	46_56°S/63_81°E	PSS	McCoy (1991), updated by Griffiths 2014 (unpublished)	<a href="https://www.node.noaa.gov/OC5/woa13/woa13data.html">https://www.node.noaa.gov/OC5/woa13/woa13data.html</a>
sediments	46_56°S/63_81°E	categorical		
seafloor_silicate_mean_1955_2012	46_56°S/63_81°E	µmol/L		
seasurface_silicate_mean_1955_2012	46_56°S/63_81°E	µmol/L	This study: Derived from World Ocean Database (Boyer et al. 2013) sea surface silicate concentration layers	<a href="https://www.node.noaa.gov/OC5/woa13/woa13data.html">https://www.node.noaa.gov/OC5/woa13/woa13data.html</a>
slope	46_56°S/63_81°E	unitless	World Ocean Circulation Experiment 2013	
seafloor_temperature_mean_1955_1964	46_56°S/63_81°E	°Celsius degrees	Smith & Sandwell 1997	
seafloor_temperature_mean_1965_1974	46_56°S/63_81°E	°Celsius degrees	This study: Derived from World Ocean Database (Boyer et al. 2013) sea surface temperature layers	<a href="https://www.node.noaa.gov/OC5/woa13/woa13data.html">https://www.node.noaa.gov/OC5/woa13/woa13data.html</a>
seafloor_temperature_mean_1975_1984	46_56°S/63_81°E	°Celsius degrees		
seafloor_temperature_mean_1985_1994	46_56°S/63_81°E	°Celsius degrees		
seafloor_temperature_mean_1995_2004	46_56°S/63_81°E	°Celsius degrees		
seafloor_temperature_mean_2005_2012	46_56°S/63_81°E	°Celsius degrees		
seafloor_temperature_mean_1955_2012	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_mean_1955_1964	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_mean_1965_1974	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_mean_1975_1984	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_mean_1985_1994	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_mean_1995_2004	46_56°S/63_81°E	°Celsius degrees	World Ocean Database (Boyer et al. 2013)	<a href="http://www.oracle.ugent.be/">http://www.oracle.ugent.be/</a>
seasurface_temperature_mean_2005_2012	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_mean_1955_2012	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_mean_2100_A1B	46_56°S/63_81°E	°Celsius degrees	BIO-ORACLE (Tyberghein et al. 2012)	<a href="http://www.oracle.ugent.be/">http://www.oracle.ugent.be/</a>
seasurface_temperature_mean_2100_A2	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_mean_2100_B1	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_mean_2200_A1B	46_56°S/63_81°E	°Celsius degrees		
seasurface_temperature_mean_2200_B1	46_56°S/63_81°E	°Celsius degrees		



Echinoids are common species of benthic communities in the Southern Ocean and on the Kerguelen Plateau (David et al. 2005). They are diversified and well-studied. Historical data are available since 1872, starting with the Challenger Expedition, and are completed with recent occurrences collected nearshore areas of the Kerguelen Islands during the PROTEKER campaigns (2013–2015).

Echinoid studies take part in conservation issues. *Ctenocidaris nutrix* is considered a Vulnerable Marine Ecosystems (VME) indicator species by CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) and is widely distributed on the Kerguelen Plateau.

On the Kerguelen Plateau, the Class Echinoidea includes five families, ten genera, and 12 species. Species distribution is shown in Figure 2.

**Phylum:** Echinodermata

**Class:** Echinoidea

**Order:** Camarodonta, Cidaroida, Holasteroida, Spatangoida

**Family:** Ctenocidarinae, Echinidae, Plexechinidae, Pourtalesiidae, Schizasteridae

**Genus:** *Abatus*, *Aporocidaris*, *Brisaster*, *Ctenocidaris*, *Dermechinus*, *Plexechinus*, *Pourtalesia*, *Rhynchocidaris*, *Sterechinus*, *Tripylus*

**Species:** *Abatus cordatus*, *Aporocidaris milleri*, *Brisaster antarcticus*, *Ctenocidaris nutrix*, *Dermechinus horridus*, *Plexechinus sulcatus*, *Pourtalesia hispida*, *Pourtalesia debilis*, *Rhynchocidaris triplopore*, *Sterechinus diadema*, *Sterechinus neumayeri*, *Tripylus abatoides*

### Spatial coverage

General spatial coverage: the Kerguelen Plateau, Southern Ocean

Coordinates: -46°S and -56°S; +63°E and +81°E

### Temporal coverage

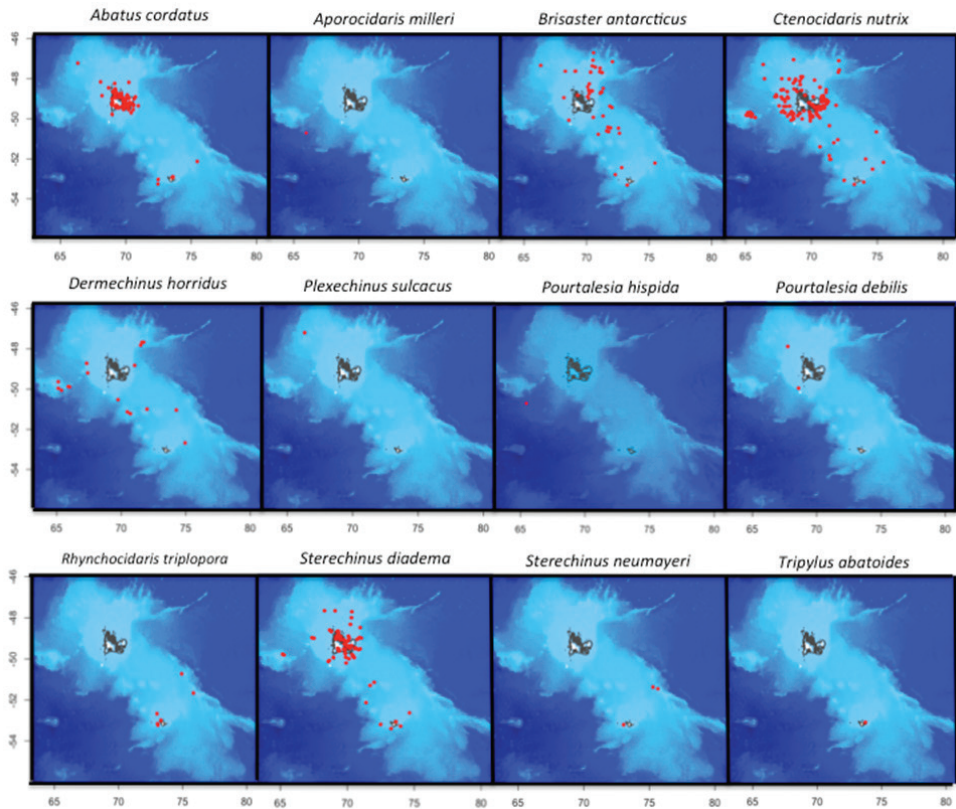
Temporal coverage: 1872–2015

### Datasets

#### Dataset occurrence description

Echinoid occurrences available on the Kerguelen Plateau. Data from 1872 to 2015 collected with different sampling strategies and objectives, during different campaigns.

**Object name:** Echinoids\_Kerguelen\_Plateau\_1872\_2015



**Figure 2.** Distribution of the 12 echinoid species based on the specimens collected since 1872 on the Kerguelen Plateau.

**Character encoding:** x-MacRoman

**Format name:** Darwin Core Archive Format

**Format version:** 3.0

**Distribution:** [http://ipt.biodiversity.aq/resource.do?r=echinoids\\_kerguelen\\_plateau\\_18-72\\_2015](http://ipt.biodiversity.aq/resource.do?r=echinoids_kerguelen_plateau_18-72_2015)

**Publication date of data:** 12/07/2016

**Language:** English

**Metadata language:** English

**Date of metadata creation:** 12/07/2016

**Hierarchy level:** Dataset

### Dataset of actual environmental parameters description

Environmental variables in the region of the Kerguelen Plateau compiled from different sources and provided in the ascii raster format (Guillaumot et al. 2016). Mean surface

and seafloor temperature, salinity and their respective amplitude data are available on the time coverage 1955–2012 and over six decades: 1955 to 1964, 1965 to 1974, 1975 to 1984, 1985 to 1994 and 1995 to 2004, and 2005 to 2012.

Future projections are provided for several parameters: they were modified after the Bio-ORACLE database (Tyberghein et al. 2012). They are based on three IPCC scenarii (B1, AIB, A2) for years 2100 and 2200 (IPCC, 4<sup>th</sup> report).

**Object name:** Environmental\_Kerguelen\_Plateau\_1955\_2012

**Format name:** Raster

**Format version:** 1.0

**Distribution:** [https://data.aad.gov.au/metadata/records/Environmental\\_Kerguelen\\_Plateau\\_1955\\_2012](https://data.aad.gov.au/metadata/records/Environmental_Kerguelen_Plateau_1955_2012)

**doi:** 10.4225/15/578ED5A08050F

**Publication date of data:** 16/07/2016

**Language:** English

**Metadata language:** English

**Date of metadata creation:** 16/07/2016

**Hierarchy level:** Dataset

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# Two new species and a remarkable record of the genus *Dendronotus* from the North Pacific and Arctic oceans (Nudibranchia)

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## Abstract

Two new species of the nudibranch genus *Dendronotus*, *D. arcticus* **sp. n.** and *D. robilliardi* **sp. n.**, are described from the Arctic and North Pacific oceans respectively, based on morphological and molecular data, and the North Pacific *D. albus* is revealed to be a species complex. The species *D. robilliardi* **sp. n.** is described from the northwestern Pacific (Kamchatka) differing from the northeastern Pacific *D. albus* by molecular and morphological data. The synonymy of *D. diversicolor* with *D. albus* is confirmed by analysis of their original descriptions. An endemic Arctic species *D. arcticus* **sp. n.** is also described here, differing substantially from all species of the genus *Dendronotus* using morphological and molecular data. An unusual record of the recently described *D. kamchaticus* Ekimova, Korshunova, Schepetov, Neretina, Sanamyan, Martynov, 2015 is also presented, the first from the northeastern Pacific, geographically separated from the type locality of this species in the northwestern Pacific by a distance *ca.* 6000 km; molecular data show them to belong to the same species.

**Keywords**

Arctic Ocean, *Dendronotus*, molecular phylogeny, new species, North Pacific Ocean, Nudibranchia, taxonomy

**Introduction**

The species of the genus *Dendronotus* are common marine invertebrates of the shallow waters in the northern hemisphere. Gordon Robilliard presented a detailed review of the genus *Dendronotus* (Robilliard 1970), and noticed an unequal number of *Dendronotus* species in the major marine regions of the northern hemisphere. In the North Atlantic at that time only two species were known, whereas in the North Pacific seven species had been recorded. Robilliard commented that “This may be an actual biological phenomenon with the northeast Pacific being the centre of evolution and radiation of the genus but it is more likely a reflection of the collection pressure” (Robilliard 1970: 475). Further studies have confirmed this prognosis, but some unexpected patterns were also revealed.

Mikael Thollessen challenged a long-standing view that only a single polymorphic species *D. frondosus* (Ascanius, 1774) inhabits European waters (Thollessen 1998). Based on morphological features and the application of allozyme electrophoresis he showed the valid status of *D. lacteus* (Thompson, 1840), which had been omitted from faunal lists for more than one century (e.g. Odhner 1907, Thompson and Brown 1984, Roginskaya 1987). Later, the validity of *D. lacteus* was confirmed in a first molecular phylogenetic study of the genus *Dendronotus* based on the 16S gene (Stout et al. 2010). They also found that one more traditional synonym of *D. frondosus* was also a valid taxon, *D. venustus* MacFarland, 1966 from the northeastern Pacific. It was originally described by Frank Mace MacFarland in his famous volume on the North American opisthobranchs (MacFarland 1966).

Stout et al. (2010: 7) also suggested that “Further examination of additional specimens from various locations may reveal a complex of species currently considered to be *D. frondosus*.” This was fulfilled in a recent revision of the genus *Dendronotus* by Ekimova et al. (2015). In this study two new species (*D. kalikal* Ekimova, Korshunova, Schepetov, Neretina, Sanamyan & Martynov, 2015 and *D. kamchaticus* Ekimova, Korshunova, Schepetov, Neretina, Sanamyan & Martynov, 2015) were described from the northwestern Pacific Kamchatka waters, both of which are very similar externally to *D. frondosus*. A further species, *D. primorjensis* Martynov, Sanamyan, Korshunova, 2015, was described from the Sea of Japan (Martynov et al. 2015a, b; Korshunova et al. 2016). Thus, *D. frondosus* is shown to be a species complex.

To date, the majority of new cryptic/semi-cryptic species of the genus *Dendronotus* from the North Pacific were discovered mostly in the *D. frondosus* species complex while other species from the North Pacific do not appear to contain obvious cryptic species complexes. Two long-debated supposedly cryptic species, *D. albus* MacFar-

land, 1966 and *D. diversicolor* Robilliard, 1970, were recently synonymised by Stout et al. (2010) and, while this paper was in review, *D. diversicolor* was removed from synonymy with *D. albus* by Ekimova et al. (prepublication).

*Dendronotus albus* and *D. diversicolor* are difficult to distinguish morphologically (Robilliard 1970; Behrens 1980, 2006) and show no genetic differences (Stout et al. 2010). Surprisingly, a high rate of the genetic divergence between supposed *D. albus* from the NW Pacific Kamchatka region (Martynov et al. 2015b) and real *D. albus* (= *D. diversicolor*, see Discussion) from the NE Pacific was found in the present study. The molecular differences were confirmed from four variably coloured specimens and an egg mass from the NW Pacific. Therefore a semi-cryptic species from the *D. albus* species complex is discovered for the first time from NW Pacific and is described here as a new species, *D. robilliardi* sp. n., in recognition of the pioneering work of Gordon Robilliard.

The second new species originates from one of the coldest region of the world, the Laptev Sea in the eastern Arctic Ocean. According to morphological and molecular data, this species differs substantially from all known *Dendronotus* species, and is described in this work as *D. arcticus* sp. n.

Finally, a remarkable new record of the recently described *D. kamchaticus* is also presented, from the NE Pacific (Washington State, USA); it is separated from the type locality in the NW Pacific (Kamchatka) by a distance *ca.* 6000 km.

## Material and methods

### Collecting data

Four specimens of *D. arcticus* sp. n. were collected in the Arctic Laptev Sea by trawling by Olga Zimina. Four specimens and one egg mass of *D. robilliardi* sp. n. were collected in the NW Pacific, Kamchatka by SCUBA diving by Nadezhda Sanamyan. A single specimen of *D. kamchaticus* and a single specimen of *D. albus* were collected in the NE Pacific, Washington State, by SCUBA diving by Karin Fletcher. For molecular phylogenetic analysis single specimens of *Doto coronata* and *Tritonia plebeia* were collected in the Barents Sea (Dalne-Zelenetskaya Bay) and Norway (Gulen Dive Resort), respectively, by SCUBA diving by Tatiana Korshunova and Alexander Martynov. All specimens were preserved in 80–95% EtOH.

### Morphological analysis

All specimens were examined with a stereomicroscope (MBS-9) and photographed using digital cameras (Nikon D-90 and D-810) with a set of extension rings. The pharynges were removed and processed with a weak solution of domestic bleach (NaOCl).

Jaws were examined using a stereomicroscope and digital cameras. The radulae were examined under a scanning electron microscope (CamScan Series II) at the electron microscopy laboratory of the Biological Faculty of Moscow State University.

## Molecular analysis

A total of eleven specimens and one egg mass was successfully sequenced for the mitochondrial genes cytochrome c oxidase subunit I (COI) and 16S, and also the nuclear gene 28S (C1-C2 domain). Additional sequences including outgroup specimens were obtained from GenBank (see Table 1 for full list of samples, localities, and voucher references).

Small pieces of tissue were used for DNA extraction with Diatom™ DNA Prep 100 kit by Isogene Lab, according to the producer's protocols. Extracted DNA was used as a template for the amplification of partial sequences of the COI, 16S, and 28S. The primers that were used for amplification are LCO 1490 (GGTCAACAAATCAT-AAAGATATTGG, Folmer et al. 1994); HCO 2198 (TAAACTTCAGGGTGAC-CAAAAAATCA, Folmer et al. 1994); 16S arL (CGCCTGTTTAACAAAAACAT, Palumbi et al. 2002); 16S R (CCGRTYTGAACCTCAGCTCACG, Puslednik and Serb 2008); 28S C1' (ACCCGCTGAATTTAAGCAT, Dayrat et al. 2001); and 28S C2 (TGAACTCTCTCTTCAAAGTTCTTTTC, Le et al. 1993). Polymerase chain reaction (PCR) amplifications were carried out in a 20-μL reaction volume, which included 4 μL of 5x Screen Mix (Eurogen Lab), 0.5 μL of each primer (10 μM stock), 1 μL of genomic DNA, and 14 μL of sterile water. The amplification of COI and 28S was performed with an initial denaturation for 1 min at 95°C, followed by 35 cycles of 15 sec at 95°C (denaturation), 15 sec at 45°C (annealing temperature), and 30 sec at 72°C, with a final extension of 7 min at 72 °C. The 16S amplification began with an initial denaturation for 1 min at 95°C, followed by 40 cycles of 15 sec at 95°C (denaturation), 15 sec at 52°C (annealing temperature), and 30 sec at 72°C, with a final extension of 7 min at 72°C. Sequencing for both strands proceeded with the ABI PRISM® BigDye™ Terminator v. 3.1. Sequencing reactions were analysed using an Applied Biosystems 3730 DNA Analyzer. Protein-coding sequences were translated into amino acids for confirmation of the alignment. All sequences were deposited in GenBank (Table 1, highlighted in bold).

Original data and publicly available sequences were aligned with the MUSCLE algorithm (Edgar 2004). Separate analyses were conducted for COI (641 bp), 16S (462 bp), and 28S (350 bp). An additional analysis was performed with all three concatenated markers (1453 bp). Evolutionary models for each data set were selected using MrModelTest 2.3 (Nylander et al. 2004) under the Akaike information criterion (Akaike 1974). The HKY+I+G model was chosen for COI. The GTR + I + G model was chosen for 16S and for the combined dataset. The GTR+G model was chosen for 28S. Two different phylogenetic methods, Bayesian inference (BI) and Maximum likelihood (ML) were used to infer evolutionary relationships. Bayesian estimation of posterior probability was performed in MrBayes 3.2. Markov chains were sampled

**Table 1.** List of specimens used for phylogenetic analyses. New specimens are highlighted in bold.

Species	Voucher	Locality	GenBank accession nos.		
			COI	16S	28S
<b><i>Dendronotus albus</i> MacFarland, 1966 (= <i>D. diversicolor</i> Robilliard, 1970)</b>	<b>ZMMU:Op-566</b>	<b>USA: Washington</b>	<b>KX788135</b>	<b>KX788123</b>	<b>KX788114</b>
<i>Dendronotus albus</i> MacFarland, 1966 (= <i>D. diversicolor</i> Robilliard, 1970)	LACM:174845	USA: California	-	GU339185	-
<i>Dendronotus albus</i> MacFarland, 1966 (= <i>D. diversicolor</i> Robilliard, 1970)	LACM:174846	USA: California	-	GU339186	-
<b><i>Dendronotus arcticus</i> sp. n.</b>	<b>ZMMU:Op-561</b>	<b>Russia: Laptev Sea</b>	<b>KX788140</b>	<b>KX788129</b>	<b>KX788118</b>
<b><i>Dendronotus arcticus</i> sp. n.</b>	<b>ZMMU:Op-562</b>	<b>Russia: Laptev Sea</b>	<b>KX788141</b>	<b>KX788130</b>	<b>KX788119</b>
<b><i>Dendronotus arcticus</i> sp. n.</b>	<b>ZMMU:Op-563</b>	<b>Russia: Laptev Sea</b>	<b>KX788142</b>	<b>KX788131</b>	<b>KX788120</b>
<i>Dendronotus dalli</i> Bergh, 1879	ZMMU:Op-295	Russia: Kamchatka	KM397001	KM397083	KM397042
<i>Dendronotus dalli</i> Bergh, 1879	ZMMU:Op-330	Russia: Kamchatka	KM396999	KM397081	KM397040
<i>Dendronotus dalli</i> Bergh, 1879	ZMMU:Op-331	Russia: Kamchatka	KM397000	KM397082	KM397041
<i>Dendronotus frondosus</i> (Ascanius, 1774)	ZMMU:Op-324	Russia: Barents sea	KM396980	KM397062	KM397021
<i>Dendronotus frondosus</i> (Ascanius, 1774)	ZMMU:Op-359	Russia: Barents sea	KM396979	KM397061	KM397020
<i>Dendronotus frondosus</i> (Ascanius, 1774)	ZMMU:Op-380	Norway	KM396976	KM397056	KM397017
<i>Dendronotus frondosus</i> (Ascanius, 1774)	ZMMU:Op-382	Russia: Barents sea	KM396977	KM397050	KM397018
<i>Dendronotus kamchaticus</i> Ekimova et al., 2015	ZMMU:Op-246.2	Russia: Kamchatka	KM396989	KM397072	KM397030
<i>Dendronotus kamchaticus</i> Ekimova et al., 2015	ZMMU:Op-247.1	Russia: Kamchatka	KM396991	KM397073	KM397032
<i>Dendronotus kamchaticus</i> Ekimova et al., 2015	ZMMU:Op-247.2	Russia: Kamchatka	KM396992	KM397074	KM397033
<b><i>Dendronotus kamchaticus</i> Ekimova et al., 2015</b>	<b>ZMMU:Op-565</b>	<b>USA: Washington</b>	<b>KX788144</b>	<b>KX788111</b>	<b>KX788121</b>
<i>Dendronotus kalikal</i> Ekimova et al., 2015	ZMMU:Op-284.3	Russia: Kamchatka	KM396988	KM397070	KM397029
<i>Dendronotus lacteus</i> (W. Thompson, 1840)	ZMMU:Op-288	Russia: Barents Sea	KM396975	KM397059	KM397016
<i>Dendronotus lacteus</i> (W. Thompson, 1840)	ZMMU:Op-335	Russia: Barents Sea	KM396973	KM397057	KM397014
<i>Dendronotus lacteus</i> (W. Thompson, 1840)	ZMMU:Op-383.1	Norway	KM396971	KM397054	KM397012
<i>Dendronotus niveus</i> Ekimova et al., 2015	ZMMU:Op-269	Russia: White Sea	KM396996	KM397078	KM397037
<i>Dendronotus niveus</i> Ekimova et al., 2015	ZMMU:Op-274.2	Russia: Barents Sea	KM396993	KM397076	KM397034
<i>Dendronotus niveus</i> Ekimova et al., 2015	ZMMU:Op-279	Russia: Barents Sea	KM396995	KM397077	KM397036
<i>Dendronotus patricki</i> Stout et al., 2011	SIO-BIC M12133	USA: California	HQ225828	HQ225829	-
<i>Dendronotus primorjensis</i> Martynov et al., 2015	ZMMU:Op-419	Russia: Japan Sea	KX672010	KX672008	KX672006



Species	Voucher	Locality	GenBank accession nos.		
			COI	16S	28S
<i>Dendronotus primoriensis</i> Martynov et al., 2015	ZMMU:Op-420	Russia: Japan Sea	KX672011	KX672009	KX672007
<i>Dendronotus regius</i> Pola & Stout, 2008	CASIZ179492	Philippines	HM162708	HM162629	-
<i>Dendronotus regius</i> Pola & Stout, 2008	CASIZ179493	Philippines	JN869451	JN869407	-
<i>Dendronotus robilliardi</i> sp. n.	ZMMU:Op-567	Russia: Kamchatka	KX788136	KX788124	KX788115
<i>Dendronotus robilliardi</i> sp. n.	ZMMU:Op-568	Russia: Kamchatka	KX788138	KX788126	KX788116
<i>Dendronotus robilliardi</i> sp. n.	ZMMU:Op-569	Russia: Kamchatka	KX788137	KX788125	KX788112
<i>Dendronotus robilliardi</i> sp. n.	ZMMU:Op-447	Russia: Kamchatka	KX788139	KX788127	KX788117
<i>Dendronotus robilliardi</i> sp. n. egg mass	ZMMU:Op-570	Russia: Kamchatka	KX788143	KX788128	-
<i>Dendronotus robustus</i> Verrill, 1870	ZMMU:Op-343	Russia: Barents sea	KM397002	KM397084	KM397043
<i>Dendronotus robustus</i> Verrill, 1870	ZMMU:Op-344	Russia: Barents sea	KM397003	KM397085	KM397044
<i>Dendronotus robustus</i> Verrill, 1870	ZMMU:Op-390.5	Russia: Barents sea	KM396968	KM397051	KM397009
<i>Dendronotus venustus</i> MacFarland, 1966	LACM174850	USA: California	HM162709	HM162630	-
<i>Dendronotus venustus</i> MacFarland, 1966	LACM:174852.1	USA: California	-	GU339199	-
<i>Doto coronata</i> (Gmelin, 1791)	ZMMU:Op-571	Russia: Barents sea	KX788145	KX788133	KX788113
<i>Doto koenneckeri</i> Lemche, 1976	CASIZ178247	Portugal: Azores Islands	HM162735	HM162658	-
<i>Marionia arborescens</i> Vayssiere, 1877	CAS:177735	Philippines	KP226855	KP226859	-
<i>Notobryon thompsoni</i> Pola et al., 2012	CASIZ176362	South Africa	JN869456	JN869413	-
<i>Notobryon wardi</i> Odhner, 1936	CASIZ177540	Philippines	JN869454	JN869411	-
<i>Tritonia plebeia</i> Johnston, 1828	ZMMU:Op-572	Norway	KX788134	KX788122	KX788132

at intervals of 500 generations. Analysis was started with random starting trees and  $10^7$  generations. Maximum likelihood-based phylogeny inference was performed in GARLI 2.0 (Zwickl 2006) with bootstrap in 1000 pseudo-replications. The program TRACER v1.6 was used to examine the convergence results. Final phylogenetic tree images were rendered in the FigTree 1.4.2. The ABGD program is available from <http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html>. COI and 16S FASTA alignments were analysed separately (excluding outgroups) using both proposed models Jukes-Cantor (JC69) and Kimura (K80). The program Mega7 (Kumar et al. 2016) was used to calculate the uncorrected p-distances between all the sequences. Pairwise uncorrected p-distances within and between clades were also examined.

## Results

### Phylogenetic analysis

In this molecular study, 44 specimens and one egg mass were included, representing 20 species and 120 sequences. The resulting combined tree provided better resolution than COI, 16S, or 28S separately (not shown). Trees of both Bayesian Inference (BI) and Maximum Likelihood (ML) were used to infer phylogenetic trees. The combined dataset yielded a sequence alignment of 1453 positions. The topology of the tree obtained by ML was the same as the one inferred by BI.

The molecular phylogenetic analysis (Fig. 5) support the presence of two distinct species, *Dendronotus arcticus* sp. n. (PP = 1, BS = 100%) and *D. robilliardi* sp. n. (PP = 1, BS = 99%). All *D. albus* specimens cluster together with maximum support (PP = 1, BS = 100%) and form a separate clade. The *D. kamchaticus* specimens from Kamchatka and from the NE Pacific (Washington State) cluster together in a single clade with maximum support (PP = 1, BS = 100%). The *D. kalikal* specimens are also clustered in a single clade but hold an unstable position on the tree (and are therefore excluded from further phylogenetic analysis). This could be explained because some of *D. kalikal* sequences are too short.

The ABGD analysis revealed fourteen potential genetic groups both for COI (the prior maximal distance ranged between 0.001 and 0.013) and 16S (the prior maximal distance ranged between 0.001 and 0.02) genes: *D. regius*, *D. robilliardi* sp. n., *D. arcticus* sp. n., *D. lacteus*, *D. kamchaticus* (including the specimen from USA), *D. niveus*, *D. dalli*, *D. albus*, *D. venustus*, *D. primorjensis*, *D. frondosus*, *D. patricki*, *D. robustus*, and *D. kalikal*.

The sensitivity of the species delineation methods are discussed in e.g. Jörger et al. (2012), Jörger and Schrödl (2013), Padula et al. (2014). To define species, we use an integrative approach (Dayrat 2005) including tree topologies, pairwise uncorrected distances, and ABGD as well as morphological data.

## Taxonomy

### Family Dendronotidae

#### *Dendronotus arcticus* sp. n.

<http://zoobank.org/6B4A9064-A864-498C-BC81-C2A00FBB6186>

Figs 1, 3A

**Type material.** Holotype, ZMMU Op-561, 19 mm long (preserved), Laptev Sea, R/V “Dalnie Zelentsy”, sta. O-48, 74°34.9'N–74°35.1'N, 115°43.4'E–115°42.2'E, 04.10.2014, depth 15 m, drague, sand, collector O.L. Zimina. 3 paratypes, ZMMU Op-562–Op-564, same locality and collectors as holotype.

**Type locality.** Laptev Sea.

**Etymology.** After the Arctic region.

**Diagnosis.** 5–6 pairs dorsolateral appendages, colour brownish with scattered distinct opaque white dots, central tooth with up to 14 small denticles and reduced furrows, vas deferens moderate in length, penis long, bent.

**Description.** Body elongate, up to 19 mm in length (Fig. 1A–C), 6–8 branched appendages of oral veil, 5–6 appendages of rhinophoral stalks, 15–18 rhinophoral lamellae, branched rhinophoral lateral papilla present, 5–6 pairs dorsolateral appendages, 15–25 lip papillae. Dorsolateral appendages with moderate primary stalk, moderately branched secondary branches, and elongated tertiary branches (Fig. 1A–C). Reproductive and anal openings placed laterally on right side. General colour brownish with scattered distinct opaque white dots on notum, tips of lateral appendages, oral appendages, lip papillae, and rhinophores (Fig. 1A–C).

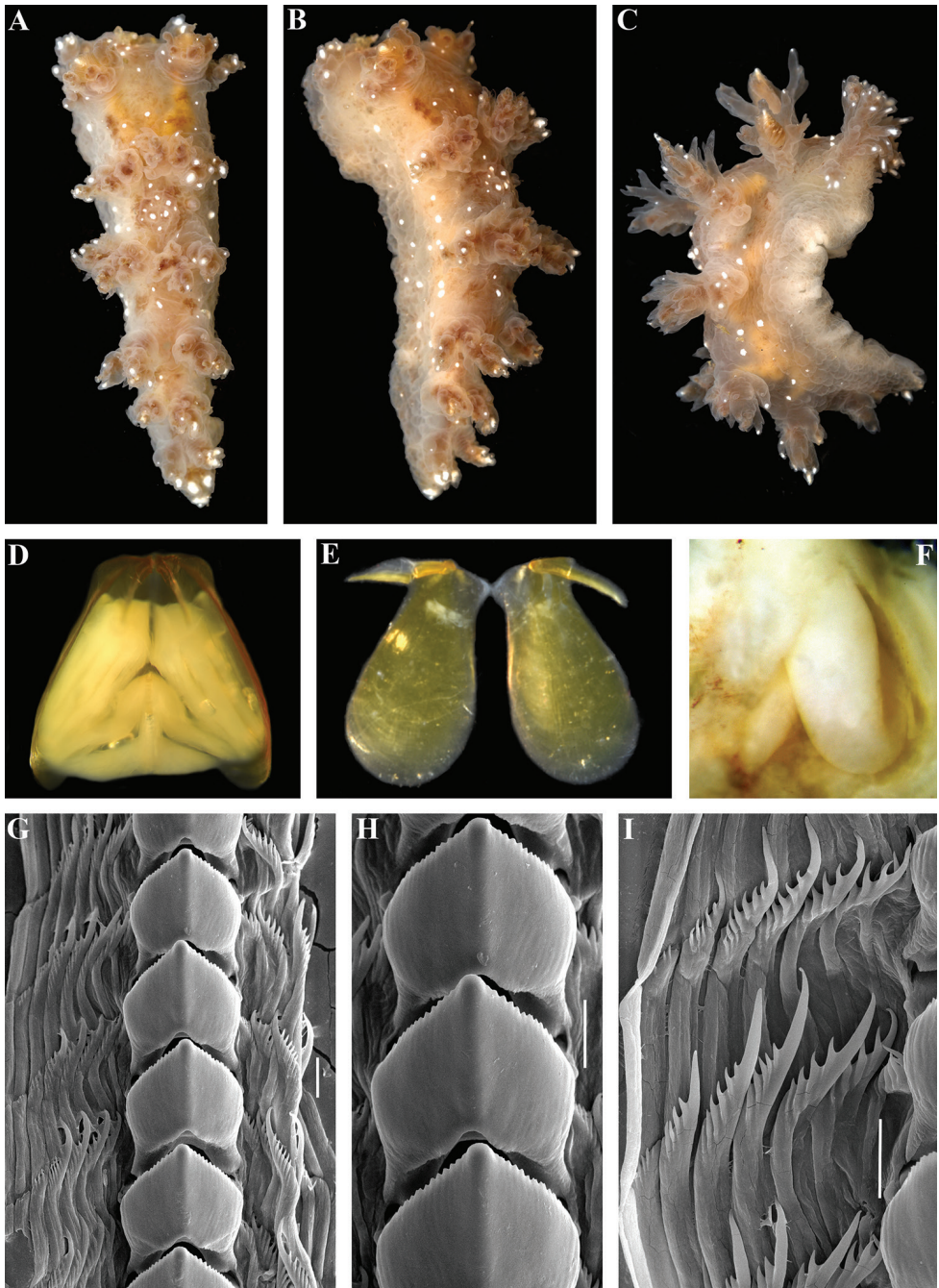
Dorsal processes of jaws inclined posteriorly at approximately 55° to longitudinal axis of jaw body and 0.47 of its length (Fig. 1D, E). Masticatory processes apparently bear indistinct denticles. Radula formula is  $38 \times 3-9.1.9-3$ . Central tooth weakly denticulated and bearing up to 14 small denticles (Fig. 1 G, H) with reduced furrows. Lateral teeth are short, slightly curved, bearing up to nine long denticles (Fig. 1I).

Reproductive system triaenic (Fig. 3A), ampulla twice folded, prostate consisting of 25–30 alveolar glands, vas deferens moderate in length expanding to voluminous penial sheath, vagina long and twisted, penis long and twisted (Fig. 1F), and bursa copulatrix is large, rounded, and elongated with small seminal receptaculum placed distally (Fig. 3A) (nomenclature of the seminal reservoirs according to Stout et al. 2011).

**Biology.** Inhabits soft substrates (sand, mud) with gravel and small stones.

**Distribution.** Central and eastern coastal waters of Arctic Ocean.

**Remarks.** *Dendronotus arcticus* sp. n. is well separated from other species of the genus *Dendronotus*: externally *D. arcticus* sp. n. is readily distinguished from all species of the genus *Dendronotus* by a light brownish ground colour with few distinct scattered white dots. There is little variation of colour in *D. arcticus* sp. n. compared to that of other *Dendronotus* species. The radula of *D. arcticus* sp. n. is similar to those of *D. albus* and *D. robilliardi* sp. n. but clearly differs by its pattern of central and lateral teeth. The



**Figure 1.** *Dendronotus arcticus* sp. n.: **A** holotype ZMMU Op-561, live, dorsal view **B** same, lateral view **C** paratype ZMMU Op-562, live, lateral view **D** holotype ZMMU Op-561, jaws and radula *in situ*, dorsal view **E** same, jaws, lateral views **F** same, penis **G** same, posterior rows of radula, SEM **H** same, details of central teeth, SEM **I** same, details of lateral teeth, SEM. Scale bars 30 µm. Photos of living specimens by Olga Zimina, other photos and SEM images by Alexander Martynov.

radular differences include the presence of reduced furrows on the central teeth of *D. arcticus* sp. n.: *Dendronotus albus* and *D. robilliardi* sp. n. have no furrows on their central teeth, whereas the central teeth of the common North Atlantic species *D. frondosus* have deep furrows. The common North Atlantic and Arctic species *D. lacteus* differs considerably from *D. arcticus* sp. n. by its radula (central teeth with deep furrows), colour, and reproductive system. Other species of the genus *Dendronotus* clearly differ from *D. arcticus* sp. n. by radular patterns. The reproductive system of *D. arcticus* sp. n. differs from those of *D. albus* and *D. robilliardi* sp. n. by the presence of a twisted penis, by the colour pattern of the dorsal appendages, by the shape of the central tooth, and by the thicker vagina. *Dendronotus arcticus* sp. n. can be clearly distinguished from the recently described NW Pacific species *D. kamchaticus*, *D. kalikal*, and *D. primorjensis* by the colour and the radular and reproductive system patterns.

Uncorrected p-distances are different between *D. arcticus* sp. n. and the sympatric Arctic species *D. lacteus* (range 10.0–10.8 % for COI, and 1.6–1.8% for 16S data set), and *D. robustus* (range 12.8–13.9% for COI, and 3.2–3.4% for 16S). *P*-distances are different between *D. arcticus* sp. n. and the North Pacific *D. kamchaticus* (range 8.6–10.0% for COI, and 2.3–2.7% for 16S), *D. kalikal* (10.1 % for COI, and 2.3–2.5% for 16S), and *D. primorjensis* (range 12.0–12.5% for COI, and 2.5–2.7% for 16S). Minimum interspecific distances of the COI marker separate *D. arcticus* sp. n. from other species with high genetic divergence: 10.1% from *D. kalikal*, 9.3% from *D. kamchaticus*, 10.5% from *D. lacteus*, 12.3% from *D. primorjensis*, and 13.4% from *D. robustus*.

### ***Dendronotus robilliardi* sp. n.**

<http://zoobank.org/2BA57DC2-EFC9-4662-8A9C-931F69589DE9>

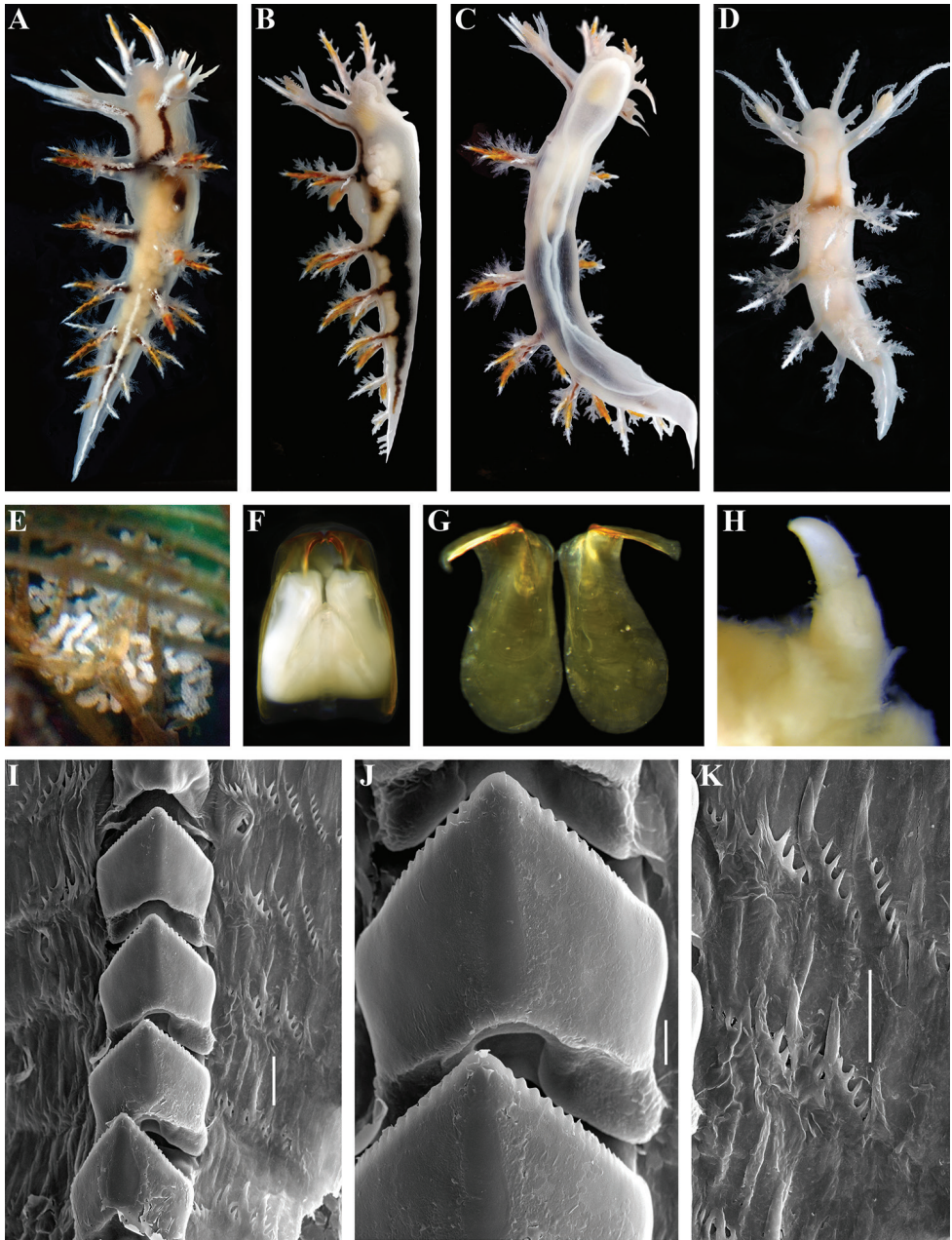
Figs 2, 3B

*Dendronotus albus*: Robilliard 1970: 466–470, pl. 64, fig 34, text figs 2–4, 6, 22–24 (excluding part of Geographical section, p. 469–Baja California); Morris et al. 1980: 332–333, part; McDonald 1983: 172, part; Koh 2006: locality information and photo; Lloyd 2007: locality information and photo; Martynov et al. 2015b: 74–75 pp, figs 2B, r; Ekimova et al. prepublication: 2–10, figs 2D–F, 3D–G, 4A (non *albus* MacFarland, 1966).

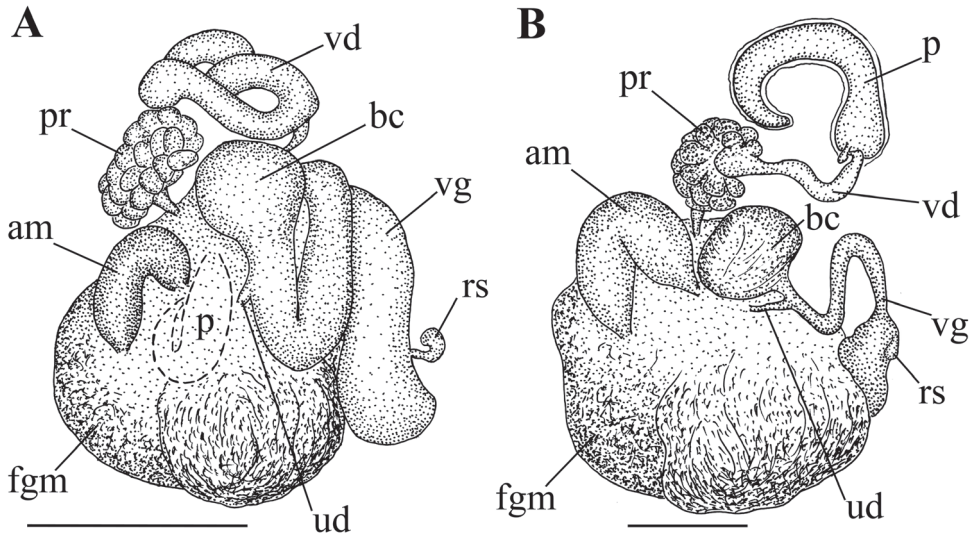
**Type material.** Holotype, ZMMU Op-568, 35 mm long (live), NW Pacific, Kamchatka, Starichkov Island, 52°47.009'N–158°36.185'E, 17.09.2015, depth 11.5 m, stones, SCUBA diving, collector N.P. Sanamyan. 1 paratype, ZMMU Op-567, same locality and collectors as holotype. 1 paratype, ZMMU Op-447, same locality and collectors as holotype. 1 paratype (egg mass only), ZMMU Op-570, same locality and collectors. 1 paratype, ZMMU Op-569, NW Pacific, Kamchatka, Zhirovaya Bay, 52°36.767'N–158°27.318'E, 12.06.2016, depth 18 m, stones, SCUBA diving, collector N.P. Sanamyan.

**Type locality.** The NW Pacific, Kamchatka, Russia.





**Figure 2.** *Dendronotus robilliardi* sp. n.: **A** holotype ZMMU Op-568, live, dorsal view **B** same, lateral view **C** same, ventral view **D** paratype ZMMU Op-569, live, dorsal view **E** egg mass *in situ*, same collection data as holotype **F** paratype ZMMU Op-567, jaws and radula *in situ*, dorsal view **G** same, jaws, lateral views **H** same, penis **I** same, posterior rows of radula, SEM **J** same, details of central teeth, SEM **K** same, details of lateral teeth, SEM. Scale bars **I**, **K** = 30  $\mu$ m **J** = 10  $\mu$ m. Photos of living specimens by Nadezhda Sanamyan, other photos and SEM images by Alexander Martynov.



**Figure 3.** Reproductive systems: **A** *Dendronotus arcticus* sp. n., holotype ZMMU Op-561 **B** *Dendronotus robilliardi* sp. n., paratype ZMMU Op-567. Abbreviations: **am** ampulla; **bc** bursa; **fgm** female gland mass; **pr** prostate; **p** penis; **rs** receptaculum semenis; **u** uterine duct; **vd** vas deferens; **vg** vagina. Drawings by Tatiana Korshunova. Scale bars 1 mm.

**Etymology.** In honour of Gordon Robilliard (Gig Harbor, Washington State, USA), the author of the classic study on the genus *Dendronotus*, including the description of *D. diversicolor* Robilliard, 1970. For a long time Robilliard attempted to resolve status of *D. diversicolor* (Behrens 2006); *D. diversicolor* was finally synonymised with *D. albus* based on molecular data forty years later by Stout et al. (2010) (see also Discussion below). Here molecular evidence is provided showing the existence of another species in the NW Pacific belonging to the *D. albus* complex; therefore, this is a good opportunity to honour the important contributions of Gordon Robilliard to the systematics of the genus *Dendronotus*, and particularly to the *D. albus* species complex problem.

**Diagnosis.** 5–6 pairs branched dorsolateral appendages, digestive gland penetrates 3–4 pairs of dorsolateral appendages, general colour translucent white, dorsolateral appendages colour variable, orange-copper pigment present or completely lacking, tips opaque white, opaque white stripes on tips of dorsal appendages and tail, central tooth with up to 15 small distinct denticles without furrows, vas deferens short, conical penis.

**Description.** Body elongate, 30–35 mm in length (Fig. 2A–D). 4–5 branched appendages of oral veil, 4–6 appendages of rhinophoral stalks, 11–12 rhinophoral lamellae, unbranched (or with few small branches) rhinophoral lateral papilla present, 5–6 pairs larger branched dorsolateral appendages and 1–3 pairs smaller unbranched appendages reaching tip of tail, 5–10 lip papillae. Dorsolateral appendages with moderate primary stalk and secondary branches, and pointed tertiary branches, digestive gland penetrates 3–4 pairs of dorsolateral appendages including posterior ones (Fig. 2A–D). Reproductive and anal openings placed laterally on right side.



General colour translucent white with opaque white stripes on oral veil appendages, rhinophoral sheaths, posterior part of dorsum and on tips of dorsal appendages; orange-copper marks in middle part of dorsal and oral processes (Fig. 2A–C), or absent (Fig. 2D).

Dorsal processes of jaws inclined posteriorly at approximately 60° to longitudinal axis of jaw body and 0.45 of its length (Fig. 2F–G). Masticatory borders with ridge-like denticles. Radula formula  $43 \times 3-9.1.9-3$ . Central tooth with up to 15 small distinct denticles (Fig. 2I, J), without furrows. Lateral teeth slightly curved, bearing up to seven distinct long denticles (Fig. 2K).

Reproductive system triaulic (Fig. 3B). Ampulla wide, folded twice. Prostate moderate in size, consists of *ca.* 19–20 alveolar glands. Vas deferens short, relatively narrow, penial sheath elongate, relatively long, curved, conical penis (Fig. 2H). Vagina narrow, bent, moderate in length, distally expanded into vestibulum. Uterine (insemination) duct short. Bursa copulatrix large, irregularly spherical, stalked, small oval seminal receptaculum placed distally on vestibulum (Fig. 3B).

**Biology.** Inhabits stones and rocky bottom. Feeds on the hydroid *Abietinaria annulata* (Kirchenpauer, 1884).

**Distribution.** The type specimens of *D. robilliardi* sp. n. originate from the NW Pacific, Kamchatka, Russia. According to the ceratal pattern, a specimen of *D. albus* recorded from cold waters of South Korea, 37°7'N, 129°E (Koh 2006) is also likely to be *D. robilliardi* sp. n.; therefore, a very broad distribution of *D. robilliardi* sp. n. is expected in the NW Pacific, from the Commander Islands in the north to Korea in the south. According to the morphological data given in Robilliard (1970) and a detailed image by Lloyd (2007) clearly showing up to six pairs of dorsolateral appendages (three of them contain digestive gland branches), the range of *D. robilliardi* sp. n. in NE Pacific reaches at least British Columbia and Washington State (San Juan Island). Robilliard and Barr (1974) also presented a record of *D. albus* from Alaska without an image. Since Robilliard consistently misidentified *D. albus* in his revision (1970) (see Discussion and Table 2), most probably the Alaskan record also belongs to the species *D. robilliardi* sp. n. However, the majority of the records *D. albus* from California and especially from Baja California (Robilliard 1970; Behrens 1980, 1991) probably represent true *D. albus*. The specimens of *D. albus* (= *D. robilliardi* sp. n.) which were studied by Robilliard (1970) originated from San Juan Island, Washington State and Albert Head, British Columbia, whereas more southern records were listed according to the information from James Lance only (Robilliard 1970: 469; Bertsch et al. 1972: 305). A selection of detailed images of several specimens of *D. albus* from the type locality of this species, Monterey Bay, California (McDonald 2016) showing only specimens with four to five pairs (the fifth pair if present is smaller) of dorsolateral appendages is in a full agreement with the first description of true *D. albus* (MacFarland, 1966). Sandra Millen (pers. comm.) has distinguished *D. albus sensu* Robilliard, 1970 from *D. diversicolor* (a synonym of *D. albus*, see Table 2) in the British Columbia region. *Dendronotus diversicolor* was also recorded without an illustration from British Columbia by Lambert (1976). A record of *D. diversicolor* by Millen (1989) from Alaska represents the northernmost range of true *D. albus* since that specimen had four ceratal pairs plus a small bump, and digestive gland extending in to the two anterior pairs (S. Millen, pers. comm.).

