

On the northernmost *Orchestina* species in China, with a first description of the female of *O. zhiwui* (Araneae, Oonopidae)

Ying Wang¹, Na Wan¹, Yanfeng Tong¹, Yuri M. Marusik^{2,3,4}

1 College of Life Sciences, Shenyang Normal University, Shenyang 110034, China **2** Institute for Biological Problems of the North RAS, Portovaya Str. 18, Magadan, Russia **3** Department of Zoology & Entomology, University of the Free State, Bloemfontein 9300, South Africa **4** Zoological Museum, Biodiversity Unit, FI-20014 University of Turku, Turku, Finland

Corresponding author: Yanfeng Tong (tyf68@hotmail.com); Yuri M. Marusik (yurmar@mail.ru)

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Abstract

Orchestina zhiwui Liu, Xu & Henrard, 2019, a species previously known only from males collected in Jiangxi Province, was found in Liaoning, ca 2200 km northeast of the type locality, including specimens of both sexes. The previously unknown female of this species is described, and the male is redescribed. A key to species of the genus *Orchestina* from China is provided.

Keywords

Fenghuang Mountain, Goblin spiders, Key to species, Taxonomy

Introduction

Orchestina Simon, 1882 is among the most speciose genera of the goblin spider family (Oonopidae), with 162 extant and 33 fossil species (WSC 2021). It has an almost global distribution and occurs in the Northern Hemisphere in the region south of 45°N (Marusik et al. 2018). In China, the genus is known from 13 species (Tong and

Li 2011, 2014; Liu et al. 2016, 2019), and the northernmost localities were previously known from Zhejiang Province (Fig. 4; Li and Lin 2016).

While studying spiders collected on Fenghuang Mountain in the Liaoning Province, China, we found *Orchestina* specimens; this locality is distant from their known range. A detailed study of the males revealed that the specimens belong to *Orchestina zhiwui* Liu, Xu & Henrard, 2019, a species known only from males collected in Jiangxi. The goals of our paper are to provide a key and distribution map to all species of *Orchestina* occurring in China, redescribe the male and provide the first description of the female *O. zhiwui* with detailed illustrations for both sexes.

Material and methods

The specimens were examined using a Leica M205C stereomicroscope. Details of body parts and measurements were studied under an Olympus BX51 compound microscope. Photos were made with a Canon EOS 750D zoom digital camera (18 megapixels) mounted on an Olympus BX51 compound microscope. Vulvae were cleared in lactic acid. For scanning electron microscopy (SEM), specimens were air-dried, sputter coated using IXRF SYSTEMS, and imaged with a Hitachi TM3030 SEM. Photos were stacked using Helicon Focus 7.6.1 and processed using Adobe Photoshop 21.1.2. All measurements in the text are expressed in millimeters. Terminology and taxonomic descriptions follow Henrard and Jocqué (2012) and Tong and Li (2011). All material studied is deposited in Shenyang Normal University (SYNU) in Shenyang, China.

The following abbreviations are used in the text and figures: **ALE** = anterior lateral eyes; **ARe** = anterior receptaculum; **AUS** = anterior uterine sclerite; **Mp** = median projection of clypeus; **PLE** = posterior lateral eyes; **PME** = posterior median eyes; **Po** = pore-like structure; **Pp** = posterior plate; **Pr** = protrusions; **Se** = serrula; **So** = slit organs; **Ss** = stomate-like structure; **To** = triangular outgrowth.

Taxonomy

Family Oonopidae Simon, 1890

Genus *Orchestina* Simon, 1882

Key to *Orchestina* species from China

Males of *O. colubrina*, *O. yinggezui*, and *O. zhengi* unknown; female of *O. multipunctata* unknown.

1 (0)	Males.....	2
–	Females.....	11
2 (1)	Carapace without any pattern.....	3
–	Carapace with reticulate pattern.....	5

- 3 (2) Endites without serrula ***O. sinensis* Xu, 1987**
 – Endites with serrula **4**
- 4 (3) Sclerotized part of endites smoothly curved; labium with a sclerotized, inverted Y-shaped pattern; sperm duct with 5 loops in prolateral view (Liu et al. 2019: figs 6B, F, 7A) ***O. bialata* Liu, Xiao & Xu, 2016**
 – Sclerotized part of endites straight; labium without Y-shaped pattern; sperm duct with 3 loops in