Both *D. robilliardi* sp. n. and true *D. albus* evidently may co-occur in some localities around at least the British Columbia/Washington waters. *Dendronotus albus* was recently recorded and illustrated from the Salish Sea (Washington) by Fletcher (2013), geographically thus very close to San Juan Island, the type locality of *D. diversicolor*, and from where also *D. “albus”* (= *D. robilliardi* sp. n. ) was already reported by Robilliard (1970). Thus *D. robilliardi* sp. n. appears to be a boreal species widely distributed in the northern Pacific and adapted for lower temperatures compared to *D. albus*. The latter species is mostly likely distributed in the NE Pacific from British Columbia southwards potentially to Baja California, in warmer temperature conditions.

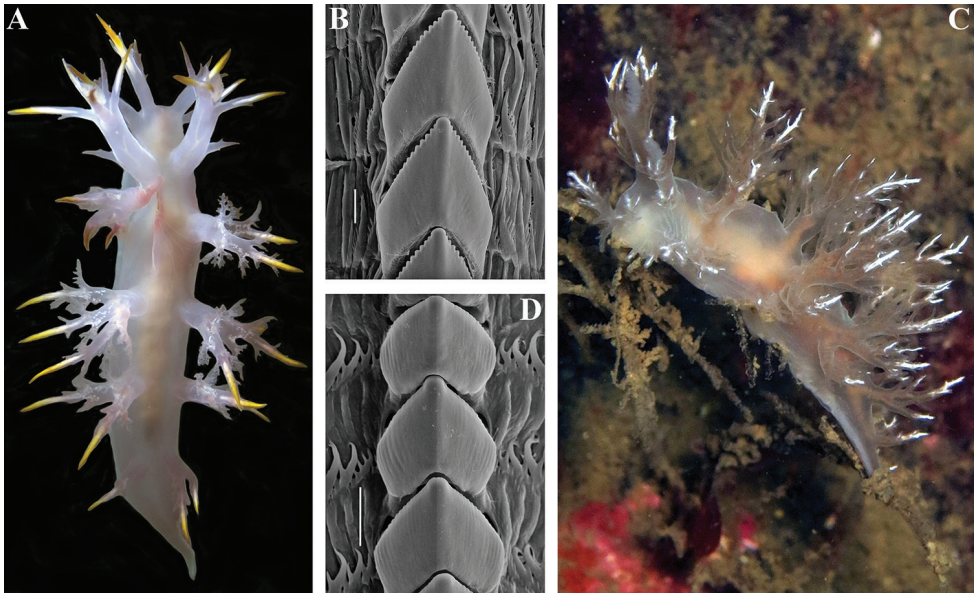
**Remarks.** There is a significant genetic gap between *D. robilliardi* sp. n. and the morphologically similar *D. albus* (13.6–14.5% for COI gene, 2.3–2.5% for 16S gene) (Fig. 5). According to Carmona et al. (2013) such values can be considered as species- and genus-‘level’ differences in the nudibranch molluscs. *Dendronotus robilliardi* sp. n. is also distinguished morphologically from the true *D. albus* MacFarland, 1966. *Dendronotus albus* (including its synonym *D. diversicolor*) has only 4–5 pairs of dorso-lateral appendages and the digestive gland penetrates only the two anteriormost pairs of the dorsolateral appendages (see also Discussion). *Dendronotus robilliardi* sp. n. has 5–9 pairs of dorsolateral appendages and the digestive gland penetrates at least 3–4 pairs of the dorsolateral appendages. In his redescription of *D. albus* Robilliard (1970) misidentified this species, as did Ekimova et al. (prepublication): *Dendronotus albus sensu* Robilliard (1970) shares a larger number of pairs of dorsolateral appendages with *D. robilliardi* sp. n. and not with *D. albus* (= *D. diversicolor*) and can be referred to this new species. Table 2 outlines the differences between these two species.

*Dendronotus robilliardi* sp. n. differs both morphologically and according to the genetic distances from its sympatric species *D. dalli* (range 12.0–14.0% for COI, and 2.7–3.2 % for 16S), *D. kalikal* (range 10.8–12.1% for COI, and 3.2 - 3.4% for 16S), and *D. kamchaticus* (range 12.5–13.7% for COI, and 2.8–3.2% for 16S). Another NW Pacific species, *D. primorjensis*, also differs from *D. robilliardi* sp. n. by external morphology, radular and reproductive features, and by *p*-distances (range 12.2–13.6% for COI, and 3.2–3.7% for 16S). Minimum interspecific distances of the COI marker separate *D. robilliardi* sp. n. from other species with high genetic divergences: 13.0% from *D. dalli*, 11.5% from *D. kalikal*, 12.9% from *D. kamchaticus*, and 12.8% from *D. primorjensis*.

### ***Dendronotus kamchaticus* Ekimova et al., 2015**

*Dendronotus kamchaticus* Ekimova, Korshunova, Schepetov, Neretina, Sanamyan & Martynov, 2015: 869–872, figs 6E, 8D, 16A, B, 17, 18A.

**Material.** 1 specimen, ZMMU Op-565, NE Pacific, Puget Sound, Rich Passage, Washington State, USA, 47°58.7'N–122°54.65'W, 17.03.2014, depth 17.4 m, stones and algae, SCUBA diving, collector Karin Fletcher.



**Figure 4.** **A** *Dendronotus albus* MacFarland, 1966, live specimen ZMMU Op-566, dorsal view, Rich Passage, NE Pacific **B** same, posterior radular teeth, SEM **C** *Dendronotus kamchaticus* Ekimova et al., 2015, live specimen ZMMU Op-565, dorsal and lateral view, Rich Passage, NE Pacific **D** same, posterior radular teeth, SEM. Scale bars **B**, **D** = 30  $\mu$ m. Photos of living specimens by Karin Fletcher, SEM images by Alexander Martynov.

**Description.** Body elongate, 30 mm in length (live specimen, Fig. 4C). Four branched appendages of oral veil, *ca.* five appendages of rhinophoral stalks, approximately ten rhinophoral lamellae, branched rhinophoral lateral papilla present, six pairs dorsolateral appendages, *ca.* 10–15 lip papillae. Dorsolateral appendages with long primary stalk and secondary branches, and elongate tertiary branches (Fig. 4C). Reproductive and anal openings placed laterally on right side. General colour pale, translucent white with few scattered brown dots and opaque white stripe on dorsal appendages (Fig. 4C).

Dorsal processes of jaws inclined posteriorly at approximately 70° to longitudinal axis of jaw body and 0.37 of its length. Masticatory borders with fine denticles. Radula formula  $44 \times 3-10.1.10-3$ . Central tooth with reduced or completely absent denticles and furrows in posterior rows (Fig. 4D); anteriormost juvenile rows denticulated. Lateral teeth short, slightly curved, bearing up to six distinct denticles.

Reproductive system triaulic. Ampulla wide, folded twice. Prostate consists of approximately 20–25 alveolar glands. Vas deferens relatively short and expands to oval penial sheath and conical penis. Vagina moderate in length. Bursa copulatrix large, rounded, elongated, with small seminal receptaculum placed distally.

**Biology.** Inhabits stony and rocky substrates.

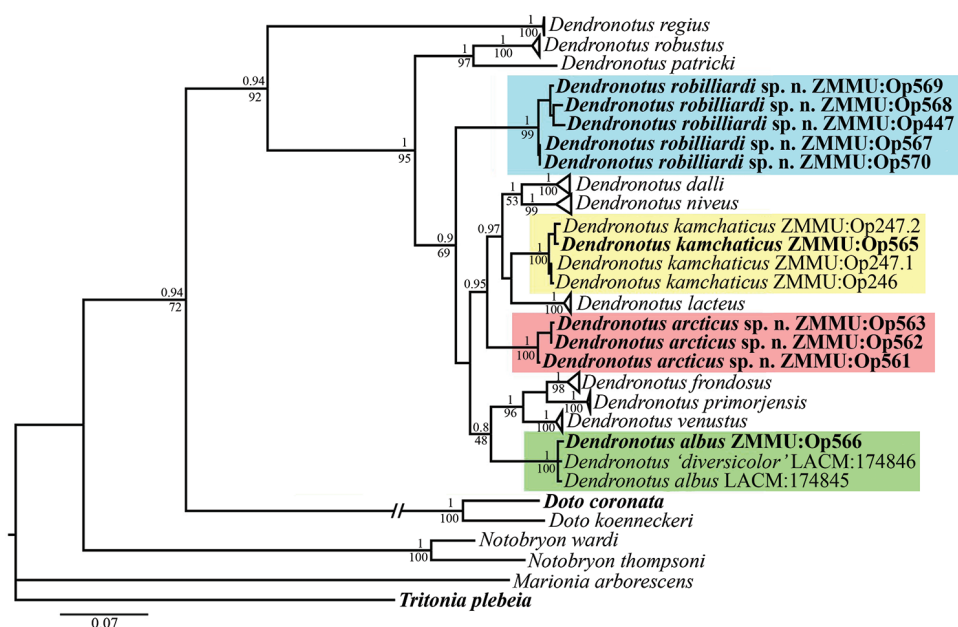
**Distribution.** According to the present data *D. kamchaticus* has a broad transpacific distribution in the northern part of the Pacific Ocean.

**Table 2.** Key diagnostic characters of *Dendronotus albus* MacFarland, 1966, its synonym *D. diversicolor* Robilliard, 1970, *D. albus* sensu Robilliard 1970 (= *D. robilliardi*), and *D. robilliardi* sp. n.

	<i>D. albus</i> (based on the original description, MacFarland 1966)	<i>D. "albus"</i> (from Robilliard 1970)	<i>D. diversicolor</i> (based on the original description, Robilliard 1970)	<i>D. diversicolor</i> (from Ekimova et al. prepublication)	<i>D. "albus"</i> (from Ekimova et al. prepublication)	<i>D. robilliardi</i> sp. n. (present study)
Locality	NE Pacific, California (type locality)	NE Pacific	NE Pacific, Washington (type locality)	NE Pacific	NW Pacific, Kamchatka and Kurile Islands	NW Pacific, Kamchatka (type locality)
Body length (live)	Up to 30 mm	Up to 40 mm	Up to 73 mm	Appr. 40 – 50 mm	Appr. 20 mm	Up to 35 mm
Number of pairs of dorsolateral appendages ("cerata")	4–5	5–7 (4–8)	4–5	4–5	5–6	5–9
Digestive gland branches in dorsolateral appendages	Only in 2 anterior pairs	Up into 6 pairs, including posterior ones	Only in 2 anterior pairs	Only in 2 anterior pairs	In 4–5 pairs	In 3–4 pairs, including posterior ones
Colour of dorsolateral appendages	"With orange-yellow stripe becoming a dark-brown termination in a clear tip"	Variable, orange, copper, tip opaque white, both orange and white pigments may completely lacking	Variable, opaque orange or opaque white, including tips	"Yellow pigment on cerata only on the tips, pigment occurs in epidermal cells"	"Internal yellow pigment near the base; tips with white pigment"	Variable, orange-copper, tip opaque white, orange pigment may completely lacking
Jaws	–	The dorsal processes at 50–60° to the longitudinal axis, 0.43 × of its length	The dorsal processes at 60° to the longitudinal axis, and about 0.4 × of its length	–	–	The dorsal processes of the jaws at approximately 60° to the longitudinal axis, and 0.45 × of its length
Denticles of jaws	Ridge-like denticles (according to Pl. 47, Fig. 4–11)	Ridge-like denticles	–	–	–	Ridge-like denticles
Radula formula	36–38 × (7.9.1.7.9)	32–38 × (6.8.1.6–8)	33–38 × (6–9.1.6–9)	34 × 8.1.8	34–38 × 7–9.1.7–9	43 × 3–9.1.9–3
Central teeth	16–20 denticles	11–14 (7–17) denticles	13–17 (7–25) denticles	10–17 denticles	10–17 denticles	Up to 15 denticles
Lateral teeth	5–7 denticles	4–6 (3–8) denticles	4–10 (2–14) denticles	4–10 denticles	4–10 denticles	up to 7 denticles

	<i>D. albus</i> (based on the original description, MacFarland 1966)	<i>D. "albus"</i> (from Robilliard 1970)	<i>D. diversicolor</i> (based on the original description, Robilliard 1970)	<i>D. diversicolor</i> (from Ekimova et al. prepublication)	<i>D. "albus"</i> (from Ekimova et al. prepublication)	<i>D. robilliardi</i> sp. n. (present study)
Ampulla	Wide, bent (according to Pl. 50, Fig. 4)	"Very wide, short, crescentic"	"Wide, which is folded against itself for most of its length"	"Well-developed, which is folded against itself for most of its length"	"Wide and short, crescent-shaped"	Wide, folded twice
Relative size of discoid prostate	Large (according to Pl. 50, Fig. 4)	"Much smaller than in <i>D. diversicolor</i> "	Large (according to Fig. 28)	"Quite large"	Small	Moderate
Number of prostatic alveolar glands	"some ten"	12–15	"30 or more"	10	10	19–20
Vas deferens	Short, widened after prostate, then narrowed (according to Pl. 50, Fig. 4)	"Relatively short, quite narrow"	Short, wide	Short, wide	Narrow	Short, relatively narrow
Penis	"Short, nearly straight, tapering to a blunt tip"	"Moderately long, narrow, tapered to a point"	"Short, wide, nearly straight, tapers gradually to a blunt tip"	Relatively straight, tapers gradually to a blunt tip (according to Fig. 4B)	Conical (according to Fig. 4A)	Relatively long, conical
Vagina	Narrow (according to Pl. 50, Fig. 4)	"Quite narrow"	Narrow	Relatively wide (according to Fig. 4B)	Narrow (according to Fig. 4A)	Narrow
Uterine (insemination) duct	Short (according to Pl. 50, Fig. 4)	Short	Short	Long	Short	Short
Bursa copulatrix	"Spherical, almost sessile"	"Spherical, stalked"	"Squashed ovoid", "stalked"	Spherical, non-stalked (according to Fig. 4B)	Spherical, non-stalked (according to Fig. 4A)	Irregularly spherical, stalked
Seminal receptaculum	"Small, pyriform"	"Long, flaccid, sac-like"	"Small, spherical"	Relatively small (according to Fig. 4B)	Relatively large (according to Fig. 4A)	Small, oval





**Figure 5.** Phylogenetic tree based on combined molecular data (COI + 16S + 28S) represented by Bayesian Inference. Numbers above branches represent posterior probabilities from Bayesian Inference. Numbers below branches indicate bootstrap values for Maximum Likelihood. Some branches are collapsed at species level. New specimens are highlighted in bold.

**Remarks.** *Dendronotus kamchaticus* was recently described from Kamchatka in the Russian NW Pacific (Ekimova et al. 2015). Here an outstanding and unexpected record of *D. kamchaticus* is presented from the American NE Pacific (Washington state). The single collected specimen matches closely with *D. kamchaticus* from the type locality, and genetic distances between the four *D. kamchaticus*, including *D. kamchaticus* from Washington waters, range from 0–1.1% for COI, and 0–0.2% for 16S. Mean *p*-distance value of the COI marker within *D. kamchaticus* group is 0.7%. Furthermore, *D. kamchaticus* from Washington waters share an important diagnostic character with those from the type locality, the central teeth with strongly reduced denticles and furrows in the posterior radular teeth (Fig. 4D) and denticulated anteriormost juvenile rows. This is the first record of *D. kamchaticus* from the NE Pacific, approximately 6000 km away from the type locality, across the ocean.

## Discussion

*Dendronotus arcticus* sp. n. is the first species of the genus described from the central Arctic region of Eurasia. Using a combination of external and internal morphological characters, *D. arcticus* sp. n. can be distinguished from all recently reviewed species of the genus *Dendronotus* (Stout et al. 2010, Ekimova et al. 2015, Martynov et al. 2015a,

b). The molecular data also support the description of *D. arcticus* sp. n. as a new species.

*Dendronotus albus* species complex is a long standing problem of the North Pacific nudibranch taxonomy. Since Robilliard (1970) described the species *D. diversicolor* there was little consensus on how to distinguish this species from *D. albus*. Recently, using morphological and molecular data, *D. diversicolor* was considered to be junior synonym of *D. albus* (Stout et al. 2010). While this paper was under review, a manuscript appeared online (Ekimova et al. prepublication): these authors recognised the presence of two species and suggested that *D. albus* inhabits the NW Pacific and that *D. diversicolor* is a separate NE Pacific species, challenging the previous synonymy by Stout et al. (2010). However, there are number of key problems with their assumptions:

- (1) Ekimova et al. (prepublication) called a species from NW Pacific “true” *D. albus* but this is in error since the first description of *D. albus* in MacFarland (1966) was based on specimens from NE Pacific (California) and fits well with the diagnostic features of *D. diversicolor* (type locality also in NE Pacific, Washington) and was previously synonymised by Stout et al. (2010).
- (2) According to the original description in Robilliard (1970: 471) *D. diversicolor* possesses four to five pairs dorsolateral appendages (cerata), and the digestive gland penetrates only the two anteriormost pairs of the cerata; precisely these characters have been reported in the original description of *D. albus* (MacFarland 1966: 275, 278–279) but were not noted by Ekimova et al. (prepublication). These facts also support the synonymy of *D. diversicolor* with *D. albus*.
- (3) Colour patterns of *D. albus* and *D. diversicolor* vary greatly (Robilliard 1970) and cannot serve as reliable diagnostic features; in Ekimova et al. (prepublication) only specimens with yellow pigment are discussed whereas white specimens without yellow/orange pigment are common (Robilliard 1970).
- (4) Ekimova et al. (prepublication) recorded the body length as approximately 20 mm as a diagnostic feature for “true *D. albus*”, while for *D. diversicolor* they recorded 40–50 mm; however, this is inaccurate since MacFarland (1966: 276) in the original description of *D. albus* recorded 30 mm, and Robilliard (1970: 466) reported the length up to 40 mm, which clearly overlaps with the size of *D. diversicolor*. The notion “true” is thus incorrect, since the species reported by Robilliard and in the publication of Ekimova et al. (prepublication) is in fact *D. robilliardi* sp. n. and not *D. albus*.
- (5) The number of prostatic alveolar glands cannot be diagnostic as pointed out by Ekimova et al. (prepublication) because there is too much variation within species; while they reported no more than ten alveoli for NW Pacific *D. albus* (= *D. robilliardi* sp. n.), the present work records no less than 19–20 alveoli in *D. robilliardi* sp. n. from the same NW Pacific region while Robilliard (1970: 473) also reported no less than 30 alveoli in the original description of *D. diversicolor*. For *D. albus* MacFarland (1966: 279) reported only “some ten” prostatic alveoli, but the prostate itself is large (MacFarland 1966, Plate 50, Fig. 4) and similar to the original description of *D. diversicolor* (Robilliard 1970, fig. 28) and not to the small pros-



tate of *D. albus sensu* Robilliard (1970, fig. 24 = *D. robilliardi*). Thus, the number of prostatic alveolar glands should be used for diagnostic purposes with great care since their number may depend on the physiological condition of a specimen, and also because it is very easy to make a mistake during counting of the alveoli under a stereomicroscope.

- (6) The same considerable variation can be mentioned for other reproductive features. E.g. the uterine (insemination) duct of *D. diversicolor* is short according to the original description (Robilliard 1970: 473–474) whereas according to Ekimova et al. (prepublication) it is long, but these authors claim that “these features were described by Robilliard (1970) for *D. diversicolor* as important for its separation from *D. albus*”. Furthermore, the bursa copulatrix (termed as receptaculum in Ekimova et al. (prepublication) although Stout et al. 2011 provided an updated nomenclature), the receptaculum semenis (termed bursa in Ekimova et al. prepublication), and the shape of the ampulla are all variable and variably described by authors (Table 2). Thus, Robilliard’s (1970) and Ekimova’s et al. (prepublication) statements that reproductive characters are important for distinguishing of *D. albus* and *D. diversicolor* should be reconsidered.

Thus, *D. albus* (according to the original description) is essentially similar to *D. diversicolor*, but differs considerably from *D. robilliardi*. All sequenced specimens of *D. albus* species complex from the NE Pacific (including the present study) show distinct species-level molecular differences compared to NW Pacific *D. robilliardi*. In this study, a very large specimen (70 mm long) of *D. albus* from the NE Pacific (Washington State, Rich Passage, 17 March 2014, 12.5 m, collector Karin Fletcher, ZMMU Op-566) (Fig. 4A, B) was studied: it had four pairs dorsal appendages, and thus morphologically matches true *D. albus* and the original description of its synonym *D. diversicolor*. In our phylogenetic analysis (Fig. 5) the *D. albus* specimen from Rich Passage is robustly placed in the same clade with the other *D. albus* (including those named *D. diversicolor*), and all four specimens of *D. robilliardi* sp. n. and its egg mass (Fig. 2E) are clustered in a single separate clade (Fig. 5). The number of radular rows in our 70 mm long *D. albus* is 38, somewhat less than the 43 rows in half as small specimen of *D. robilliardi*. The number of prostatic lobules in *D. albus* from Rich Passage is ca. 25–27, thus approaching the range reported for *D. diversicolor* by Robilliard (1970) and supports the size-dependence theory of the number of prostatic alveoli.

This work confirms the synonymy of *D. diversicolor* Robilliard, 1970 as a junior synonym of *D. albus* MacFarland, 1966 as suggested by Behrens (2006) and realized by Stout et al. (2010), and the existence of a third species described herein as *D. robilliardi* sp. n. (Table 2). Further work on more material is desirable to confirm the actual range of this species in the northeastern Pacific.

*Dendronotus kamchaticus* was described recently (Ekimova et al. 2015) and was thought to be endemic of the NW Pacific. However, in this study a surprising record of *D. kamchaticus* from NE Pacific is documented. The specimen from the Puget Sound, Rich Passage, agrees well with *D. kamchaticus* from the NW Pacific in radular patterns and molecular data but differs in having a much paler ground colour and the presence of dense white pigment (Fig. 4C). The pale ground colour is similar to that of another species, *D. dalli*, and to the pale variants of *D. venustus*. Misidentifications with *D. dalli* and *D. venustus* may explain the absence of records of *D. kamchaticus* from the NE Pacific, and records of these two species need to be re-examined in light of this study. Other explanations may include anthropogenic transportation by ships, either in the biofouling organisms or as larvae in ballast tanks; however, *D. kamchaticus* may prove to be a species with a natural transpacific distribution. We also observe differences from the original description in Ekimova et al. (2015), including the shape of the dorsal processes (long slender branches of the dorsal processes not short bulbous ones described by Ekimova et al. 2015) and patterns of the masticatory processes of jaws. Therefore, the diagnosis of *D. kamchaticus* is expanded to include denticles on the masticatory processes of the jaws and elongated dorsal processes.

## Conclusions

In this study new data on the taxonomy, phylogeny, and biogeography of the genus *Dendronotus* are presented. A true Arctic species *D. arcticus* sp. n. from the central Eurasian coastal zone is described. This species is well supported by both morphological and molecular data. A long-standing problem of *D. albus* species complex is revisited and for the first time it is clearly concluded that Robilliard (1970) in the course of his revision of the genus *Dendronotus* misidentified true *D. albus* as it was originally described by MacFarland (1966) (Table 2). The key diagnostic characters of *D. albus* fully agree with the original description of *D. diversicolor* Robilliard, 1970, and the latter is confirmed a junior synonym of *D. albus*. At the same time, a species that was redescribed by Robilliard (1970) under the name *D. albus* has considerable differences from the true *D. albus* but is the newly described *D. robilliardi* from the NW Pacific. Finally, a remarkable record of *D. kamchaticus* is presented here for the first time from NE Pacific, extending its range to the east by some 6000 km.

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# The jumping spiders from Xishuangbanna, Yunnan, China (Araneae, Salticidae)

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## Abstract

Twenty one jumping spider species from South Yunnan are reported, diagnosed, described and illustrated; 19 of them are described as new: *Afraflacilla ballarini* Cao & Li, **sp. n.** (♂), *Agorius tortilis* Cao & Li, **sp. n.** (♂♀), *Bavia exilis* Cao & Li, **sp. n.** (♂), *Carrhotus kevinlii* Cao & Li, **sp. n.** (♂♀), *Carrhotus sarahcrewsae* Cao & Li, **sp. n.** (♂), *Chinattus wengnanensis* Cao & Li, **sp. n.** (♂♀), *Chinophrys mengyangensis* Cao & Li, **sp. n.** (♂♀), *Cocalus menglaensis* Cao & Li, **sp. n.** (♂♀), *Cosmophasis xiaolonghaensis* Cao & Li, **sp. n.** (♂♀), *Cytaea yunnanensis* Cao & Li, **sp. n.** (♂), *Gedea pinguis* Cao & Li, **sp. n.** (♂), *Gelotia zhengi* Cao & Li, **sp. n.** (♂), *Icius bamboo* Cao & Li, **sp. n.** (♂), *Nannenus menghaiensis* Cao & Li, **sp. n.** (♂♀), *Pancorius latus* Cao & Li, **sp. n.** (♂), *Phintella lepidus* Cao & Li, **sp. n.** (♂♀), *Phintella sancha* Cao & Li, **sp. n.** (♂), *Ptocasius paraweyersi* Cao & Li, **sp. n.** (♂♀), and *Stenaelurillus fuscus* Cao & Li, **sp. n.** (♂). Females of *Bavia capistrata* (C.L. Koch, 1846) and *Phintella suavisoides* Lei & Peng, 2013 are described for the first time. DNA barcodes of 12 species were obtained for future use.

## Keywords

Description, diagnosis, new species, Southeast Asia, taxonomy

## Introduction

Of 598 salticid genera and 5912 species known worldwide (World Spider Catalog 2016), 95 genera and 473 species are recorded from China, with 44 genera and 94 species recorded from Yunnan (Li and Lin 2016). The lists are far from being complete as large parts of the country are still poorly studied.

Being a border area with Vietnam, Laos and Myanmar, Yunnan shares the jumping spider taxa with those countries, of which the fauna of Vietnam is the best studied, with 56 genera and 116 species (Ono et al. 2012), the majority described and recorded by Žabka (1985). From other countries, 18 species are known from Laos and 55 from Myanmar (World Spider Catalog 2016).

While studying spiders in Xishuangbanna in South Yunnan, 21 salticid species were found. The goal of this paper is to report these species, including descriptions of 19 new species and the redescriptions of two known species.

## Material and methods

The material came from Xishuangbanna in South Yunnan (21°08'N–22°36'N, 99°56'E–101°50'E). The area belongs to the transitional zone from tropical South to subtropical East Asia (Zhu et al. 2004). The region has an area of 19,120 km<sup>2</sup>, with mountain ridges running north-south, and the elevation decreasing southwards. The current study is based on 10 years of collecting in Xishuangbanna. More details on the spider diversity in the area and collection methods can be found in Zheng et al. (2015).

The specimens were preserved in 95% ethanol and were examined and measured with Olympus SZX12 and BX41 microscopes. Photos were taken with an Olympus C7070 wide zoom digital camera mounted on an Olympus SZX12 stereomicroscope. The images were processed with Helicon image stacking software. Vulvae were removed and digested with lactic acid or a 10% warm solution of potassium hydroxide (KOH). All measurements are in millimetres. References to figures in the cited papers are listed in lowercase type (fig. or figs); figures in this paper are noted with an initial capital (Fig. or Figs).

## Abbreviations used

**AER** anterior eye row;  
**ALE** anterior lateral eyes;  
**AL** abdomen length;  
**AME** anterior median eyes;  
**AW** abdomen width;  
**CD** copulatory ducts;

**CL** carapace length;  
**CO** copulatory opening;  
**CW** carapace width;  
**DB** dorsal-basal bulge;  
**DTA** dorsal tibial apophysis;  
**E** embolus;



<b>EB</b>	embolus base;	<b>RBB</b>	retrolateral bulbal bump;
<b>EC</b>	extension of cymbium;	<b>RP</b>	retrolateral process;
<b>EFL</b>	length of eye field;	<b>RTA</b>	retrolateral tibial apophysis;
<b>FD</b>	fertilization ducts;	<b>RVA</b>	retrolateral ventral tibial apophysis;
<b>H</b>	hood;	<b>S</b>	serration;
<b>LP</b>	lamellar process;	<b>SA</b>	sclerotized apophysis;
<b>P</b>	pocket;	<b>SD</b>	seminal duct;
<b>PE</b>	posterior extension;	<b>RP</b>	retrolateral process;
<b>PER</b>	posterior eye row;	<b>SDA</b>	seminal duct angle;
<b>PLE</b>	posterior lateral eyes;	<b>TA</b>	tegular apophysis;
<b>PME</b>	posterior median eyes;	<b>TD</b>	translucent duct;
<b>PP</b>	prolateral process;	<b>TP</b>	tegulum protrusion;
<b>R</b>	receptacles;	<b>VTa</b>	ventral tibial apophysis.

The leg spination pattern is given after Platnick and Shadab (1975): d, p, v, r for dorsal, prolateral, ventral and retrolateral sides of a segment.

For 12 species the DNA barcodes were obtained for future use (the samples collected in 2006, 2007 and 2009 were not extracted successfully). A partial fragment of the mitochondrial gene cytochrome oxidase subunit I (COI) was amplified and sequenced following the protocol in Miller et al. (2010). Primers used in this study are: LCO1490 (5'-CWACAAAYCATARRGATATTGG-3') and HCO-N-2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al. 1994). Voucher information and GenBank accession number for all samples are listed in Table 1. All specimens, including voucher specimens, are deposited in the Institute of Zoology, Chinese Academy of Sciences (IZCAS) in Beijing, China.

**Table 1.** Voucher specimen information,

Species	Sequence length	GenBank accession number	Collecting localities in Xishuangbanna
<i>Agorius tortilis</i> sp. n.	629 bp	KU893260	Mengyang, Jinghong
<i>Bavia capistrata</i>	629 bp	KU893261	Menglun, Mengla
<i>Carrhotus kevinlii</i> sp. n.	629 bp	KU893263	Menglun, Mengla
<i>Carrhotus sarahcrewsae</i> sp. n.	629 bp	KU893264	Menglun, Mengla
<i>Chinattus wengnanensis</i> sp. n.	629 bp	KU893265	Menga, Jinghong
<i>Chinophrys mengyangensis</i> sp. n.	629 bp	KU893266	Mengyang, Jinghong
<i>Cocalus menglaensis</i> sp. n.	629 bp	KU893267	Xiaolongha, Mengla
<i>Cosmophasis xiaolonghaensis</i> sp. n.	629 bp	KU893268	Xiaolongha, Mengla
<i>Nannenus menghaiensis</i> sp. n.	629 bp	KU893269	Menghai, Jinghong
<i>Phintella lepidus</i> sp. n.	629 bp	KU893270	Mengyang, Jinghong
<i>Phintella suavisoides</i>	629 bp	KU893271	Menglun, Mengla
<i>Procasius paraweyersi</i> sp. n.	629 bp	KU893272	Menglun, Mengla

## Taxonomy

Family Salticidae Blackwall, 1841

Genus *Afraflacilla* Berland & Millot, 1941

*Afraflacilla ballarini* Cao & Li, sp. n.

<http://zoobank.org/898EE80F-6D26-4FFB-B9F4-832A81944515>

Figs 1–2, 43

**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Menglun Town, rubber plantation (21°54.684'N, 101°16.319'E, 585 m), 7 March 2006, G. Zheng leg.

**Etymology.** The new species is named after Francesco Ballarin (IZCAS) for his study on the spiders of Asia; noun (name) in genitive case.

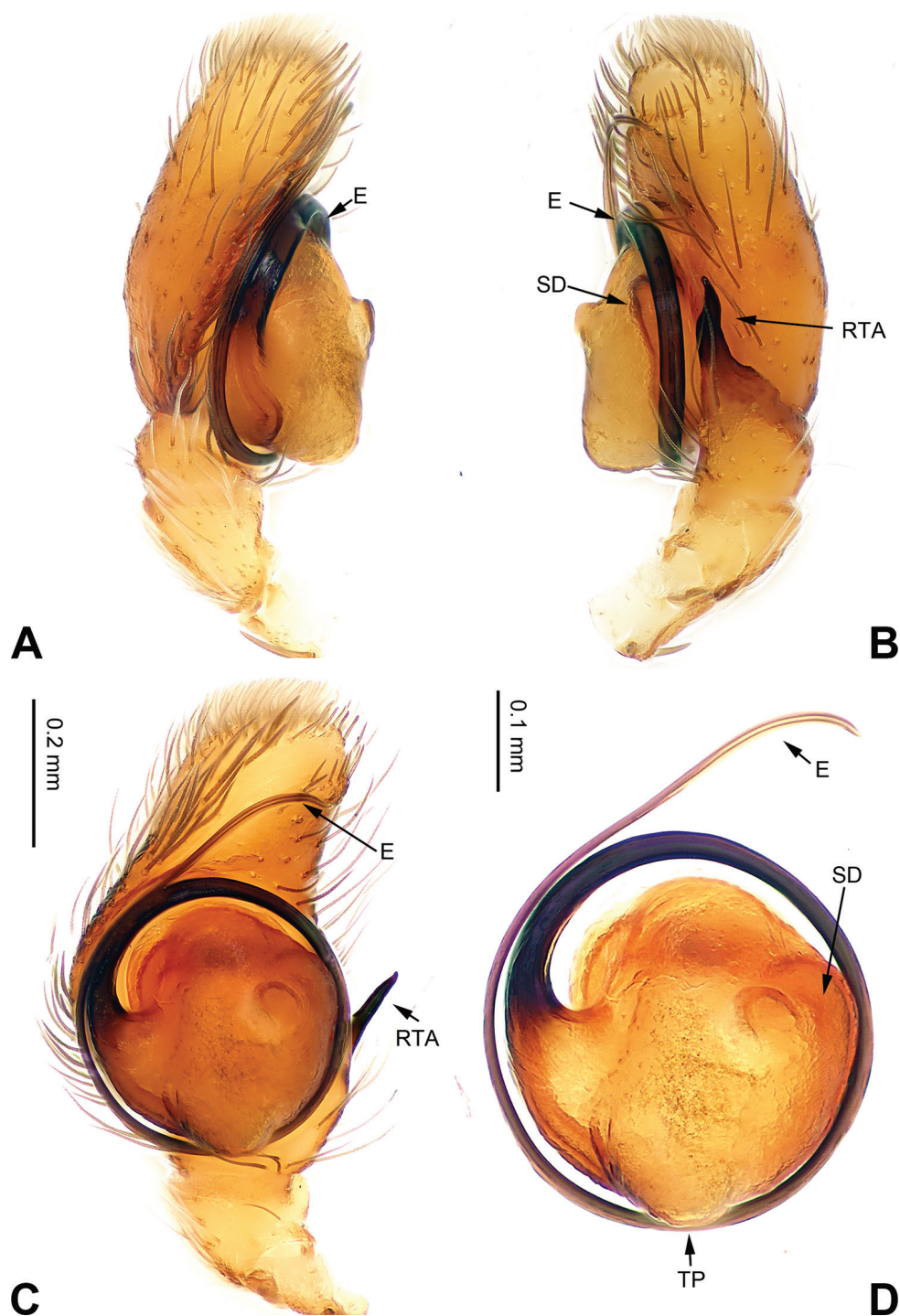
**Diagnosis.** The male resembles *A. grayorum* Żabka, 1993 (Żabka 1993: figs 7A–D, 8A–C) by having similar embolus (Fig. 1C–D) and body shape (Fig. 2), but differs in the shape of the tegulum (Fig. 1D) and embolus set at nine o'clock vs. six o'clock in *A. grayorum*. Also, the course of the seminal duct and tegular protrusion are in different positions (six o'clock vs. four o'clock in *A. grayorum*). The tibial apophysis lacks a dorsolateral protrusion (vs. this character in *A. grayorum*) (Fig. 1B).

**Description.** Male (holotype). Total length 3.85, CL 1.85, CW 1.20, AL 2.00, AW 1.40. Eye measurements: AME 0.32 ALE 0.18 PME 0.08 PLE 0.15; AER 1.00, PER 1.00, EFL 0.85. Clypeus 0.12 high. Legs: I 3.58 (1.05, 0.70, 0.85, 0.60, 0.38); II 2.31 (0.78, 0.33, 0.50, 0.40, 0.30); III 2.60 (0.80, 0.35, 0.55, 0.50, 0.40); IV 3.34 (1.00, 0.50, 0.75, 0.64, 0.45).

Carapace brown with grey and white hairs (Fig. 2A). Sides and clypeus with white marginal band. Ocular area dark brown. Chelicerae and labium brown. *Maxillae* brown with white tips. Sternum greyish brown. Abdomen oval, brownish, anterior and sides with white hairs. Venter and spinnerets dark brown. Leg I more robust and darker than the other legs, which are yellowish. Spination of leg I: femur d2-1-1; tibia p0-1-0, metatarsus v2-0-2. Palpal tibia short, about 1/3 length of cymbium. Cymbial tip about 1.5 times as long as tibia. RTA pointed, subequal to the length of the tibia (Fig. 1B). Bulb oval, with blunt outgrowth and posterior protrusion (Fig. 1D). Seminal duct with loops. Embolus elongate, starting at nine o'clock and coiled more than once around the bulb (Fig. 1C).

Female. Unknown.

**Distribution.** Known only from the type locality.



**Figure 1.** Palp of *Afraflacilla ballarini* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.



**Figure 2.** Habitus of *Afraflacilla ballarini* sp. n., male holotype. **A** dorsal **B** lateral.

### Genus *Agorius* Thorell, 1877

#### *Agorius tortilis* Cao & Li, sp. n.

<http://zoobank.org/4BB85C25-617E-4601-9310-F134823897BE>

Figs 3–4, 43

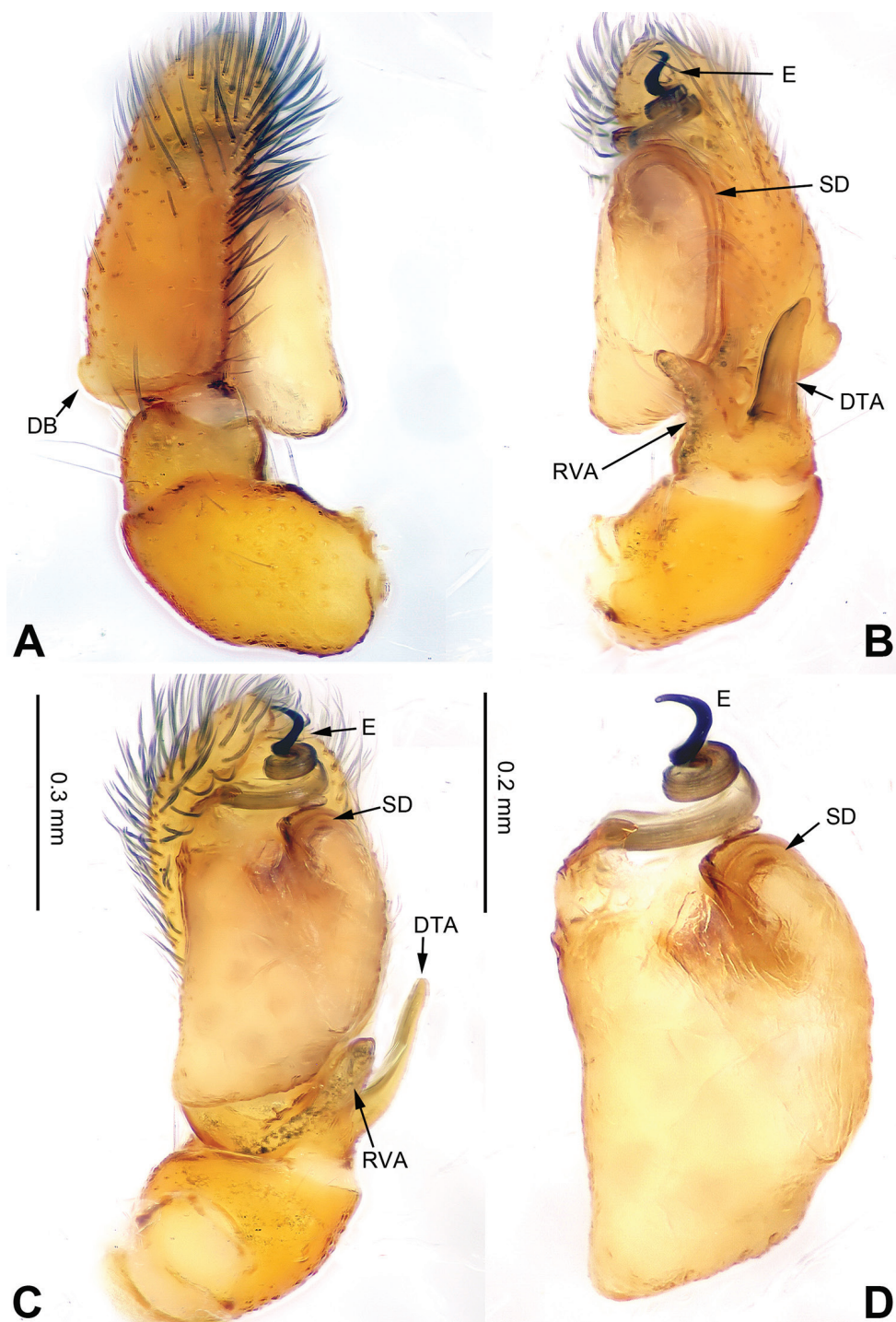
**Type. Holotype** ♂: CHINA, Yunnan, Jinghong City, Mengyang Town, tunnel in Mt. Baihuashan (22°69.529'N, 101°55.210'E, 856 m), 16 July 2012, Q. Zhao & Z. Chen leg. **Paratype**: 1♀, same data as holotype.

**Etymology.** From Latin *tortilis* (coiled), in reference to the shape of embolus; adjective.

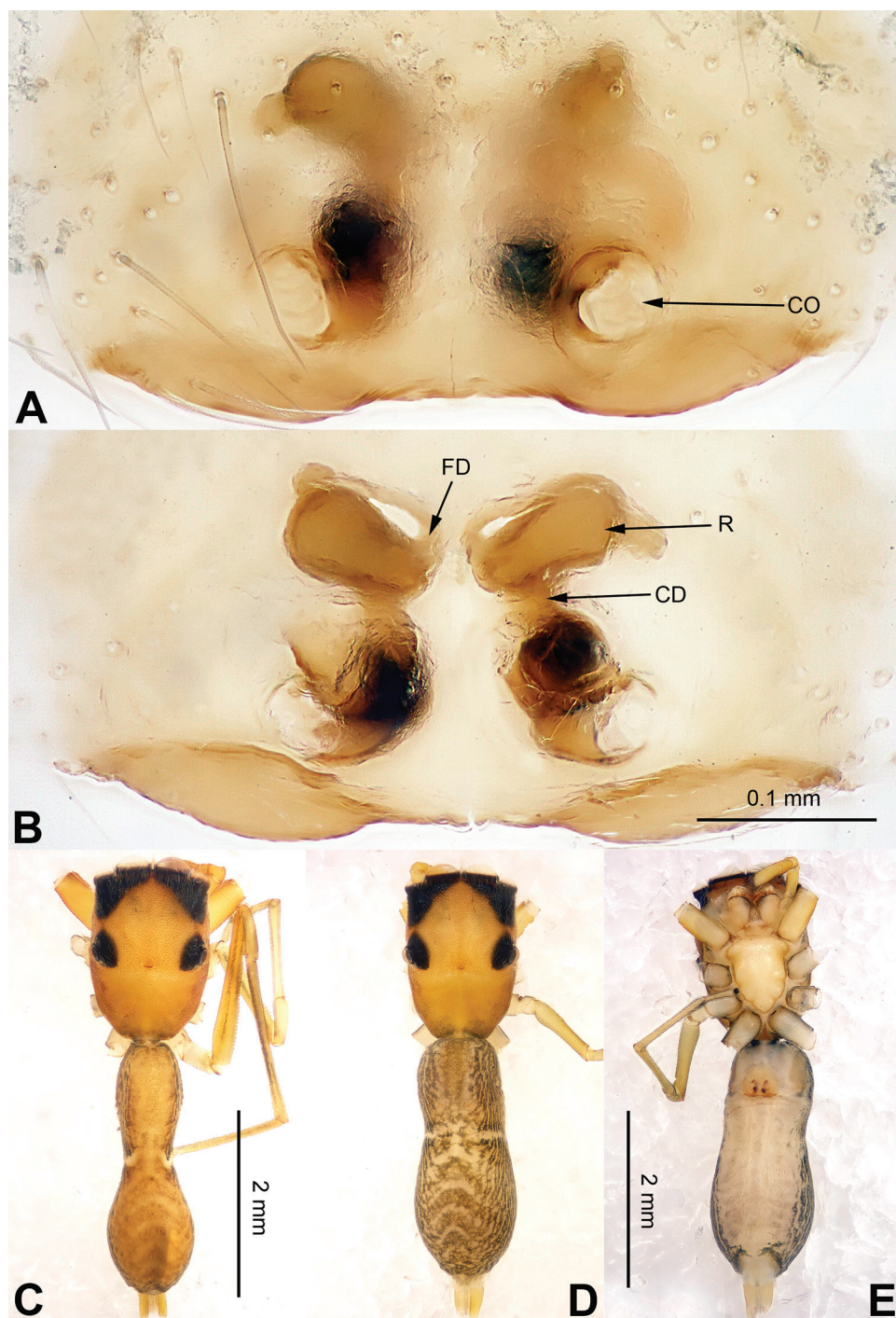
**Diagnosis.** The male is similar to that of *A. lindu* Prószyński, 2009 (Prószyński 2009: figs 7–8, 29–30, 54, 59) by body shape (Fig. 4C) and tegulum (Fig. 3C–D), but the embolus has 3 coils (Fig. 3D) vs. 1; dorsal-retrolateral tibial apophysis lacking, without terminal hook (Fig. 3B), which is present in *A. lindu*. The female differs from that of *A. lindu* by the shape of the copulatory openings (Fig. 4A), which are small circular holes vs. slanted ovals in *A. lindu*, and the copulatory openings are separated by about two diameters vs. only 1/4 diameter in *A. lindu*.

**Description.** Male (holotype). Total length 5.23, CL 1.83, CW 1.50, AL 3.40, AW 1.09. Eye measurements: AME 0.48, ALE 0.27, PME 0.01, PLE 0.25, AER 1.48,





**Figure 3.** Palp of *Agorius tortilis* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.



**Figure 4.** *Agorius tortilis* sp. n., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male habitus, dorsal **D** female habitus, dorsal **E** female habitus, ventral. Scale bar equal for **A** and **B**; equal for **D** and **E**.

PER 1.49, EFL 1.47. Clypeus 0.04 high. Legs: I 18.26 (3.28, 4.00, 2.64, 0.50, 0.46); II 3.95 (1.55, 0.55, 1.31, 1.06, 0.45); III missing; IV 7.50 (2.13, 0.73, 2.13, 1.88, 0.63).

Carapace greyish-yellow (Fig. 4C). *Chelicerae* yellow, sparsely covered with fine grey hairs. *Maxillae* yellow with black anterior margin and grey hairs on inner margins. *Labium* dark yellow, tip with black hairs. *Sternum* yellowish. Abdomen thin, elongate with median constriction. Venter and spinnerets yellow. Legs I thin and long, especially the patella. Spination of leg I: tibia v2-2-2-2; metatarsus p2-0-2. Palp: patella large, thicker than tibia. Tibia with two large apophyses, RVA and DTA (Fig. 3B). Cymbium with dorsal-basal small bulge (Fig. 3A). Tegulum with a broad prolateral flap. Seminal duct encircling retrolateral part of tegulum. Embolus with tapering spiral (Fig. 3C).

Female (paratype). Total length 5.54, CL 2.35, CW 1.38, AL 3.19, AW 1.23. Eye measurements: AME 0.44, ALE 0.25, PME 0.01, PLE 0.25, AER 1.30, PER 1.32, EFL 1.36. Clypeus 0.04 high. Legs: I 7.64 (2.50, 2.56, 1.80, 0.40, 0.38); II 4.15 (1.25, 0.56, 1.04, 0.90, 0.40); III missing; IV 4.31 (1.22, 0.56, 1.09, 1.00, 0.44).

Abdomen higher and broader than in male, other characters similar. Epigyne heavily sclerotised along the posterior margin (Fig. 4A). Copulatory opening grooves round and separated from each other by two diameters, located 1 diameter from the posterior margin. Vulva: copulatory ducts short and sclerotised, anterior part thicker than the posterior. Receptacles pyriform. Fertilisation ducts elongate and located at the posterior part of the receptacles (Fig. 4B).

**Distribution.** Known only from the type locality.

## Genus *Bavia* Simon, 1877

### *Bavia capistrata* (C.L. Koch, 1846)

Figs 5–6, 43

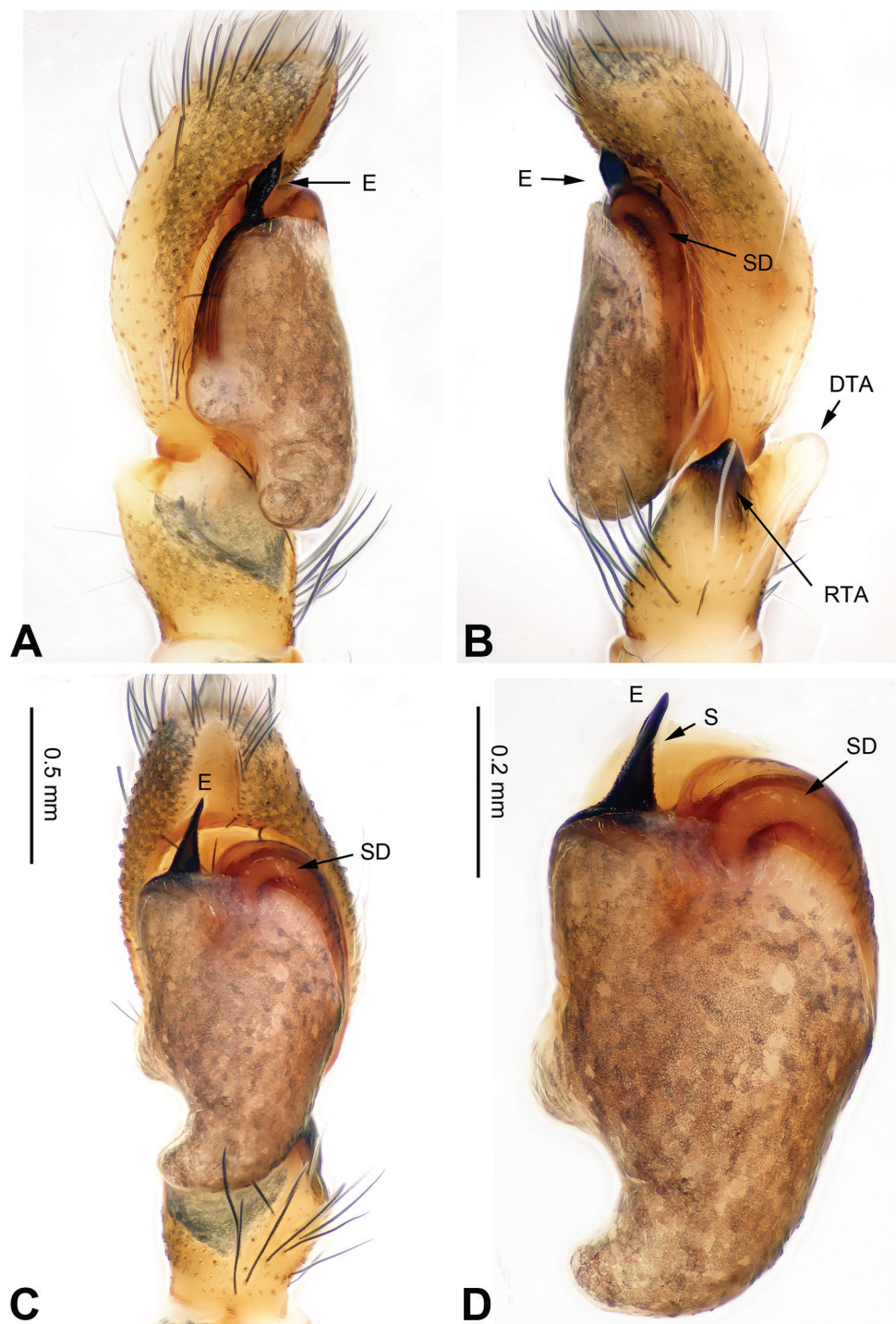
*Maevia capistrata* C.L. Koch, 1846: 76, fig. 1331 (♂).

*Bavia capistrata*: Żabka 1988: 435, figs 37–39 (♂, removed from synonymy with *Evarcha flavocincta*).

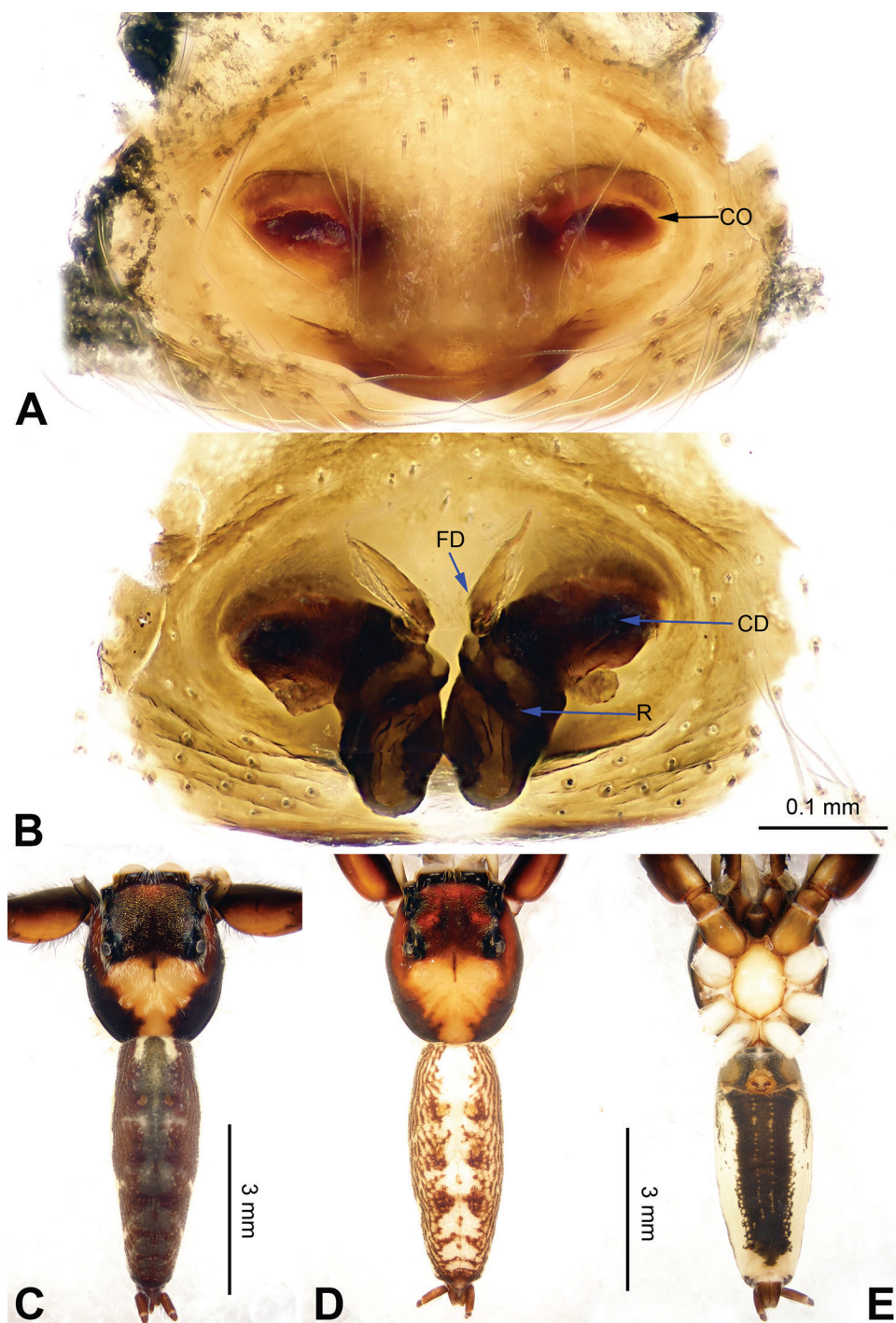
**Material examined.** 1♂, CHINA, Yunnan, Mengla County, Menglun Town, Xishuangbanna Nature Reserve: nearby fish pond (21°57.883'N, 101°12.147'E, 839 m), ravine rainforest, 15 August 2011, Q. Zhao & Z. Chen leg.; 1♀, CHINA, Yunnan, Mengla County, Xiaolongha Village, Xishuangbanna Nature Reserve: Biological diversity corridor (21°24.265'N, 101°37.300'E, 653 m), seasonal rainforest, 27 June 2012, Q. Zhao & Z. Chen leg.

**Diagnosis.** Differs from the closely related *B. aericeps* Simon, 1877 (see Żabka 1988: figs 29–36) by the tibia with a distinct dorsal apophysis (Fig. 5B) and serrated embolus (Fig. 5D). The females differ from *B. aericeps* by the horizontal position of the





**Figure 5.** Palp of *Bavia capistrata*, male from Xishuangbanna. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.



**Figure 6.** *Bavia capistrata*, female and male from Xishuangbanna. **A** epigyne, ventral **B** vulva, dorsal **C** male habitus, dorsal **D** female habitus, dorsal **E** female habitus, ventral. Scale bars equal for **A** and **B**; equal for **D** and **E**.

copulatory openings (Fig. 6A) vs. the inclined copulatory organs and the arc-shaped posterior epigynal margin (Fig. 6A) vs. triangular.

**Description.** Male. Well described by Žabka (1988).

Female. Total length 8.70, CL 3.44, CW 2.75, AL 5.26, AW 1.92. Eye measurements: AME 0.69, ALE 0.28, PME 0.06, PLE 0.29, AER 2.00, PER 2.00, EFL 1.88. Clypeus 0.16 high. Legs: I 6.92 (2.13, 1.35, 1.75, 1.14, 0.55); II 5.50 (1.70, 1.06, 1.26, 0.98, 0.50); III 5.33 (1.60, 0.95, 1.00, 1.19, 0.59); IV 9.09 (2.25, 1.00, 1.74, 1.74, 0.63).

Carapace reddish-brown, lighter dorsally, ocular area dark brown (Fig. 6C) with white setae. Chelicerae dark brown. *Maxillae* elongate with white tips. Labium dark brown with white tips. Sternum yellowish. Abdomen long with light broad median stripe and grey margins. Venter with few longitudinal rows of white dots. Spinnerets brownish grey. Legs I more robust and darker than others. Legs II–IV yellowish. Spination of leg I: femur d2-1-0; tibia v2-2-2, metatarsus p2-0-2. Epigyne strongly sclerotised along the posterior midline margin (Fig. 6A). Copulatory openings slit shaped, with strongly sclerotised edges. Distance between the openings subequal to 1.5 times the length of a copulatory opening. Copulatory ducts short and strongly sclerotised, receptacles close to each other. The length and width of receptacles subequal to the copulatory ducts. Fertilisation ducts located at the joined part of the copulatory ducts and receptacles (Fig. 6B).

**Distribution.** Malaysia to Australia, Pacific Islands, and South China.

**Remark.** Female of *B. capistrata* is described for the first time.

### ***Bavia exilis* Cao & Li, sp. n.**

<http://zoobank.org/2DC9C8CF-27F1-4E1C-86D4-F4303CE1C907>

Figs 7–8, 43

**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Xiaolongha Village, Xishuangbanna Nature Reserve: Biological diversity corridor (21°24.230'N, 101°36.262'E, 715 m), seasonal rainforest, 4 June 2012, Q. Zhao & Z. Chen leg.

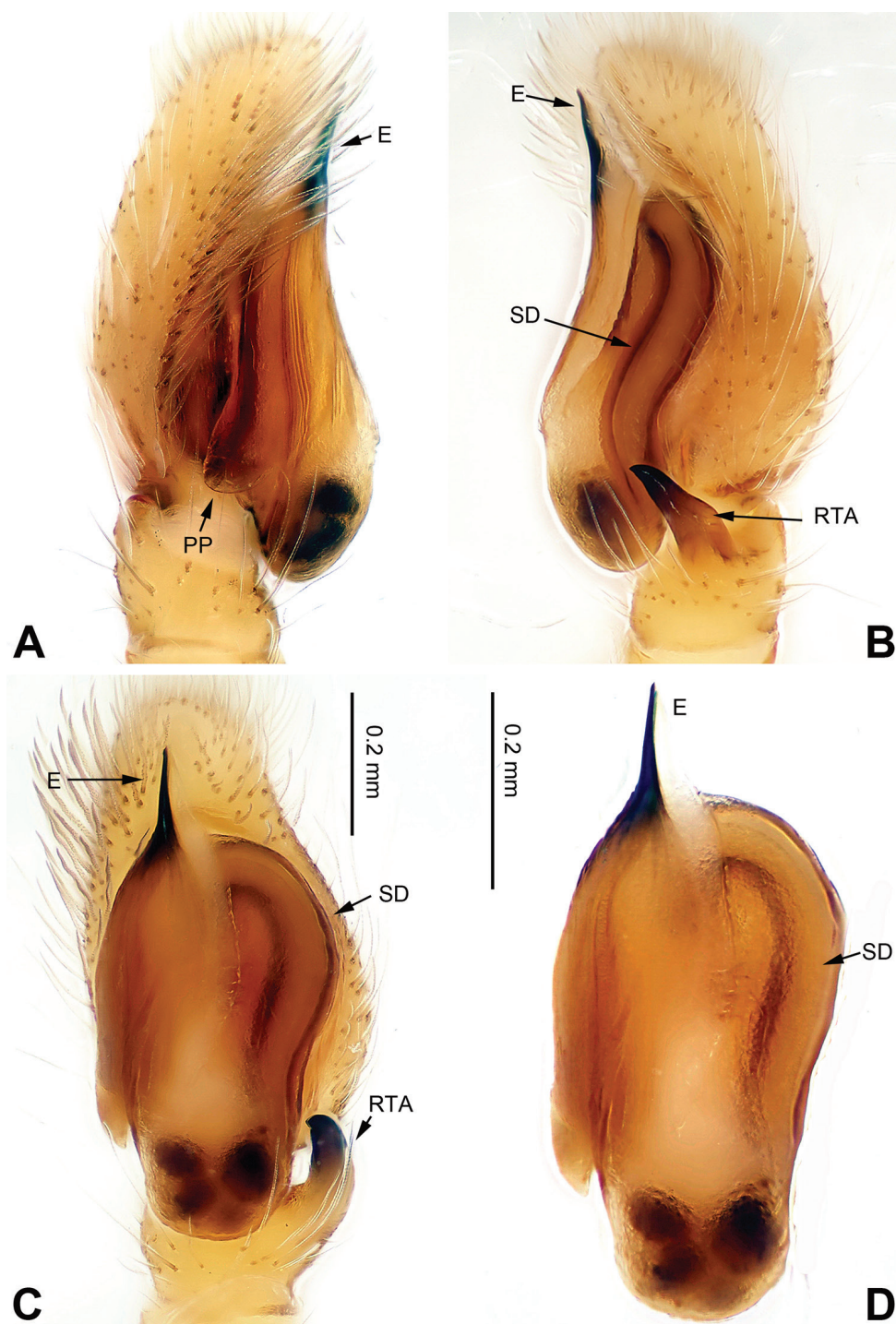
**Etymology.** From Latin *exilis* (slender), in reference to the shape of the abdomen; adjective.

**Diagnosis.** Similar to *B. aericeps*, but RTA much larger (Fig. 7B) and embolus with retrolateral membranous margin (Fig. 7C). Compared to *B. capistrata* (Fig. 5B–D), the tibia lacks a distinct dorsal apophysis, and the embolus is not serrated.

**Description.** Male (holotype). Total length 6.65, CL 2.75, CW 1.75, AL 3.90, AW 1.10. Eye measurements: AME 0.60, ALE 0.21, PME 0.06, PLE 0.16, AER 1.52, PER 1.55, EFL 1.41. Clypeus 0.08 high. Legs: I 6.15 (1.75, 1.00, 1.55, 1.00, 0.85); II 4.00 (1.15, 0.70, 0.85, 0.70, 0.60); III 3.55 (1.00, 0.60, 0.65, 0.80, 0.50); IV 4.35 (1.25, 0.65, 0.90, 1.00, 0.55).

Carapace dark brown with central lighter trapezoid dorsally (Fig. 8A). Chelicerae brown. Maxillae and labium brown, light tips with greyish-brown hairs. Sternum yellowish.





**Figure 7.** Palp of *Bavia exilis* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.



**Figure 8.** Habitus of *Bavia exilis* sp. n., male holotype. **A** dorsal **B** ventral.

lowish. Abdomen elongate, slender and grey. Venter and spinnerets dark greyish. Legs I more robust and darker than others, legs II–IV yellowish. Spination of leg I: femur d1-0-0; tibia v2-2-2; metatarsus v2-0-2. Palp: tibia short, about 1/4 length of cymbium. Tibial apophysis bent, subequal to the length of tibia (Fig. 7B). Embolus short and pointed, with retrolateral membranous margin (Fig. 7C).

Female. Unknown.

**Distribution.** Known only from the type locality.

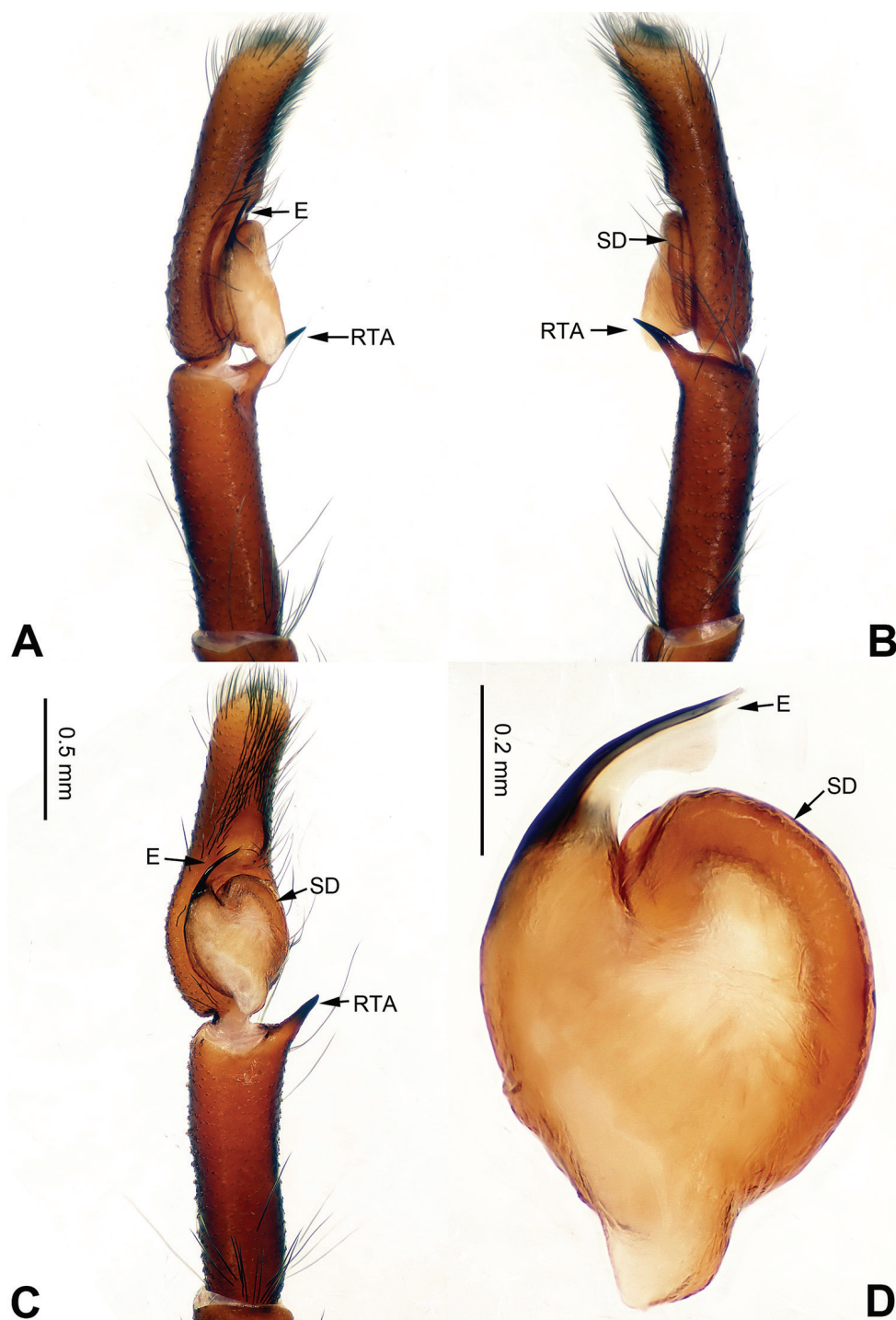
### Genus *Carrhotus* Thorell, 1891

#### *Carrhotus kevinlii* Cao & Li, sp. n.

<http://zoobank.org/C2408FE6-35E7-45B4-9858-FE61B1747C3B>

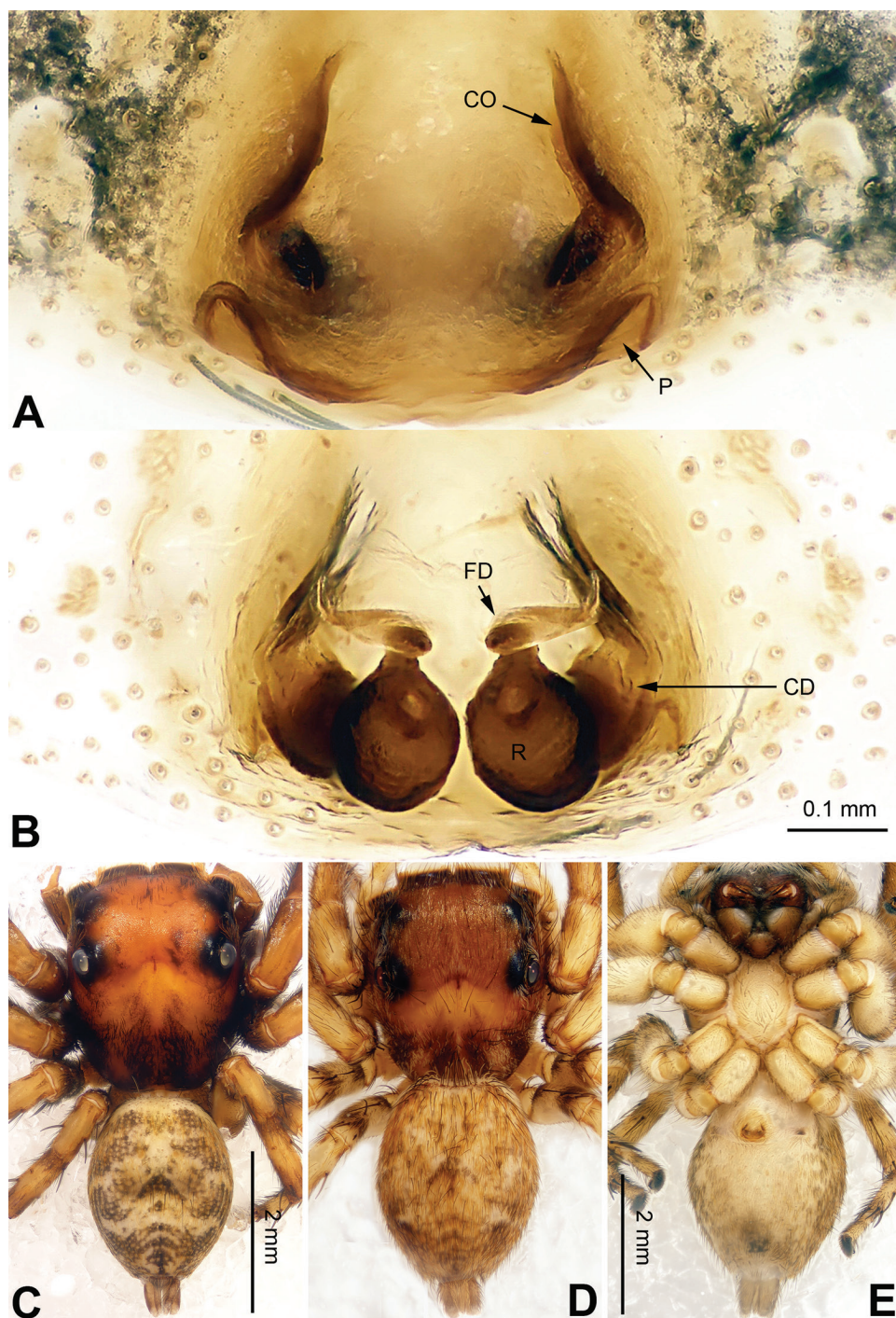
Figs 9–10, 43

**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Menglun Town, Lüshilin (21°54.398'N, 101°16.754'E, 705 m), seasonal rainforest, 19 August 2011, K. Li leg. **Para-**  
**types:** 1♂, same data as holotype; 1♂2♀, CHINA, Yunnan, Mengla County, Xiaolong-  
ha Village, Xishuangbanna Nature Reserve: Biological diversity corridor (21°24.213'N,  
101°36.995'E, 834 m), seasonal rainforest, 3 June 2012, Q. Zhao & Z. Chen leg.



**Figure 9.** Palp of *Carrhotus kevinlii* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.





**Figure 10.** *Carrhotus kevinlii* sp. n., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male habitus, dorsal **D** female habitus, dorsal **E** female habitus, ventral. Scale bars equal for **A** and **B**; equal for **D** and **E**

**Etymology.** The new species is named after Mr Kevin Li (=Kaiwen Li) for his assistance in field work; noun (name) in genitive case.

**Diagnosis.** Cymbium twice as long as bulb (Fig. 9C) vs. approximately equal to bulb length in other congeners and embolus accompanied by a membrane (Fig. 9D). The female resembles *C. viduus* (see Prószyński 2009b: figs 22–23), but the copulatory openings are highly sclerotised (Fig. 10A) vs. oval in *C. viduus*. Also, the receptacles are subglobose (Fig. 10B) vs. irregular in *C. viduus*.

**Description.** Male (holotype). Total length 6.08, CL 3.20, CW 2.64, AL 2.88, AW 1.95. Eye measurements: AME 0.55, ALE 0.24, PME 0.08, PLE 0.37, AER 2.41, PER 2.35, EFL 2.00. Clypeus 0.24 high. Legs: I 5.93 (1.85, 1.10, 1.38, 0.82, 0.78); II 5.86 (1.80, 1.12, 1.30, 0.86, 0.78); III 6.37 (2.15, 1.00, 1.36, 1.26, 0.60); IV 6.48 (0.70, 1.47, 1.41, 0.94, 1.96).

Carapace brown (Fig. 10C). Lower margin and area around eyes darker with white hairs, clypeus brown. Chelicerae dark brown, *maxillae* and labium brown with white tips. Sternum yellowish. Abdomen grey with irregular beige patches and beige sides, entire surface covered with a few short, whitish hairs. Venter grey. Spinnerets grey-brown. Legs dark brown. Spination of leg I: femur d3-1-1; patella p0-1-0, r0-1-0; tibia v2-2-2, p2-0-1, r1-0-0; metatarsus v2-0-2, p1-0-0. Palpal tibia and cymbium long, tibia about 4/5 length of cymbium. Retrolateral apophysis almost as wide as tibia, with pointed tip (Fig. 9B). Cymbium with long and dark brown bristles. Bulb about half the length of the cymbium. Embolus with membrane, bow-shaped, and subequal to half the length of the tegulum (Fig. 9C).

Female (one of paratypes) very similar to the male, with clypeus brown and legs light brown. Total length 7.05, CL 3.25, CW 2.66, AL 3.80, AW 2.97. Eye measurements: AME 0.75, ALE 0.39, PME 0.08, PLE 0.37, AER 2.45, PER 2.55, EFL 1.36. Clypeus 0.24 high. Legs: I 6.17 (1.90, 1.28, 1.41, 0.95, 0.63); II 5.68 (1.84, 1.22, 1.20, 0.79, 0.63); III 6.66 (2.15, 1.02, 1.36, 1.33, 0.80); IV 7.07 (2.15, 1.22, 1.41, 1.45, 0.84). Spination of leg I: femur d3-1-1; patella p0-1-0, r0-1-0; tibia v2-2-2, p1-0-0, r1-0-0; metatarsus v2-0-2. Copulatory openings slit shaped with strongly sclerotised edges. The distance between openings subequal to the length of openings (Fig. 10A). Copulatory ducts short and broad. Receptacles subglobular and diameter equal to the width of copulatory ducts. Fertilisation ducts located at the anterior part of the receptacles (Fig. 10B).

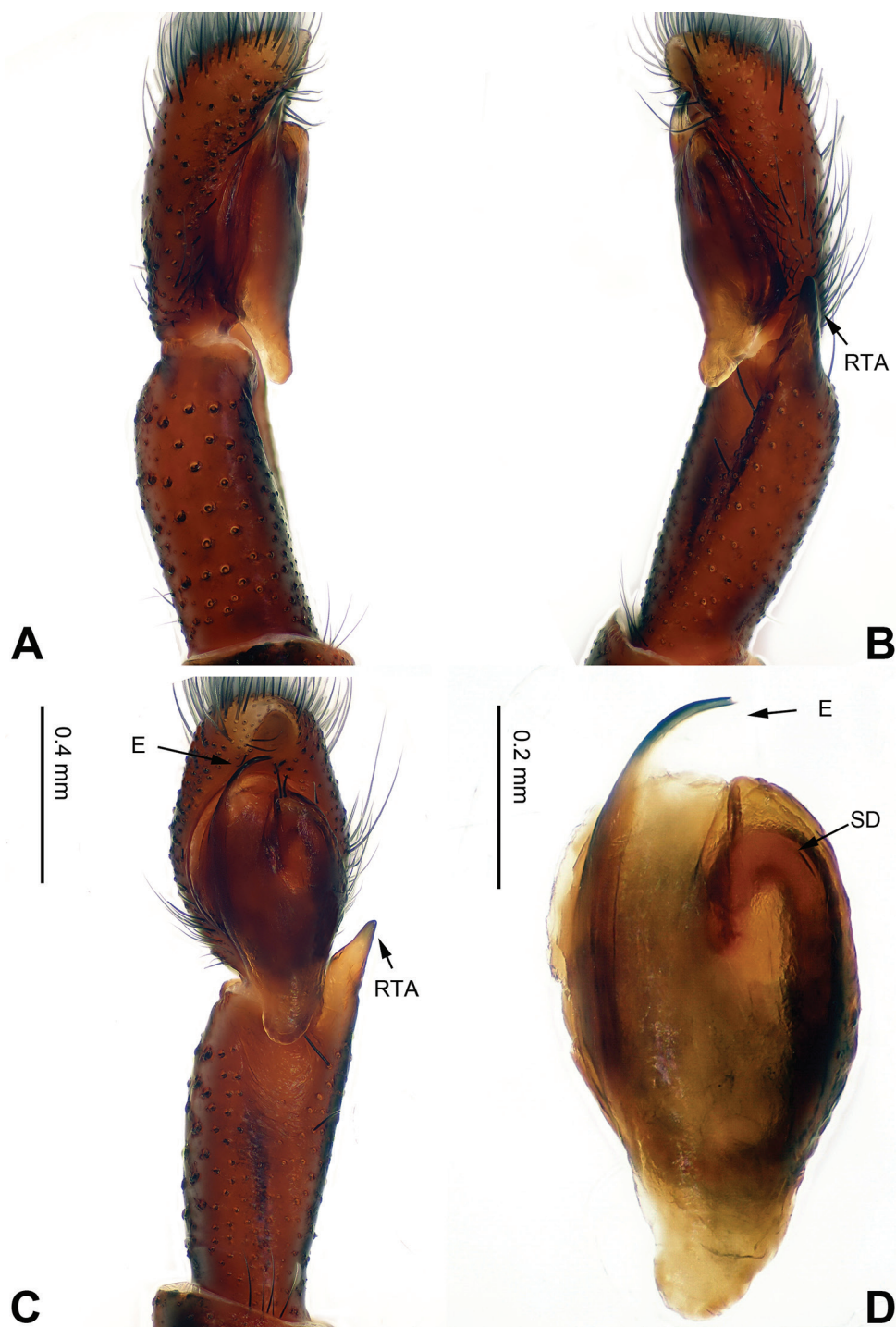
**Distribution.** Known from several localities in Xishuangbanna.

***Carrhotus sarahcrewsae* Cao & Li, sp. n.**

<http://zoobank.org/E1FE66AD-EFBB-4913-9F55-C7708AC8A80C>

Figs 11–12, 43

**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Menglun Town, 48 km landmark in Nature Reserve (21°38.853'N, 101°09.625'E, 1001 m), seasonal rainforest, 30 July 2012, Q. Zhao & Z. Chen leg.



**Figure 11.** Palp of *Carrhotus sarahcrewsae* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.





**Figure 12.** Habitus of *Carrhotus sarahcrewsae* sp. n., male holotype. **A** dorsal **B** lateral. Scale bar equal for **A** and **B**.

**Etymology.** The new species is named after Dr Sarah Crews for her contribution to the study of the spider family Selenopidae; noun (name) in genitive case.

**Diagnosis.** The male resembles that of *C. sannio* (see Žabka 1985: figs 63–65), but the length of the tibia is nearly equal to the cymbium (Fig. 11A) vs.  $2/3$  of the length of the cymbium in *C. sannio*, and the cymbium has no apical process (Fig. 11C). Compared to *C. kevinlii* sp. n., the bulb length is subequal to the cymbium vs. less than half the length, the embolus has no membrane and the angle between the RTA and tibia is early  $20^\circ$  vs. about  $45^\circ$  in *C. kevinlii* sp. n.

**Description.** Male (holotype). Total length 5.77, CL 2.97, CW 2.25, AL 2.80, AW 1.94. Eye measurements: AME 0.63, ALE 0.29, PME 0.05, PLE 0.25, AER 1.84, PER 1.70, EFL 1.64. Clypeus 0.25 high. Legs: I 8.22 (2.25, 1.40, 2.13, 1.64, 0.80); II 6.38 (1.96, 1.06, 1.48, 1.25, 0.63); III 6.44 (2.00, 1.00, 1.33, 1.30, 0.81); IV 6.47 (1.93, 1.00, 1.41, 1.34, 0.79).

Carapace dark brown, margin and area around eyes dark with white hairs (Fig. 12A). Chelicerae dark brown, with dense greyish hairs. *Maxillae* and labium dark brown, tips with dark setae. Sternum light brown. Abdomen dark grey with irregular beige patches. Venter and spinnerets dark greyish. Legs brown. Spination of leg I: femur d3-1-1; patella p0-1-0; tibia v2-2-2, p2-0-2, r2-0-2; metatarsus v2-0-2, p1-0-1, r1-0-1. Palp: tibia subequal to the length of cymbium. Cymbium with long, dark

brown bristles. Tibial apophysis triangular (Fig. 11B). Bulb equal to the length of the cymbium. Embolus short, about 1/4 the length of the tegulum, bent (Fig. 11D).

Female. Unknown.

**Distribution.** Known only from the type locality.

### Genus *Chinattus* Logunov, 1999

#### *Chinattus wengnanensis* Cao & Li, sp. n.

<http://zoobank.org/1E75B981-6EB3-4955-9223-126169A81614>

Figs 13–14, 43

**Type. Holotype** ♂: CHINA, Yunnan, Jinghong, Menga Town, Wengnan Village (22°05.020'N, 100°22.087'E, 1118 m), secondary forest, 24 July 2012, Q. Zhao & Z. Chen leg. **Paratypes**: 2♀, same data as holotype; 1♂, CHINA, Yunnan, Mengla County, Menglun Town, 48 km landmark in Nature Reserve (21°53.997'N, 101°16.957'E, 593 m), secondary forest, 11 August 2011, Q. Zhao & Z. Chen leg.

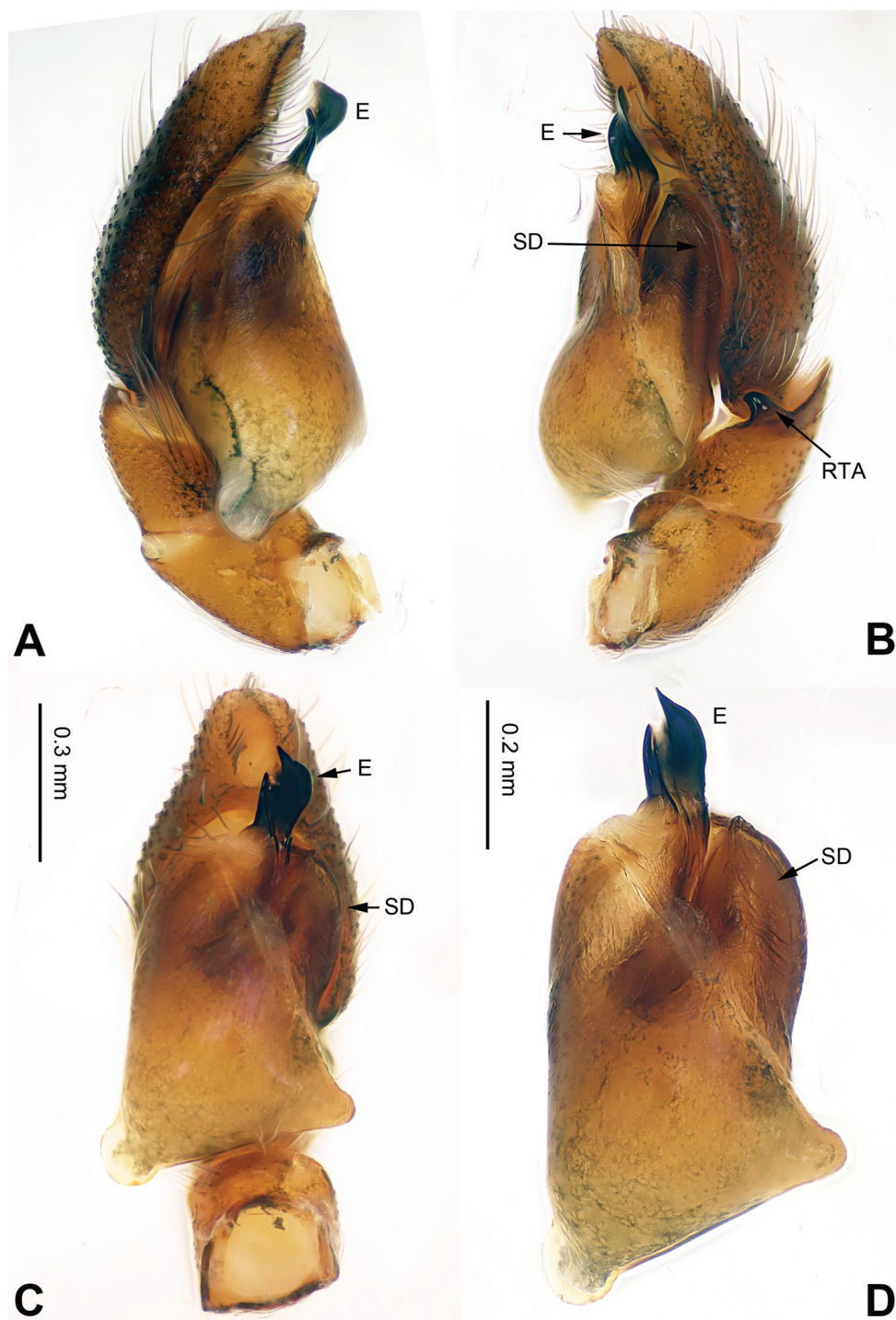
**Etymology.** The species name is derived from the name of type locality; adjective.

**Diagnosis.** The male can be distinguished from the other congeners by the broad and bifurcate embolus and the nearly rectangular tegulum (in ventral view) (Fig. 13C–D). The female is similar to *C. undulatus* (Song & Chai, 1992) (see Prószyński 1992: figs 22–27), but the copulatory openings have a semicircular highly-sclerotised lobe (Fig. 14A), epigyne with posterior projection and two pockets vs. only one in *C. undulatus* (Fig. 14A).

**Description.** Male (holotype). Total length 4.25, CL 2.25, CW 1.75, AL 2.00, AW 1.44. Eye measurements: AME 0.49, ALE 0.34, PME 0.09, PLE 0.24, AER 1.72, PER 1.56, EFL 1.40. Clypeus 0.13 high. Legs: I 4.85 (1.50, 0.86, 1.13, 0.80, 0.56); II 5.93 (1.25, 0.69, 0.85, 0.70, 0.44); III 4.73 (1.56, 0.80, 0.90, 1.00, 0.47); IV 4.40 (1.41, 0.59, 0.90, 1.00, 0.50).

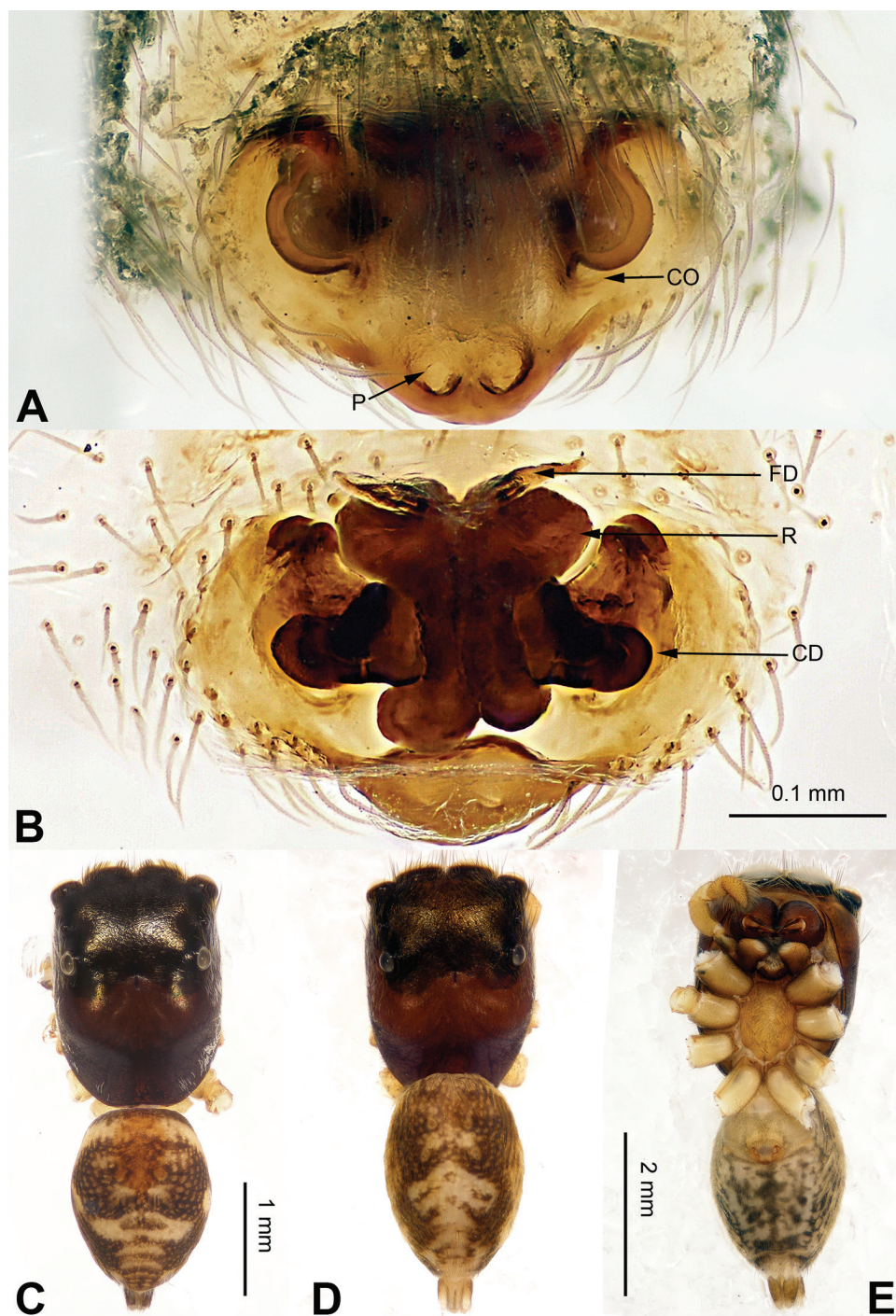
Carapace dark brown (Fig. 14C). *Chelicerae* dark brown, *maxillae* brown with white tips, grey hairs on inner margins. *Labium* dark brown, light at tip with black hairs. *Sternum* greyish brown. Abdomen oval, greyish brown. Venter and spinnerets dark greyish. Legs I more robust and darker than others, which are yellow and black. Spination of leg I: femur d2-1-1; tibia p0-2-0, r0-2-0; metatarsus v2-0-2. Palp: tibia short, subequal to half the length of the cymbium. Tibial apophysis triangular and very short, about 1/5 the length of the tibia (Fig. 13B). Tegulum large, nearly rectangular. Embolus short, broad with bifurcate tip (Fig. 13D).

Female (one of paratypes) very similar to the male. Total length 6.00, CL 3.00, CW 2.10, AL 3.00, AW 1.76. Eye measurements: AME 0.60, ALE 0.40, PME 0.09, PLE 0.27, AER 2.00, PER 1.84, EFL 1.60. Clypeus 0.20 high. Legs: I 4.96 (1.50, 1.00, 1.13, 0.80, 0.53); II 4.31 (1.41, 0.75, 0.90, 0.75, 0.50); III 5.62 (1.85, 0.94, 1.13, 1.00, 0.70); IV 5.38 (1.64, 0.71, 1.13, 1.20, 0.70).



**Figure 13.** Palp of *Chinattus wengnanensis* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.





**Figure 14.** *Chinattus wengnanensis* sp. n., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male habitus, dorsal **D** female habitus, dorsal **E** female habitus, ventral. Scale bars equal for **A** and **B**; equal for **D** and **E**.

Legs light brown. Spination of leg I: femur d2-1-1; tibia v2-2-2; metatarsus v2-0-2. Epigyne wider than long, with posterior projection and two pockets (Fig. 14A). Copulatory openings with two semicircular highly sclerotised lobes. Copulatory ducts broad, anteriorly broader, receptacles massive, slightly curved and closely spaced. Fertilisation ducts at the anterior part of the receptacles (Fig. 14B).

**Distribution.** Known from several localities in Xishuangbanna.

## Genus *Chinophrys* Zhang & Maddison, 2012

### *Chinophrys mengyangensis* Cao & Li, sp. n.

<http://zoobank.org/045A5227-44EB-4D6B-953E-DDEFB089A229>

Figs 15–16, 43

**Type. Holotype** ♂: CHINA, Yunnan, Jinghong City, Mengyang Town, seasonal rainforest (22°09.765'N, 100°52.553'E, 862 m), 22 July 2012, Q. Zhao & Z. Chen leg. **Paratypes:** 1♂, same data as holotype; 1♀, CHINA, Yunnan, Mengla County, Menglun Town, 48 km landmark of Nature Reserve (21°38.853'N, 101°09.625'E, 1001 m), seasonal rainforest, 30 July 2012, Q. Zhao & Z. Chen leg.; 1♂1♀, CHINA, Yunnan, Mengla County, Menglun Town, 48 km landmark in Nature Reserve (21°58.704'N, 101°19.748'E, 1088 m), seasonal rainforest, 12 August 2011, Q. Zhao & Z. Chen leg.

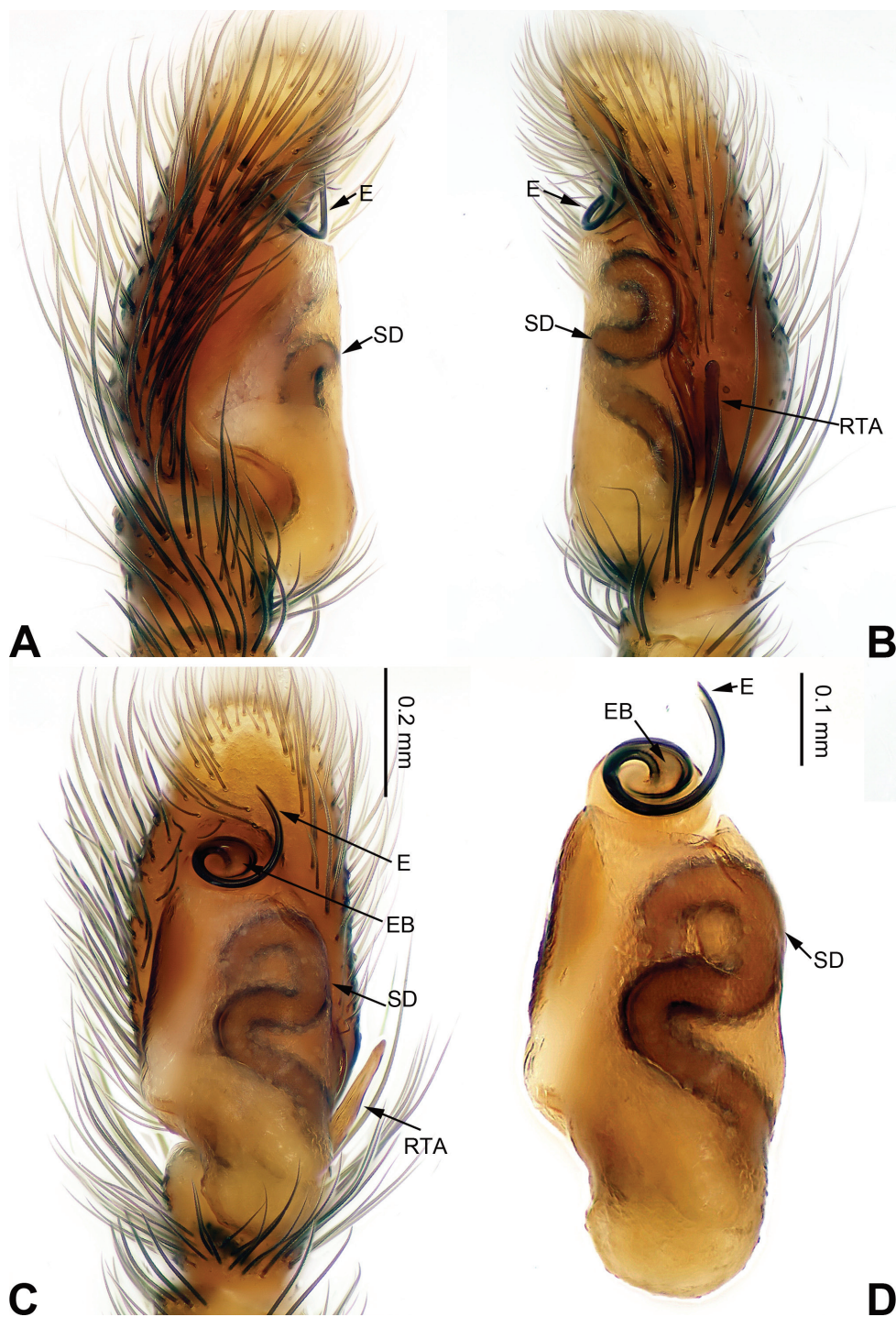
**Etymology.** The species name is derived from the name of type locality; adjective.

**Diagnosis.** Similar to *C. liujiapingensis* (Yang & Tang, 1997) (cf. Yang and Tang 1997: figs 6–10) in having a similar tegulum (Fig. 15D), but the embolus base is much wider. Compared to *C. pengi* (Zhang and Maddison 2012: figs 1–9), the tibial apophysis is located retrolaterally vs. dorso-retrolaterally. The epigyne of the new species resembles that of *C. pengi*, but the copulatory openings are different (the copulatory openings of the new species have fewer coils than in *C. pengi*) (Fig. 16A), and the receptacles lack spherical terminals vs. have spherical terminals in *C. pengi* (Fig. 16B).

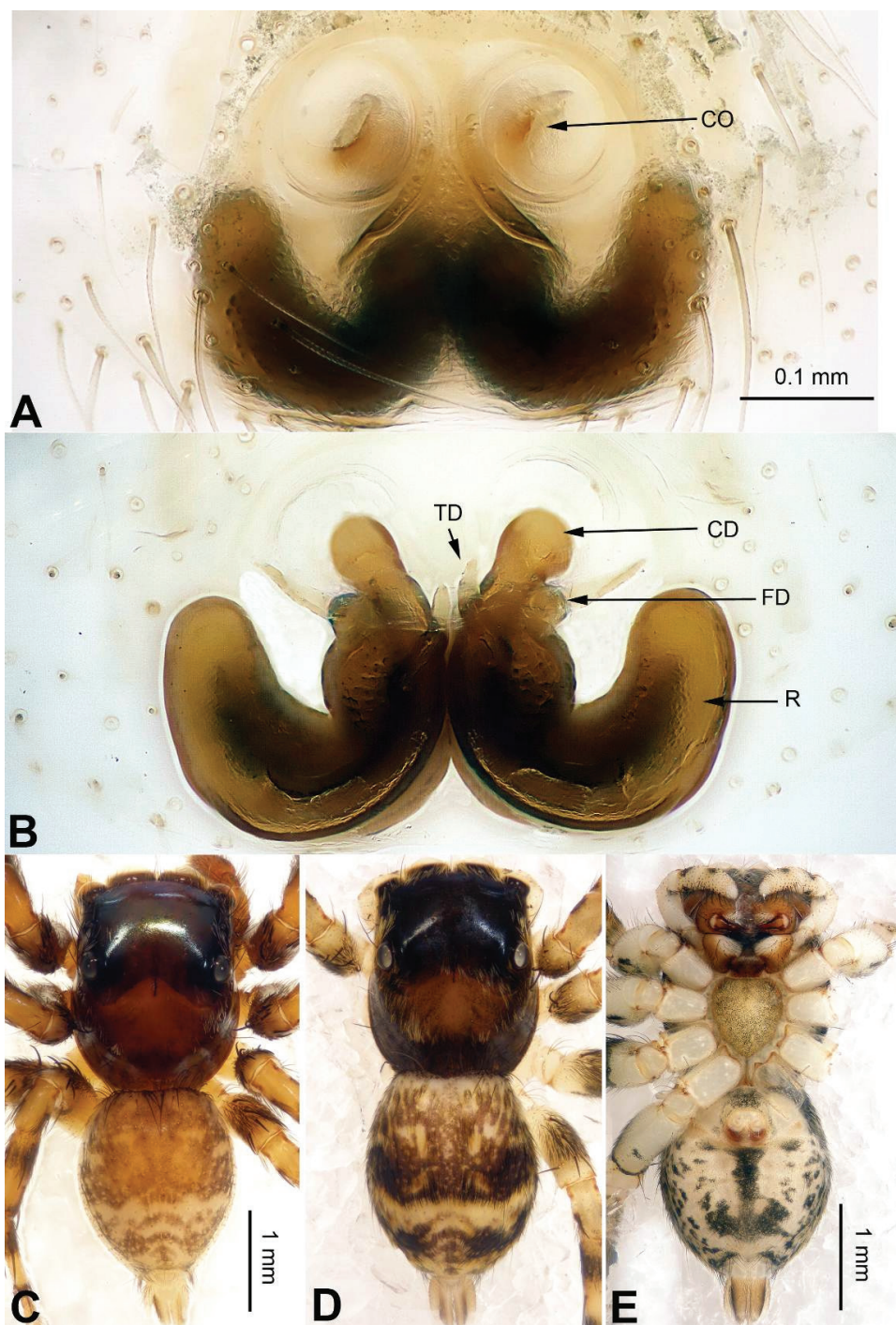
**Description.** Male (holotype). Total length 4.80, CL 2.25, CW 1.75, AL 2.55, AW 1.60. Eye measurements: AME 0.48, ALE 0.31, PME 0.05, PLE 0.29, AER 1.62, PER 1.70, EFL 1.44. Clypeus 0.10 high. Legs: I 4.40 (1.45, 0.70, 1.05, 0.70, 0.50); II 3.95 (1.30, 0.65, 0.80, 0.70, 0.50); III 4.60 (1.40, 0.50, 1.00, 1.00, 0.70); IV 4.85 (1.40, 0.60, 1.00, 1.10, 0.75).

Carapace dark brown, tegument iridescent with a few sparse colourless setae (Fig. 16C). Chelicerae, *maxillae* and labium greyish brown with white tips. Sternum greyish yellow. Abdomen oval and greyish brown. Venter and spinnerets grey. Legs light brown. Spination of leg I: femur d5-1-1; patella p0-1-0; tibia v2-2-2, p1-0-1, r1-0-1; metatarsus v2-0-2, p1-0-1 r1-0-1. Palp: tibia short, about 1/3 the length of the cymbium. Tibial apophysis straight, rod-like and subequal to the length of the tibia (Fig. 15B). Cymbium with long, dark brown bristles. Tegulum twice as long as wide. Seminal duct broad and coiled. Embolus a narrow helix (Fig. 15C).





**Figure 15.** Palp of *Chinophrys mengyangensis* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.



**Figure 16.** *Chinophrys mengyangensis* sp. n., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male habitus, dorsal **D** female habitus, dorsal **E** female habitus, ventral. Scale bars equal for **A** and **B**; equal for **D** and **E**.



Female (one of paratypes). Total length 4.73, CL 2.30, CW 2.03, AL 2.43, AW 1.94. Eye measurements: AME 0.60, ALE 0.33, PME 0.03, PLE 0.29, AER 1.79, PER 1.81, EFL 1.44. Clypeus 0.10 high. Legs: I 4.24 (1.39, 0.75, 0.90, 0.75, 0.45); II 4.04 (1.38, 0.70, 0.85, 0.66, 0.45); III 4.93 (1.60, 0.80, 0.93, 1.05, 0.55); IV 5.32 (1.56, 0.75, 1.13, 1.25, 0.63).

Abdomen dark brown. Legs grey. Other characters similar to those of male. Epigyne: Copulatory ducts stout, receptacles kidney-shaped, with anteriorly bent translucent ducts (Fig. 16B). Fertilisation ducts located at the anterior part of the receptacles (Fig. 16B).

**Distribution.** Known from several localities in Xishuangbanna.

### Genus *Cocalus* C.L. Koch, 1846

#### *Cocalus menglaensis* Cao & Li, sp. n.

<http://zoobank.org/A97C770D-4BF5-49DF-947E-F24ED92C29FE>

Figs 17–18, 43

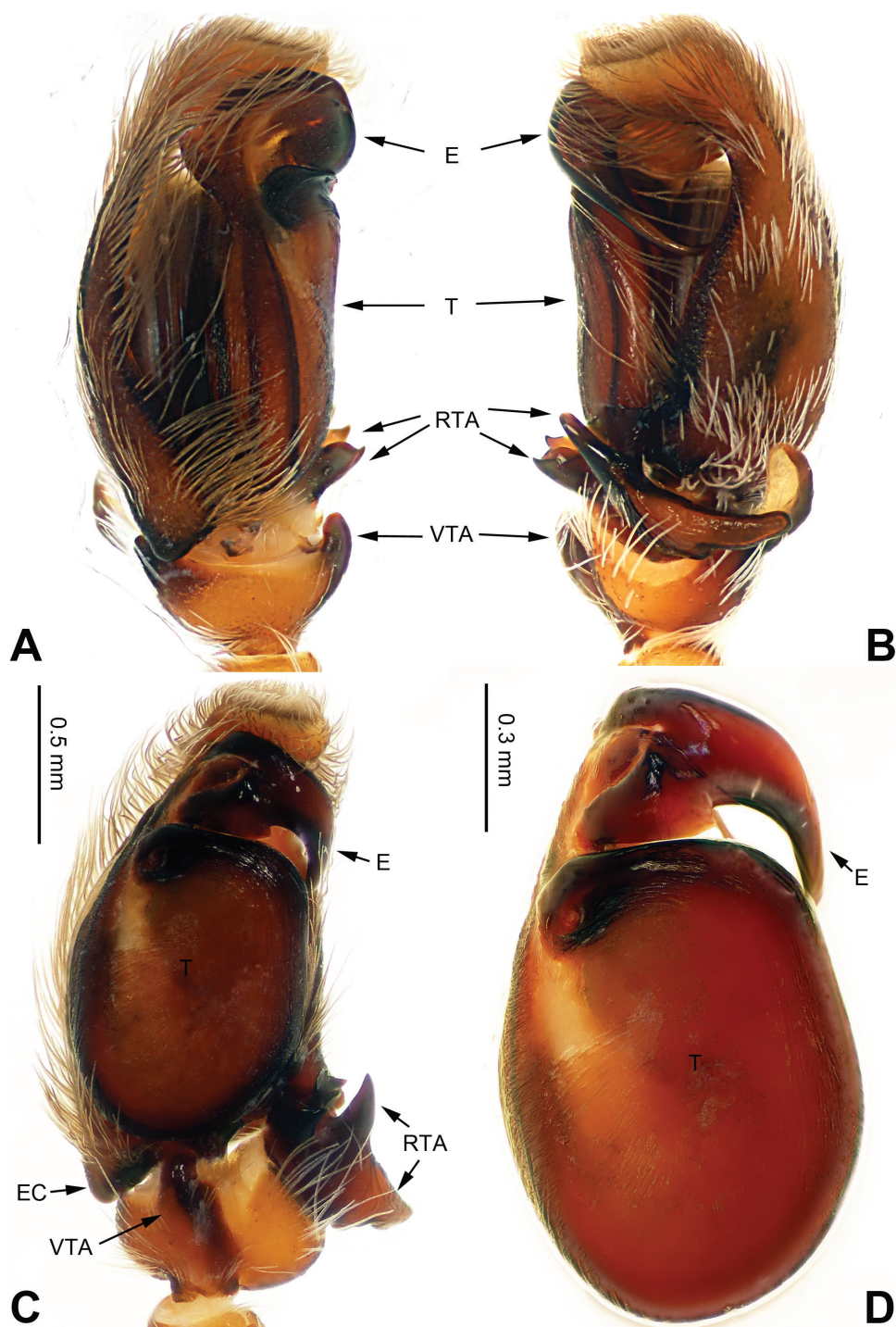
**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Xiaolongha Village, Xishuangbanna Nature Reserve, Biological diversity corridor (21°24.330'N, 101°37.002'E, 801 m), secondary forest, 30 June 2012, Q. Zhao & Z. Chen leg. **Paratypes:** 1 ♀, CHINA, Yunnan, Mengla County, Xiaolongha Village, Xishuangbanna Nature Reserve, Biological Diversity Corridor (21°24.265'N, 101°37.300'E, 653 m), seasonal rainforest, 27 June 2012, Q. Zhao & Z. Chen leg.; 1 ♀, CHINA, Yunnan, Mengla County, Menglun Town, 48 km landmark in Nature Reserve (21°58.704'N, 101°19.748'E, 1088 m), seasonal rainforest, 12 August 2011, Q. Zhao & Z. Chen leg.

**Etymology.** The species name is derived from the name of the type locality; adjective.

**Diagnosis.** Similar to *C. gibbosus* Wanless, 1981 (see Wanless 1981: fig. 4A–D) by the shape of tegulum and embolus (Fig. 17C–D), but different in the shape of RTA. Female copulatory openings (Fig. 18A) resemble *C. murinus* Simon, 1899 (see Wanless, 1981: 256, fig. 3A–E), but the epigynal plate has two rectangular and strongly sclerotised posterior projections (Fig. 18A)

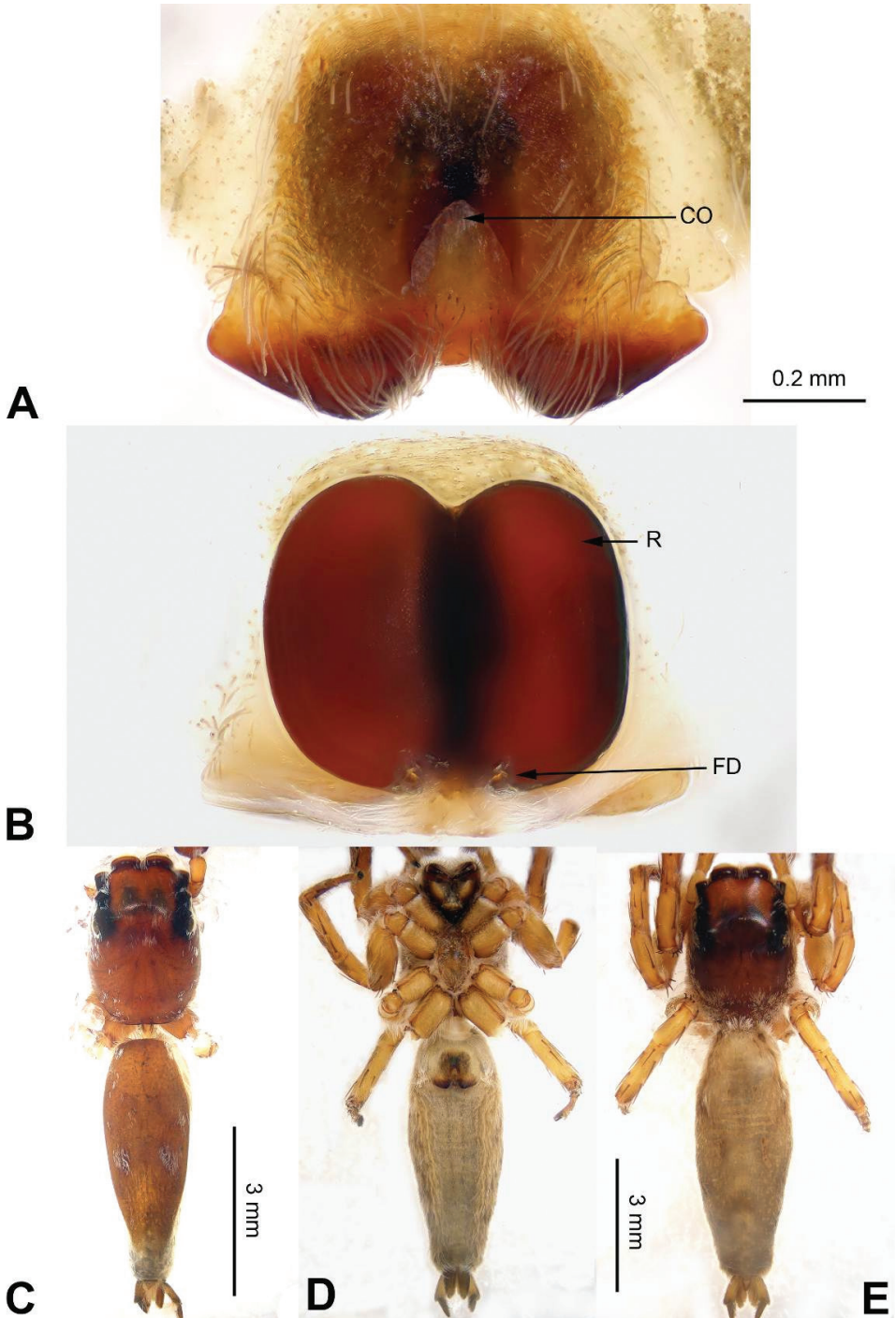
**Description.** Male (holotype). Total length 8.75, CL 3.75, CW 2.25, AL 5.00, AW 1.50. Eye measurements: AME 0.60, ALE 0.25, PME 0.22, PLE 0.26, AER 1.86, PER 2.00, EFL 1.74. Clypeus 0.31 high. Legs: I 8.10 (2.10, 1.25, 2.00, 1.75, 1.00); II 6.80 (2.00, 1.00, 1.50, 1.50, 0.80); III 7.27 (1.95, 1.20, 1.75, 1.57, 0.80); IV 8.95 (2.50, 1.15, 2.00, 2.20, 1.10).

Carapace dark brown with short recumbent and white setae (Fig. 18C). Eyes surrounded with black except AME. Clypeus covered with dark grey hairs. *Chelicerae* dark brown, sparsely covered with fine black hairs. *Maxillae* brownish with dull white tips and dark grey hairs on inner margins. *Labium* dark brown, tip dull white. *Sternum* grey-brown, with few black hairs. Abdomen dorsally orange-brown to greyish brown, clothed in short recumbent white hairs. Venter dark greyish. Spinnerets dark brown.



**Figure 17.** Palp of *Cocalus menglaensis* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.





**Figure 18.** *Cocalus menglaensis* sp. n., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male habitus, dorsal **D** female habitus, dorsal **E** female habitus, ventral. Scale bars equal for **A** and **B**; equal for **D** and **E**.

Legs generally amber. Spination of leg I: femur d4-1-1; patella p0-1-0; tibia v2-0-2, p1-1-1, r1-1-1; metatarsus v0-2-0, p0-1-0 r0-1-0 d2-1-2. Palp: densely covered by hairs. Cymbium with posterior triangular extension prolaterally (Fig. 17C). Tegulum ovoid, with tegular furrow and dark peripheral seminal duct. Embolus stout, bending ventrally (Fig. 17C).

Female (one of the paratypes). Total length 10.67, PL 4.00, PW 2.67, OL 6.67, OW 2.19. Eye measurements: AME 0.60, ALE 0.30, PME 0.25, PLE 0.35, AER 2.00, PER 2.45, EFL 1.74. Clypeus 0.20 high. Legs: I 8.08 (2.23, 1.53, 2.05, 1.47, 0.80); II 7.10 (2.00, 1.36, 1.74, 1.25, 0.75); III 7.27 (2.10, 1.20, 1.66, 1.41, 0.90); IV 9.91 (2.66, 1.40, 2.25, 2.40, 1.20).

Abdomen dorsally greyish. Spination of leg I: femur d4-1-1; patella p0-1-0, r0-1-0; tibia v2-2-2, p1-0-1, r1-0-1, d1-1-1; metatarsus v0-2-0, d2-0-2. Other characters similar to those of male. Epigyne: dark amber clothed in creamy hairs. Epigyne with two rectangular and strongly sclerotised posterior projections (Fig. 18A). Receptacles massive and phaseoliform, fertilisation ducts located at the posterior part of the receptacles (Fig. 18B).

**Distribution.** Known from several localities in Xishuangbanna.

## Genus *Cosmophasis* Simon, 1901

### *Cosmophasis xiaolonghaensis* Cao & Li, sp. n.

<http://zoobank.org/D0DE08D5-D373-49A7-A206-5CA130E41DE9>

Figs 19–20, 43

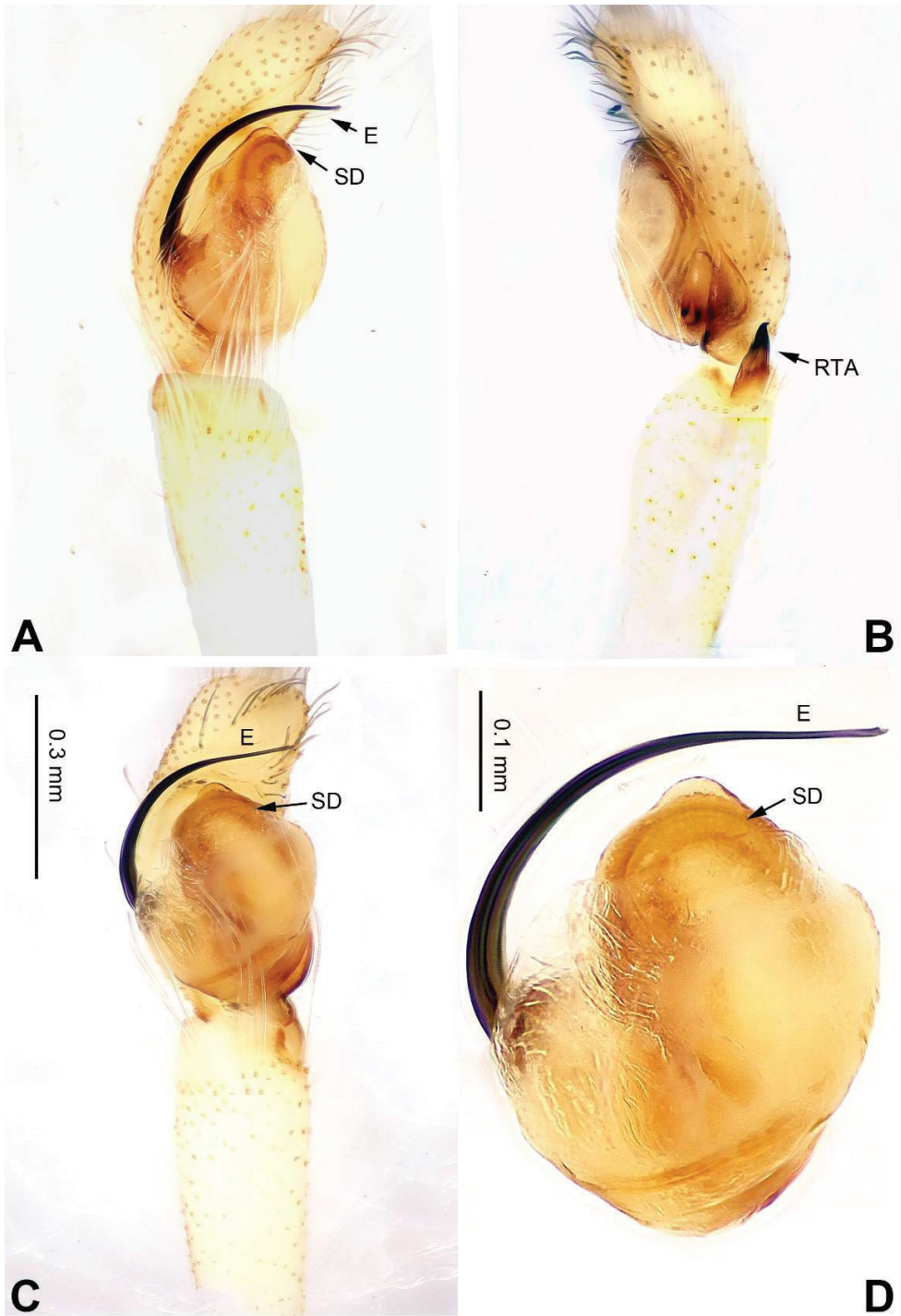
**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Xiaolongha Village, Xishuangbanna Nature Reserve: Biological diversity corridor (21°24.798'N, 101°37.880'E, 693 m), seasonal rainforest, 28 June 2012, Q. Zhao & Z. Chen leg. **Paratypes:** 1♂1♀, same data as holotype; 1♀, CHINA, Yunnan, Mengla County, Xiaolongha Village, Xishuangbanna Nature Reserve: Biological diversity corridor (21°24.230'N, 101°36.262'E, 715 m), seasonal rainforest, 4 June 2012, Q. Zhao & Z. Chen leg.

**Etymology.** The species name is derived from the name of the type locality; adjective.

**Diagnosis.** Similar to *C. courti* Żabka & Waldock, 2012 (Żabka and Waldock 2012: figs 52A–H, 53A–D), but tibia is subequal to cymbium (Fig. 19A–B) vs. twice as long in *C. courti*, RTA with one small apical hook (Fig. 19B), lacking in *C. courti*. Copulatory openings widely separated (Fig. 20A), about three diameters vs. only 1/4 the diameter of a copulatory opening.

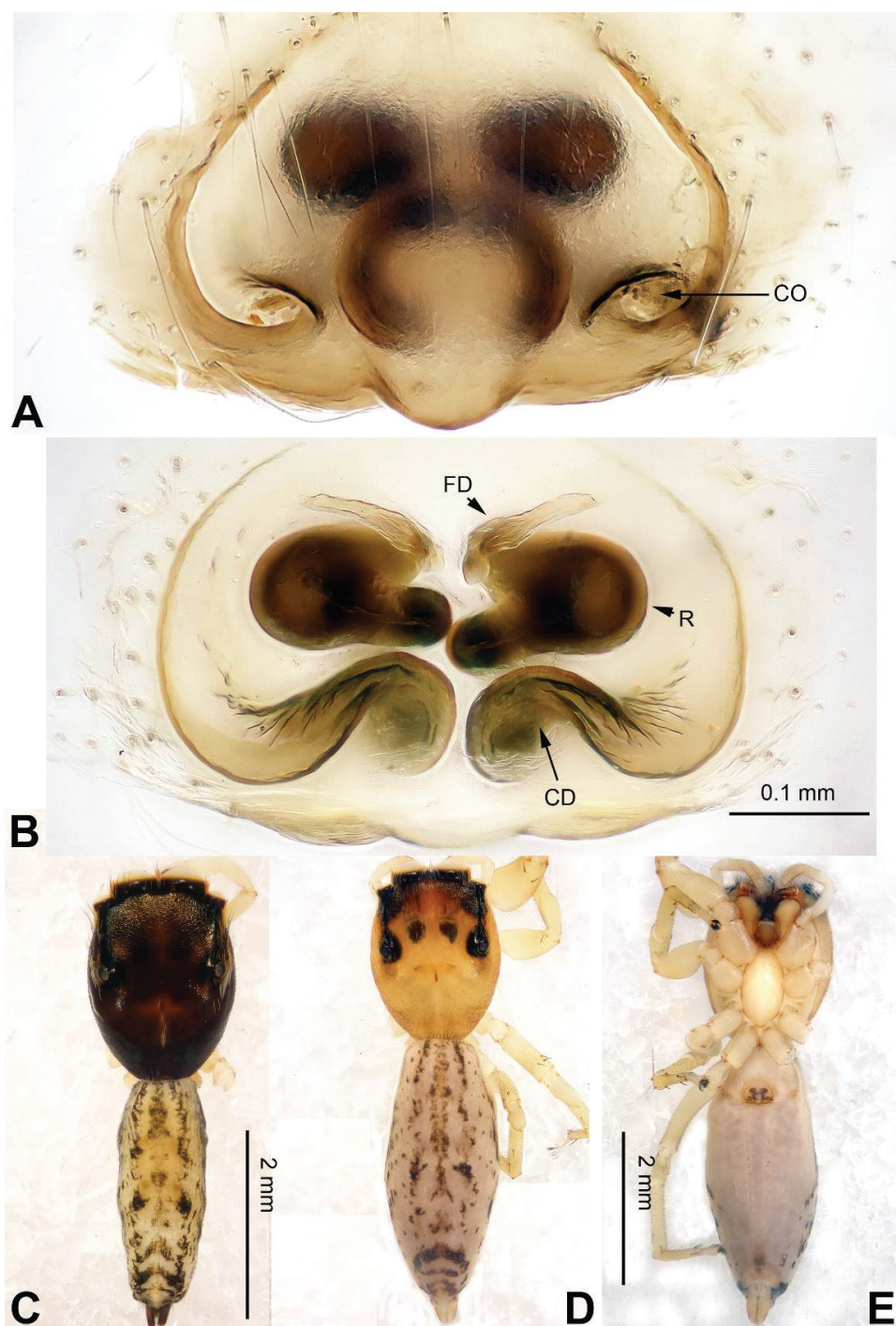
**Description.** Male (holotype). Total length 5.20, CL 2.30, CW 1.72, AL 2.90, AW 1.05. Eye measurements: AME 0.55, ALE 0.24, PME 0.05, PLE 0.20, AER 1.59, PER 1.59, EFL 1.44. Clypeus 0.09 high. Legs: I 4.34 (1.34, 0.94, 1.00, 0.56, 0.50); II 3.64 (1.13, 0.70, 0.76, 0.58, 0.47); III 3.84 (1.30, 0.55, 0.71, 0.80, 0.48); IV 4.31 (1.41, 0.56, 0.70, 1.06, 0.50).

Carapace dark brown (Fig. 20C). *Chelicerae* dark brown, sparsely covered with fine grey hairs. *Maxillae* brown with light tips and grey hairs on inner margins.



**Figure 19.** Palp of *Cosmophasis xiaolonghaensis* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.





**Figure 20.** *Cosmophasis xiaolonghaensis* sp. n., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male habitus, dorsal **D** female habitus, dorsal **E** female habitus, ventral. Scale bars equal for **A** and **B**; equal for **D** and **E**.

*Labium* brown, tip with black hairs. Abdomen light, with irregular black patches. Venter and spinnerets dark grey. Legs I more robust and darker than others. Spination of leg I: femur d2-1-0; tibia v2-2-2; metatarsus v2-0-2. Palpal tibia white, subequal to the cymbium. The apophysis short, about 1/4 the length of the cymbium, with a small apical hook (Fig. 19B). Embolus starting at the prolateral part of the bulb, bent (Fig. 19C).

Female (same locality of holotype). Total length 6.46, CL 2.66, CW 1.90, AL 3.80, AW 1.64. Eye measurements: AME 0.60, ALE 0.22, PME 0.06, PLE 0.22, AER 1.59, PER 1.59, EFL 1.44. Clypeus 0.08 high. Legs: I 4.34 (1.34, 0.94, 1.00, 0.56, 0.50); II 3.64 (1.13, 0.70, 0.76, 0.58, 0.47); III 3.84 (1.30, 0.55, 0.71, 0.80, 0.48); IV 4.31 (1.41, 0.56, 0.70, 1.06, 0.50).

Carapace yellow (Fig. 20D). Abdominal venter grey-white. Legs yellowish. Spination of leg I: femur d2-1-0; tibia v2-2-2; metatarsus v2-0-2. Other characters similar to those of male. Epigynal plate weakly sclerotized. Copulatory opening grooves with sclerotised edges, openings widely separated (about three diameters). Posterior margin projecting in midline (Fig. 20A). Copulatory ducts broad, located posteriorly. Receptacles round, strongly sclerotised. Fertilisation ducts elongate, located at the anterior part of the receptacles (Fig. 20B).

**Distribution.** Known from several localities in Xishuangbanna.

## Genus *Cytaea* Keyserling, 1882

### *Cytaea yunnanensis* Cao & Li, sp. n.

<http://zoobank.org/0A78F858-FEC9-41E2-B86F-95FC8B1714ED>

Figs 21–22, 43

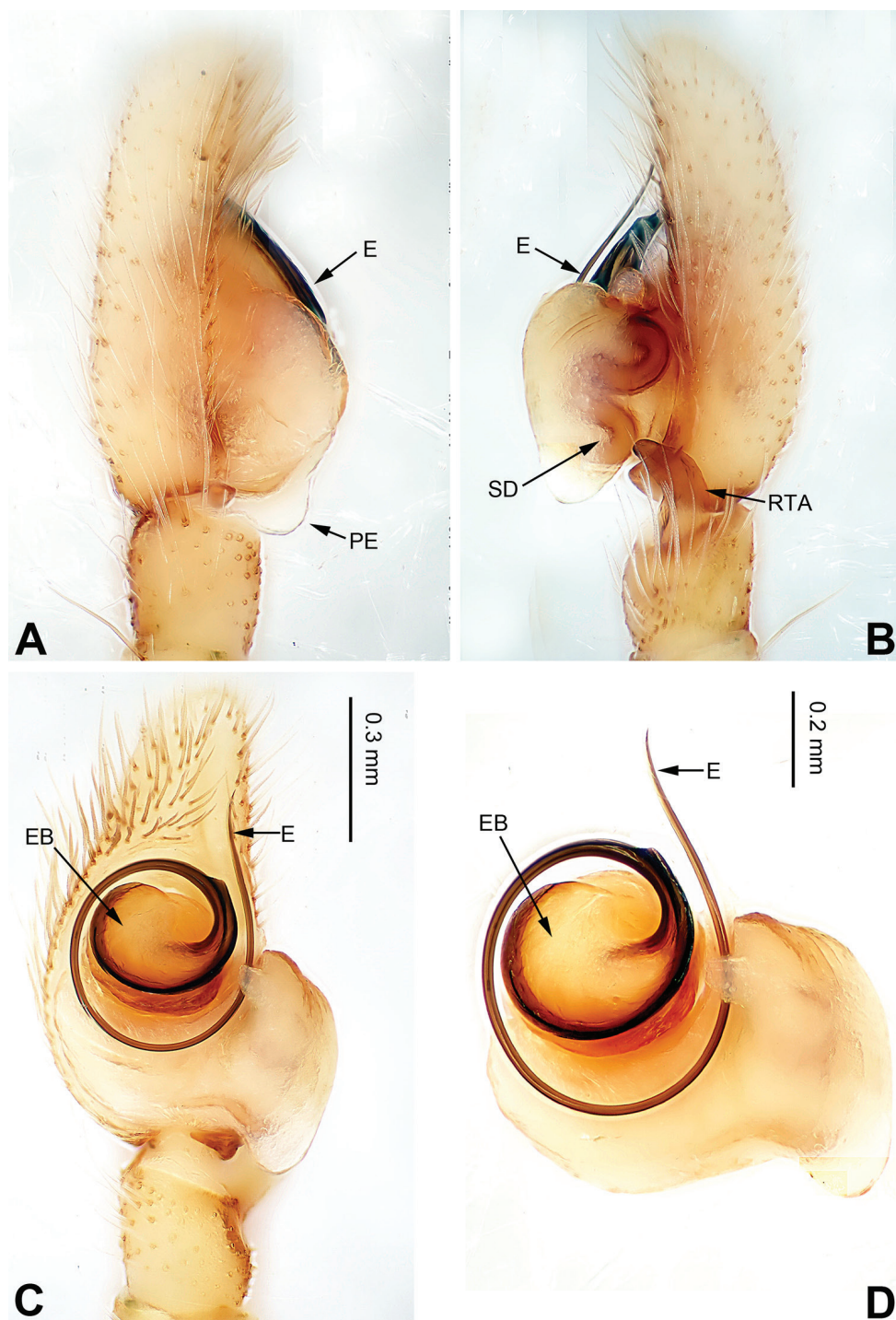
**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Menglun Town, Menglun Nature Reserve (21°57.669'N, 101°11.893'E, 790 m), 23 April 2007, G. Zheng leg.

**Etymology.** The species name derived from the name of the type locality; adjective.

**Diagnosis.** Differs from all known congeners by the shape of the tegulum (prolateral large bulge and posterior translucent extension) (Fig. 21).

**Description.** Male (holotype). Total length 5.75, CL 2.75, CW 2.05, AL 3.00, AW 1.75. Eye measurements: AME 0.55, ALE 0.36, PME 0.10, PLE 0.36, AER 1.90, PER 1.80, EFL 1.50. Clypeus 0.13 high. Legs: I 4.76 (1.38, 0.75, 1.13, 0.90, 0.60); II 5.56 (1.63, 0.88, 1.20, 0.95, 0.90); III missing; IV 5.63 (1.63, 0.75, 1.30, 1.20, 0.75).

Carapace brown, covered with dense, white setae (Fig. 22A). Lateral eyes surrounded with black. *Chelicerae* dark orange-brown. *Maxillae* brownish, with dull white tips. *Labium* dark brown, tip dull white. *Sternum* light brown. Abdomen oval, dorsally greyish brown, narrower than carapace. Venter greyish. Spinnerets light greyish. Legs whitish. Spination of leg I: femur d2-1-1; tibia v2-2-2, p1-0-1; metatarsus v2-0-2, p0-1-0. Palpal tibia short, about 1/4 length of cymbium. The tibial apophysis subequal to the tibia, with a slightly bent tip (Fig. 21B). Cymbium whitish. Tegulum with



**Figure 21.** Palp of *Cytaea yunnanensis* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.





**Figure 22.** Habitus of *Cytaea yunnanensis* sp. n., male holotype. **A** dorsal **B** lateral.

meandering seminal duct and prominent prolateral bulge. Embolus with circular basal pad (Fig. 21C).

Female. Unknown.

**Distribution.** Known only from the type locality.

### Genus *Gedea* Simon, 1876

#### *Gedea pinguis* Cao & Li, sp. n.

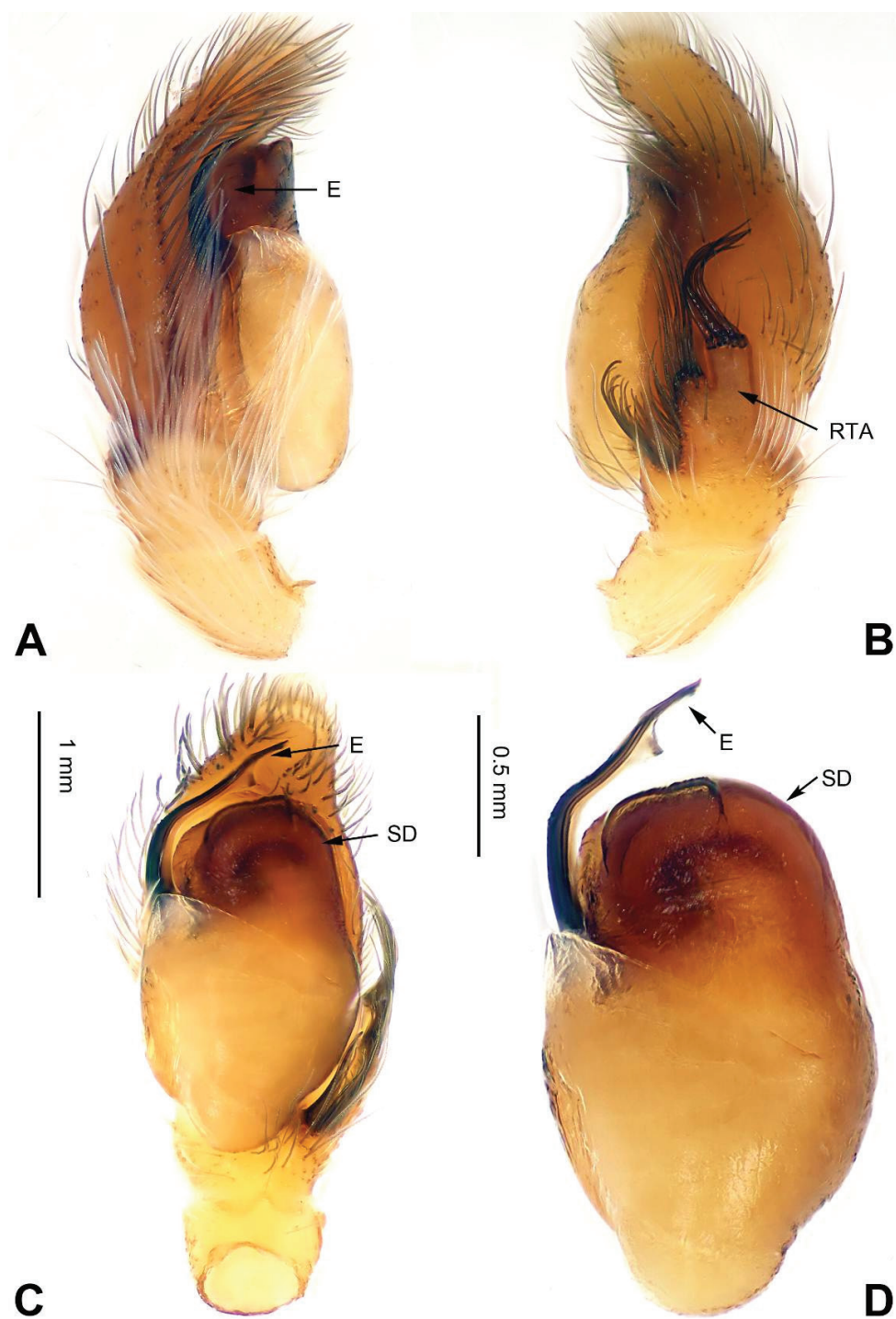
<http://zoobank.org/8B648ACB-2493-4AAE-B632-C88649335E2E>

Figs 23, 43

**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Menglun Town, Xishuangbanna Nature Reserve, G213 road, Banyan tree (21°54.089'N, 101°17.024'E, 579 m), 28 November 2009, G. Tang & Z. Yao leg.

**Etymology.** From Latin *pinguis* (fat), in reference to the shape of the palp; adjective.

**Diagnosis.** Similar to *G. tibialis* Żabka, 1985 (see Żabka 1985: figs 263–267), but the cymbium is shorter (about 1/3 the length of the bulb in the new species vs. nearly equal in *G. tibialis*), embolus base with membrane (without in *G. tibialis*) (Fig. 23C–D),



**Figure 23.** Palp of *Gedeia pinguis* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.

tibial apophysis with two branches, both with clusters of long apical bristles (only one without bristles in *G. tibialis*) (Fig. 23B).

**Description.** Male (holotype). In poor condition. Precise description of the habitus unavailable. Palpal tibia short, subequal to the tip of the cymbium, about 1/3 the length of the bulb. Tibial apophysis with two branches, each with clusters of long apical bristles (Fig. 23B). Tegulum with posterior lobe, and the width about 2/3 of the length. Embolus base hidden by the fold of the membranous structure of the tegulum (Fig. 23C). Embolus accompanied by a membrane, membrane with a triangular outgrowth (Fig. 23D).

Female. Unknown.

**Distribution.** Known only from the type locality.

### Genus *Gelotia* Thorell, 1890

#### *Gelotia zhengi* Cao & Li, sp. n.

<http://zoobank.org/8C8AD320-9364-481E-B657-B707C24B3CD8>

Figs 24–25, 43

**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Menglun Town, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences: Lvshilin (21°54.705'N, 101°16.898'E, 656 m), 11 November 2009, G. Zheng leg.

**Etymology.** The specific is named in honour of the collector Guo Zheng from Shenyang Normal University; noun (name) in genitive case.

**Diagnosis.** Differs from the similar *G. bouchardi* (Simon, 1903) (see Prószyński and Deeleman-Reinhold 2012: figs 47–50) by the shorter embolus (subequal to the tip of the cymbium vs. nearly twice as long in *G. bouchardi*) (Fig. 24C) and the straight RTA (Fig. 24B) vs. bent in *G. bouchardi*.

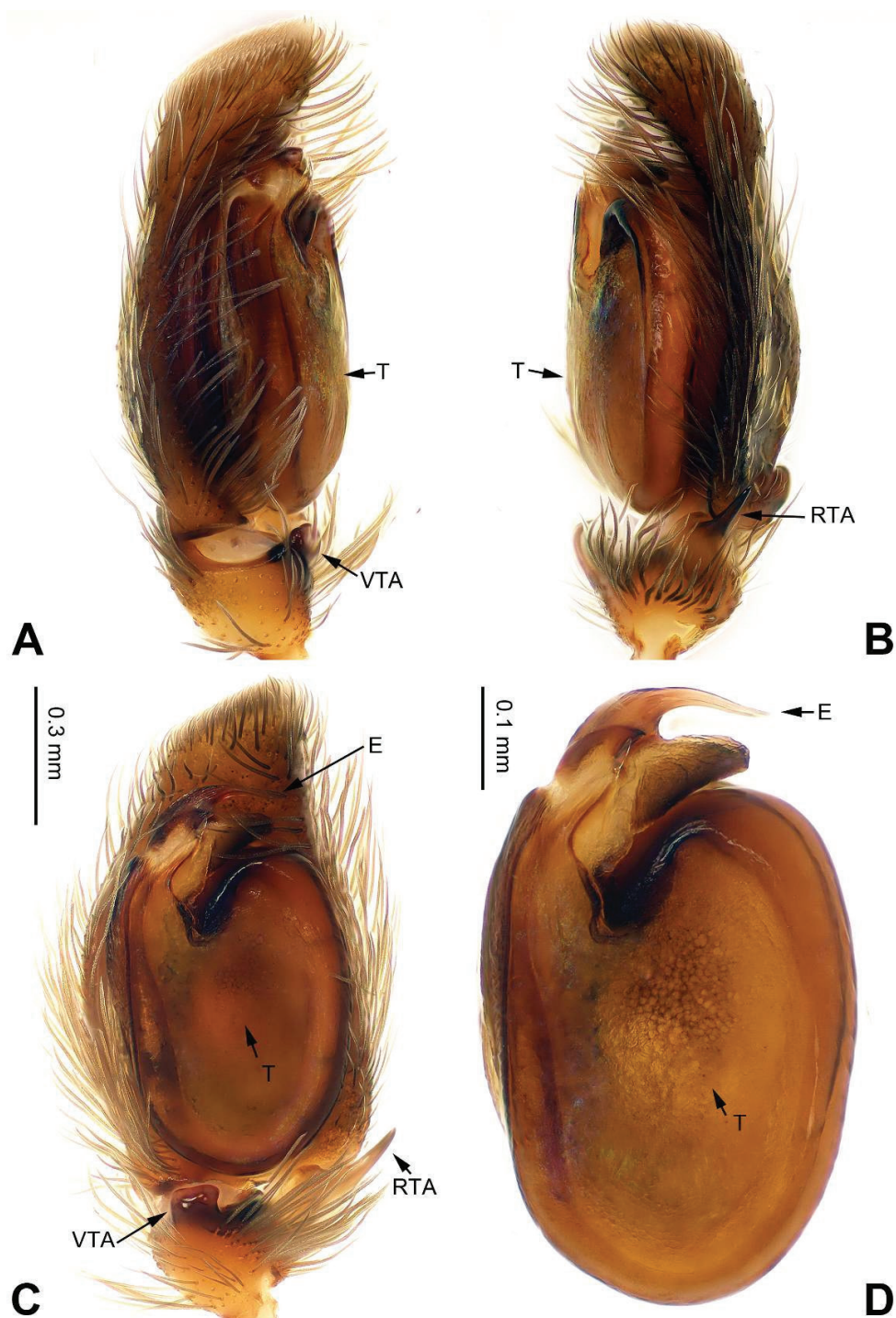
**Description.** Male (holotype). Total length 5.90, CL 2.75, CW 1.80, AL 3.15, AW 1.60. Eye measurements: AME 0.50, ALE 0.28, PME 0.15, PLE 0.20, AER 1.68, PER 1.68, EFL 1.40. Clypeus 0.25 high. Legs: I 8.15 (2.05, 0.85, 2.10, 2.10, 1.05); II 6.85 (1.90, 0.80, 1.75, 1.55, 0.85); III 6.30 (1.75, 0.70, 1.45, 1.55, 0.85); IV 8.30 (2.15, 0.85, 1.90, 2.35, 1.05).

Carapace dark brown (Fig. 25A), sides and clypeus margins encircled with a wide band of white hairs. Chelicerae light brown, inner margin with greyish brown setae. *Maxillae brown, tips with grey hairs.* Labium dark brown, light tip with grey hairs. Sternum greyish brown. Abdomen oval, greyish brown. Venter and spinnerets dark greyish. Legs brown, slender. Spination of leg I: femur d4-1-1; patella p0-1-0, r0-1-0; tibia v2-2-2, p1-0-1, d1-1-1, r1-0-1; metatarsus v2-0-2, p1-1-1, d2-0-2, r1-1-1. Palpal tibia short, about 1/5 the length of the cymbium. The ventral tibial apophysis short and obtuse, retrolateral apophysis broad at the base and sharp apically (Fig. 24B). Cymbium flattened and semilunar. Tegulum subovoid with peripheral seminal duct. Embolus base with one stout lobe (Fig. 24D).

Female. Unknown.

**Distribution.** Known only from the type locality.





**Figure 24.** Palp of *Gelotia zhengi* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.



**Figure 25.** Habitus of *Gelotia zhengi* sp. n., male holotype. **A** dorsal **B** lateral.

### Genus *Icius* Simon, 1876

#### *Icius bamboo* Cao & Li, sp. n.

<http://zoobank.org/71D1D871-F4BE-434B-8956-B0CC0CB4CB33>

Figs 26–27, 43

**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Menglun Town, Bamboo plantation, G213 (21°53.646'N, 101°16.975'E, 589 m), 26 November 2009, G. Tang & Z. Yao leg.

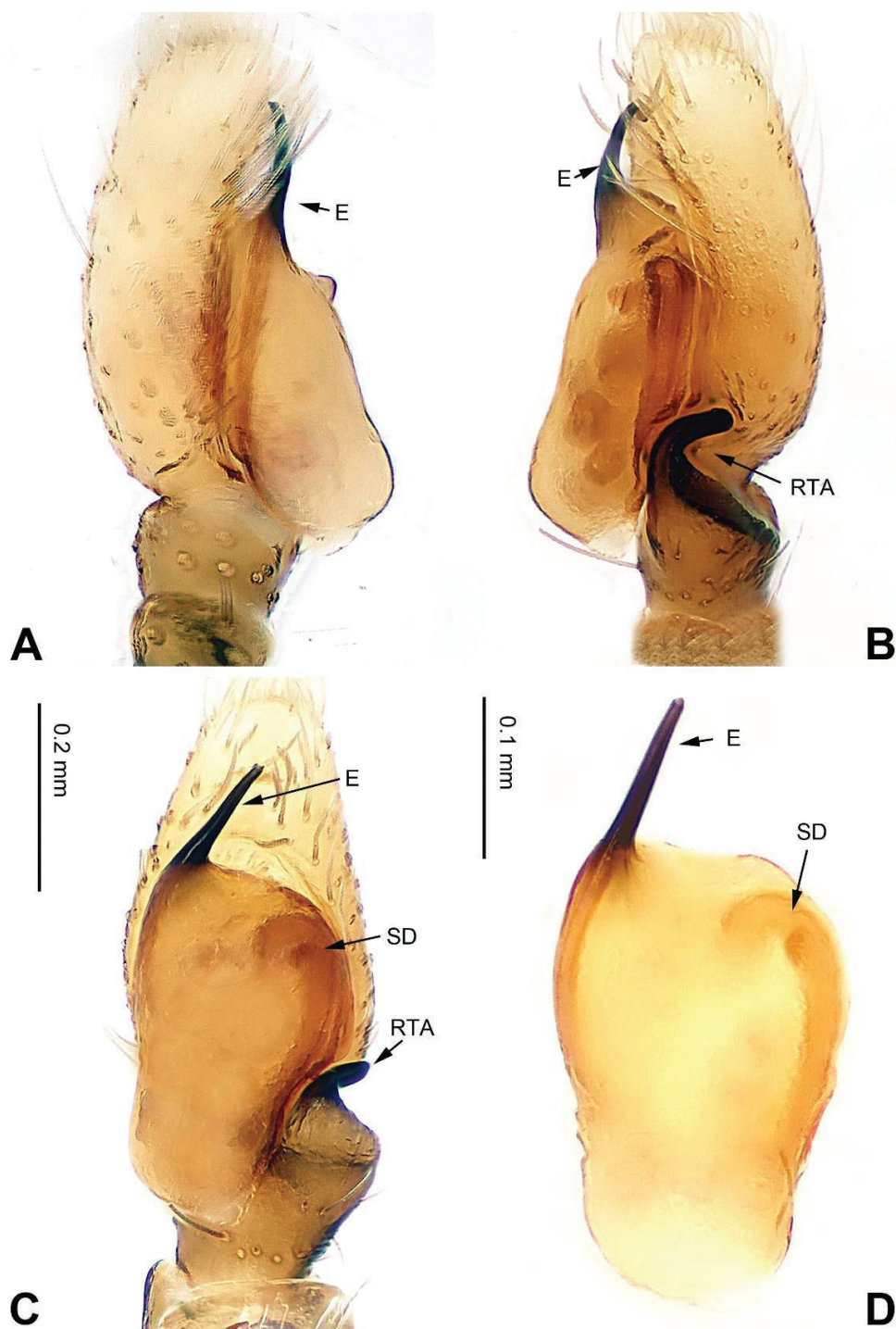
**Etymology.** The species was collected from a bamboo plantation; noun.

**Diagnosis.** The male resembles *I. hamatus* (see Andreeva et al. 1984: figs 1–4), but the embolus is straight and digitiform (Fig. 26D) vs. bent and needle-like; the RTA is entire (unbranched) and bent dorsally (Fig. 26B) vs. with two branches and nearly triangular apophyses in *I. hamatus*.

**Description.** Male (holotype). Total length 4.23, CL 1.53, CW 0.90, AL 1.70, AW 0.80. Eye measurements: AME 0.31, ALE 0.15, PME 0.03, PLE 0.16, AER 1.00, PER 1.10, EFL 0.81. Clypeus 0.05 high. Legs: I 2.05 (0.65, 0.39, 0.49, 0.30, 0.22); II 1.70 (0.50, 0.30, 0.38, 0.27, 0.25); III 1.81 (0.56, 0.25, 0.40, 0.35, 0.25); IV 2.25 (0.75, 0.32, 0.46, 0.44, 0.28).

Carapace dark brown (Fig. 27A). Sides and clypeus margins with a strip of white hairs. Chelicerae dark brown. *Maxillae* greyish yellow, inner margin with dense setae.





**Figure 26.** Palp of *Icius bamboo* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bars: equal for **A**, **B** and **C**.



**Figure 27.** Habitus of *Icius bamboo* sp. n., male holotype. **A** dorsal **B** lateral.

Labium brown, tip with greyish hairs. Sternum greyish brown. Abdomen oval, with transverse alternating dark and light stripes. Venter and spinnerets grey. Legs I more robust and darker than other legs, which are yellowish. Spination of leg I: femur d4-1-1; tibia v2-0-2; metatarsus v2-0-2. Palpal tibia short, about 1/3 the length of cymbium, RTA bent, strong and with blunt tip (Fig. 26B). Bulb about twice as long as wide. Seminal duct encircling tegulum retrolaterally. Embolus short, digitiform, (Fig. 26D).

Female. Unknown.

**Distribution.** Known only from the type locality.

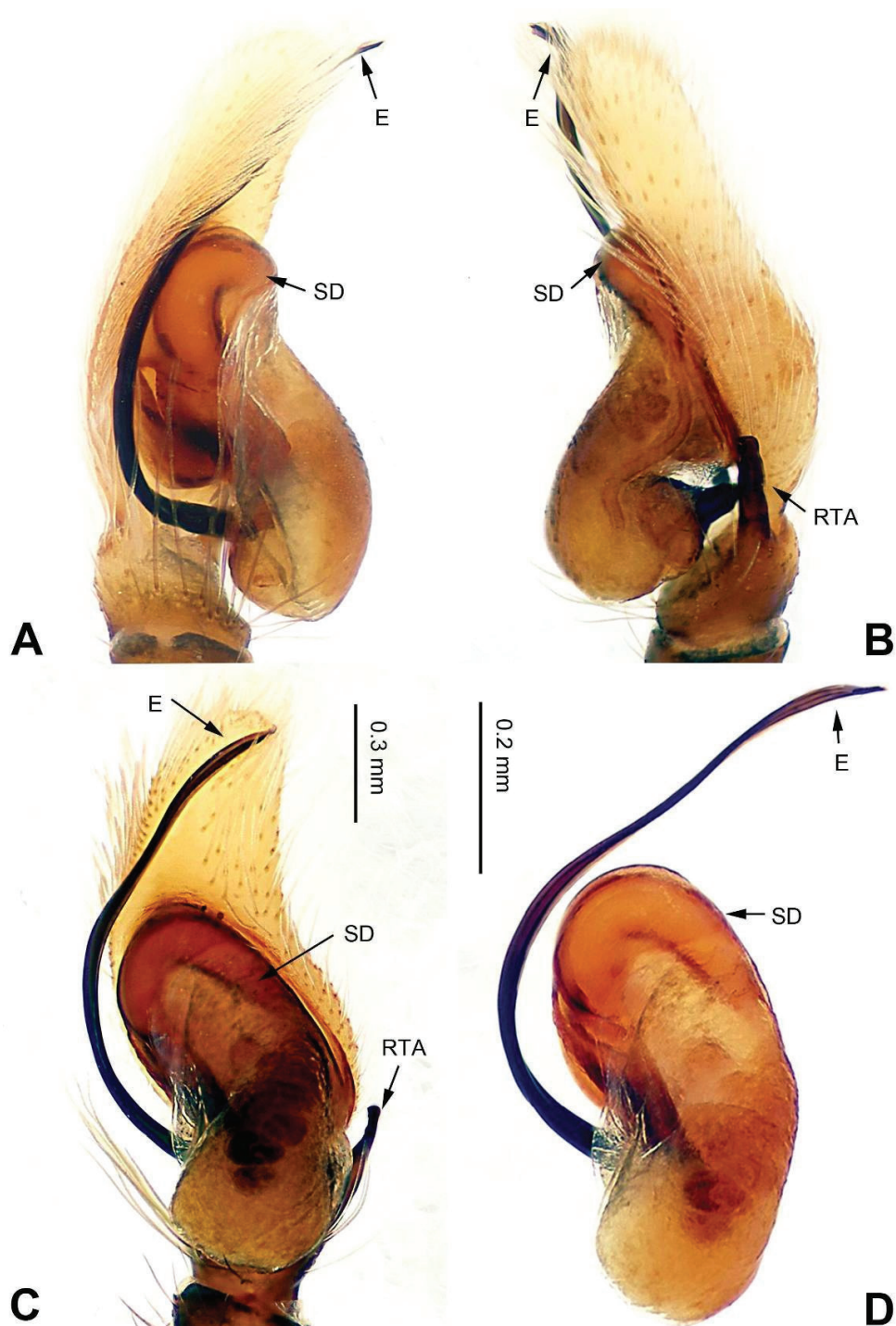
### Genus *Nannenus* Simon, 1902

#### *Nannenus menghaiensis* Cao & Li, sp. n.

<http://zoobank.org/BF65EB9F-B57D-48B7-818C-F8A7FE33DC53>

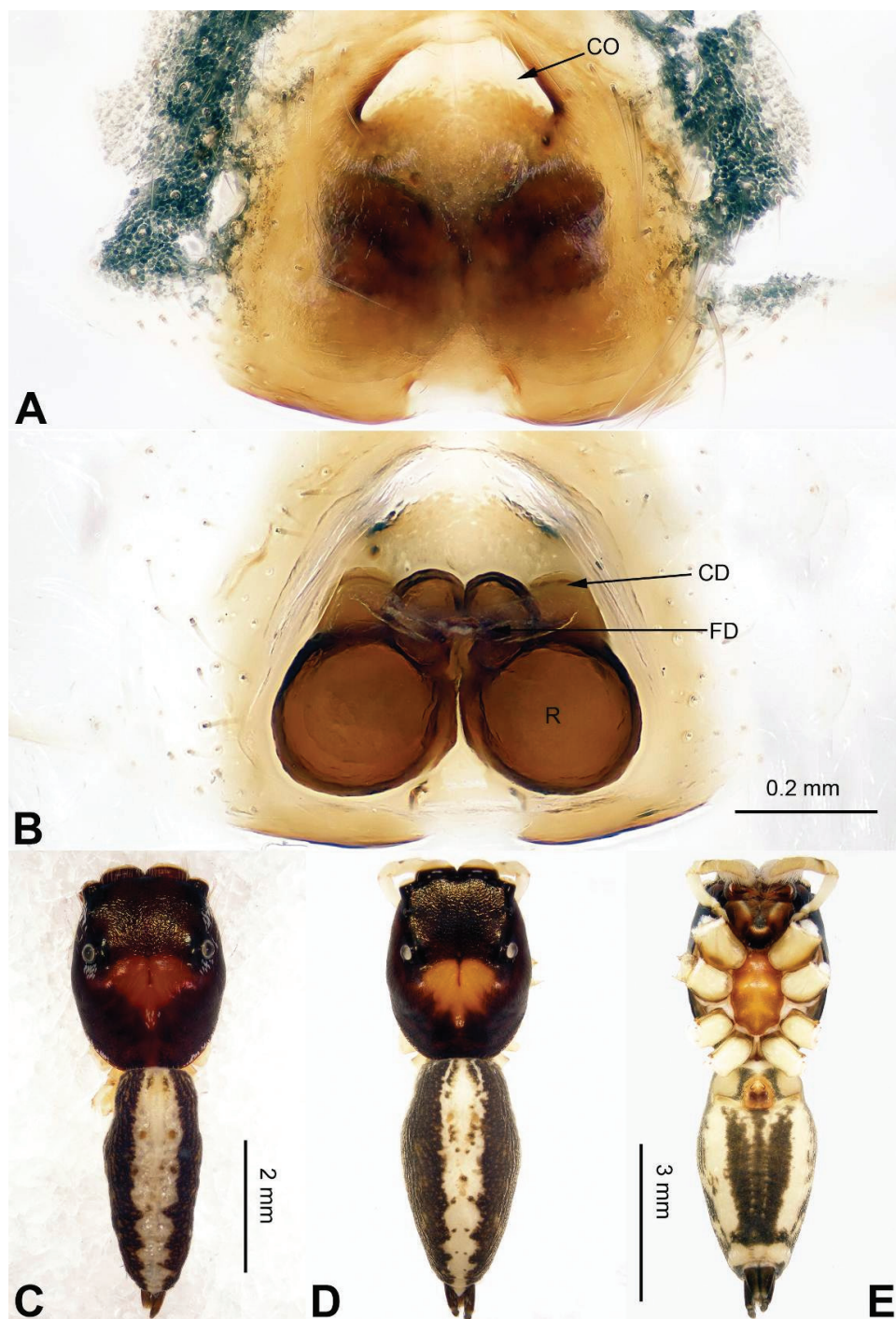
Figs 28–29, 43

**Type. Holotype** ♂: CHINA, Yunnan, Jinghong City, Menghai County, Menghai Village (22°01.702'N, 100°23.700'E, 1188 m), secondary forest, 28 July 2012, Q. Zhao & Z. Chen leg. **Paratypes:** 1 ♀, same data as holotype; 1 ♀, CHINA, Yunnan, Mengla County, Xiaolongha Village, Xishuangbanna Nature Reserve, Biological diversity corridor (21°24.213'N, 101°376.995'E, 834 m), seasonal rainforest, 3 June 2012, Q. Zhao & Z. Chen leg.



**Figure 28.** Palp of *Nannenus menghaiensis* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.





**Figure 29.** *Nannenus menghaiensis* sp. n., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male habitus, dorsal **D** female habitus, dorsal **E** female habitus, ventral. Scale bars equal for **A** and **B**; equal for **D** and **E**.



**Etymology.** The species name is derived from the name of the type locality; adjective.

**Diagnosis.** The male resembles that of *N. maughami* Prószyński & Deeleman-Reinhold, 2012 (see Prószyński and Deeleman-Reinhold 2012: figs 97–99), but the RTA is straight and shorter, about 1/4 the length of the cymbium (Fig. 28B) vs. apically bent in *N. maughami*. The female can be distinguished from other congeners by the boomerang-like copulatory openings (Fig. 29A).

**Description.** Male (holotype). Total length 7.25, CL 3.50, CW 2.43, AL 3.75, AW 1.50. Eye measurements: AME 0.70, ALE 0.32, PME 0.15, PLE 0.25, AER 2.10, PER 2.15, EFL 1.80. Clypeus 0.25 high. Legs: I 6.00 (2.00, 1.10, 1.25, 0.90, 0.75); II 5.45 (1.65, 1.00, 1.20, 0.85, 0.75); III 5.48 (1.70, 0.85, 1.00, 1.10, 0.83); IV 6.52 (1.95, 0.92, 1.50, 1.35, 0.80).

Carapace dark brown (Fig. 29C). Lateral eyes with surrounded with black. *Chelicerae* dark orange-brown, sparsely covered with fine grey hairs. *Maxillae* brownish with dull white tips and with grey hairs on the inner margins. *Labium* dark brown, with dull white tip and black hairs. *Sternum* orange-brown. Abdomen with central light stripe, black laterally. Venter dark greyish. Spinnerets black. Legs I more robust and darker than the other legs, which are yellow. Spination of leg I: femur d2-1-1; tibia v2-2-2; metatarsus v2-0-2. Palpal tibia short, about 1/5 the length of the cymbium, RTA straight, as long as tibia (Fig. 28B). Cymbium bent. Bulb elongate, set obliquely, with peripheral seminal duct. Embolus arising from basal-retrolateral part of the bulb, running parallel to bulb and extending to the tip of the cymbium (Fig. 28C).

Female (one of paratypes, same locality as holotype). Total length 9.26, CL 4.00, CW 2.56, AL 5.26, AW 2.38. Eye measurements: AME 0.79, ALE 0.39, PME 0.08, PLE 0.34, AER 2.28, PER 2.30, EFL 2.10. Clypeus 0.13 high. Legs: I 6.57 (2.15, 1.34, 1.48, 0.90, 0.70); II 6.02 (1.90, 1.20, 1.25, 0.95, 0.72); III 6.11 (1.90, 1.08, 1.00, 1.34, 0.79); IV 7.77 (2.28, 1.18, 1.72, 1.80, 0.79).

Spination of leg I: femur d0-1-0; tibia v2-2-2; metatarsus v2-0-2. Other characters similar to those of male. Epigyne with two rectangular posterior projections and central bulge formed by the copulatory ducts (Fig. 29A). Copulatory openings boomerang-like, located anteriorly. Copulatory ducts short, receptacles round, fertilisation ducts at the anterior part of the receptacles (Fig. 29B).

**Distribution.** Known from several localities in Xishuangbanna.

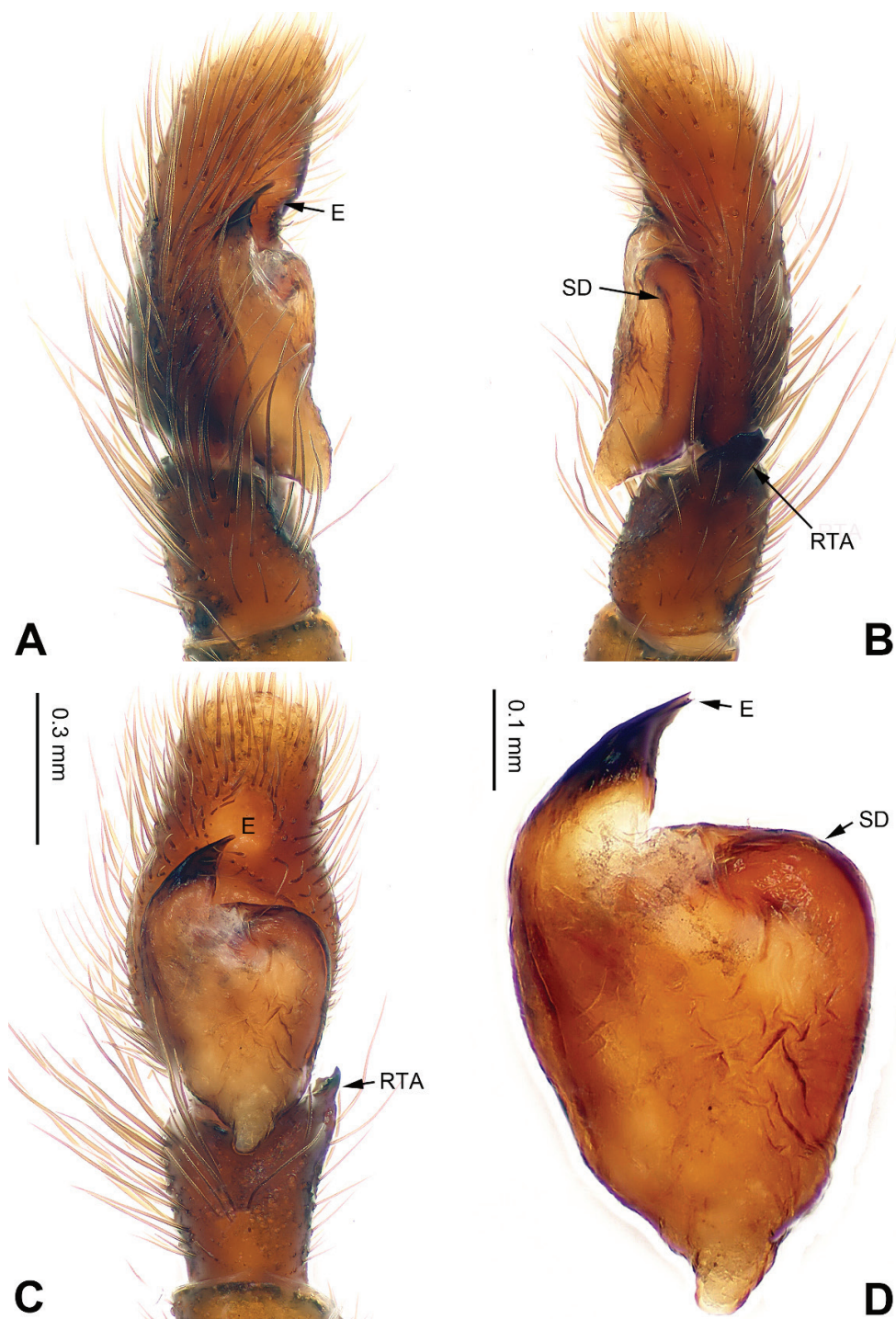
## Genus *Pancorius* Simon, 1902

### *Pancorius latus* Cao & Li, sp. n.

<http://zoobank.org/7DD1BEB1-7962-45C6-9AA9-709AEDABB168>

Figs 30–31, 43

**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Menglun Town, *Paramichelia baillonii* plantation (21°54.200'N, 101°16.923'E, 608 m), 7 April 2007, leg. G. Zheng Guo.



**Figure 30.** Palp of *Pancorius latus* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.



**Figure 31.** Habitus of *Pancorius latus* sp. n., male holotype. **A** dorsal **B** lateral.

**Etymology.** From Latin *latus* (wide), in reference to the shape of the carapace; adjective.

**Diagnosis.** Similar to *P. crassipes* (Karsch, 1881) (see Žabka 1997: figs 108–109), but bulb triangular (Fig. 30D) vs. oval, embolus beak-like with broad base (Fig. 30C) vs. needle-like; RTA rectangular with three little tips (Fig. 30B) vs. triangular in *P. crassipes*.

**Description.** Male (holotype). Total length 6.45, CL 3.20, CW 2.80, AL 3.25, AW 1.80. Eye measurements: AME 0.60, ALE 0.36, PME 0.07, PLE 0.36, AER 2.25, PER 2.20, EFL 1.90. Clypeus 0.31 high. Legs: I 8.40 (2.35, 1.25, 2.30, 1.60, 0.90); II 6.35 (2.00, 0.95, 1.45, 1.20, 0.75); III 6.80 (1.00, 1.30, 1.45, 0.95, 2.10); IV missing.

Carapace dark brown, moderately high and slightly broadened posteriorly, with white or greyish hairs and lighter mediodorsally (Fig. 31A). Clypeus with dense white setae. Chelicerae dark brown, with greyish hairs. *Maxillae* and labium dark brown, tips with dark setae. Sternum light brown. Abdomen oval, generally grey. Venter and spinnerets greyish–brown. Legs brown with hairs and spines. Spination of leg I: femur d3-1-1; patella p0-1-0; tibia v2-2-2, p1-0-1; metatarsus v2-0-2, p1-0-0. Palpal tibia about 1/2 the length of the cymbium. RTA rectangular, with three little apical tips (Fig. 30B). Bulb with posterior lobe. Embolus beak-like with broad base, subequal to the length of the RTA (Fig. 30C).

Female. Unknown.

**Distribution.** Known from the type locality.

**Genus *Phintella* Strand, 1906*****Phintella lepidus* Cao & Li, sp. n.**

<http://zoobank.org/D3974470-7A73-42D5-A2CC-0B3FBB801E8A>

Figs 32–33, 43

**Type. Holotype** ♂: CHINA, Yunnan, Jinghong City, Mengyang Town (22°09.765'N, 100°52.553'E, 862 m), seasonal rainforest, 22 July 2012, Q. Zhao & Z. Chen leg.

**Paratypes:** 1♂1♀, CHINA, Yunnan, Mengla County, Xiaolongha Village, Xishuangbanna Nature Reserve, Biological diversity corridor (21°24.192'N, 101°37.025'E, 657 m), seasonal rainforest, 29 July 2012, Q. Zhao & Z. Chen leg.

**Etymology.** From Latin *lepidus* (nice), in reference to the body appearance; adjective.

**Diagnosis.** Male can be distinguished from other congeners by the wrench-like structure comprising the embolus and lamellar process (Fig. 32C–D). The epigyne (Fig. 33A–B) resembles that of *P. piatensis* Barrion & Litsinger, 1995 (see Barrion and Litsinger 1995: fig. 36a–f), but the copulatory ducts are broader, about 1/2 the length of the receptacle diameter vs. 1/4 the length in *P. piatensis*.

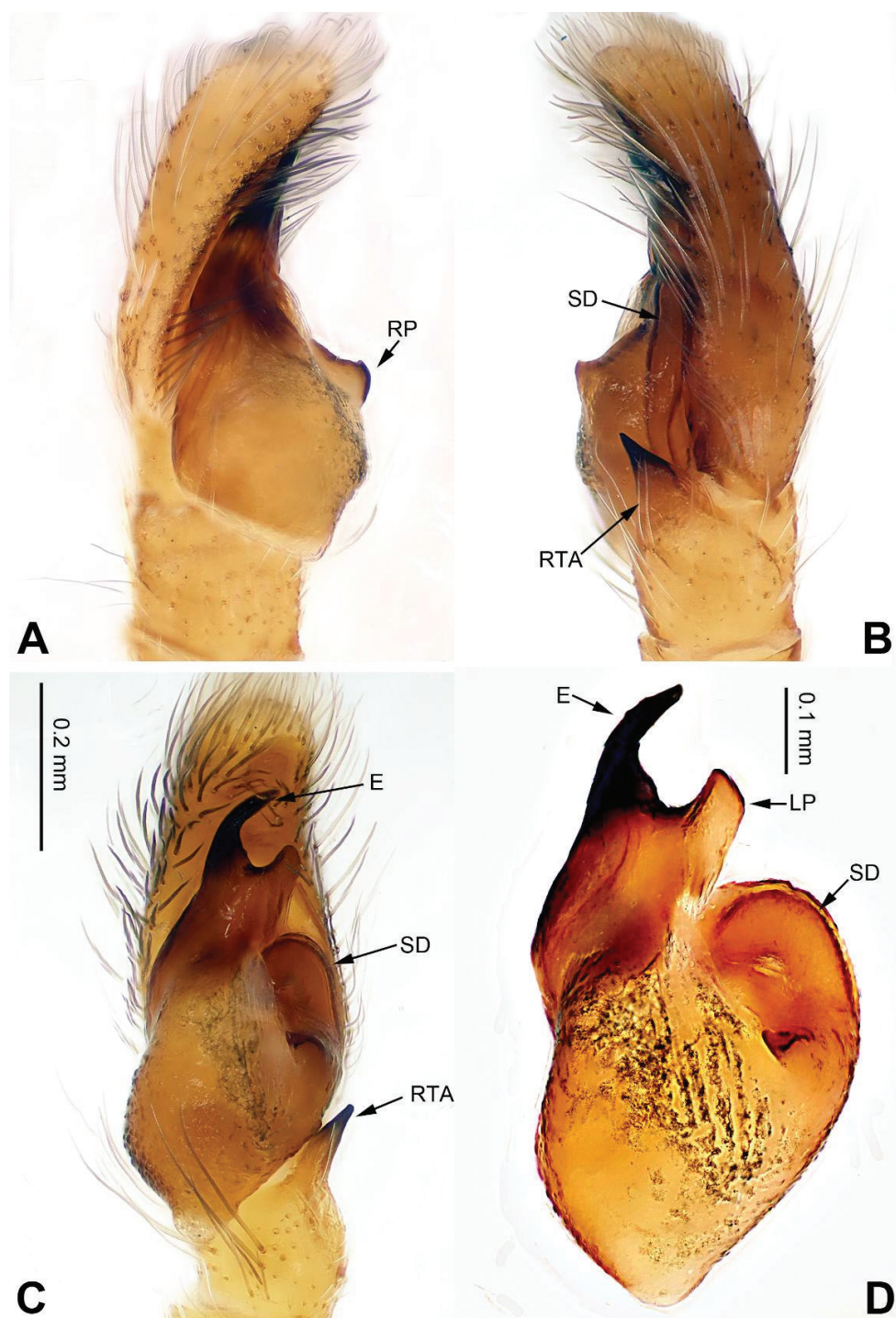
**Description.** Male (holotype). Total length 5.10, CL 2.25, CW 1.75, AL 2.85, AW 1.50. Eye measurements: AME 0.50, ALE 0.30, PME 0.05, PLE 0.20, AER 1.75, PER 1.70, EFL 1.35. Clypeus 0.40 high. Legs: I 6.25 (1.75, 1.00, 1.50, 1.25, 0.75); II 4.83 (1.35, 0.73, 1.15, 0.90, 0.70); III 5.60 (1.60, 0.70, 1.25, 1.30, 0.75); IV 5.80 (1.65, 0.70, 1.35, 1.35, 0.75).

Carapace dark brown (Fig. 33C). Ocular area with metallic lustre, anteriorly with black hairs. Posterior median and margin with white strip of hairs. Clypeus with white strip of hairs. Chelicerae dark brown. *Maxillae* and labium greyish brown, tips with grey hairs. Sternum yellow with dark margin. Atrium with distinct anterior margin. Abdomen oval, dorsomedially yellow, the rest dark grey with a metallic lustre. Venter dark grey. Spinnerets grey-brown. Legs I more robust and darker than others, which are yellowish. Spination of leg I: femur d3-1-1; tibia v2-2-2-2; metatarsus v2-0-2. Palp: tibia short, about 1/3 the length of the cymbium. Tibial apophysis about 2/3 the length of the tibia, with pointed tip (Fig. 32B). Bulb about twice as long than wide, with distinct outgrowth and one retrolateral process (in prolateral or retrolateral views). Embolus subequal to length of the RTA, accompanied with one lamellar process (Fig. 32D).

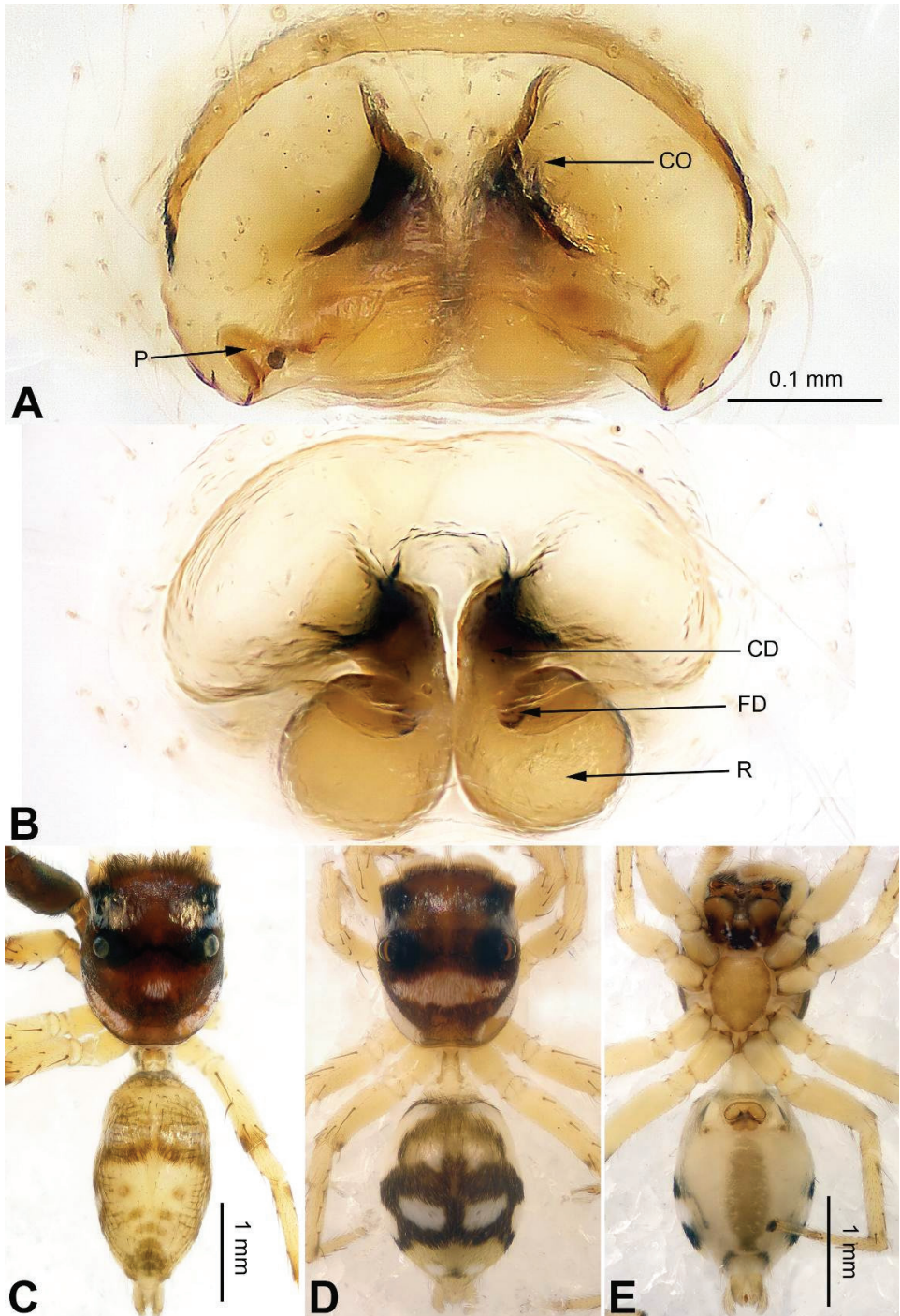
Female (one of paratypes). Total length 4.42, CL 1.70, CW 1.30, AL 2.72, AW 1.72. Eye measurements: AME 0.43, ALE 0.22, PME 0.04, PLE 0.23, AER 1.25, PER 1.23, EFL 1.13. Clypeus 0.37 high. Legs: I 3.35 (0.92, 0.62, 0.91, 0.61, 0.39); II 3.34 (0.90, 0.63, 0.88, 0.56, 0.37); III 3.57 (1.06, 0.50, 0.71, 0.86, 0.44); IV 4.15 (1.33, 0.47, 0.96, 0.87, 0.52).

Posterior part of carapace with broader white stripe of hairs than in male. Abdomen with broad, dark decorative pattern. Legs yellowish. Spination of leg I: femur d2-1-1; tibia v2-2-2-2; metatarsus v2-0-2. Other characters similar to these of male. Epigyne sclerotised along the anterior margin (Fig. 33A). Copulatory openings with





**Figure 32.** Palp of *Phintella lepidus* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.



**Figure 33.** *Phintella lepidus* sp. n., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male habitus, dorsal **D** female habitus, dorsal **E** female habitus, ventral. Scale bars equal for **A** and **B**; equal for **D** and **E**.

strongly sclerotised edges. Two pockets near posterolateral edge. Copulatory ducts bent, short. Receptacles spherical, their diameter about 2 times as wide as copulatory ducts. Fertilisation ducts located anteriorly to the receptacles (Fig. 33B).

**Distribution.** Known from two localities in Xishuangbanna.

***Phintella sancha* Cao & Li, sp. n.**

<http://zoobank.org/43D9664A-155C-4373-A6E2-7C32C044F02A>

Figs 34–35, 43

**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Menglun Town, rubber plantation (21°54.684'N, 101°16.319'E, 585 m), 8 April 2007, G. Zheng leg.

**Etymology.** From Chinese Pinyin *san cha* (trident), in reference to the trifurcate RTA; noun.

**Diagnosis.** Similar to *P. suavisoides* Lei & Peng, 2013 (Fig. 36), but can be distinguished by: (1) trifurcate RTA in new species (Fig. 34B) vs. bifurcate in *P. suavisoides*; (2) the terminal seminal duct angle almost 30° (Fig. 34C) vs. about 60° in *P. suavisoides*; (3) the embolus of the new species is accompanied by one digitiform lamellar process (Fig. 34D), lacking in *P. suavisoides*.

**Description.** Male (holotype). Total length 3.60, CL 1.75, CW 1.40, AL 1.85, AW 1.09. Eye measurements: AME 0.45, ALE 0.13, PME 0.04, PLE 0.14, AER 1.25, PER 1.20, EFL 1.06. Clypeus 0.15 high. Legs: I 4.63 (1.50, 0.80, 1.13, 0.80, 0.40); II 3.50 (1.05, 0.6, 0.75, 0.65, 0.45); III 4.08 (1.25, 0.55, 0.88, 0.90, 0.50); IV 4.10 (1.05, 0.50, 1.00, 1.00, 0.55).

Carapace brown (Fig. 35A). Chelicerae dark brown. *Maxillae* and labium brown, tips white with greyish hairs. Sternum light brown. Abdomen oval, greyish. Venter and spinnerets grey. Legs I more robust and darker than others, which are yellowish. Spination of leg I: femur d2-1-1; tibia v2-2-2; metatarsus v2-0-2. Palp: tibia short, about 1/3 the length of the cymbium. RTA trifurcate (Fig. 34B), short, about 1/4 the length of the cymbium. Bulb 2 times longer than wide, with anterior semi-transparent lobe. Embolus very short, slightly bent (Fig. 34C).

**Female.** Unknown.

**Distribution.** Known only from the type locality.

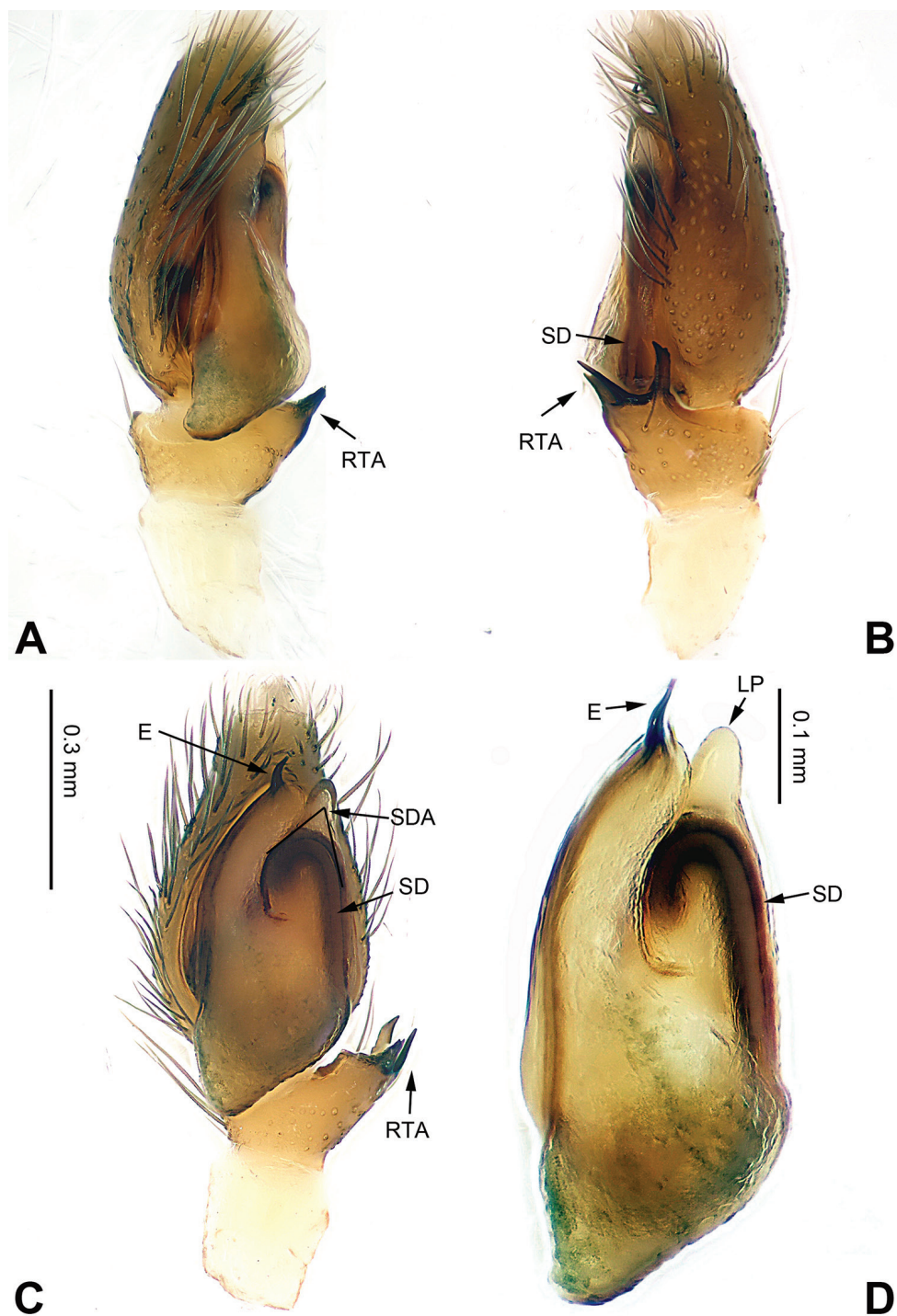
***Phintella suavisoides* Lei & Peng, 2013**

Figs 36–37, 43

*Phintella suavisoides* Lei & Peng, 2013: 103, figs 5, 6a–e (♂).

**Material examined.** 1♂1♀: CHINA, Yunnan, Mengla County, Menglun Town, 48 km landmark in Nature Reserve (21°38.853'N, 101°09.625'E, 1001 m), seasonal rain-forest, 30 July 2012, Q. Zhao & Z. Chen leg. 1♂, CHINA, Yunnan, Jinghong City,





**Figure 34.** Palp of *Phintella sancha* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.





**Figure 35.** Habitus of *Phintella sancha* sp. n., male holotype. **A** dorsal **B** ventral.

Menga Town, Wengnan Village (22°05.020'N, 100°22.086'E, 1118 m), secondary forest, 24 July 2012, Q. Zhao & Z. Chen leg.; 1♀, CHINA, Yunnan, Jinghong City, Menghai County, Manda Village (22°01.702'N, 100°23.700'E, 1188 m), secondary forest, 28 July 2012, Q. Zhao & Z. Chen leg.

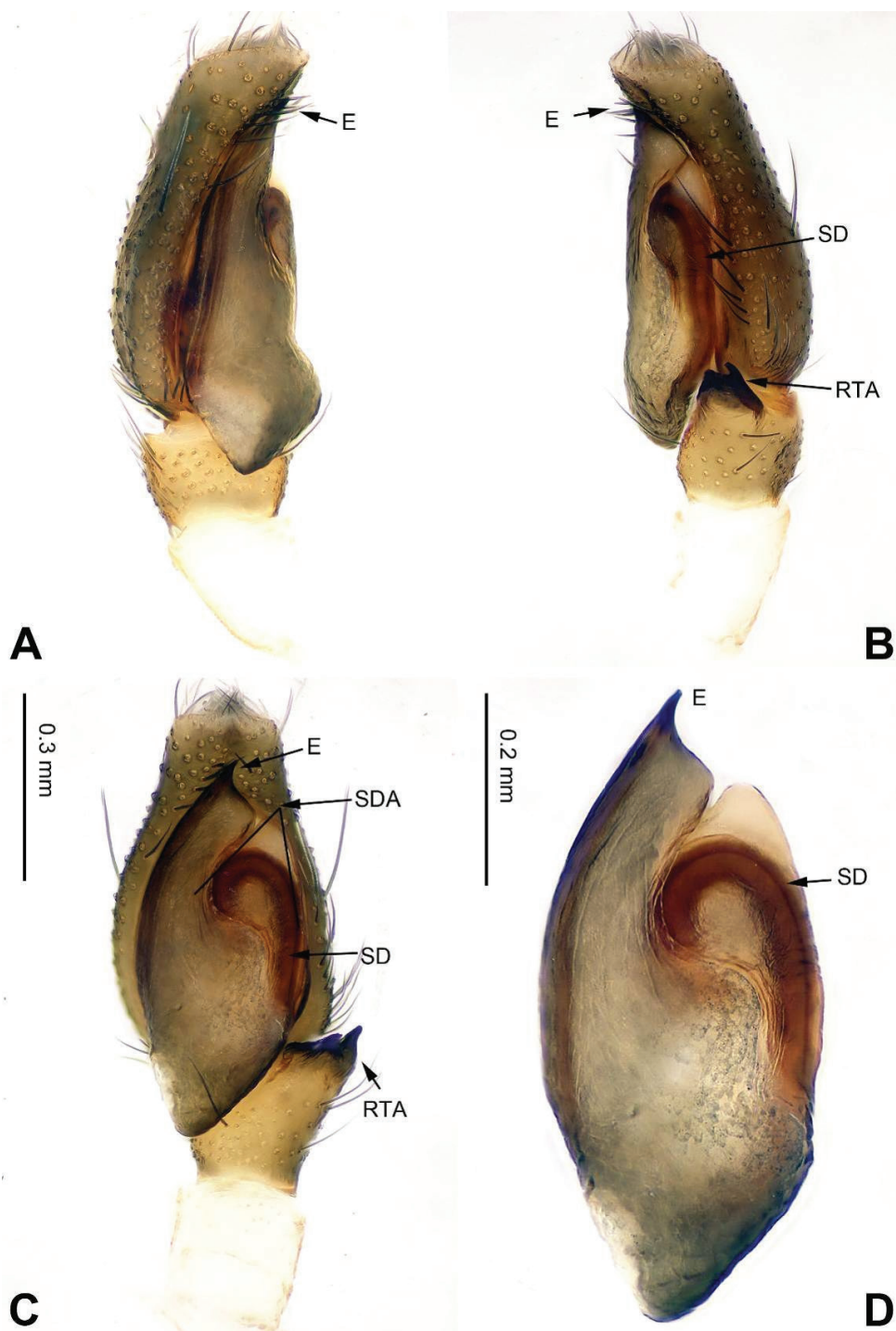
**Comparative material examined.** **Holotype** ♂ (Hunan Normal University, China): CHINA, Yunnan, Tengchong County, Jietou Township, Zhoujiapo Village (25°32.086'N, 98°40.139'E, 1620 m), 13 May 2006, C. Yin, X. Peng, J. Hu & P. Hu leg.

**Diagnosis.** Male well diagnosed by Lei and Peng (2013). The female resembles *P. cavaleriei* (Schenkel, 1963) (see Peng et al. 1993: figs 537–539), but the copulatory openings and copulatory ducts located medially (Fig. 37A–B) vs. laterally; copulatory ducts bent dorsally (Fig. 37B) vs. facing each other in *P. cavaleriei*.

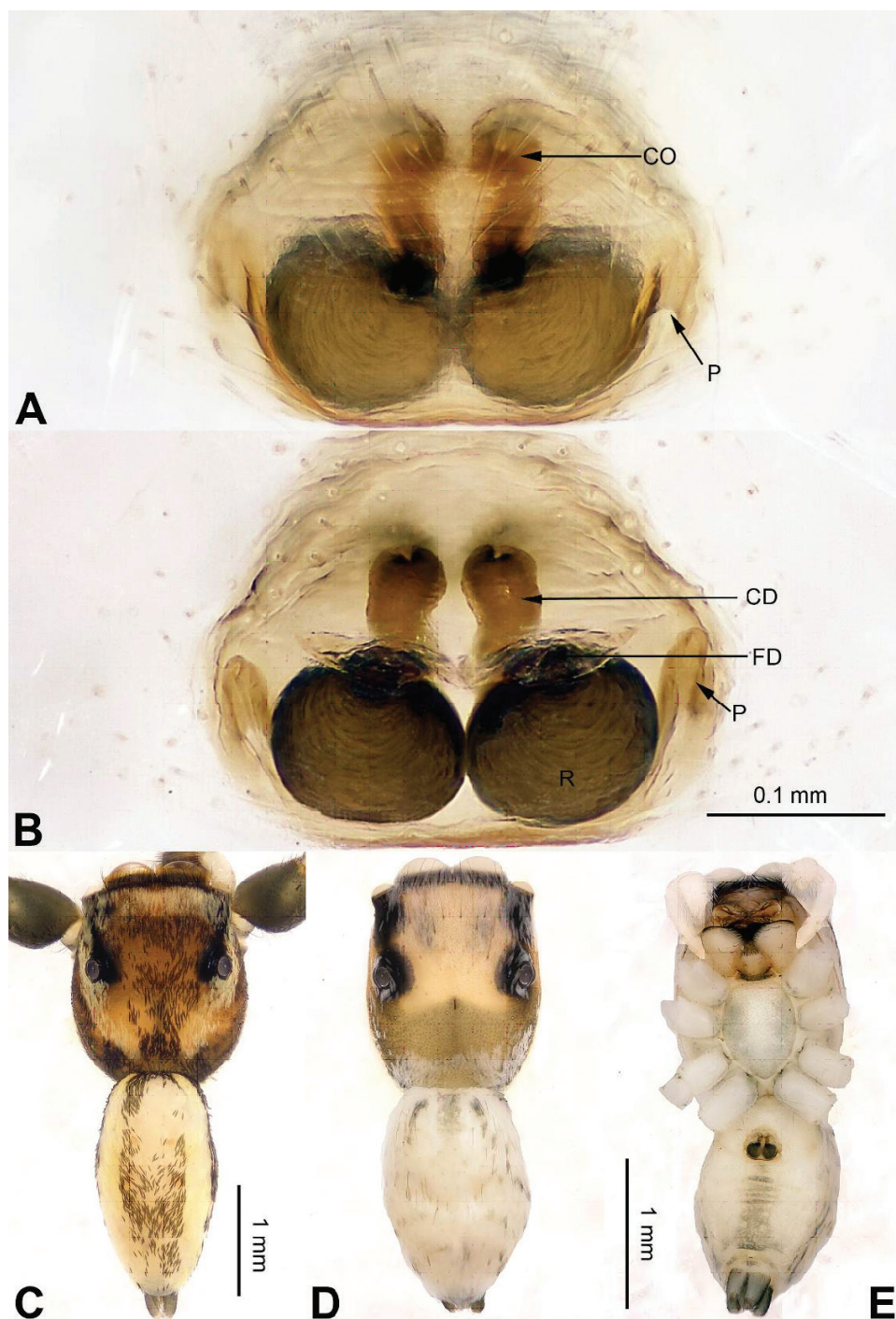
**Description.** Male. Well described by Lei and Peng (2013).

Female. Total length 3.25, CL 1.50, CW 1.28, AL 1.75, AW 1.10. Eye measurements: AME 0.38, ALE 0.20, PME 0.03, PLE 0.15, AER 1.19, PER 1.20, EFL 1.00. Clypeus 0.10 high. Legs: I 3.01 (0.98, 0.50, 0.63, 0.50, 0.40); II 2.62 (0.80, 0.40, 0.52, 0.50, 0.40); III 3.09 (1.00, 0.40, 0.56, 0.73, 0.40); IV 3.73 (1.18, 0.44, 0.85, 0.86, 0.40).

Carapace light grey with dense setae (Fig. 37C). Clypeus light brown, covered by white, flat hairs. Chelicerae brown. Maxillae and labium greyish, tips with black hairs. Sternum greyish brown with light margin. Abdomen oval and white, clothed



**Figure 36.** Palp of *Phintella suavisoides*, male from Xishuangbanna. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.



**Figure 37.** *Phintella suavisoides*, female and male from Xishuangbanna. **A** epigyne, ventral **B** vulva, dorsal **C** male habitus, dorsal **D** female habitus, dorsal **E** female habitus, ventral. Scale bars equal for **A** and **B**; equal for **D** and **E**.

in dense setae. Venter greyish. Spinnerets green-grey. Legs white. Spination of leg I: femur d0-1-0; tibia v2-2-2; metatarsus v2-0-2. Copulatory openings small and located anteromedially (Fig. 37A). Copulatory ducts bent, short. Receptacles spherical, diameters four times wider than copulatory ducts. Fertilisation ducts located anteriorly to receptacles (Fig. 37B).

**Distribution.** Known from Gaoligong Mountains and Xishuangbanna in Yunnan, China.

### Genus *Ptocasius* Simon, 1885

#### *Ptocasius paraweyersi* Cao & Li, sp. n.

<http://zoobank.org/641FCCBC-0024-43AC-AE43-AE7FADBF0EB4>

Figs 38–39, 43

**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Menglun Town, 48 km landmark in Nature Reserve (21°58.704'N, 101°19.748'E, 1088 m), seasonal rainforest, 12 August 2011, Q. Zhao & Z. Chen leg. **Paratypes:** 1♂2♀, CHINA, Yunnan, Mengla County, Xiaolongha Village, Xishuangbanna Nature Reserve, Biological diversity corridor (21°24.192'N, 101°37.025'E, 657 m), seasonal rainforest, 29 June 2012, Q. Zhao & Z. Chen leg.

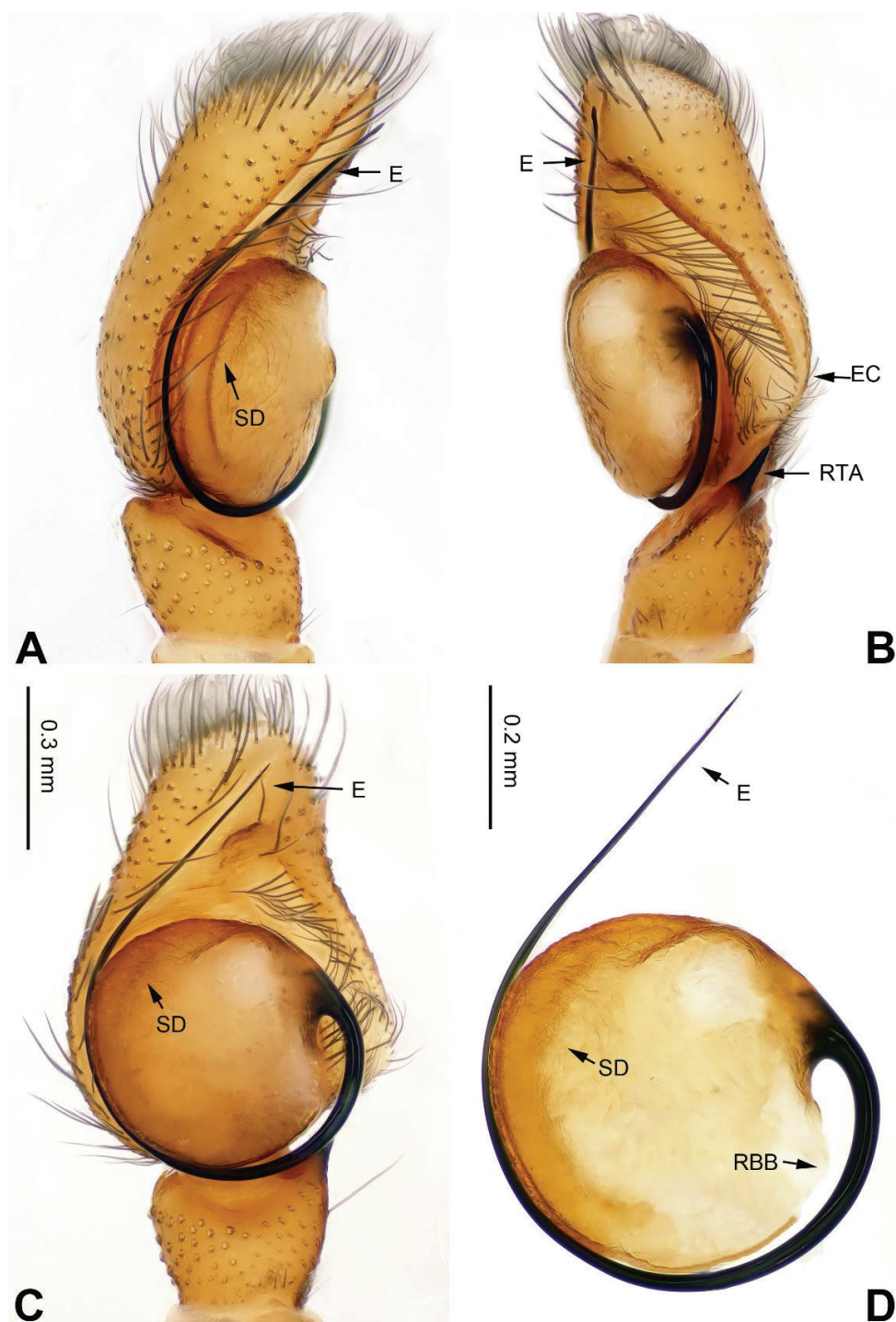
**Etymology.** From Greek prefix *para* and *weyersi*, a patronym from Weyers, referring to similarities with *P. weyersi*.

**Diagnosis.** Similar to *P. weyersi* (see Żabka 1985: figs 530–532), but the tegulum has one small bump (Fig. 38D) and the RTA is straight (Fig. 38B) vs. bent backward in *P. weyersi*. The female resembles *P. weyersi*, but differs by having two epigynal hoods (Fig. 39A) vs. one. Compared to *P. songi* Logunov, 1995, the hoods are located medially (Fig. 39A) vs. laterally and the receptacles are elongate (Fig. 39B) vs. spherical.

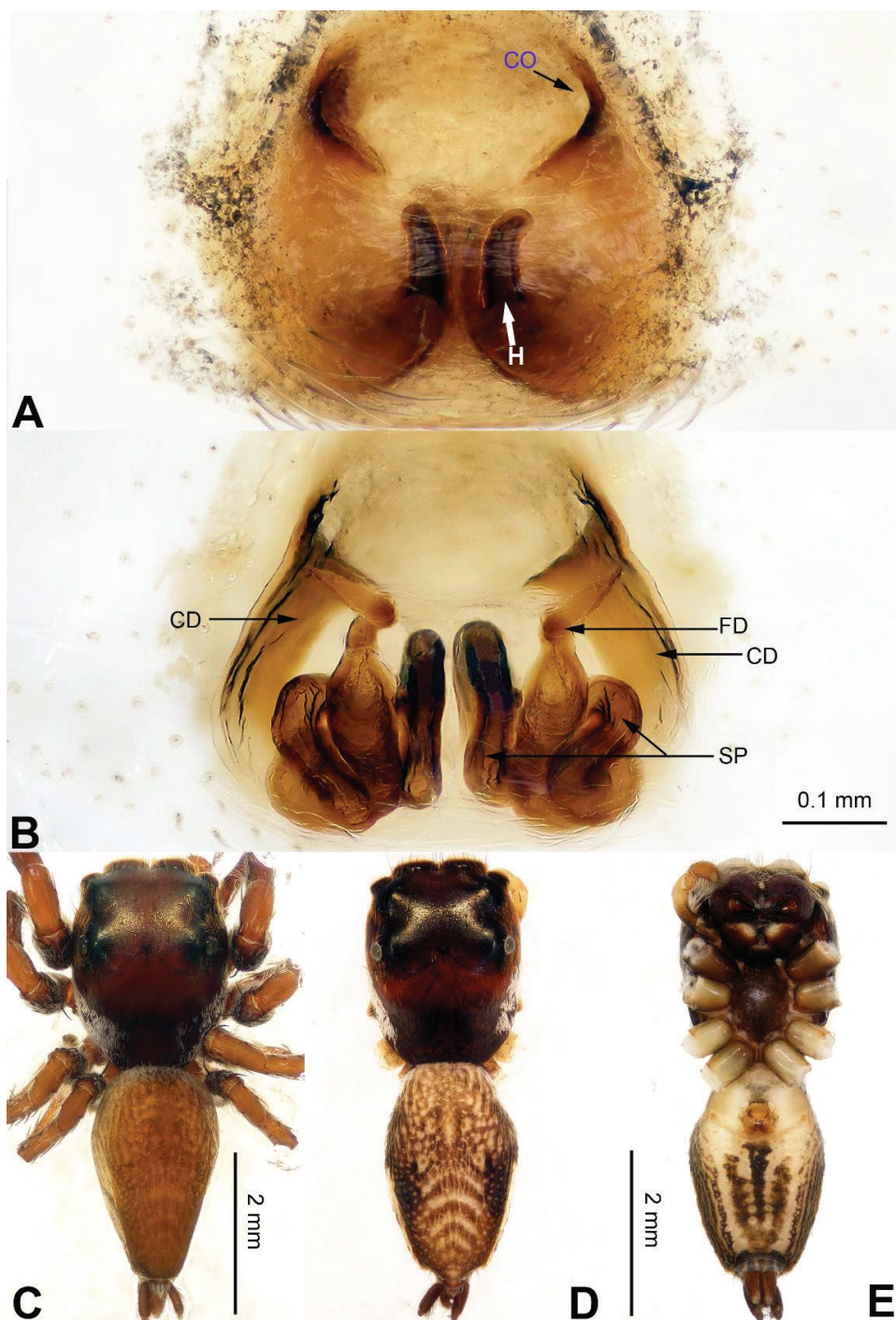
**Description.** Male (holotype). Total length 6.10, CL 2.60, CW 2.00, AL 3.50, AW 1.65. Eye measurements: AME 0.63, ALE 0.31, PME 0.05, PLE 0.30, AER 1.90, PER 1.90, EFL 1.60. Clypeus 0.15 high. Legs: I 5.20 (1.50, 1.00, 1.25, 0.85, 0.60); II 4.45(1.35, 0.75, 1.10, 0.70, 0.55); III 5.15 (1.55, 0.75, 1.10, 1.05, 0.70); IV 5.25 (1.55, 0.75, 1.10, 1.10, 0.75).

Carapace dark brown with dense white hairs on both sides of the posterior edge (Fig. 39C). Chelicerae, clypeus and labium dark brown. *Maxillae* brown with wide, white tips. Sternum dark brown. Abdomen elongate, brownish. Venter puce with longitudinal rows of dots. Legs dark brown. Spination of leg I: femur d5-1-1; patella p0-1-0, r0-1-0; tibia v2-2-2, p1-1-1, r1-1-1; metatarsus v2-0-2, p1-0-1, r1-0-1. Palp: tibia short, about 1/3 the length of the cymbium. RTA short, with a pointed tip (Fig. 38C). Cymbium nearly flabellate with retrolateral fold. Seminal duct encircling tegulum prolaterally. Embolus elongate, its base at two o'clock (Fig. 38C–D).





**Figure 38.** Palp of *Ptocasius paraเวย์ersi* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.



**Figure 39.** *Procasis paraweyersi* sp. n., female paratype and male holotype. **A** epigyne, ventral **B** vulva, dorsal **C** male habitus, dorsal **D** female habitus, dorsal **E** female habitus, ventral. Scale bars equal for **A** and **B**; equal for **D** and **E**.

Female (one of paratypes). Total length 6.25, CL 2.81, CW 2.03, AL 3.44, AW 1.85. Eye measurements: AME 0.63, ALE 0.33, PME 0.05, PLE 0.28, AER 1.98, PER 2.00, EFL 1.72. Clypeus 0.10 high. Legs: I 4.57 (1.41, 1.00, 1.00, 0.63, 0.53); II 4.37 (1.41, 0.90, 0.93, 0.63, 0.50); III 4.80 (1.56, 0.76, 1.00, 0.92, 0.56); IV 5.37 (1.70, 0.80, 1.13, 1.10, 0.64).

Abdomen light brown with irregular white patches. Venter yellowish with black longitudinal stripe. Spination of leg I: femur d3-1-1; patella p0-1-0; tibia v2-2-2, p1-0-1; metatarsus v2-0-2. Other characters similar to the male. Copulatory ducts long, broad and located laterally. Receptacles long and convoluted, forming four loops. Fertilisation ducts located at the anterior part of the receptacles (Fig. 39B).

**Distribution.** Known from several localities in Xishuangbanna.

### Genus *Stenaelurillus* Simon, 1886

#### *Stenaelurillus fuscus* Cao & Li, sp. n.

<http://zoobank.org/33962F70-D32A-46C9-8684-83B8E7228F07>

Figs 40–42, 43

**Type. Holotype** ♂: CHINA, Yunnan, Mengla County, Menglun Town, Rubber-Tea plantation (21°55.551'N, 101°16.923'E, 561 m), 11 December 2006, G. Zheng leg.

**Etymology.** From Latin *fuscus* (dark), in reference to the dark carapace; adjective.

**Diagnosis.** Similar to *S. minutus* Song & Chai, 1991 (see Wesołowska 2014: fig. 4A–D), but embolus straight (Fig. 40C) vs. bent; sclerotized apophysis (the longer one) located anteriorly to embolus (Fig. 40C) vs. posteriorly; RTA almost triangular (Fig. 40B) vs. broad with thin, long, pointed apex in *S. minutus*.

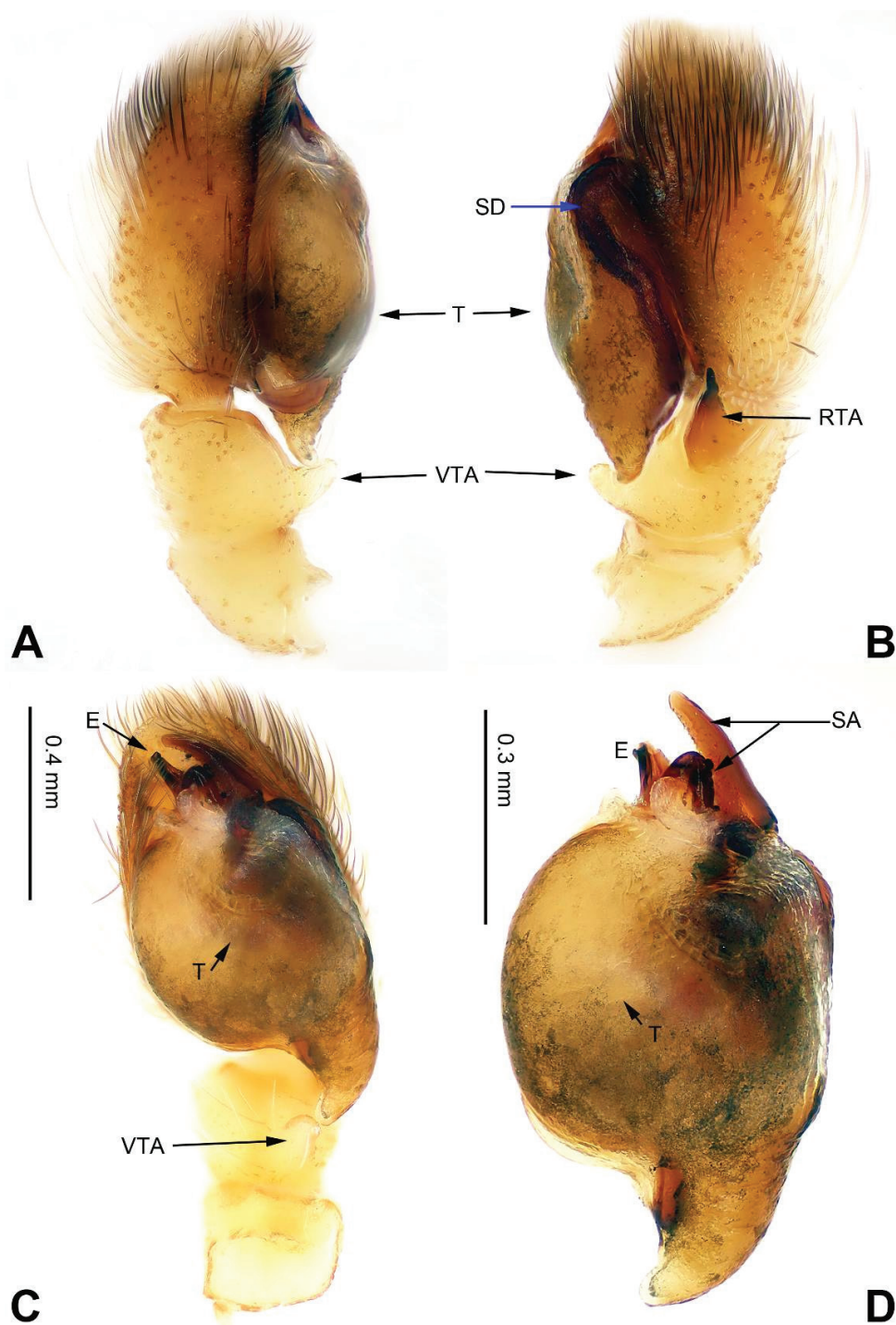
**Description.** Male (holotype). Total length 5.30, CL 2.80, CW 2.35, AL 2.50, AW 1.60. Eye measurements: AME 0.48, ALE 0.30, PME 0.06, PLE 0.29, AER 1.75, PER 1.60, EFL 1.30. Clypeus height 0.31 high. Legs: I 4.50 (1.50, 0.75, 1.00, 0.75, 0.50); II 6.85 (1.50, 0.65, 0.95, 0.70, 0.50); III 5.35 (1.80, 0.70, 1.15, 1.15, 0.55); IV 5.85 (2.00, 0.75, 1.25, 1.25, 0.60).

Carapace dark, moderately high and slightly broadened posteriorly (Fig. 42A). Lateral carapace margins with long, dense brush-like setae. Chelicerae dark brown. *Maxillae* and labium brown, tips light with greyish hairs. Sternum dark, oval. Abdomen shield-shaped, anterior edge with long dense bristles. Venter and spinnerets dark grey. Legs dark with dense hairs and numerous spines. Palpal tibia white and short, about 1/3 the length of the cymbium. Tibia with ventral, digitiform, obtuse apophysis and triangular RTA (Fig. 40B). Seminal duct encircling retrolateral part of tegulum. Tegulum oval, with long and triangular posterior lobe.

**Female.** Unknown.

**Distribution.** Known only from the type locality.





**Figure 40.** Palp of *Stenaelurillus fuscus* sp. n., male holotype. **A** prolateral **B** retrolateral **C** ventral **D** bulb, ventral. Scale bar equal for **A–C**.

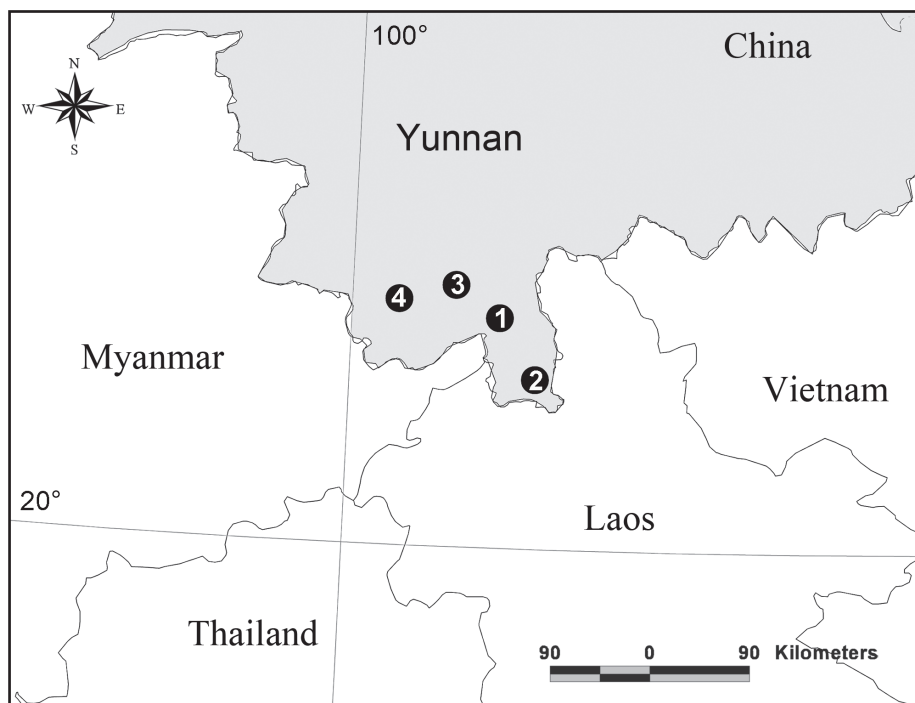




**Figure 41.** *Stenaelurillus fuscus* sp. n., male holotype. **A** embolus, prolateral **B** embolus, retrolateral **C** embolus, dorsal **D** habitus, front. Scale bars equal for **A–C**.



**Figure 42.** Habitus of *Stenaclurillus fuscus* sp. n., male holotype. **A** dorsal **B** lateral.



**Figure 43.** Four main collection localities in Xishuangbanna, Yunnan, China. **1** Mengla Town **2** Menglun Town **3** Mengyang Town **4** Menghai Town.

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# First record of the genus *Pycnodictya* with its subspecies *P. galinieri galinieri* from Egypt (Orthoptera, Acrididae)

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## Abstract

The band-winged *Pycnodictya galinieri galinieri* (Reiche & Fairmaire, 1849) and its genus *Pycnodictya* Stål, 1873 (Orthoptera: Acrididae: Oedipodinae) are recorded for the first time for the Egyptian fauna. The species was collected from Gabal Elba, in the southeastern corner of Egypt. This record expands the known distributional range of *P. galinieri* towards the north of Africa. Descriptions of the genus and the Egyptian subspecies are given using multiple diagnostic characters. The descriptions are supplemented by drawings and photographs of the specimen collected. It is proposed that the genus *Pycnodictya* belongs to the tribe Locustini.

## Keywords

Egypt, new record, Oedipodinae, *Pycnodictya galinieri*

## Introduction

The genus *Pycnodictya* Stål, 1873 is a member of the subfamily Oedipodinae. At present it includes 14 species, one of which contains two subspecies (Eades et al. 2016), mainly distributed over the Afrotropical region (Johnston 1956, Dirsh 1965), with three species (*P. dentata* Krauss, 1902; *P. galinieri* Reiche & Fairmaire, 1849; *P. gracilis* Uvarov, 1936) reaching the Arabian Peninsula (Popov 1980, Ingrisch 1999, Eades et al. 2016).

*Pycnodictya* is arguably one of the rarer but morphologically distinct genera in the Oedipodinae. However, its species are not easily distinguished morphologically as many previous descriptions considered the color of hind wing and leg as main diagnostic characters (Uvarov 1929). *Pycnodictya* is unique in having an expanded lower marginal area of the hind femur, by which it can be easily distinguished from related genera of Oedipodinae, such as *Chloeobora* and *Scintharista* described by Saussure in 1884 (Dirsh 1965). Generally most Oedipodinae have brightly colored hind wings, are characterized by the absence of a prosternal process, the hind legs are missing an external apical spine at the knee and stridulatory serration on the inner surface of hind femur, and by presence of an intercalary vein in medial area of tegmina and the vertical frons (Bolívar 1876, Siddiqui and Shamim 2013).

Previously, the subfamily Oedipodinae was represented in Egypt by 44 species and subspecies, belonging to five tribes: Acrotylini, Epacromiini, Locustini, Oedipodini, and Sphingonotini (Abdel-Dayem et al. 2005, Haggag et al. 2008, Haggag 2011). The genus *Pycnodictya* is currently listed under Oedipodinae without assignment to any of the tribes (Eades et al. 2016); in this article, the tribe Locustini is proposed for this genus following Johnston (1956), who used tribe names as group names, and included *Pycnodictya* in the group Locustae (valid tribe Locustini).

*Pycnodictya* was established by Stål (1873) to include *P. obscura* Linnaeus, 1758 and *P. rosacea* Serville, 1838, but the latter has been recently considered a synonym of the first (Eades et al. 2016). Some species of this genus are only known by only one of the two sexes and descriptions are often based upon a single specimen, as for *P. citripennis* Saussure, 1888; *P. dentata* Krauss, 1902; *P. herero* Karny, 1910; and *P. kelleri* Schulthess, 1894. Thus a revision of the genus including a key to the species is necessary.

Sporadic faunistic investigations had been made to record Egyptian insect species in different regions of the country. Some information about the insect fauna of Gabal Elba was reported by Hassan and Fadl (2000); however, they did not record *Pycnodictya galinieri* (Reiche & Fairmaire, 1849).

Gabal Elba covers approximately 10,000 km<sup>2</sup>, includes a group of six mountains, and is considered a distinct phytogeographic region of Egypt (Al-Gohary 2008). Moreover, it is considered to be a transitional zone between the Afrotropical and the Palearctic biogeographical regions with a special ecogeographical area located in Egypt that lead to its declaration as a natural protectorate in 1984 (Hassan and Fadl 2000).

This contribution is the first record for the Afrotropical genus *Pycnodictya* Stål from Egypt. Based on microscopic observations of external morphological characters and a comparison to earlier literature dealing with the description of different species of this genus, especially from East Africa and Yemen (Ingrisch 1999), the available band winged specimen was identified as *P. galinieri galinieri* (Reiche & Fairmaire), which was described originally from Ethiopia and has been recorded further from Eritrea, Kenya, Oman, Somalia, South Africa, Sudan, Tanzania and Yemen (Johnston 1956, 1968; Dirsh 1965; Popov 1980; Ingrisch 1999; Eades et al. 2016).

## Material and methods

The specimen was collected from Haliab, during an extensive survey by Egyptian taxonomists to the natural protectorate of Gabal Elba, who brought it with other orthopteroid specimens to me to identify as specialist in Egyptian Orthoptera, and then it was dry mounted. The terminology of morphological characters used here is adopted from Chopard (1943) and Dirsh (1965). Morphological features were measured with an ocular micrometer and drawn with aid of a *camera lucida* attached to a Hund Wetzelar SM33 stereomicroscope. Drawings and photographs were modified with Adobe Photoshop C5 software and the distributional map was produced with Arc View 3.2. Photographs of the species were taken by a Nikon D5300 digital camera, Af-S zoom, Nikkor 18–55 mm 1:3.5–5.6 GII.

The measurements are in millimeters and the whole length of the specimen was measured along the midline from fastigium of the vertex to the distal end of the external genitalia, that of hind femur was measured from the basal to the most apical point, and the tegminal length was measured laterally along its greatest length.

## Taxonomy

### Family Acrididae

### Subfamily Oedipodinae

### Tribe Locustini

### Genus *Pycnodictya* Stål, 1873

*Pycnodictya* Stål, 1873: 116, 121.

**Type-species.** *Gryllus obscurus* Linnaeus, 1758: 433.

**Diagnosis** (adapted from Stål 1873, Saussure 1884, Dirsh 1965). Species belonging to this robust genus are well recognized by their thick hind femur having the upper carina serrated and the lower marginal area highly expanded, as well as by their robust, rugose head and pronotum, and their brightly colored hind wings with dark or at least smoky transverse fascia. They are also generally characterized by their globular heads with prominent eyes and filiform antennae, a distinct median carina of the pronotum crossed by the third transverse sulcus that continues on the lateral lobes, while the lateral carinae are absent and the posterior margin is acutely angular; the meso- and metasternal interspace are very wide. The elongate supra-anal plate is angular, the cerci are narrowly conical with subacute apices, and the subgenital plate is conical with an obtuse apex in males. The female ovipositor valves are short, robust with curved apices.

***Pycnodictya galinieri galinieri* (Reiche & Fairmaire, 1849)**

Figs 1–14

*Oedipoda galinieri* Reiche & Fairmaire, 1849: 432.*Humbe hyalodes* Karsch, 1896: 265.*Humbe miniatipennis* Karsch, 1896: 265.

**Type specimen.** Unspecified male collected from Ethiopia deposited in Muséum national d'Histoire naturelle Paris, France (MNHN).

**Material examined.** 1♀, Halaib II in Gabal Elba (22°11'16"N, 36°22'14"E), 2003 [CUE, Efflatoun Bey Collection, Entomology Department, faculty of science, Cairo University, Egypt].

**Description.** The body of the female is robust, medium-sized, and brownish, with sparse hairs on pronotum, sternum, legs, and mouth parts. Head (Figs 1, 9) rugose, prominent, and straight. Eyes rounded with obtuse rounded apex. Frons (Fig. 3) with rounded obtuse angle to fastigium of vertex. Frontal ridge shallowly sulcate with obtuse lateral carinulae, wide above ocellus, excurved between antennae then straight below ocellus, not reaching clypeus; surface coarsely punctured and wrinkled above ocellus. Fastigial foveolae shallow and oval. Fastigium of vertex wide, shallow with obtuse margins. Vertex broad and convex with low carinula between eyes. Antennae (Fig. 12) yellowish brown, filiform, with 27 flagellomers, shorter than head and pronotum together.

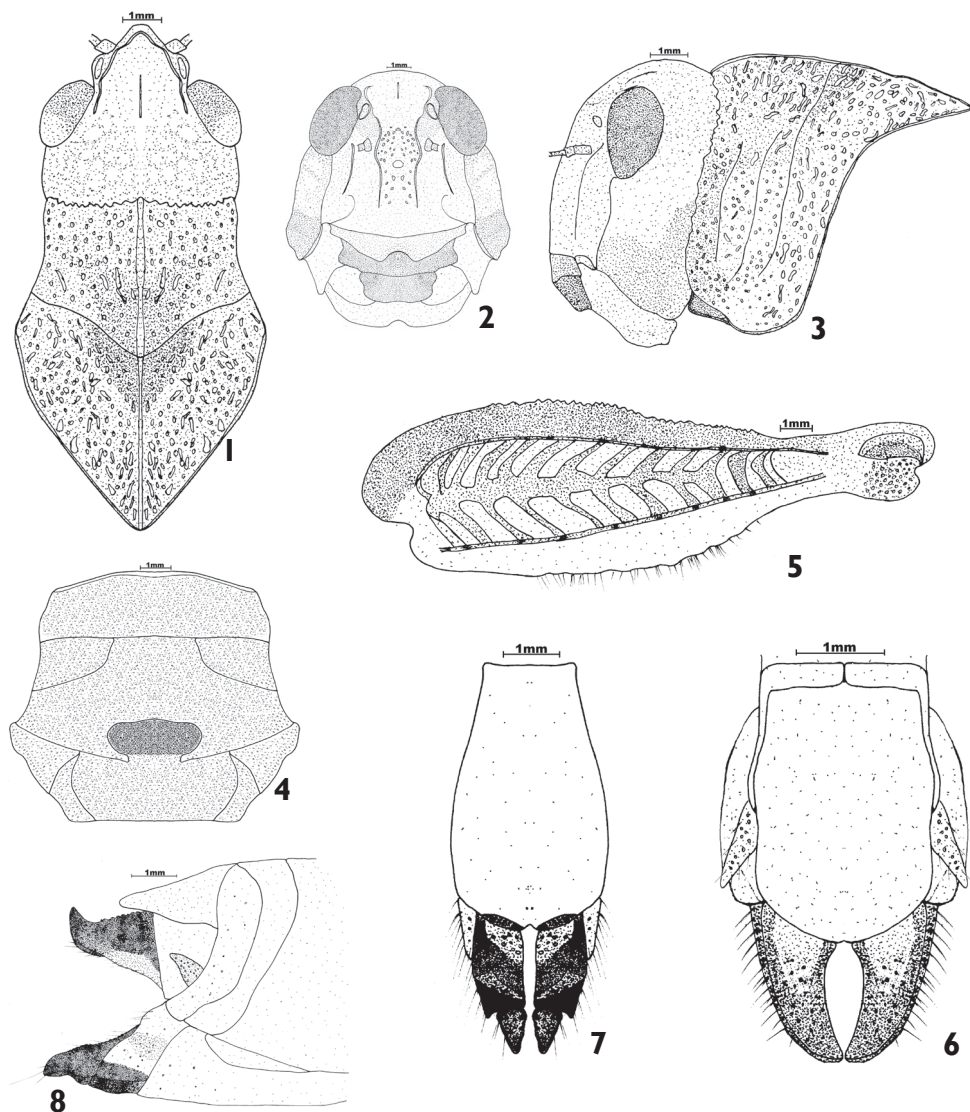
*Pronotum* (Figs 1, 9, 13) constricted in the posterior half of prozona, coarsely punctured and wrinkled especially in metazona; anterior margin dentate with slightly acute angle at median carina; third transverse sulcus sharp; metazona coarsely wrinkled with tubercles, its length slightly longer than prozona, posterior angle highly acute angular, median carina obtuse, distinct, crossed by third transverse sulcus only and raised in prozona. Lateral lobes (Figs 2, 10, 11) with three transverse sulci, with anterior and posterior margin straight, anterior and posterior lower angle obtusely rounded and lower margin distinctly convex from second sulcus to posterior margin. Mesosternal interspace (Fig. 4) about three times as broad as long and metasternal interspace about 3.25 times as broad as long.

*Elytra* (Fig. 9) wide, about 4.25 times as long as its maximum width, slightly narrowing toward obliquely truncate apex; opaque and with obtuse dark spots that do not form definite transverse bands, leaving the apical third transparent with brownish veins; second branch of medial vein with five branches apically; intercalary vein straight then raised apically, behind middle closer to cubital vein.

*Wings* (Fig. 9) approximately twice as long as its maximum width, with orange red basal half, surrounded by a dark, moderately narrow, transverse semicircular band that does not reach posterior margin, with short anterior projection toward base; veins darkened in transparent apical part.

*Hind femora* (Figs 5, 10) thick, their lengths approx. 3.25 times their maximum widths; upper margins distinctly serrate and lower marginal areas expanded with irregular

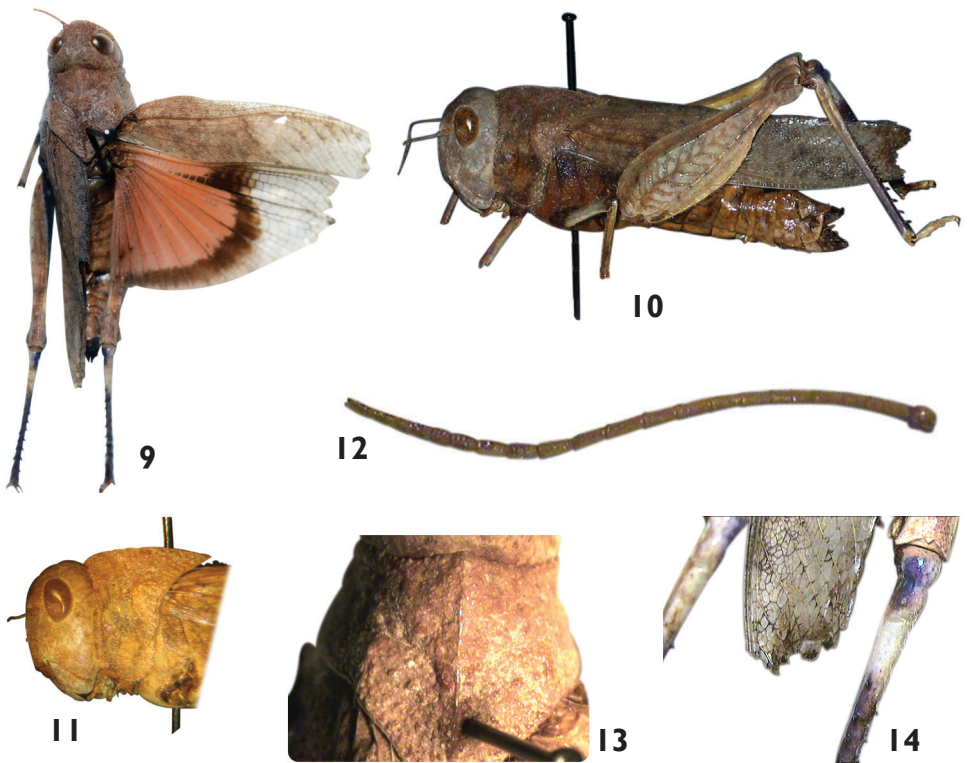




**Figures 1–8.** ♀ *Pycnodictya galinieri galinieri*. **1** dorsal view of head and pronotum **2** lateral view of head and pronotum **3** anterior view of head **4** ventral view of meso- and metasternum **5** external side of hind femur **6** dorsal view of abdominal apex **7** ventral view of abdominal apex **8** lateral view of abdominal apex.

edges; upper and lower external carinulae with dark dots; inner sides blackish below upper carina and with dark crest at knee.

*Hind tibiae* (Fig. 14) blackish violet except for yellowish ring in basal third and blackish violet condyle internally; shorter than femora with ten spines on outer, eleven on inner side.



**Figures 9–14.** Digital photos of female *Pycnodictya galinieri galinieri* **9** dorsal view **10** lateral view **11** lateral view of head & pronotum **12** antenna **13** dorsal view of pronotum **14** dorsal view of base of hind tibia.

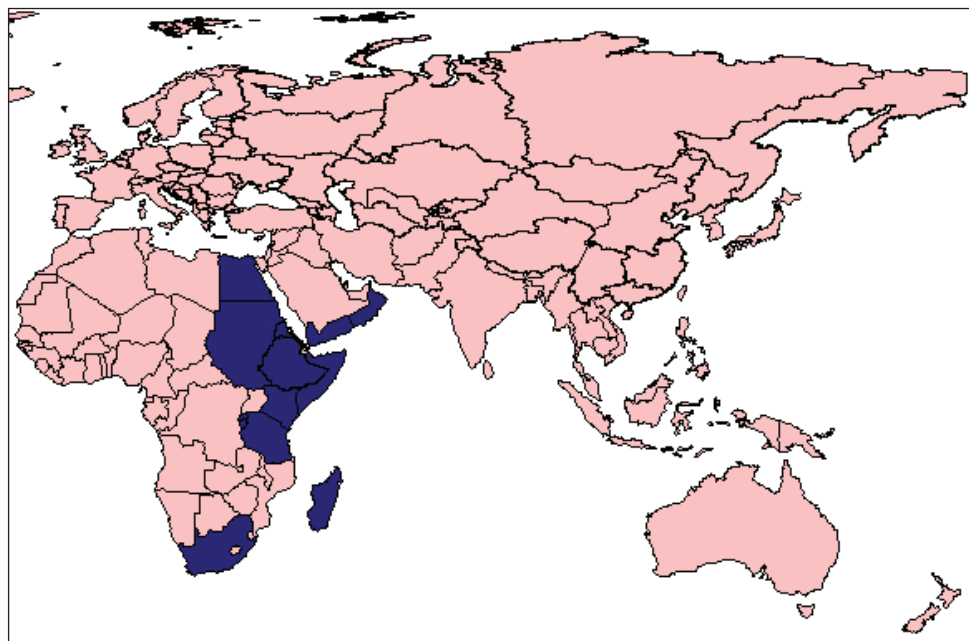
**Table 1.** Measurements (in mm) of female *Pycnodictya galinieri galinieri* from Egypt (male after Saussure 1884).

Sex	Body	Pronotum	Elytron	Wing	Hind femur	Hind tibia
♀ (mm)	33	9	28	27	17.5	15
♂ (mm)	25	7	26	-	16	-

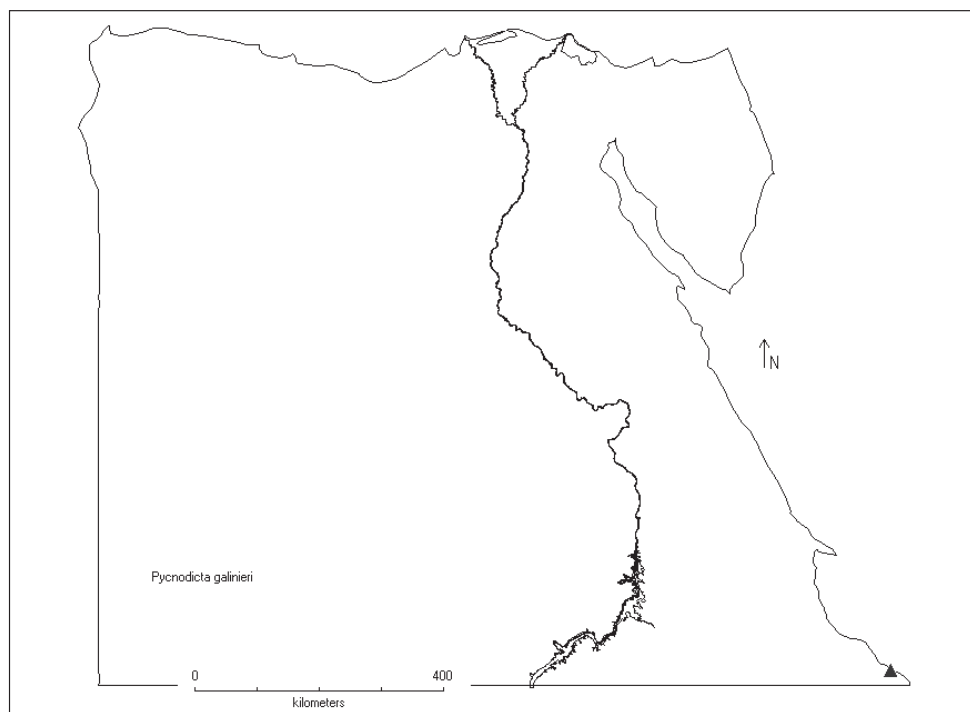
*Abdominal extremity* (Figs 6, 7, 8) with ovipositor valves robust, short with curved apex. The male is noted to be similar to the female but smaller in size; hind wings bright orange red; hind tibiae with a less distinct pale basal ring (Ingrisch 1999).

**Measurements.** (Table 1).

**Distribution.** Afrotropical species distributed along the Indian Ocean in the eastern half of the African continent from Sudan in the north to South Africa (Johnston 1956, 1968; Dirsh 1965; Eades et al. 2016), expanding north eastwards to the south of the Arabian Peninsula to Yemen (Ingrisch 1999) and Oman (Popov 1980), and reaching, with the new record presented here, the southern corner of Egypt at the Red Sea (Figs 15, 16).



**Figure 15.** Map of the known country records of *Pycnodictya galinieri galinieri*.



**Figure 16.** Map of Egypt showing the local distribution of *Pycnodictya galinieri galinieri*.

## Discussion

The classification of Egyptian Oedipodinae species was previously reviewed by Abdel-Dayem et al. (2005) and Haggag et al. (2008), and tribe Epacromiini was revised under Acridinae by Haggag (2011). The genus *Pycnodictya* belongs to the subfamily Oedipodinae with its brightly colored hind wings, vertical frons, and by the presence of an intercalary vein in medial area of fore wings. Also it lacks the prosternal process of other Acridid subfamilies (e.g. Calliptaminae, Cyrtacanthacridinae and Eyprepocnemidinae) and stridulatory serration on the inner surface of hind femur of other subfamilies (e.g. Gomphocerinae and Eremogryllinae). The genus *Pycnodictya* is recorded here as its subspecies *P. galinieri galinieri* and new for the Egyptian fauna from Gabal Elba.

The expanded lower marginal area of the hind femur is very characteristic for *Pycnodictya* by which it can easily be separated from related genera such as *Chloeobora* Saussure, 1884 and *Scintharista* Saussure, 1884 (Dirsh 1965).

The different species of the genus *Pycnodictya* are similar to one another in general appearance, and the most features used for their identification are the color of the hind wings and hind legs, which are easily viewed by eye (Uvarov 1929, Ingrisch 1999). The previous description of *P. galinieri* by Saussure (1884) is superannuated and insufficient but recognizable, and thus, a description of the Egyptian subspecies is given in this paper with additional line drawings and photographs that are not available elsewhere. *Pycnodictya galinieri galinieri* is well-differentiated from other species of the genus by its characteristic hind wings with orange red bases, moderately narrow dark band with an anterior projection that is separated from the posterior margin, and the clearly dentate anterior margin of the pronotum. In addition, the hind tibia is blackish violet with a yellowish basal ring and the hind femur is blackish on its inner side.

*Pycnodictya galinieri* has a dentate anterior margin of pronotum resembling the situation in *P. dentata* Krauss, 1902 but lacks the sinuated posterior lower angle of the pronotal lateral lobes of the latter. However, *P. kelleri* Schulthess and the other subspecies *P. galinieri citrina* Kevan, 1961 described from Somalia and restricted to it (Eades et al. 2016), differentiated well from *P. galinieri galinieri* with their sulphorous or yellowish wings, respectively. Only the two species *P. diluta* Ramme, 1929 and *P. zinae* Uvarov, 1949 resemble *P. galinieri* in the purplish hind tibia, but *P. diluta* with disappeared fascia of the hind wings and *P. zinae* with crested pronotal median carina. Moreover, *P. gracilis* Uvarov and *P. kilosana* Miller, 1929 distinguished from *P. galinieri* as their hind tibia is honey yellow or light brown not blackish violet as the latter.

*Pycnodictya galinieri* is widespread along the eastern part of the African continent. The high mobility of Oedipodinae as very strong fliers (Alexander 1964) may explain the wide distribution of *P. galinieri* from South Africa to Egypt. It is not clear, whether the subspecies has so far been overlooked in Egypt or whether it has expanded its range. The new finding and previous new records from Egypt (Haggag et al. 2008, Haggag 2011) highlight the importance of making a thorough survey of Acridoidea in diverse regions of the country.



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# Systematics of *Ecnomiohyla tuberculosa* with the description of a new species and comments on the taxonomy of *Trachycephalus typhonius* (Anura, Hylidae)

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## Abstract

*Ecnomiohyla tuberculosa* is an Amazonian hylid of uncertain phylogenetic position. Herein DNA sequences of mitochondrial and nuclear genes are used to determine its phylogenetic relationships. New sequences and external morphology of *Trachycephalus typhonius* are also analyzed to assess the status of Ecuadorian and Peruvian populations. The phylogeny shows unequivocally that *Ecnomiohyla tuberculosa* is nested within the genus *Tepuihyla*, tribe Lophiohylini. This position was unexpected because the remaining species of *Ecnomiohyla* belong to the tribe Hylini. To solve the paraphyly of the genus *Ecnomiohyla*, *E. tuberculosa* is transferred to the genus *Tepuihyla*. Comparisons of DNA sequences, external morphology, and advertisement calls between populations of *Ecnomiohyla tuberculosa* from Ecuador and Peru indicate that the Peruvian population represents an undescribed species. The new species is described and a species

account is provided for *Ecnomiophyla tuberculosa*. *Trachycephalus typhonius* is paraphyletic relative to *T. cunauaru*, *T. hadroceps*, and *T. resinifictrix*. The phylogenetic position of populations from western Ecuador indicates that they represent a species separate from *T. typhonius sensu stricto*. We resurrect the name *Hyla quadrangulum* (*Trachycephalus quadrangulum* **comb. n.**) for those populations. Amazonian populations of “*T. typhonius*” from Ecuador and Peru are genetically and morphologically distinct from *T. typhonius sensu stricto* and are conspecific with the holotype of *Hyla macrotis*. Therefore, we also resurrect *Hyla macrotis*, a decision that results in *Trachycephalus macrotis* **comb. n.**

## Keywords

Advertisement call, Amazon basin, biodiversity, Ecuador, Lophiohylini, Peru, phylogeny, *Tepuihyla*

## Introduction

Fringe-limbed frogs, genus *Ecnomiophyla* Faivovich et al. 2005, are a group of 14 species distributed in Central America, the Chocó region of Colombia and Ecuador and the Amazon Basin (Batista et al. 2014). Their morphology is distinctive and characterized by large size, proportionally enlarged hands and feet, extensive webbing between fingers, moss-like dorsal coloration, and dermal fringes on the limbs (Batista et al. 2014; Savage and Kubicki 2010). These canopy dwellers that breed on phytotelmata and are rarely found in the lower forest strata (Batista et al. 2014; Mendelson et al. 2008) are scarce in scientific collections with few specimens known for some species.

One of the most enigmatic members of the genus is *Ecnomiophyla tuberculosa* (Boulenger 1882), a species only known from the holotype until the work of Duellman (1974). Its occurrence has been documented at scattered localities along the upper Amazon basin of Brazil, Colombia, Ecuador and Peru (Frost 2014). *Ecnomiophyla tuberculosa* was grouped with other species of *Ecnomiophyla* by Firschein and Smith (1956) and Duellman (1961; 1970) under the “*Hyla tuberculosa*” group. Based on those assignments, Faivovich et al. (2005) included it tentatively in the genus *Ecnomiophyla*. Mendelson et al. (2008) and Savage and Kubicki (2010), based on morphological characters, suggested that *E. tuberculosa* was not a member of *Ecnomiophyla*. Neither publication proposed an alternative phylogenetic position for *E. tuberculosa* and they considered it *insertae sedis*. Nevertheless, Batista et al. (2014) maintained the binomial *Ecnomiophyla tuberculosa* and noted that additional information was needed to determine its generic position. Recently, Duellman et al. (2016) placed *E. tuberculosa* in the genus *Hypsiboas*. We do not follow that assignment because it lacked justification.

Another enigmatic Neotropical hyliid is *Trachycephalus typhonius* (Linnaeus 1758). Its identity was recently defined by Lavilla et al. (2010). Previously this species was referred as “*Trachycephalus venulosus*” or “*Phrynohyas venulosa*” (e.g., Duellman 1970; 1971; Faivovich et al. 2005). According to its current definition, *T. typhonius* is distributed from southern México to northern Argentina and includes populations in the Guianan region, Amazon Basin, and Chocó (Lavilla et al. 2010). Several authors have reported considerable morphological variation that suggests that it may represent



a species complex (e.g., Savage 2002). The existence of at least two species is also suggested by its biogeography. *Trachycephalus typhonius* occurs in the lowlands east and west of the Andes of Ecuador, an unusual pattern only seen in 3 out of 174 species of amphibians: *Hypsiboas boans*, *Rhinella marina* and *T. typhonius*. Because the Andes are a formidable barrier to dispersal, this distribution is likely a artifact of incorrect delimitation of species boundaries (dos Santos et al. 2015). The existence of separate species on both sides of the Andes in *T. typhonius* is supported by unambiguous morphological differences between both distribution ranges (Ron and Read 2011). Genetic data could conclusively define the status of trans-Andean populations of *T. typhonius*.

Fieldwork in Ecuador and Peru has resulted in the collection of additional specimens and genetic samples of *E. tuberculosa* and *T. typhonius*. Based on new specimens of *E. tuberculosa*, we infer its phylogenetic position and also describe its calling behavior. We show that a distinctive population from Amazonian Peru represents an undescribed species, which we describe here. Finally, we take advantage of the new phylogenetic analysis to include samples of *Trachycephalus typhonius* from Ecuador and Peru and determine their taxonomic status. We show that those populations represent two valid species currently considered junior synonyms of *Trachycephalus typhonius*.

## Materials and methods

### Nomenclature

Generic names follow Faivovich et al. (2005) and AmphibiaWeb (2016).

### DNA extraction amplification and sequencing

DNA was extracted from muscle or liver tissue preserved in 95% ethanol or tissue storage buffer, using standard phenol–chloroform extraction protocols (Sambrook et al. 1989). We used a polymerase chain reaction (PCR) to amplify DNA fragments for mitochondrial genes 12S rRNA (12S), Cytochrome Oxidase sub-unit I (COI), two overlapping fragments for the last ~320 bp of 16S rRNA (16S), NADH dehydrogenase subunit 1 (ND1) and adjacent tRNAs (tRNA<sup>Leu</sup>, tRNA<sup>Ile</sup> and tRNA<sup>Gln</sup>), and the nuclear gene POMC, using the primers listed in Goebel et al. (1999), Moen and Wiens (2009) and Wiens et al. (2005). PCR amplification was performed under standard protocols and sequenced by the MacroGen Sequencing Team (MacroGen Inc., Seoul, Korea). The combined DNA matrix had up to 3792 bp.

The newly generated DNA sequences are available on GenBank under accession numbers listed on Table 1. To optimize taxon sampling within Hylidae, we blasted our *E. tuberculosa* 12S and ND1 sequences to the GenBank database (blastn procedure). These searches shown unequivocally that the most similar samples belonged

**Table 1.** New sequences generated for the phylogenetic analysis.

Voucher	Species	12S	16S-ND1	COI	POMC	GenSeq Nomenclature
CORBIDI 12513	<i>Tepuihyla shushupe</i>	KY013372	KY013419	KY013396	-	genseq-1
QCAZ 52855	<i>Tepuihyla tuberculosa</i>	KY013373	KY013417	-	-	genseq-4
QCAZ 53147	<i>Tepuihyla tuberculosa</i>	KY013374	KY013416	-	-	genseq-4
QCAZ 53542	<i>Tepuihyla tuberculosa</i>	KY013375	KY013418	KY013415	-	genseq-4
105BM	<i>Trachycephalus coriaceus</i>	KY013376	KY013420	-	-	-
QCAZ 19305	<i>Trachycephalus cunauaru</i>	KY013388	KY013440	KY013395	KY013462	genseq-4
QCAZ 20808	<i>Trachycephalus cunauaru</i>	-	KY013443	KY013398	KY013465	genseq-4
QCAZ 20809	<i>Trachycephalus cunauaru</i>	KY013389	KY013441	-	KY013463	genseq-4
QCAZ 46436	<i>Trachycephalus cunauaru</i>	KY013390	KY013442	KY013413	KY013464	genseq-4
CORBIDI 9556	<i>Trachycephalus macrotis</i>	KY013392	-	-	-	genseq-4
CORBIDI 9559	<i>Trachycephalus macrotis</i>	KY013393	-	-	-	genseq-4
CORBIDI 9560	<i>Trachycephalus macrotis</i>	KY013394	KY013430	-	-	genseq-4
QCAZ 18198	<i>Trachycephalus macrotis</i>	-	KY013428	KY013397	KY013451	genseq-4
QCAZ 21283	<i>Trachycephalus macrotis</i>	-	KY013421	KY013400	KY013445	genseq-4
QCAZ 23997	<i>Trachycephalus macrotis</i>	-	KY013422	-	KY013444	genseq-4
QCAZ 32492	<i>Trachycephalus macrotis</i>	-	KY013426	KY013405	KY013449	genseq-4
QCAZ 38075	<i>Trachycephalus macrotis</i>	KY013380	KY013427	KY013406	KY013450	genseq-4
QCAZ 38774	<i>Trachycephalus macrotis</i>	KY013377	KY013423	KY013407	KY013446	genseq-4
QCAZ 39565	<i>Trachycephalus macrotis</i>	KY013378	KY013424	KY013409	KY013447	genseq-4
QCAZ 43017	<i>Trachycephalus macrotis</i>	KY013379	KY013425	KY013412	KY013448	genseq-4
QCAZ 47319	<i>Trachycephalus macrotis</i>	KY013381	KY013429	KY013414	KY013452	genseq-4
QCAZ 21282	<i>Trachycephalus quadrangulum</i>	-	KY013439	KY013399	KY013461	genseq-4
QCAZ 23472	<i>Trachycephalus quadrangulum</i>	-	KY013438	KY013401	KY013460	genseq-4
QCAZ 23485	<i>Trachycephalus quadrangulum</i>	KY013387	KY013437	KY013402	KY013459	genseq-4
QCAZ 28530	<i>Trachycephalus quadrangulum</i>	KY013383	KY013432	KY013403	KY013454	genseq-4
QCAZ 31271	<i>Trachycephalus quadrangulum</i>	KY013382	KY013431	KY013404	KY013453	genseq-4
QCAZ 38205	<i>Trachycephalus quadrangulum</i>	-	KY013434	-	KY013456	genseq-4
QCAZ 39360	<i>Trachycephalus quadrangulum</i>	KY013385	KY013435	KY013408	KY013457	genseq-4
QCAZ 39782	<i>Trachycephalus quadrangulum</i>	KY013386	KY013436	KY013410	KY013458	genseq-4
QCAZ 40219	<i>Trachycephalus quadrangulum</i>	KY013384	KY013433	KY013411	KY013455	genseq-4
163MC	<i>Trachycephalus typhonius</i>	KY013391	-	-	-	-

to the genera *Osteocephalus* and *Tepuihyla*, tribe Lophiohylini. For example, a blastn for the ND1 sequence of *E. tuberculosa* QCAZ 53542 retrieved 50 most similar sequences with identity values ranging from 82.7% to 89.1%. All 50 sequences be-

longed to the Lophiohylini tribe (*Corythomantis*, *Osteocephalus*, *Osteopilus*, *Tepuihyla*, and *Trachycephalus*). To confirm the close relationships between *E. tuberculosa* and *Tepuihyla*, we carried out an additional exploratory analysis based on Pyron (2014) matrix for the genes 12S and 16S. We included our sequences as well as those from all species of the tribes Hylini (including *Ecnomiohyla*) and Lophiohylini from Pyron (2014) matrix. We also included several species of *Agalychnis*, *Litoria* and *Phyllomedusa* as outgroups. The final matrix had 169 terminals. A maximum likelihood phylogenetic analysis using GARLI 2.0 (Zwickl 2006) confirmed with strong support that *Ecnomiohyla tuberculosa* is not closely related to other *Ecnomiohyla*. Instead, it is a member of the tribe Lophiohylini and is nested within *Tepuihyla*. The phylogeny based on Pyron (2014) matrix is available as Suppl. material 1.

For final phylogenetic analysis we included GenBank sequences from all available species of Lophiohylini as well as sequences from representative species of all other tribes within Hylinae (Cophomantini, Dendropsophini, and Hylini). GenBank sequences were originally published by Darst and Cannatella (2004), Faivovich et al. (2005), Salducci et al. (2005), Wiens et al. (2005), Moen and Wiens (2009), Moravec et al. (2009), Salerno et al. (2012), Jungfer et al. (2013), and Salerno et al. (2015). Samples of *Phyllomedusinae* were included as outgroups (*Agalychnis spurrelli*, *Phyllomedusa tomopterna*, and *Phyllomedusa perineros*). We also added new sequences from 25 individuals of Ecuadorian and Peruvian *Trachycephalus* to assess their taxonomic status.

Preliminary sequence alignment was done with MAFFT 7.2 software with the L-INS-i algorithm (Katoh and Standley 2013). All sequences in the matrix were visually examined and translated in MESQUITE (version 3.01; Maddison and Maddison 2014). The matrix was partitioned to allow independent inferences of models of evolution by gene and by codon position in coding genes. We used software PARTITION-FINDER v. 1.1.1 (Lanfear et al. 2012) to simultaneously estimate both the best-fit model for each partition and the best partition strategy for our data.

## Phylogeny

Phylogenetic trees were obtained using maximum likelihood and Bayesian inference. Maximum likelihood searches were carried out with software GARLI 2.0 (Zwickl 2006). We made two independent searches with 10 replicates each. The first search started with random trees and the second with stepwise addition trees. We modified the settings for the number of generations without topology improvement required for termination (genthreshfortopoterm = 200000) and the maximum range for localized SPR topology changes (limsprrange = 10) to increase exhaustiveness of the tree space search. Other settings were set on default values. Node support was assessed with 200 pseudoreplicate non-parametric bootstraps (npb), configured with the same settings of the full search, but with three replicates per run.

Bayesian inference was performed with MARBAYES 3.2.1 (Ronquist et al. 2012). The analysis consisted of four parallel runs of the Metropolis-coupled Monte Carlo Markov chain for  $5 \times 10^6$  generations; each run had six chains with a temperature of 0.08. We used TRACER 1.6 (Rambaut et al. 2014) to assess convergence and stationarity of the runs and to obtain effective sample sizes (ESS) for all model parameters. The search was considered finished when all ESS were  $> 200$ . Each run was sampled every 1000 generations. The first 25% of the samples was discarded as “burn-in”, using the remaining samples to estimate the Bayesian tree, posterior probabilities (pp) and other model parameters.

## Morphology

Diagnostic characters and comparisons are based on specimens from the following institutions. Ecuador: Fundación Herpetológica Gustavo Orcés, Quito (FHGO); Museo de Zoología at Pontificia Universidad Católica del Ecuador, Quito (QCAZ). Peru: Centro de Ornitología y Biodiversidad, Lima (CORBIDI); Colección Referencial de Biodiversidad del Instituto de Investigaciones de la Amazonía Peruana, Iquitos (IIAP). United States of America: American Museum of Natural History, New York, (AMNH); National Museum of Natural History, Washington DC (USNM); Natural History Museum at the University of Kansas, Lawrence (KU). United Kingdom: Natural History Museum, London (BMNH). Venezuela: Museo de Historia Natural La Salle, Caracas (MHNLS). Our comparisons included the revision of the holotype of *Hyla tuberculosa* (Natural History Museum, London, BMNH 1947.2.13.34) and photographs of the holotype of *Hyla macrotis* (Swedish Museum of Natural History, Stockholm, NRM 1958). Examined specimens are listed as Suppl. material 2. Character definitions follow Duellman (1970) and Luna et al. (2012) for nuptial excrescences. Notation for hand and foot webbing is based on Myers and Duellman (1982). Sex was determined by presence of nuptial pads or vocal slits, and by gonadal inspection. Descriptions of coloration in life are based on digital photographs. Adults were measured with digital calipers for the following eight morphological variables, following Duellman (1970): (1) SVL; (2) head length; (3) head width; (4) tympanum diameter; (5) femur length; (6) tibia length; (7) foot length; and (8) eye diameter. Additionally, we measured the hand length (HAL) from proximal edge of palmar tubercle to tip of third finger for the new species described herein following Batista et al. (2014).

Morphometric analyses were performed based on measurements of adult males (number of specimens in parenthesis): *E. tuberculosa* (5), *T. shushupe* sp. n. (1), *T. edelcae* (17), *T. obscura* (17), and *T. rodriguezi* (14; see Suppl. material 2). We did a  $\log_{10}$  transformation of the dataset, a common practice in morphometric analyses due to the multiplicative nature of allometric growth and to make measurement variances comparable. A principal components analysis was later performed on the data. We used



Principal Component 1 as a proxy for size and its effects, given that most variation is due to size and size effect differences. Other principal components were interpreted as a proxy for shape (Bookstein 1989). We also performed a Discriminant Analysis with species as group priors, in order to determine if they can be diagnosed from each other with morphometric characters.

### **Bioacoustics**

Calls were analyzed from two adult males, QCAZ 53699 from Juyuintza, Pastaza province, Ecuador (2.110°S, 76.190°S, 200 m of elevation) and CORBIDI 12513 from Ere River, Putumayo Basin, Loreto Department, Peru (1.67903°S, 73.7197°W, 145 m). Male QCAZ 53699 was recorded at night on 22 June 2012 (23.9°C / relative humidity ~86.0%). Male CORBIDI 12513 was recorded at night of 18 October 2012 (21.3°C / relative humidity ~95.8%). Recordings were saved in PCM format, with a sample rate of 48000 Hz and 24-bits. Call variables were measured with RAVEN PRO 1.4 (Charif et al. 2010), under a Hanning function, 2048 DFT sample size and a grid spacing of 23.4 Hz. After a preliminary screening of the sound spectrogram, we clipped values below 90.0 db and applied a filter band-pass between 350 and 2420 Hz, to reduce background noise and facilitate the measurement of the acoustic parameters. Fourteen acoustic parameters (modified from Cocroft and Ryan 1995) were measured to describe the structure of each call: (1) Call duration = time from beginning to end of one call, measured from waveform analyzer screen; (2) Call rate = number of calls per minute; (3) Call interval = time from the end of the call to the beginning of the next call; (4) Call rise time = time from beginning of call to point of maximum amplitude; (5) Notes per call = number of notes per call; (6) Note rate = (number of notes-1)/time from beginning of first note to beginning of last note; (7) Note length = average time from beginning to end of a note; (8) Note rise time = time from beginning of note to point of maximum amplitude; (9) Note shape = note rise time/note length; (10) Frequency band = difference between the upper and lower frequencies measured along the entire call; (11) Fundamental frequency = frequency with the highest energy on the 1st harmonic in the call; (12) Dominant frequency = frequency with the highest energy along the entire call. In order to analyze the modulation of dominant frequency, we divided the call in three sections corresponding to the beginning, the middle and the end of the call; (13) Fundamental frequency ratio = number of notes with the dominant frequency in the first harmonic/total number of notes; and (14) Frequency modulation = (frequency with the most energy at end of call – frequency with the most energy at beginning of call)/call duration; values equal or near 0 represent calls lacking frequency modulation. Recordings are deposited in the Sound Archive of Museo de Zoología of Pontificia Universidad Católica del Ecuador (available at AmphibiaWebEcuador website, <http://zoologia.puce.edu.ec/vertebrados/anfibios/>).

## Results

### Phylogeny

The Maximum Likelihood and the Bayesian analyses yielded similar topologies with differences pertaining only to weakly supported nodes. The phylogeny shows strong support for the inclusion of *E. tuberculosa* within the tribe Lophiohylini, genus *Tepuihyla* Ayarzagüena et al. 1993 “1992” (Fig. 1B). *Ecnomiophyla tuberculosa* is sister to all species of *Tepuihyla*, except *T. warreni* from Ayanganna, Guyana. *Tepuihyla warreni* is polyphyletic because a sample from the Maringma Tepui, Guyana, clusters with *T. aecii*, *T. edelcae*, *T. obscura*, and *T. rodriguezi* instead of the other samples of *T. warreni* (Fig. 1A). The distance of the type locality of *T. warreni* from Ayanganna is approximately 90 km and from Maringma is 15 km. These distances suggest that the Ayanganna population represents an undescribed species.

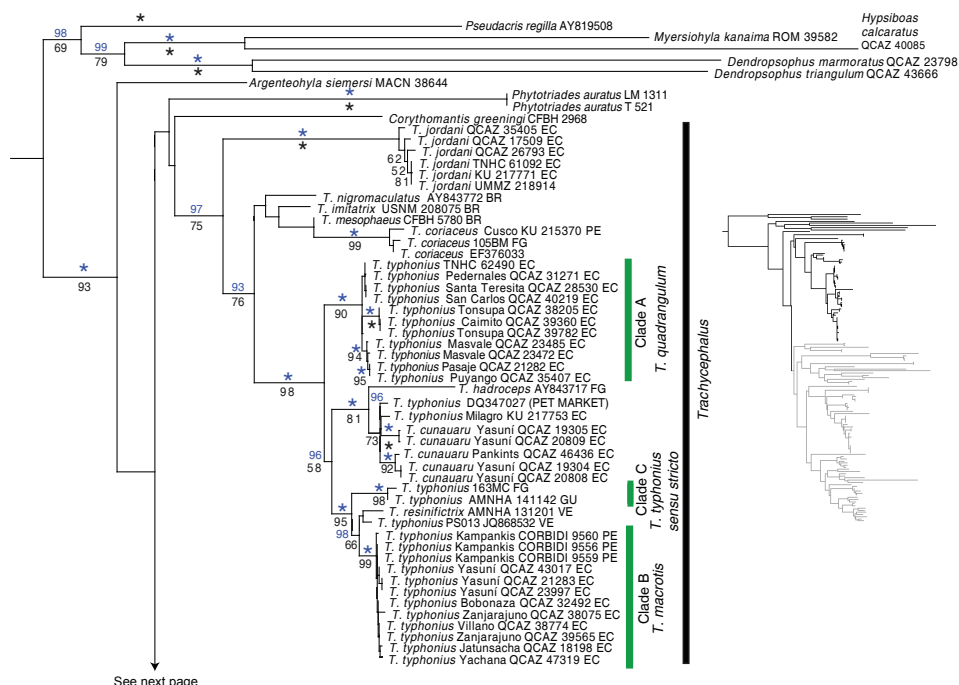
There is strong support for the tribe Lophiohylini. However, the relationships between basal clades within Lophiohylini are weakly supported. Within *Trachycephalus*, the recently described *T. cunauaru* is sister to *T. hadroceps*. *Trachycephalus typhonius* (previously referred as “*T. venulosus*”) is widely paraphyletic. The new sequences of *T. typhonius* from the Ecuadorian Chocó are sister to a clade composed of *T. cunauaru*, *T. hadroceps*, *T. resinifictrix*, *T. typhonius* from Guyana, French Guiana, Venezuela, and the upper Amazon basin in Ecuador and Peru. Populations of *T. typhonius* from Amazonian Peru and Ecuador are sister to a clade composed of *T. resinifictrix* and one sample of *T. typhonius* from Venezuela (Fig. 1A).

As in previous phylogenies (e.g., Pyron 2014) we found a clade composed by *Dryaderces* + *Tepuihyla* + *Osteocephalus*. Two samples of *Dryaderces* do not cluster together. This is likely a result of the use of short and non-overlapping sequences between both samples. Therefore, our results do not challenge the monophyly of *Dryaderces*.

### Morphometry

The first Principal Component, a proxy for size covariation, explains 97% of the variance and has very similar proportions for all variables (Table 2). The second Principal Component is mostly made up of Eye Diameter, but the variance seems to be higher within rather than among groups (Fig. 2). The third principal component is mainly composed of Tympanum Diameter.

Morphometric analyses do not show differences in shape among species (Fig. 2). The only morphometric difference pertains to size (Principal Component 1; not shown) as *E. tuberculosa* is much larger than the other species. The Discriminant Function Analysis graph (not shown) is similar to the PCA in not showing interspecific differences. Group assignment proportions are all very low (between 0.02–0.31), indicating very little power of morphometric discrimination among groups, even when attempting to maximize differences with species/lineage priors.



**Figure 1.** Maximum likelihood phylogram showing the position of *Tepuihyla tuberculosa* comb. n. and *Tepuihyla shushupe* sp. n. within Hylidae. Phylogram derived from analysis of 3792 bp of mitochondrial (gene fragments *12S*, *16S*, *ND1*, *COI*, *tRNA<sup>Leu</sup>*, *tRNA<sup>Ile</sup>*, *tRNA<sup>Gln</sup>*) and nuclear DNA (*POM-C*). Voucher no. (or, if unavailable, GenBank accession no.) is shown for each sample. Clade posterior probabilities (pp × 100) resulting from Bayesian Markov chain Monte Carlo searches appear above branches in blue. Non-parametric bootstrap (npb) support values, from 200 pseudoreplicates, are shown below. Asterisks represent values of 100. Outgroups are not shown. Abbreviations are: BR = Brazil, EC = Ecuador, FG = French Guiana, GU = Guyana, PE = Peru, VE = Venezuela

### Comparisons between populations of *Ecnomiohyla tuberculosa*

The four samples of *E. tuberculosa* form three well-supported clades (pp/npb = 100). The sample from Ere River, Peru, is sister to the Yasuní + Juyuintza in Ecuador. The Juyuintza samples are sister to each other. All genetic distances reported below are uncorrected distances for the gene *12S*. Genetic distances between Ere River, Peru, and the Ecuadorian populations (Juyuintza and Yasuní) range from 5.3 to 5.9%; distances between Yasuní and Juyuintza are both 1.2%. Samples from Juyuintza are identical to each other. The genetic distances between Ere River and the other populations are above distances between several closely related species in *Tepuihyla* and *Osteocephalus* (e.g., *O. buckleyi*-*O. cabrerai* 2.8%, *O. oophagus*-*O. taurinus* 1.3–1.8%, *O. cannatellai*-*O. cabrerai* 2.6%, *O. cannatellai*-*O. vilmae* 2.4%, *T. rodriguezi*-*T. exophthalma* 4.5–4.6%, *T. rodriguezi*-*T. edelcae* 1.3–1.5%).

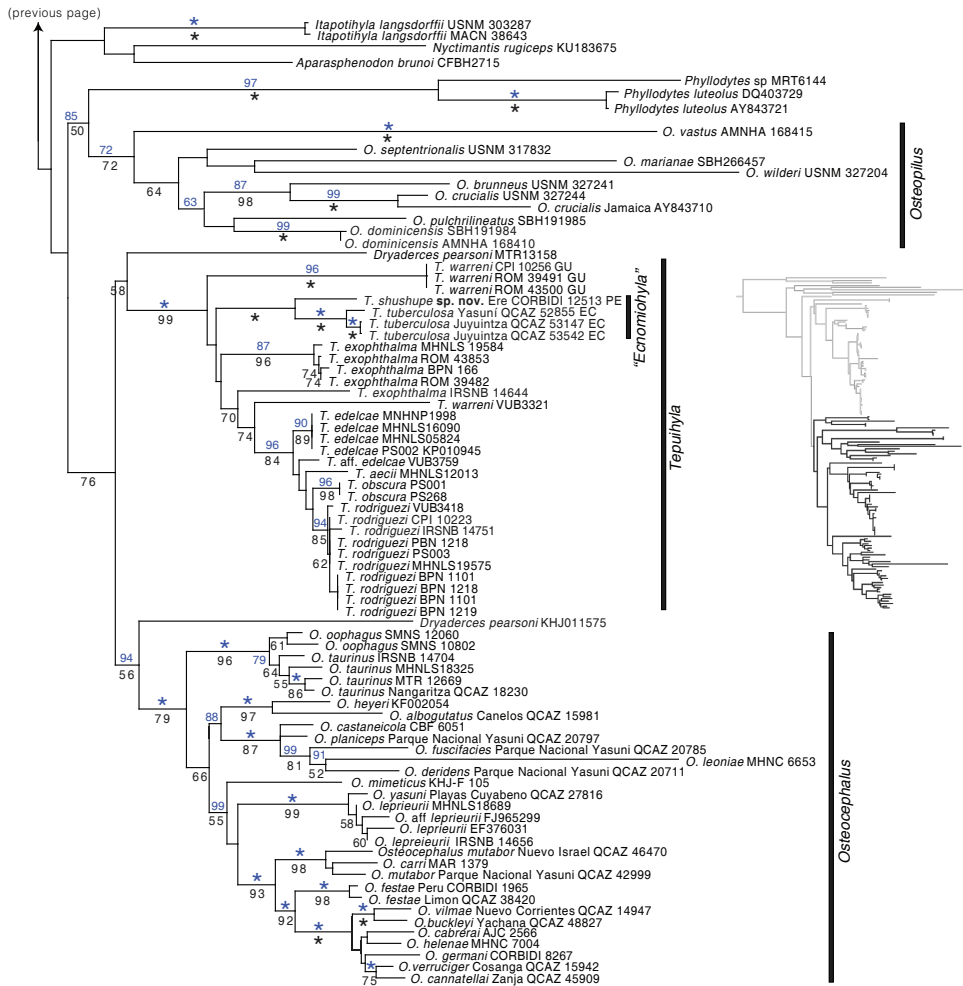


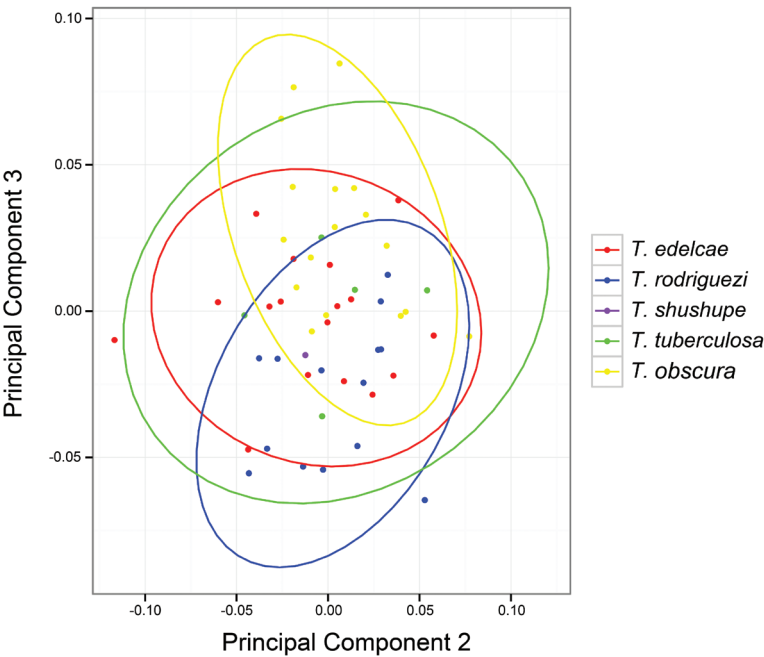
Figure 1. Continue.

Morphologically, the individual from Ere River differs from all other populations (in parenthesis) in having a cream iris with red periphery (entirely cream to reddish cream; Fig. 3G vs. 3H) and dorsum with small tubercles intermixed with abundant large tubercles (small tubercles intermixed with few large tubercles; Fig. 4A vs. 4C and 5). We found differences in advertisement calls between Río Ere and Juyuintza. Calls consist of a cackle of short notes repeated at a fast rate (Table 3; Fig. 6). Note amplitude and note rate increases markedly along the first half of the call. The call from Juyuintza differs from the call from Ere River in temporal and spectral variables. The former has shorter duration, fewer notes, and lower note rate (Ere River 3.37–3.38,  $3.37 \pm 0.01$ ; Juyuintza 2.63–2.86,  $2.74 \pm 0.16$ ; Table 3). Harmonic structure is markedly different between calls. The call from Ere River has



**Table 2.** Character loadings and cumulative proportion of variance for Principal Components. The analysis was based on eight morphometric variables of adult males of *Tepuihyla tuberculosa* comb. n., *Tepuihyla shushupe* sp. n., *Tepuihyla edelcae*, *Tepuihyla obscura*, and *Tepuihyla rodriguezi*. PCs 6–8 not shown. Abbreviations are: SVL = snout-vent length; FOOT = foot length; HL = head length; HW = head width; ED = eye diameter; TD = tympanum diameter; TL = tibia length; FL = femur length.

	PC1	PC2	PC3	PC4	PC5
Cumulative variance	0.978	0.987	0.996	0.997	0.998
SVL	-0.371	0.052	-0.117	0.079	-0.302
FOOT	-0.421	0.221	0.267	-0.413	0.707
HL	-0.329	0.054	0.078	0.417	-0.072
HW	-0.379	0.000	-0.008	0.643	0.204
ED	-0.323	-0.898	0.205	-0.186	-0.082
TD	-0.272	-0.074	-0.912	-0.176	0.137
TL	-0.393	0.229	0.168	0.005	-0.197
FL	-0.316	0.284	0.076	-0.412	-0.545



**Figure 2.** Principal Components 2 and 3 from analysis of eight morphological variables. See Table 2 for character loadings on each component.

two harmonics with similar energy content while the call from Juyuintza has one well-defined harmonic with high energy and a second harmonic with low energy, barely evident in the power spectra (Fig. 6).

**Table 3.** Quantitative and qualitative characteristics of the advertisement call of *Tepuihyla* from Ecuador and Peru. The recording in Peru was made in the Loreto Department, Putumayo River basin, Rio Ere on 18 October 2012, air temperature of 21.3 C. The recording in Ecuador was made in Pastaza Province, Juyuintza on 22 June 2012, air temperature 23.9 C.

	<i>Tepuihyla shushupe</i> sp. n. (CORBIDI 12513)	<i>Tepuihyla tuberculosa</i> comb. n. (QCAZ 53699)
Calls analyzed (specimens)	3(1)	2 (1)
Call duration (s)	16.4–17.2 (16.7±0.47)	12.2–13.1
Call rate (calls/minute)	0.45	0.37
Call interval (s)	117.024	~150
Call rise time (s)	12.7–15.7 (13.74±1.69)	6.96–11.8
Notes per call (total notes analyzed)	56–59 (171)	35 (70)
Note rate (average ± sd)	3.37–3.38 (3.37±0.01)	2.63–2.86 (2.74±0.16)
Note length (average ± sd)	0.08–0.26 (0.13±0.04)	0.17–0.43 (0.24±0.05)
Note rise time (average ± sd)	0.02–0.14 (0.06±0.03)	0.05–0.23 (0.1±0.03)
Note shape	0.2–0.94 (0.44±0.13)	0.19–0.98 (0.43±0.13)
Frequency band	96.9–5102.9	150.7–2452.1
Fundamental frequency	404.3–585.9 Hz (500.08±28.3)	515.6–796.9 Hz (619.1±77.2)
Dominant frequency (DF)	515.6 Hz (1st harmonic)	562.5–632.8 (1st harmonic)
DF beginning (% of notes)	404.3–585.9 Hz (100% in the 1st harmonic)	515.6–703.1 Hz (100% in the 1st harmonic)
DF middle (% of notes)	509.8–1210 Hz (75% in the 2nd harmonic)	585.9–1195.3 Hz (90% in the 1st harmonic)
DF end (% of notes)	445.3–539.1 Hz (100% in the 1st harmonic)	585.9–679.7 Hz (100% in the 1st harmonic)
Fundamental frequency ratio	0.75±0.44	0.97±0.06
Frequency modulation	-1.0–0.0	0.0–5.3

The combined evidence from genetics, morphology, and bioacoustics indicates the existence of two species within “*E. tuberculosa*”. Specimens from Yasuní and Juyuintza have similar coloration and dorsal tuberculation to the holotype of *E. tuberculosa* (BMNH 1947.2.13.34), therefore we assign them to *E. tuberculosa sensu stricto*. The specimen from Rio Ere belongs to an undescribed species that we describe in the following sections. Our species description is based on a single specimen and therefore we cannot characterize the variation in the new species. However, we examined 11 specimens of *E. tuberculosa*, which allow us to characterize *E. tuberculosa* morphological variation and show that the single specimen of the new species falls outside the range of variation of *E. tuberculosa*. Hence, we demonstrate that the new species is, in fact, distinct from *E. tuberculosa*. Our morphological evidence is corroborated by genetic and bioacoustic characters.

**Taxonomic Review of *Ecnomiophyla tuberculosa***

Recent phylogenies of Hylidae (Wiens et al. 2010) and all amphibians (Pyron 2014) show, with strong support, that *Ecnomiophyla* is part of Hylini, a tribe composed by the

genera *Acris*, *Anotheca*, *Bromeliophyla*, *Charadrahyla*, *Diaglena*, *Duellmanohyla*, *Ecnomiophyla*, *Exerodonta*, *Hyla*, *Isthmohyla*, *Megastomatohyla*, *Plectrohyla*, *Pseudacris*, *Ptychohyla*, *Smilisca*, *Tlalocohyla*, *Triprion*. Wiens et al. (2010) and Pyron (2014) phylogenies only included 3 out of 14 species of *Ecnomiophyla*: *E. milaria*, *E. minera*, and *E. miotympanum*. Batista et al. (2014) analyzed one fragment of the mitochondrial gene 16S from seven species of *Ecnomiophyla*. Their outgroup was limited to two genera within Hylini and was not suitable to assess the phylogenetic position of *Ecnomiophyla* within Hylidae. Nevertheless, they provided the most complete phylogeny for *Ecnomiophyla* to date.

In our phylogeny, *E. tuberculosa* is part of the tribe Lophiohylini. Because all other species of *Ecnomiophyla* are part of the tribe Hylini (Pyron 2014; Wiens et al. 2010; Suppl. material 2), the phylogenetic position of *Ecnomiophyla tuberculosa* renders the genus *Ecnomiophyla* polyphyletic and the genus *Tepuihyla* paraphyletic (Fig. 1). We solve both problems by assigning *Hyla tuberculosa* Boulenger 1882 to the genus *Tepuihyla*. This change results in *Tepuihyla tuberculosa* (Boulenger 1882) comb. n.

Below we present the species account for *T. tuberculosa* and we describe the new species from Ere River, Peru. Under this new taxonomy, the genus *Tepuihyla* contains ten species distributed in the Pantepui region of Venezuela, Guyana and in the Amazon region of Brazil, Colombia, Ecuador, and Peru (AmphibiaWeb 2016; Salerno et al. 2015; Kok et al. 2015).

### ***Tepuihyla tuberculosa* (Boulenger 1882)**

*Hyla tuberculosa* Boulenger 1882. Holotype BMNH 1947.2.13.34

*Ecnomiophyla tuberculosa*: Faivovich et al. 2005

**Holotype.** Sub adult female with SVL 67.6 mm (Fig. 4C–E). The description of the holotype provided by Boulenger (1882) is adequate.

**Diagnosis.** In this section coloration pertains to preserved specimens unless otherwise noted. A large-sized *Tepuihyla* differing from other known species in the genus by the following combination of characters: (1) SVL in males 79.3–86.2 mm ( $n = 5$ ), SVL in females 67.6–85.7 mm ( $n = 2$ ); (2) skin on dorsum coarsely tuberculate, covered by small tubercles with scattered large tubercles; tubercles without keratinized tips; (3) skin on flanks covered by large tubercles; (4) webbing between fingers extensive but without reaching the proximal border of the disks, hand webbing formula  $I2 - 2 III1 - 2 III1\frac{1}{2} - 1 IV$  to  $I2 - 2 + II1 - 2 III2 - 1 IV$  (Fig. 7A); webbing between toes extensive and reaching the proximal border of the disks on at least three toes, foot webbing formula  $I0 + - 1 + II0 + - 1 III0 + - 1 + IV1 + - 0 + V$  to  $I1 + - 1\frac{1}{2} III1 - 1 + III1 + - 1\frac{1}{2} IV1\frac{1}{2} - 0 + V$  (Fig. 7B); (5) dorsal coloration in life greenish cream or brownish cream with scattered dark brown reticulations, anterior and posterior surfaces of thighs and hidden surfaces of shanks yellowish orange; (6) ventral coloration whitish cream and webbing between fingers and toes pale orange; (7) suborbital mark absent, clear

labial stripe present, faint and with some brown spots; (8) coloration on flanks similar to dorsal coloration except for greenish yellow axilla and groins and whitish gray ventrolateral area; (9) skin on upper surface of head not co-ossified with underlying cranial elements, cranial crest slightly exostosed; (10) in life, bones green; (11) small triangular dermal flaps form serrate fringe along the ventrolateral margin of the forearm and along the outer edge of Finger IV; heels bearing two or three enlarged fleshy conical tubercles surrounded by few smaller round tubercles; small triangular dermal flaps form serrate fringe along ventrolateral margin of tarsus and outer margin of Toe V; (12) adults, in life, have cream iris with a coppery hue and scattered thin black reticulations; (13) vocal sac is white, single and subgular, (14) a juvenile is similar to adults in coloration but with dorsal background coloration brownish cream and a black medial stripe in the iris; (15) larvae unknown.

*Tepuihyla tuberculosa* differs from all congeneric species (in parenthesis), except *T. shushupe* sp. n., in having a larger size: SVL in males 79.3–86.2 mm ( $n = 5$ ), SVL in females 67.6–85.7 mm ( $n = 2$ ) (maximum SVL 59.2 mm in other *Tepuihyla*), having extensive webbing in the hands (basal webbing) and a serrate fringe along the ventrolateral margin of the forearm (absent). Other differences are listed on Table 4.

*Tepuihyla tuberculosa* is most similar to *T. shushupe* sp. n. It differs from *T. shushupe* sp. n. (character states in parenthesis) in having cream iris in life (iris cream with reddish periphery), dorsum covered with small tubercles intermixed with few large tubercles (dorsum covered with small tubercles intermixed with abundant large tubercles; Figs 3–5); in preservative, its dorsum is light cream or cream with a coppery hue and brownish cream to creamy coppery large tubercles (dorsum light brown with large brownish cream or creamy coppery tubercles with a dark brown posterior border). *Tepuihyla tuberculosa* also resembles the Amazonian *Trachycephalus cunauaru* and *T. resinifictrix* but differs from both species in having serrate fringes on the limbs and tubercles on the lower jaw (both absent in *Trachycephalus*; Fig. 8). *Tepuihyla tuberculosa* is easily distinguished from all other large Amazonian treefrogs in having fully webbed hands and feet, coarsely tubercular skin on dorsum, and serrate dermal fringes on the outer margin of the forearm and foot. *Cruziophyla craspedopus* and *Dendropsophus marmoratus* also have dermal fringes on the outer margin of the foot, but the former is distinguished by its deep green dorsum, vertically elliptical pupils in a bicolored iris (pale silver with yellow borders), smooth skin on dorsum and elongate calcar on the heel. The smaller *Dendropsophus marmoratus* exhibits a bright yellow belly with black spots or mottling (uniform yellowish-tan in *T. tuberculosa*).

**Variation.** In this section, coloration refers to preserved specimens unless otherwise noted. Morphometric data for adult specimens are summarized in Table 5, whereas variation in dorsal coloration of preserved specimens is shown in Figure 5. Dorsal coloration varies between light cream (e.g., QCAZ 55423) and cream suffused with a coppery hue (e.g., QCAZ 52855) with brownish cream or creamy coppery enlarged tubercles, bearing scattered dark brown reticulations or marks. In all specimens the belly and ventral areas of thighs are lighter than those of the holotype probably



**Table 4.** Qualitative morphological characters of frogs of the genus *Tepuihyala*. Data was obtained from Ayarzagüena et al. 1992; Duellman and Hoogmoed 1992; Gorzula and Señaris 1998; Kok and Kalamandeen 2008; Kok et al. 2015; Mijares-Urrutia et al. 1999).

	Serrate fringes on limbs	Maximum size females (mm)	Dorsum	Tubercles on jaw	Webbing between fingers	Vocal sac
<i>T. acsii</i>	absent	36.8	smooth (females) to spiculate (males)	absent	absent	subgular
<i>T. edelrae</i>	absent	45.7	smooth (females) to spiculate (males)	absent	absent	subgular
<i>T. exophthalma</i>	absent	42.5	smooth with few tubercles	absent	absent	subgular
<i>T. luteolabris</i>	absent	59.2	granular	absent	absent	subgular
<i>T. rodriguezi</i>	absent	50.3	smooth (females) to spiculate (males)	absent	absent	subgular
<i>T. shushupe</i> sp. n.	forelimbs and hindlimbs	–	tuberculate	present	extensive	subgular
<i>T. tuberculosa</i> comb. n.	forelimbs and hindlimbs	85.7	tuberculate	present	extensive	subgular
<i>T. obscura</i>	absent	38.4	smooth (females) to spiculate (males)	absent	absent	subgular
<i>T. warreni</i>	absent	36.2	smooth	absent	basal	subgular

**Table 5.** Descriptive statistics for measurements of adult Amazonian *Tepuihyla*. Mean  $\pm$  SD is given with range in parenthesis. Abbreviations are: SVL = snout-vent length; FOOT = foot length; HL = head length; HW = head width; ED = eye diameter; TD = tympanum diameter; TL = tibia length; FL = femur length. All measurements are in mm.

	<i>Tepuihyla shushupe</i> sp. n. Male CORBIDI 12513	<i>Tepuihyla tuberculosa</i> comb. n. Female QCAZ 32716	<i>Tepuihyla tuberculosa</i> comb. n. males (n = 5)
SVL	85.4	85.7	82.9 $\pm$ 2.9 (79.3–86.2)
FOOT	35.5	35.8	35.53 $\pm$ 2.4 (33.5–39.5)
HL	26.6	25.7	26.0 $\pm$ 1.0 (25.1–27.5)
HW	28.9	29.2	28.9 $\pm$ 1.6 (27.8–31.7)
ED	7.7	7.5	7.5 $\pm$ 0.9 (6.3–8.9)
TD	5.5	4.8	5.3 $\pm$ 0.5 (4.9–5.8)
TL	46.9	45.6	46.3 $\pm$ 2.2 (44.1–49.9)
FL	35.9	36.6	36.8 $\pm$ 1.3 (35.0–38.3)

because they were collected more recently. Head is rounded in dorsal view, wider than long; the snout is truncate in dorsal view and truncate (e.g. QCAZ 32716) in profile. The largest male has 86.2 mm SVL (average =  $82.9 \pm 2.7$  mm,  $n = 5$ ) and the largest female 85.7 mm (Table 5).

**Coloration in life.** Dorsal coloration is greenish cream with scattered brown marks or reticulations, top and sides of head are more greenish in some specimens (e.g. QCAZ 52855); lips greenish with scattered small dark brown marks; supratympanic fold delineated by a thin brown edge, tympanic membrane lighter than the background; flanks with coloration similar to dorsum; axilla and groin pale orange, ventrolateral region whitish cream, limbs with faint brown transversal bands; dorsal surfaces of hands and feet, including webbing, greenish cream with scattered dark brown marks; discs pale green. Throat, chest and belly are white but some specimens have an orange hue on the belly (e.g. QCAZ 55423); serrate fringes along forearms and tarsus white; webbing, thighs and concealed surfaces of shanks orange. Iris is cream with a light coppery hue bearing some scattered black venations. Juvenile specimen QCAZ 55413 is similar to adult specimens but has a brownish cream dorsum with scattered faint brown blotches (Fig. 3E–F).

**Advertisement call.** Quantitative characteristics of the advertisement call of *T. tuberculosa* (QCAZ 53699) are detailed in Table 3. The call consists of a cackle of short notes repeated at a fast rate with amplitude modulation (Fig. 6). Note amplitude and note rate increase markedly along the first half of the call, decreasing at the end. The call has two harmonics but most of the energy located on the first. Fundamental frequency of the notes ranges from 515.6 to 796.9 Hz (mean = 619.1, SD = 77.2). Two notes located at ~50% of the call duration have their greatest energy in the second harmonic, at 1078.1 and 1195.3 Hz. All other notes have their greatest energy in the first harmonic. The dominant frequency of the entire call ranges from 562.5 to 632.8

Hz. Interestingly, the call of this species is feared by natives in the lower Pastaza basin (Shiwar, Sapara, Shuar, Achuar people), because it is commonly confused with the “calling” of the bushmaster *Lachesis muta* (Squamata: Viperidae). This belief almost certainly incorrect as *L. muta* cannot vocalize. See also the Etymology section in *E. shushupe* sp. n. description.

**Distribution and natural history.** Localities documented for this species are shown in Figure 9. Duellman (1974) reported four specimens: two from Pastaza province in Ecuador, one from the mouth of Rio Santiago in northern Peru, and one juvenile from Rio Uaupes at junction of Rio Querari, Amazonas, Brazil. Given its geographic location, the latter probably corresponds to *T. shushupe* sp. n., but its identity requires confirmation. We recorded five additional localities in the Amazon lowlands of Ecuador and two in Peru (Fig. 9). Elevation range is 132 to 1076 m above sea level. The southernmost and highest locality is Cordillera Escalera, San Martin department, in northeastern Peru (CRBIIAP 1252).

All specimens with ecological data were collected at night perching on vegetation 1.5 to 3.0 m above the ground. One specimen from Yasuní (QCAZ 52855) and one from Juyuintza (QCAZ 53542; Fig. 10B) were collected on primary forest (M. Read and H. M. Ortega-Andrade field notes). The specimen recorded at Juyuintza was calling from a tree hole 1.5 m above the ground in *Terra Firme* forest. The hole had a depth of ~15 cm and a diameter of 10 cm, and was  $\frac{3}{4}$  flooded with water. Two individuals were calling nearby, at distances of approximately 100 to 200 m. No amplexant pairs, clutches, or tadpoles have been observed.

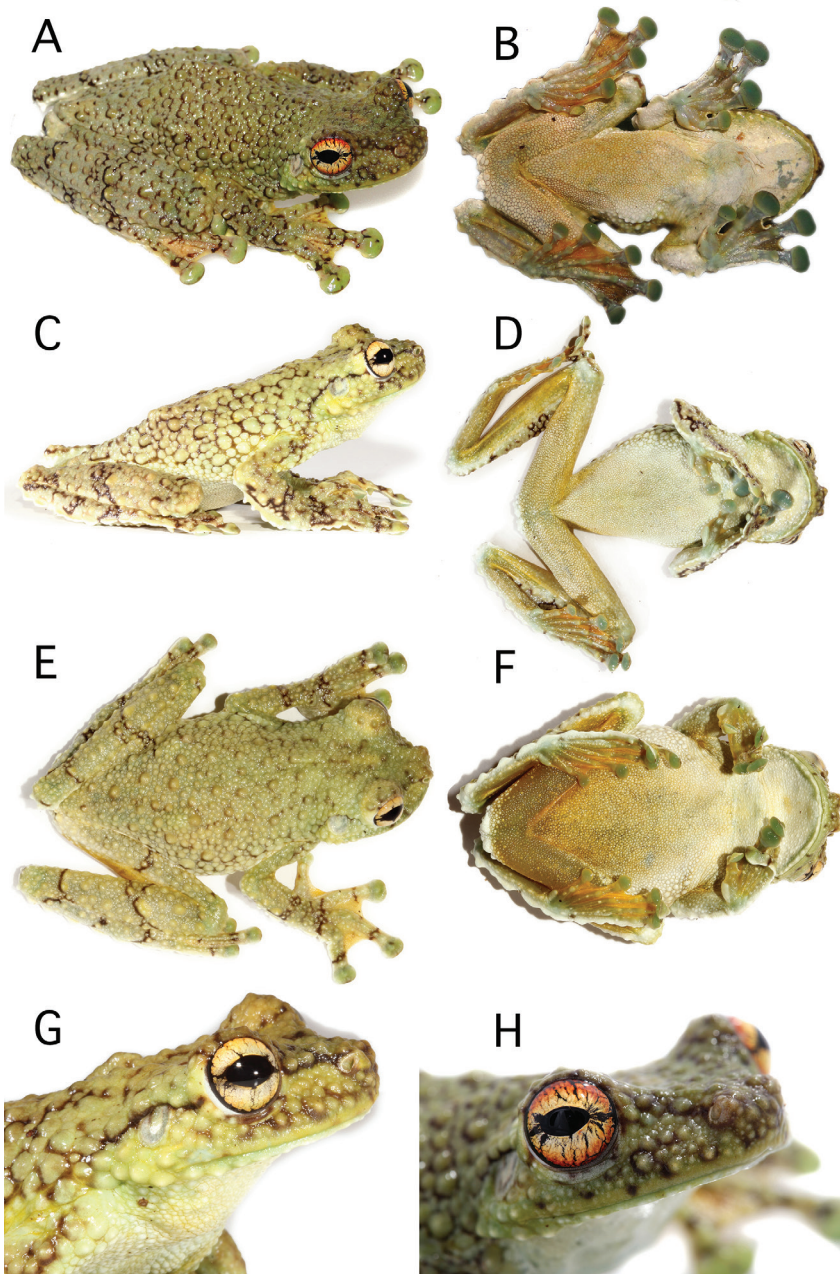
**Conservation status.** The scarcity of records of *E. tuberculosa*, even at thoroughly sampled localities, like Yasuni National Park, could be a consequence of small populations sizes or an artifact of low capture probabilities. Our finding of a male calling from a tree hole containing water suggests that *E. tuberculosa* breeds on tree holes and is unlikely to be found on ground-level surveys. Therefore, lack of records probably results from low capture probabilities consequence of microhabitat preferences. Because population status is unknown, we suggest that the Red List category of *T. tuberculosa* is Data Deficient according to IUCN (2001) guidelines. Searches of the species will benefit from audio sampling to detect the advertisement call described here.

***Tepuihyla shushupe* sp. n.**

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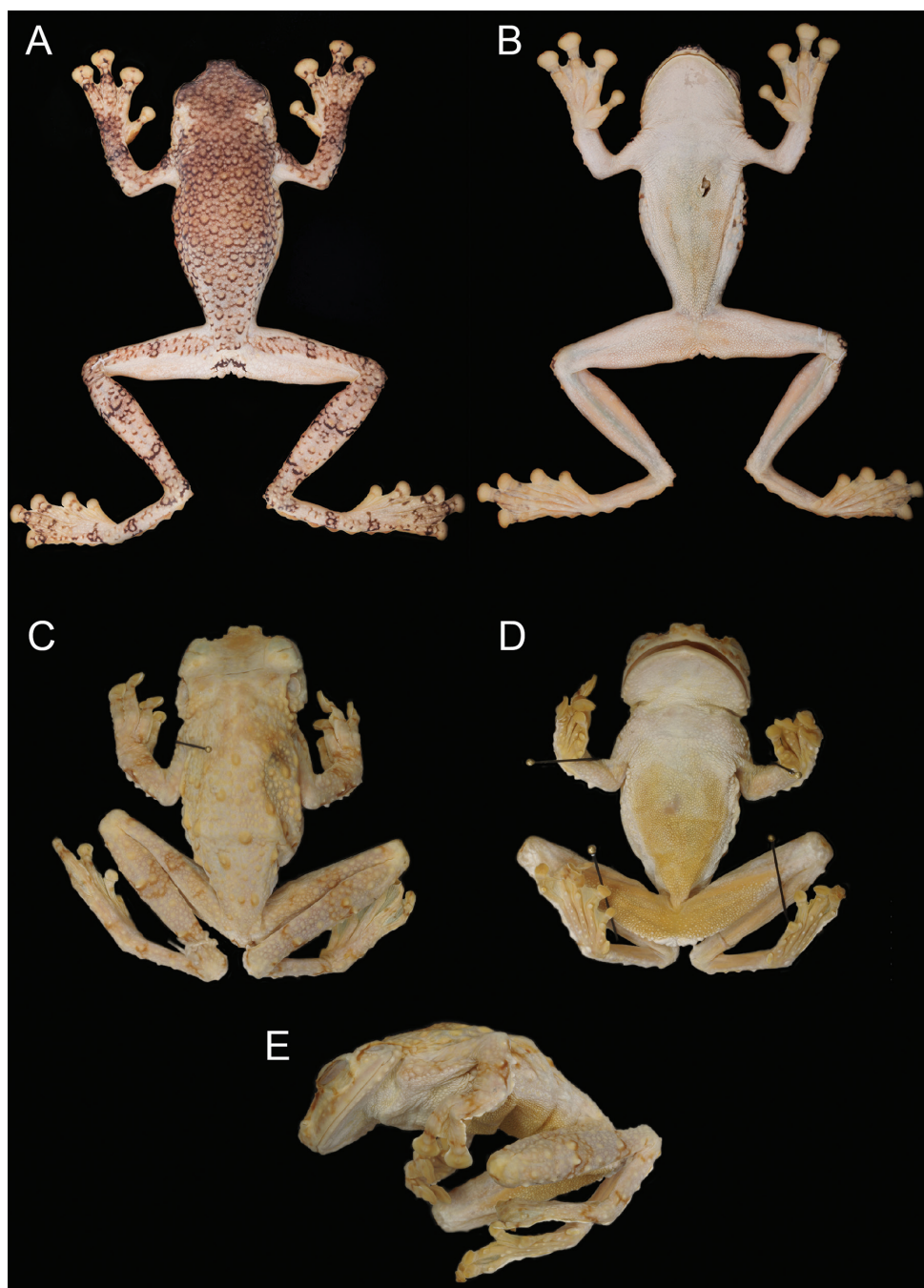
*Ecnomiohyla tuberculosa*: Venegas and Gagliardi-Urrutia (2013). Species misidentification in their Figures 8B and 8G.

**Holotype.** (Figs 3–4, 6, 10C) CORBIDI 12513, adult male from Peru, Loreto department, Maynas province, head waters of rivers Ere and Campuya, Putumayo River basin (1.6790°S, 73.7197°W), 145 m above sea level, collected by P. J. Venegas and G. Gagliardi-Urrutia on 19 October 2012.



**Figure 3.** External morphology of *Tepuihyla shushupe* sp. n. and *Tepuihyla tuberculosa* comb. n. **A–B** *Tepuihyla shushupe* sp. n. CORBIDI 12513 (holotype), adult male, SVL = 85.3 mm, Ere river, Peru **C–D** *Tepuihyla tuberculosa* comb. n. QCAZ 55423, adult male, SVL = 83.1 mm, Parque Nacional Yasuní, Tambococha, Ecuador; **E–F** *Tepuihyla tuberculosa* comb. n., QCAZ 55413 juvenile, SVL = 58.1 mm, Parque Nacional Yasuní, Tambococha, Ecuador **G–H** iris coloration of *Tepuihyla tuberculosa* comb. n. (QCAZ 55423) and *Tepuihyla shushupe* sp. n., (CORBIDI 12513). Photographs: **A–B, H** by P. Venegas, **C–G** by D. Quirola.

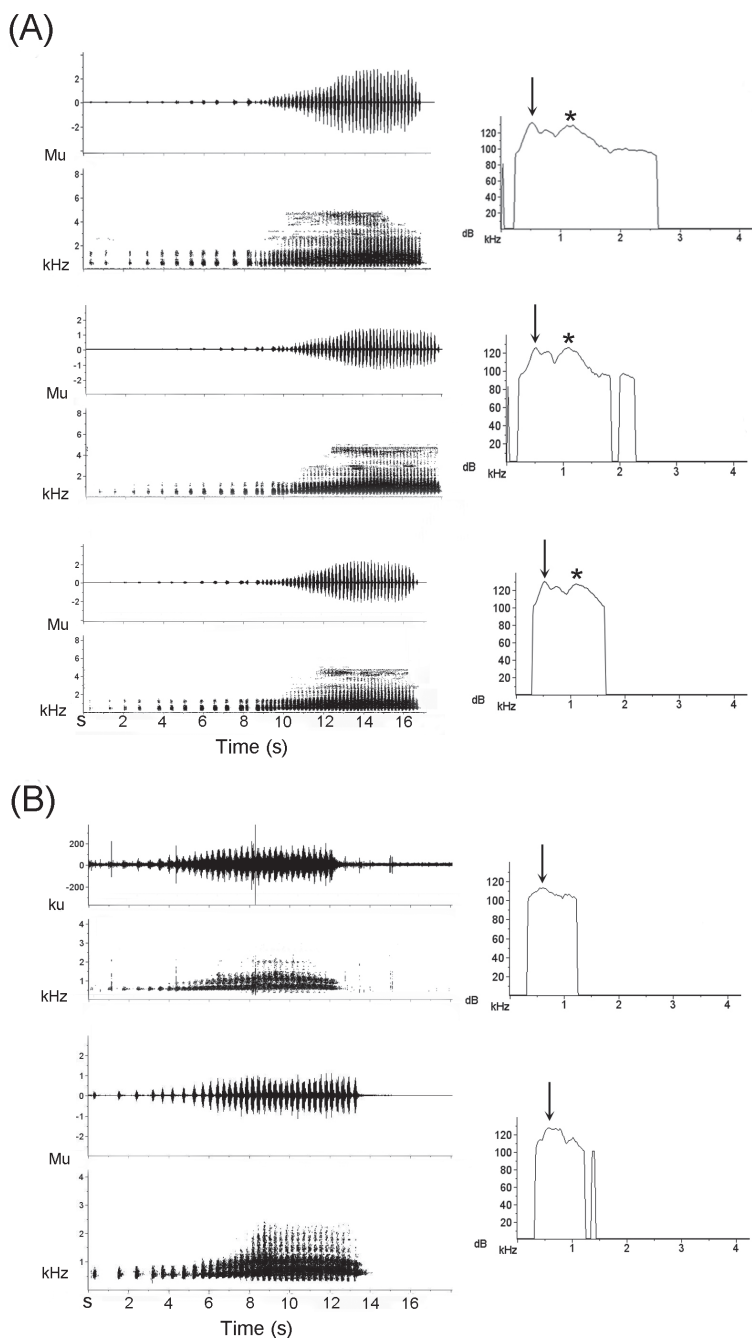




**Figure 4.** Holotypes of *Tepuihyla shushupe* sp. n. (**A–B** CORBIDI 12513) and *Tepuihyla tuberculosa* comb. n. (**C–E** BMNH 1947.2.13.34). Photos of *Tepuihyla tuberculosa* comb. n. by M. R. Bustamante.



**Figure 5.** Variation in dorsal coloration of preserved specimens of adult *Tepuihyla tuberculosa* comb. n. Left to right, upper row: QCAZ 52855 (male), QCAZ 53542 (male); lower row: QCAZ 53147 (male), QCAZ 55423 (male). See Suppl. material 2 for locality data. Specimens are shown at the same scale.



**Figure 6.** Oscillogram, sound spectrogram (first column), and power spectrum (second column) of advertisement calls of *Tepuihyla shushupe* sp. n. (A) and *Tepuihyla tuberculosa* comb. n. (B). Note differences in call length and number of notes (first column). Both species have the dominant frequency (arrows) in the first harmonic but in *Tepuihyla shushupe* sp. n. the second harmonic has similar energy content (asterisk), while in *Tepuihyla tuberculosa* comb. n. it has much less.

**Diagnosis.** In this section coloration pertains to preserved specimens unless otherwise noted. A large-sized *Tepuihyla* differing from other species in the genus by the following combination of characters: (1) SVL in males 85.4 mm ( $n = 1$ ), females unknown; (2) skin on dorsum coarsely tuberculate, covered by small tubercles intermixed with large tubercles; tubercles without keratinized tips; (3) skin on flanks similar to skin on dorsum; (4) webbing between fingers extensive but without reaching the proximal border of disks; hand webbing formula  $\text{I2—2III—2III}1\frac{1}{2}\text{—1+IV}$  (Fig. 7C); webbing between toes extensive, reaching the proximal border of the disks on at least three toes; foot webbing formula  $\text{I1—1+II0+—1+III0+—1}\frac{1}{2}\text{IV}1\frac{1}{2}\text{—0+V}$  (Fig. 7D); (5) dorsal coloration in life brownish green, anterior and posterior surfaces of thighs and hidden surfaces of shanks yellowish orange; (6) ventral coloration whitish gray and webbing between fingers and toes pale orange; (7) suborbital mark absent, clear labial stripe present, faint and with some brown spots; (8) coloration on flanks similar to dorsal coloration except for greenish yellow axilla and groins and whitish gray ventrolateral area; (9) skin on upper surface of head not co-ossified with underlying cranial element, cranial crest slightly exostosed; (10) in life, bones green; (11) small triangular dermal flaps form serrate fringe along the ventrolateral margin of the forearm and along the outer edge of Finger IV; heels bearing two enlarged fleshy conical tubercles surrounded by few smaller round tubercles; small triangular dermal flaps form serrate fringe along ventrolateral margin of tarsus and outer margin of Toe V; (12) in life, iris reddish peripherally turning cream towards to the center, with irregular black reticulations; (13) vocal sac is white, single and subgular, (14) juveniles unknown; (15) larvae unknown.

*Tepuihyla shushupe* differs from all species of the genus (in parenthesis), except *T. tuberculosa*, in being larger, having extensive hand webbing (basal webbing) and a serrate fringe along the ventrolateral margin of the forearm (absent). Other differences are listed on Table 4.

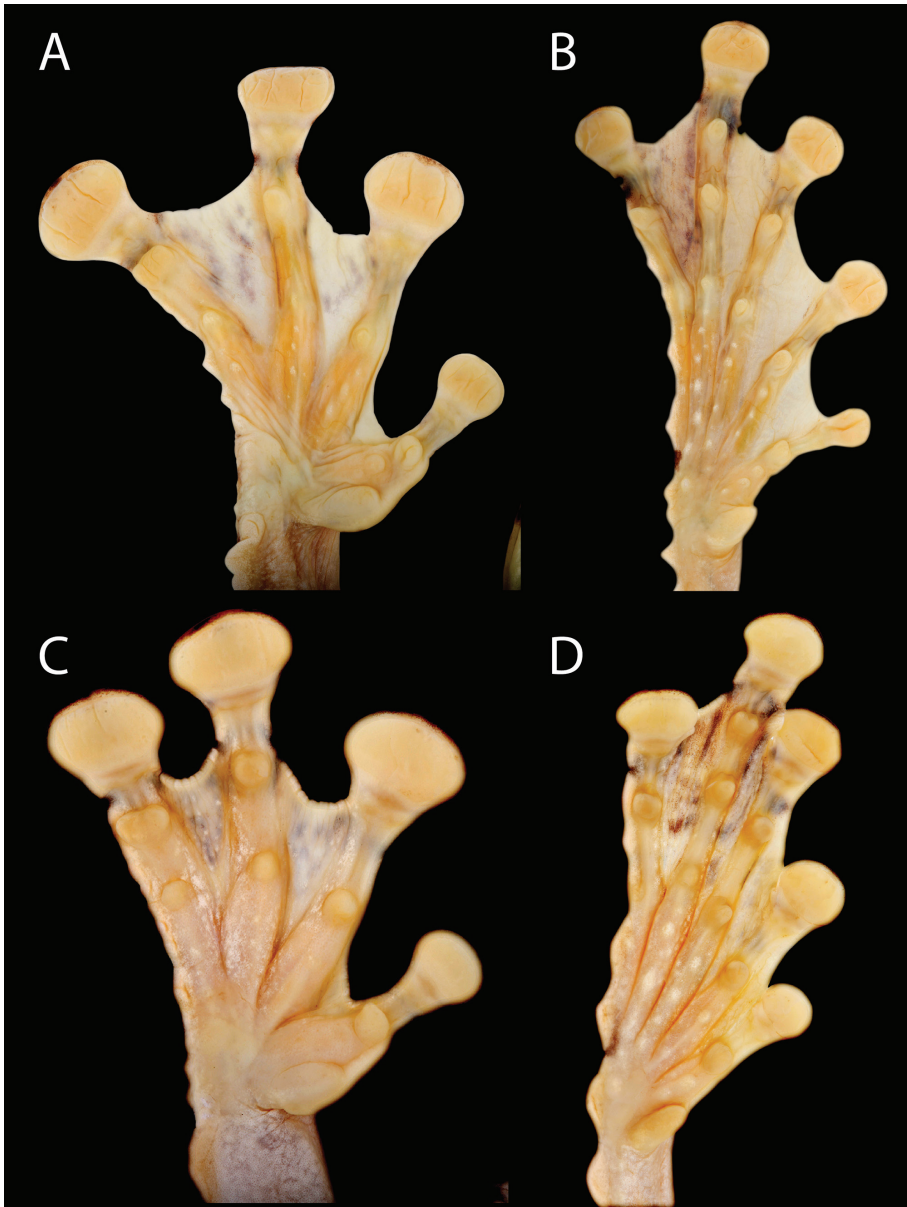
*Tepuihyla shushupe* is most similar to *T. tuberculosa*. It differs from *T. tuberculosa* (character states in parenthesis) in having, in life, a cream iris with red periphery (iris cream without red periphery), dorsum covered by small tubercles intermixed with abundant large tubercles (dorsum covered by small tubercles intermixed with few large tubercles); in preservative, dorsum cream with a brownish mantle (dorsum light cream or cream suffused with a coppery hue) and the posterior border of large dorsal tubercles dark brown (tubercles brownish cream or creamy coppery). In coloration, size, and texture of dorsal skin *Tepuihyla shushupe* resembles the Amazonian *Trachycephalus resinifictrix* and *Trachycephalus cunauaru*. It can be distinguished from both species by the presence of serrate fringes on the limbs and tubercles in the lower jaw (both absent in *Trachycephalus*) and the iris having red periphery and lacking a vertical black bar below the pupil (iris without red and with a vertical black bar below the pupil in both *Trachycephalus*).

**Description of the holotype.** Adult male (CORBIDI 12513), 85.4 mm SVL, head length 26.6, head width 28.9, eye diameter 7.7, tympanum diameter 5.5, femur length 35.9, tibia length 46.9, foot length 35.9. Head rounded in dorsal view, wider



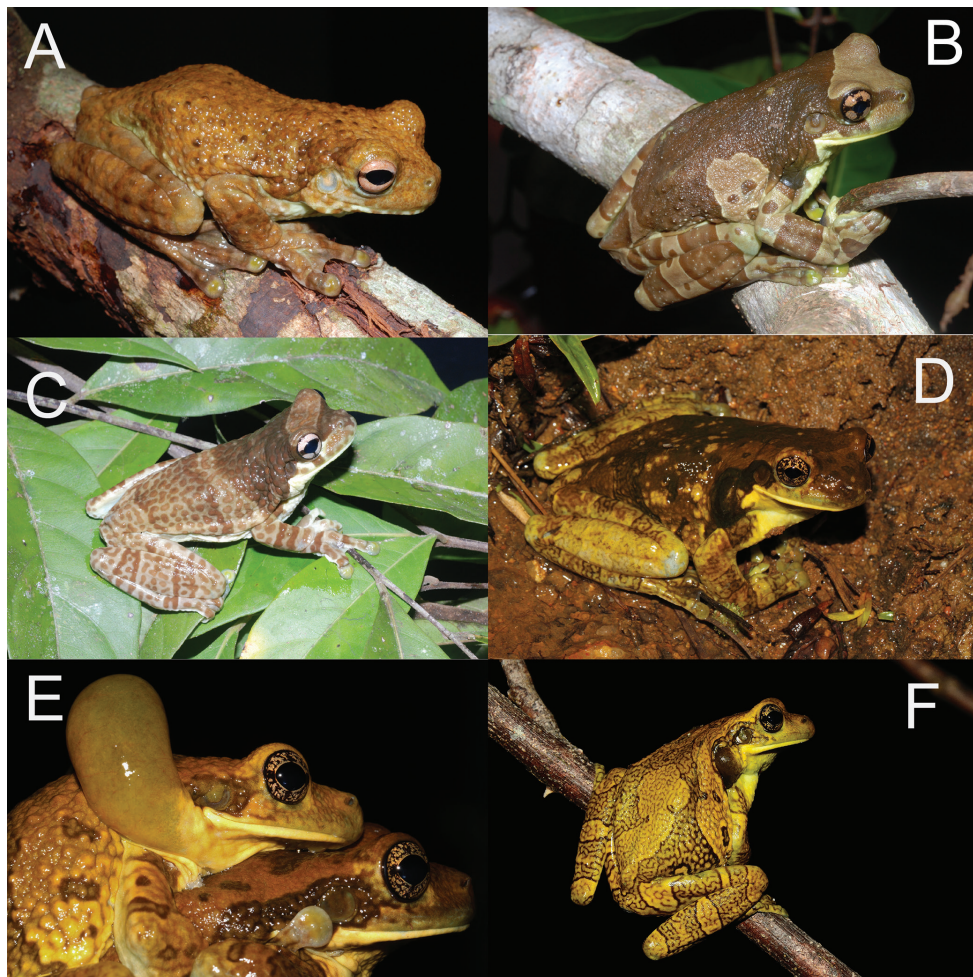
than long (HL/HW = 92%); snout truncate in dorsal view and slightly protruding in profile; nostrils are directed laterally, near tip of the snout; top of head tuberculate; canthus rostralis concave in dorsal view, straight in profile; skin on upper surface of head not co-ossified with underlying cranial elements, cranial crests slightly exostosed; loreal region concave; skin on dorsal surface of head, body and limbs coarsely tuberculate, tubercles are either small or large and lack keratinous spines; lower eyelid pigmented; distinct supratympanic fold formed by a row of round tubercles running from midpoint of posterior margin of eye; tympanum prominent, opaque, smooth, 71% of eye diameter, separated from eye by 3.8 mm; small triangular dermal flaps form serrate fringe along the ventrolateral margin of the forearm and the outer edge of Finger IV, fringe more conspicuous on forearm than on finger; hands moderate in length (HAL/SVL = 31.2%); Finger lengths  $I < II < IV < III$ , terminal disk on Finger I 63.2% of diameter of disks on Fingers II–IV; diameter of Fingers II–IV ~1.2 times tympanum diameter; distal subarticular tubercles on Fingers I–III large and rounded, on Finger IV larger and bifid; supernumerary tubercles indistinct; prepollical tubercle large, obtuse and elliptical; bony prepollical projection absent; keratinous nuptial pad with dark epidermal projections covering the surface of the thumb up to the distal edge of its subarticular tubercle; fingers considerably webbed although web does not reach base of disks; webbing formula  $I2-2III1-2III1\frac{1}{2}-1\frac{1}{4}IV$ ; legs relatively long and slender (tibia length 54.8% of SVL), thigh length 35.9 mm; heels bearing two enlarged conical tubercles surrounded by few lower round tubercles; fleshy, dermal flaps form serrate fringe along ventrolateral margin of tarsus and outer margin of Toe V extending to base of disk, scallops are deeply incised, largest on tarsus, smaller along toe; outer metatarsal tubercle small, inner metatarsal tubercle moderately large, ovoid, and flat; toe lengths  $I < II < III = V < IV$ ; disks on toes ~70% of diameter of disks on fingers, equal between Toes III–V; subarticular tubercles round; supernumerary tubercles present, ill defined; webbing in toes extensive, reaching the base of disks on at least three toes; webbing formula  $I1-1III1-1\frac{1}{4}III\frac{3}{4}-1IV1-\frac{3}{4}V$ ; gular skin smooth with small pointed tubercles along the jaw, venter finely granulate, weak granulation on undersides of arms and finely on ventral surfaces of thighs, smooth skin on anterior surfaces of thighs and ventral surfaces of legs; cloacal opening directed posteriorly at upper-level of thighs, some indistinct small tubercles on the upper edge of vent, skin under the vent covered by small flattened but conspicuous tubercles with two enlarged prominent fleshy tubercles posterolateral to the vent (one on each side); tongue cordiform; vomerine ridges transverse, oblique in the middle, narrowly separated medially, placed between the posterior margins of the large subrectangular choanae; vomerine teeth 6 to 11; vocal slits present.

**Color of holotype in life (Figs 3, 10).** Based on digital photographs. Dorsal and lateral surfaces of body and limbs pale green; posterior edge of each enlarged tubercle, dark brown; lips paler than the rest of head; lower flanks, forearms, tibia, and tarsus white; dorsal surfaces of hindlimbs with narrow dark brown transversal stripes; axillar region, groins, anterior and posterior surfaces of thighs, and hidden surfaces of shanks greenish yellow; dorsally, webbing between fingers and toes pale greenish yellow with



**Figure 7.** Ventral views of the left hand and foot of *Tepuihyla*. **A–B** *Tepuihyla tuberculosa* comb. n. (Parque Nacional Yasuní, Ecuador, SVL = 86.2 mm, QCAZ 52855, adult male) **C–D** *Tepuihyla shushupe* sp. n. (Ere River, Peru, SVL = 85.4 mm, CORBIDI 12513, adult male).

scattered dark brown marks, ventrally greenish orange. Venter whitish gray with an orange tone on belly and ventral surfaces of thighs; ventral surfaces of arms and elbows greenish yellow; ventral surfaces of tibia, tarsus, palms, fingers, soles, toes and discs water green; limb bones green; iris cream with red periphery and irregular black reticulations.

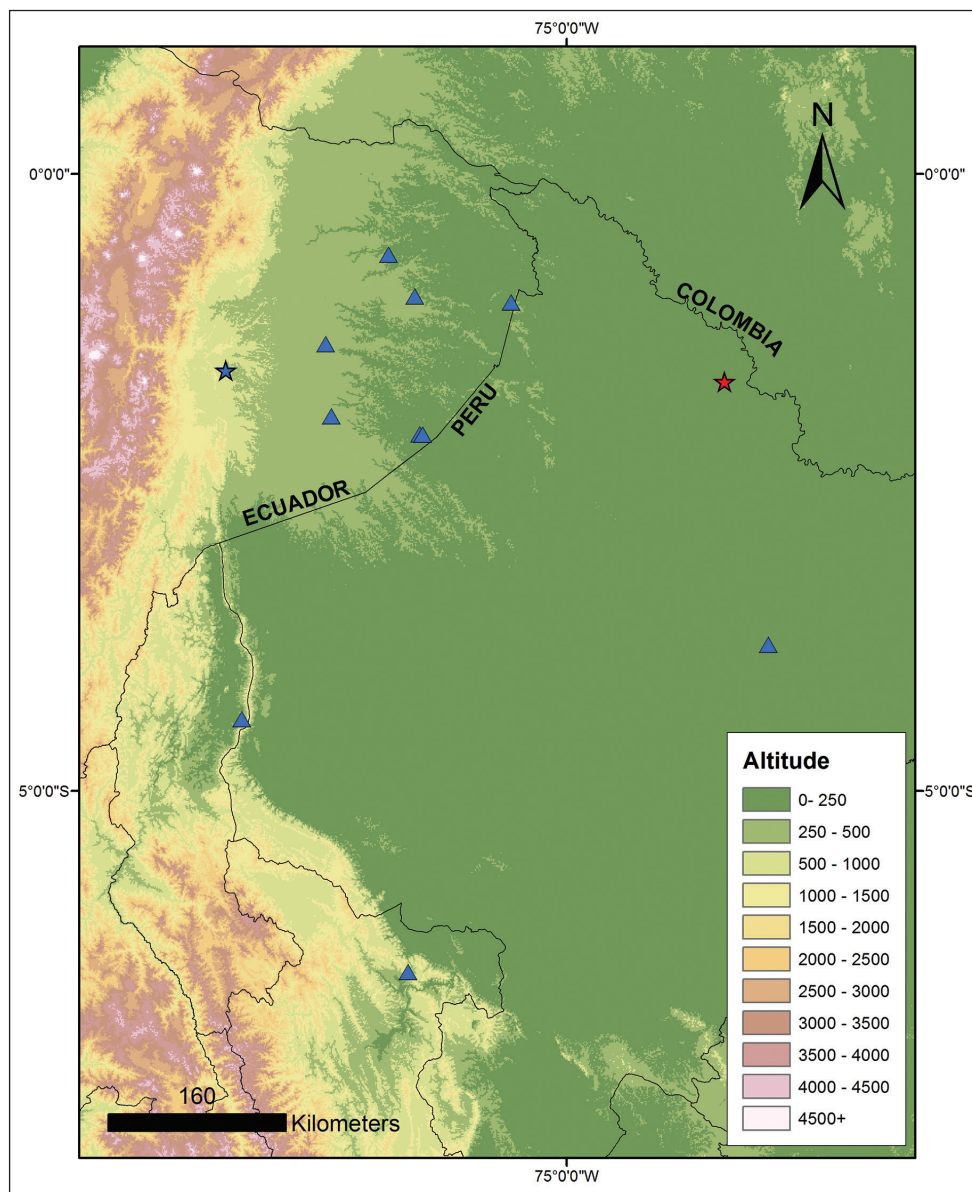


**Figure 8.** Dorsolateral views of Amazonian *Trachycephalus*. **A** *Trachycephalus helioi*, Juruti, Pará, Brazil **B** *Trachycephalus resinifictrix*, Juruti, Pará, Brazil **C** *Trachycephalus cunauaru*, Santa Isabel do Rio Negro, Amazonas, Brazil **D–E** *Trachycephalus typhoni*, Village de Ouanary, French Guiana **F** *Trachycephalus typhoni*, Matiti, French Guiana. Photographs: **A–C** by M. Gordo, **D–E** by Daniel Baudain, **F** by Vincent Premel.

**Color of holotype in preservative (Figs 4A–B, 5C–D).** Dorsal surfaces of head, body and forelimbs, including fingers, are tan; large dorsal tubercles have a dark brown margin; dorsal surfaces of hindlimbs and toes dirty cream bearing scattered light tubercles with dark brown margins and narrow dark brown transversal stripes; posterior surfaces of thighs light cream; dorsal surfaces of discs on fingers and toes are light cream with dark brown marks. Venter is whitish cream.

**Advertisement call.** Quantitative characteristics of the advertisement call *T. shushupe* (CORBIDI 12513) are detailed in Table 3. The call consists of a cackle of short notes repeated at a fast rate with amplitude modulation (Fig. 6). Note amplitude

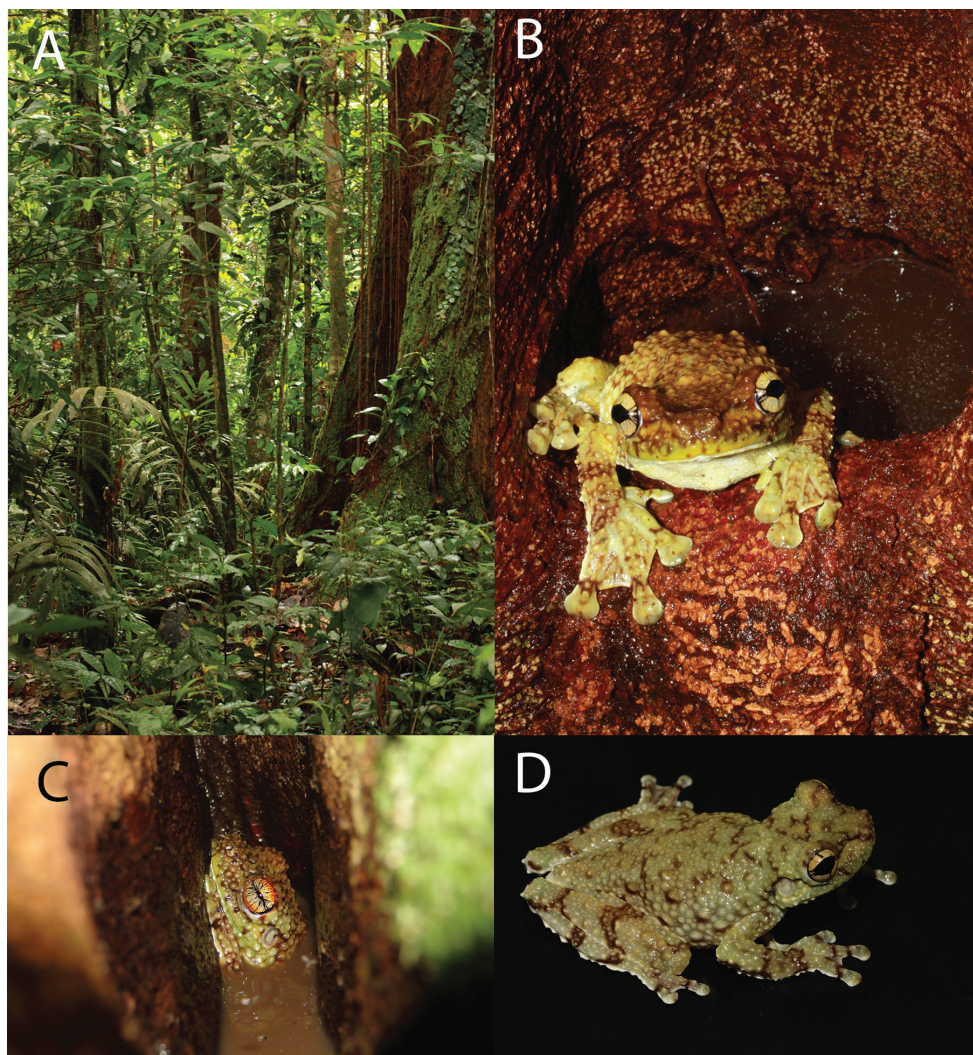




**Figure 9.** Records of *Tepuihyla shushupe* sp. n. and *Tepuihyla tuberculosa* comb. n. *Tepuihyla shushupe* sp. n., red star; *Tepuihyla tuberculosa* comb. n., blue triangles and blue star for type locality. Locality data from specimens deposited at Natural History Museum (BMNH), London, Centro de Ornitología y Biodiversidad (CORBIDI), and Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ).

and note rate increases markedly along the first half of the call, decreasing again at the end. The call has two harmonics, the first harmonic has slightly more energy than the second (Fig. 6). Fundamental frequency of individual notes ranges from 404.3 to





**Figure 10.** Life individuals and habitat of *Tepuihyla shushupe* sp. n. and *Tepuihyla tuberculosa* comb. n. **A** habitat of *Tepuihyla tuberculosa* comb. n. at Juyuintza, Provincia Pastaza, Ecuador **B** Adult male of *Tepuihyla tuberculosa* comb. n. (QCAZ 53542) sitting at the entrance of the tree hole where he was calling **C** Adult male of *Tepuihyla shushupe* sp. n. (CORBIDI 12513, holotype) partly submerged in the water accumulated on the tree hole where he was calling **D** *Tepuihyla tuberculosa* comb. n. (CRBIIAP 1839) from the vicinity of Puerto Almendras, Loreto, Peru. Photographs: **A, B** by M. Ortega, **C** by A. Del Campo, **D** by G. Gagliardi-Urrutia.

585.9 Hz (mean = 500.08, SD = 28.3). The dominant frequency of the entire call is 515.6 Hz. Midway through the call, nearly 25% of the notes have the greatest energy in the second harmonic (range 1016.6 to 1210 Hz).

**Distribution and natural history.** *Tepuihyla shushupe* is only known from the type locality in the headwaters of rivers Ere and Campuya, at an elevation of 145 m,

in the Putumayo river basin near the boundary between Peru and Colombia. According with Vriesendorp (2013), the type locality consists of a complex of forest terraces, at elevations between 90 and 170 m above sea level, with a canopy reaching 35 to 40 m; terraces have heavy loads of leaf litter (~50 cm deep) and a dense mat of fine roots; the depressions between terraces have small palm swamps (~10 m wide) of *Oenocarpus bataua*; the soil varies between sandy and clayey; most streams have a muddy bottom, few have gravel and sand, and one has big cobbles.

The holotype was calling at the base of a big tree inside a narrow hole, 150 cm above the ground. The hole had 30 cm of height and had water accumulated. The frog had most of its body submerged (Fig. 10C) and the top of its head was covered by flies (probably *Corethrella* midges). We recorded its call and immediately made playbacks. The male answered by calling quickly and perching on the hole entrance. We detected at least six individuals during 18 hours of visual encounter surveys (0.375 individuals/hour,) in areas nearby where the holotype was found (primary forest). All individuals were detected by their advertisement calls and none could be collected. No females, amplexant pairs, clutches, or tadpoles have been observed.

**Etymology.** The specific epithet is a noun in apposition. The word *shushupe* is used by native people to refer to the bushmaster *Lachesis muta* (Squamata: Viperidae), the largest viper in the Americas. Our field assistants in Ere river, Alpahuayo Mishana (Peru) and Juyuintza (Ecuador) believed that the advertisement calls of *T. shushupe* and *T. tuberculosa* were produced by *L. muta*. The belief that *L. muta* can sing seems to be widespread among hunters, colonists, and indigenous people from the Amazon basin (Lamar 1998). The association of the calls from *Tepuihylla* with *L. muta* by people on widely separated localities in Amazonian Peru and Ecuador deserves investigation.

**Conservation status.** *Tepuihylla shushupe* is only known from a single individual collected at the type locality. Calling behavior suggests that *T. shushupe* breeds on tree holes and is a canopy dweller. The detection of the calls of six additional individuals at the type locality suggests that the species can be relatively abundant. However, the species may be difficult to observe in ground-level surveys. Given the uncertainty in its population status, we suggest that its Red List category is Data Deficient according to IUCN (2001) guidelines.

**Remarks.** The juvenile specimen (USNM 193866) from Rio Querari (Amazonas, Brazil) reported as *E. tuberculosa* by Duellman (1974) probably correspond to *T. shushupe*, but a taxonomic validation is needed to confirm its identity.

### **Taxonomic status of populations of *Trachycephalus typhonius* from Ecuador and Peru**

Several authors have discussed the considerable morphological variation in *T. typhonius* (Duellman 1971; McDiarmid 1968; Savage 2002) and have suggested that it may represent a species complex (Cochran and Goin 1970; Duellman 2005). The paraphyly of *Trachycephalus typhonius* (Fig. 1A) also suggests the existence of undescribed species.

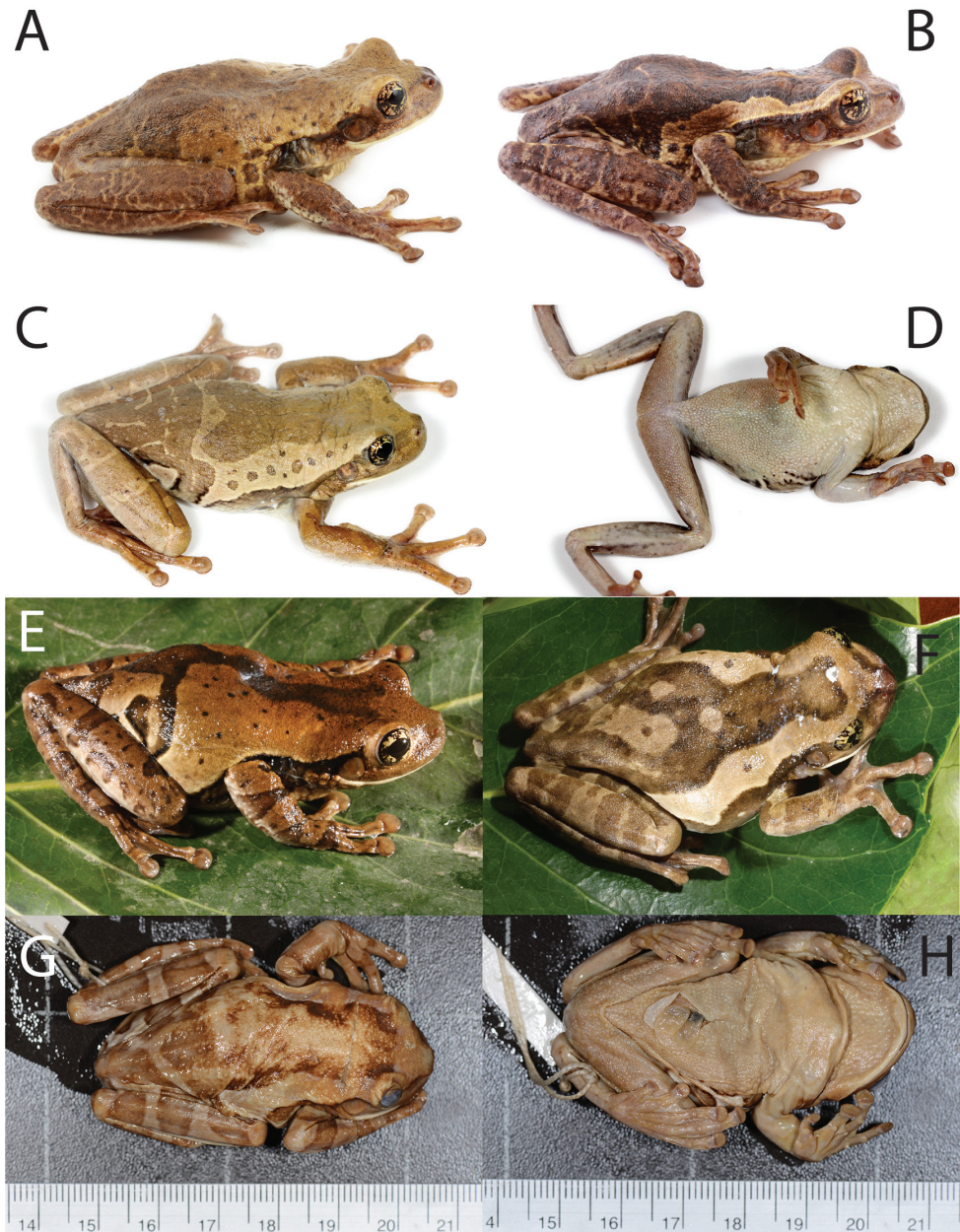
The resolution of the taxonomy of *T. typhonius* is challenging given the large number of available synonyms (Duellman 1971; Lavilla et al. 2010). However, the identification of the type locality of *T. typhonius* as Paramaribo, Suriname, by Lavilla et al. (2010) allows inferring the phylogenetic position of *T. typhonius sensu stricto*. The type locality is geographically close to samples from Guyana (AMNH-A 141142) and French Guiana (163MC), Clade C in Figure 1A. Therefore, we consider Clade C to represent *T. typhonius sensu stricto*. Two lineages from Ecuador and Peru are distinct from Clade C and each has an available name. Below we discuss their status.

### **“*Trachycephalus typhonius*” from the lowlands of western Ecuador**

Populations from western Ecuador are sister to a clade composed of *T. cunauaru*, *T. hadroceps*, *T. resinifictrix* and *T. typhonius*. Their phylogenetic position demonstrates that they are not conspecific with *T. typhonius sensu stricto* or other species of *Trachycephalus*. One binomial available for *Trachycephalus* from western Ecuador is *Hyla quadrangulum* Boulenger 1882 (type locality “western Ecuador”). Duellman (1971) synonymized *Hyla quadrangulum* under *T. coriaceus* stating that the holotype is “indistinguishable from *P. coriacea*”. He also questioned its type locality because “several species contained in the Fraser collections supposedly from western Ecuador have been found subsequently only in the Amazon Basin”. Our examination of a large series of specimens from western Ecuador and *T. coriaceus* from the Amazon basin show unequivocally that the holotype of *H. quadrangulum* (Fig. 11G–H) is not conspecific with *T. coriaceus*. Although the holotype has a quadrangular dorsal blotch, also present in *T. coriaceus*, we found the same pattern in specimens from western Ecuador (e.g., QCAZ 23427, 31302, 39361, 51746). Moreover, the holotype lacks the dark blue blotch above the arm characteristic of *T. coriaceus*. We conclude that the type locality is correct and *Hyla quadrangulum* is a valid species. The resurrection of *Hyla quadrangulum* Boulenger 1882 results in *Trachycephalus quadrangulum* (Boulenger 1882) comb. n.

Names under *T. typhonius* that could be senior synonyms to *T. quadrangulum* include *Hyla spilomma* Cope 1877 (type locality Veracruz, México), *Hyla paenulata* Brocchi 1879 (“versant occidental du Guatemala”), and *Hyla nigropunctata* Boulenger 1882 (several localities in Mexico). We exclude from this list synonyms with type localities east of the Andes based on our phylogeny, which shows that *T. quadrangulum* is restricted to the Chocó region. The phylogeny is consistent with a general biogeographic pattern showing that humid lowlands east and west from the Andes do not share amphibian species as result of the vicariant effect of the Andes (dos Santos et al. 2015). The phylogenetic and biogeographic evidence indicates that it is highly unlikely that available binomials with type localities in the Amazon basin or Guianan region are conspecific with *T. quadrangulum*. The resolution of the taxonomic identity of populations from Central America and the Chocó region is beyond the scope of this article. Nevertheless, the resurrection of *T. quadrangulum* provides a name to an evolutionary lineage separate from *T. typhonius*. Even if provisional, this new ar-





**Figure 11.** External morphology of *Trachycephalus quadrangulum* comb. n. from the Chocó region, western Ecuador. **A** QCAZ 39360, adult male, SVL = 74.1 mm, Caimito, Provincia de Esmeraldas, Ecuador **B** QCAZ 39361, adult male, SVL = 73.2 mm, same locality as A **C–D** QCAZ 51746, adult female, SVL = 80.3, Bosque Pacocha, Provincia Manabí, Ecuador **E** QCAZ 35406, adult male (SVL = 69.5), Bosque Protector Puyango, Provincia El Oro, Ecuador **F** QCAZ 28530, adult male (SVL = 64.5), Hacienda Santa Teresita, Provincia del Guayas, Ecuador; (G–H) Holotype of *Hyla quadrangulum*, adult female; scale, in cm, shown for reference. Photographs: **A–F** by S. R. Ron, **G–H** by Jeff Streicher.



rangement better reflects the evolutionary uniqueness of Chocoan populations and contributes to a more accurate characterization of the species diversity of the Chocoan amphibiofauna. It also improves our understanding of the conservation status of the *T. typhonius* species complex.

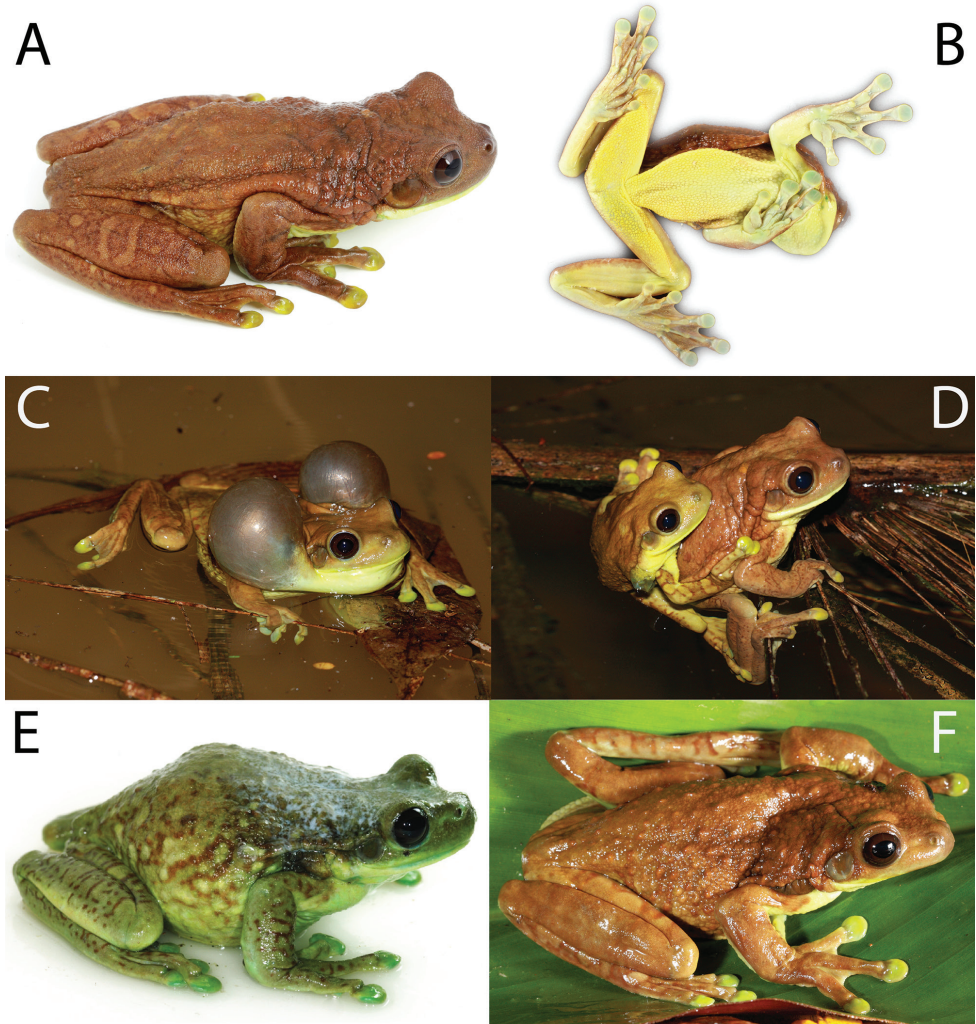
### **“*Trachycephalus typhonius*” from Amazonian Ecuador and Peru**

According to the phylogeny (Fig. 1A), populations from Amazonian Ecuador and Peru (Clade B) are sister to *T. resinifictrix* and this clade is sister to *T. typhonius sensu stricto*. Clade B is morphologically distinct from *T. resinifictrix* and comparisons of live individuals of clade B with photographs of the holotype of *T. typhonius* published by Lavilla et al. (2010) reveal that they belong to separate species as well. The holotype of *T. typhonius* (Uuzm 134) shows the clear iris with dark reticulations, also characteristic of populations from French Guyana (Fig. 8D–F). Clade B, in contrast, is characterized by having a dark brown iris without reticulations (Fig. 12).

Given its phylogenetic position and distinct external morphology, we conclude that Clade B is not conspecific with *T. typhonius*. We propose a solution for the status of those populations by resurrecting the binomial *Hyla macrotis* Andersson 1945 from its synonymy under *T. typhonius* proposed by Duellman (1971). The resurrection is based in the similarity between the holotype of *H. macrotis* (Fig. 13) and specimens from Clade B (Fig. 12). Within the region where the holotype was collected, “Río Pastaza watershed, Ecuador”, only clade B is morphologically similar. This allows us to confidently conclude that the holotype of *H. macrotis* and clade B are conspecific. The resurrection of *Hyla macrotis* results in *Trachycephalus macrotis* (Andersson 1945) comb. n.

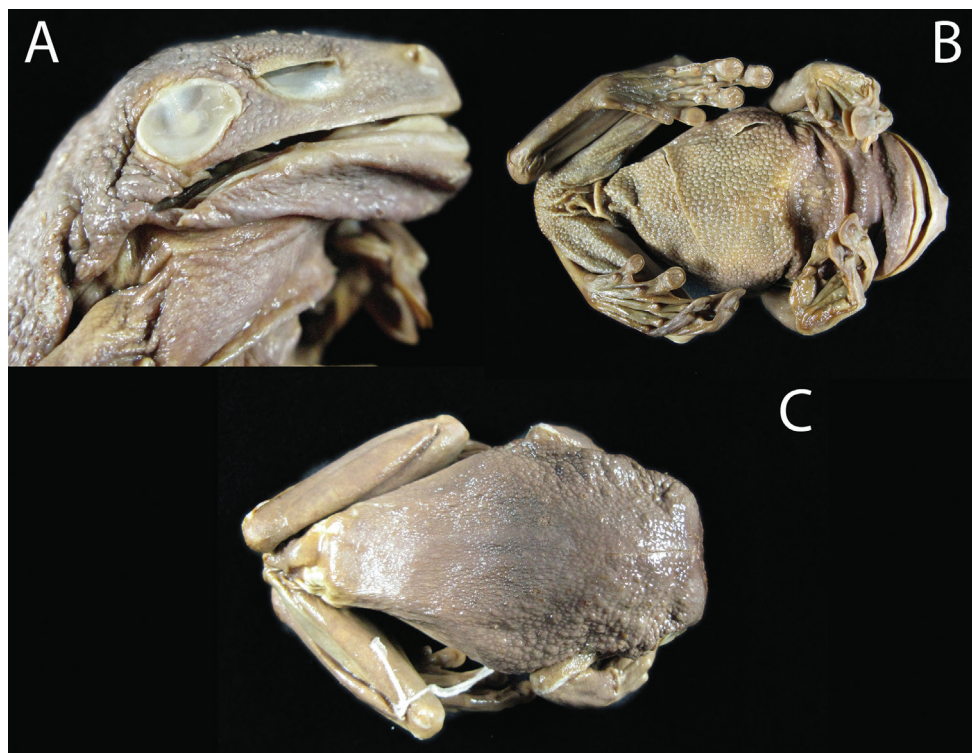
It seems unlikely that other synonyms under *T. typhonius* are senior synonyms to *T. macrotis* because most of them are from the Guianan region and Central America and are geographically distant from the range of *T. macrotis*. The resurrection of *T. macrotis* provides a name to an evolutionary lineage separate from *T. typhonius*. As in *T. quadrangulum*, the recognition of *T. macrotis* better reflects the biology of its populations.

We could not examine the voucher specimens for the GenBank sequences of *Trachycephalus* used in our phylogeny. Some of those identifications could be incorrect and should be reevaluated. For example, specimen KU 217753 is identified as *T. venulosus* (= *T. typhonius*) from the Chocó region of Ecuador. However, in the phylogeny it is nested within *T. cunauaru* from Amazonian Ecuador. Both the identification and locality are incongruent with its phylogenetic position suggesting that the tissue actually belongs to *T. cunauaru* from the Amazon region. The same error applies to GenBank sequence DQ347027, a sample that was obtained from the pet market. GenBank sequence JQ868532 (field number PS013) is identified as *T. venulosus* (= *T. typhonius*). The specimen is likely lost and its correct identification appears to be *T. resinifictrix*. Despite these potential identification errors, our taxonomic conclusions are only dependent on the correct identifications of the samples



**Figure 12.** External morphology of *Trachycephalus macrotis* comb. n. **A–B** QCAZ 39565, adult female, SVL = 101.1 mm, Reserva Zanjarauno, Ecuador **C** calling male, Reserva Zanjarauno, Ecuador **D** amplexant pair, QCAZ 39565, adult female (SVL = 101.12) and QCAZ 39566, adult male (SVL = 81.38), Reserva Zanjarauno, Ecuador **E** CORBIDI 9544, adult male, (SVL = 82.9), Peru **F** QCAZ 43017, adult male, SVL = 91.5 mm, Parque Nacional Yasuní, km 22 Pompeya-Iro road, Ecuador. Photographs by S. R. Ron except for (**E**) by A. Catenazzi.

of *T. typhonius* from Guyana and French Guyana, which are reliable. We obtained photographs of populations from French Guyana (Fig. 8) from the same collector who provided the tissues for individual 163MC. Therefore, the identification of the tissue should be correct. Sequences for the specimen from Guyana were published by Faivovich et al. (2005). They have a voucher specimen (AMNHA 121142), which should be correctly identified.



**Figure 13.** Holotype of *Hyla macrotis* Anderson 1945, NHRM 1958. **A** lateral view of the head **B** ventral view **C** dorsal view. The holotype is an adult female, SVL = 120 mm (Anderson 1945). Photographs by Bo Delling.

### Morphological comparisons between *Trachycephalus quadrangulum* and *T. macrotis*

The external morphology of *T. quadrangulum* is distinct from that of *T. macrotis*. Populations from western Ecuador (Fig. 1; Fig 11) are smaller (adult males average SVL = 69.0 mm, range 53.4–76.9,  $n = 9$ ; adult females SVL = 75.5 mm, 60.5–80.8 mm;  $n = 10$ ; Ron and Read 2011), have brown to cream disks on the fingers, and a bronze iris with irregular black reticulations (Fig. 11); *T. macrotis* (clade B, Fig. 1) are larger (adult males average SVL = 84.58 mm, range 69.8–91.5,  $n = 12$ ; adult females SVL = 103.2 mm, 93.9–118.7,  $n = 4$ ), have green discs on the fingers, and a dark brown iris (Fig. 12). The morphologic and genetic differences between both clades corroborate that they represent separate species.

### Discussion

These results show, for the first time, the evolutionary affinities of *Tepuihyla tuberculosa*, a species of controversial position within Hylidae (Faivovich et al. 2005; Savage and Kubicki 2010). The inclusion of *T. tuberculosa* within the clade *Tepuihyla* was

unexpected because it has a highly divergent morphology compared to other congeners. *Tepuihyla tuberculosa* and *T. shushupe* differ from all other *Tepuihyla* in having tuberculate skin texture in the dorsum, extensive webbing between the fingers and toes, serrate fringes on limbs, and calling behavior from tree-holes (Ayarzagüena et al. 1992; Duellman and Hoogmoed 1992; Gorzula and Señaris 1998; Kok and Kalamandeen 2008; Mijares-Urrutia et al. 1999). Except for size, all these characters are putative synapomorphies for *T. tuberculosa* and *T. shushupe* because they are absent in other *Tepuihyla* and its sister clade, *Dryaderces* + *Osteocephalus*. The distinctiveness of *T. tuberculosa* and *T. shushupe* is remarkable considering that both *Tepuihyla* and *Osteocephalus* lack phenotypic synapomorphies except for juvenile color pattern in *Osteocephalus* (Jungfer et al. 2013). Phytotelmata breeding, in contrast, is shared between all *Tepuihyla* and could be a synapomorphy for the genus or for a larger clade that also includes *Osteocephalus* and *Trachycephalus* because both genera have species that breed in phytotelmata (e.g., Gordo et al. 2013; Jungfer et al. 2000).

The morphological similarity between *T. tuberculosa* and *Ecnomiohyla* could be the result of convergence resulting from a similar reproductive mode and microhabitat. *Ecnomiohyla* are large frogs that call and lay eggs on tree holes partly filled with water (McCranie et al. 2003; Mendelson et al. 2008; Savage 2002; Savage and Kubicki 2010). Our observations of males of *T. tuberculosa* and *T. shushupe* calling from tree holes containing water suggest they share a similar reproductive mode. Convergence in external morphology and reproductive mode in *Ecnomiohyla* and Amazonian *Tepuihyla* suggests that both sets of characters are correlated. This hypothesis is reinforced by the morphological similarity between *T. tuberculosa* and *Trachycephalus cunauaru*, *Trachycephalus hadroceps* and *Trachycephalus resinifictrix* (Fig. 8). These three species of *Trachycephalus* are among the few Amazonian hylids that also call and breed on tree holes (Duellman and Trueb 1976; Gordo et al. 2013; Moser 2010). They represent an additional independent origin of this mode of reproduction. As in *Ecnomiohyla*, *Tepuihyla tuberculosa*, and *T. shushupe*, large size, mossy coloration, ornamented skin, and large hands characterize their external morphology.

The phylogenetic position of *T. tuberculosa* is consistent with the biogeography of Hylinæ. Most species of the tribe Hylini (including *Ecnomiohyla*) occur in Central and North America; only *Ecnomiohyla phantasmagoria* and three species of *Smilisca* are present in South America and none of them occur in the Amazon basin (Wiens et al. 2006). According to the biogeographic reconstruction by Wiens et al. (2011), the most recent common ancestor (MRCA) of Hylini inhabited either Central América or North America while the MRCA of *Ecnomiohyla* inhabited Central America. Therefore, the assignment of “*Hyla tuberculosa*” to the genus *Ecnomiohyla* was at odds with the distribution of the rest of the tribe. The tribe Lophiohylini, on the other hand, is primarily distributed in South America. The MRCA of *Tepuihyla* probably occurred in the Guyana region, the MRCA of *Osteocephalus* in the Amazon basin and that of *Tepuihyla* + *Osteocephalus* + *Dryaderces* in Guyana-Amazon or Amazon basin exclusively (Wiens et al. 2011). The phylogenetic relationships of *T. tuberculosa* reported here imply a more parsimonious biogeographic scenario because they do not require a



recent dispersal event between Central America and the Amazon Basin. Further analyses with a more complete taxon sampling are needed to more confidently infer the geographic origin of *Tepuihyla*.

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## Supplementary material 1

### **Majority rule consensus for maximum likelihood phylogenetic analysis based on Pyron (2014) matrix for genes 12S and 16S rRNA with additional sequences of Amazonian *Tepuihyla***

Authors: Santiago R. Ron, Pablo J. Venegas, H. Mauricio Ortega-Andrade, Giuseppe Gagliardi-Urrutia, Patricia Salerno

Data type: Phylogeny

Explanation note: The consensus was obtained from 100 non-parametric bootstrap pseudoreplicates. Bootstrap Support values are shown on nodes.

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## Supplementary material 2

### **Examined material**

Authors: Santiago R. Ron, Pablo J. Venegas, H. Mauricio Ortega-Andrade, Giuseppe Gagliardi-Urrutia, Patricia Salerno

Data type: Specimen and occurrence data

Explanation note: Specimens are deposited in the following institutions. Ecuador: Fundación Herpetológica Gustavo Orcés, Quito (FHGO); Museo de Zoología at Pontificia Universidad Católica del Ecuador, Quito (QCAZ). Peru: Centro de Ornitología y Biodiversidad, Lima (CORBIDI); Colección Referencial de Biodiversidad del Instituto de Investigaciones de la Amazonía Peruana, Iquitos (IIAP). United States of America: American Museum of Natural History, New York, (AMNH); National Museum of Natural History, Washington DC (USNM); Natural History Museum at the University of Kansas, Lawrence (KU). United Kingdom: Natural History Museum, London (BMNH). Venezuela: Museo de Historia Natural La Salle, Caracas (MHNLS).

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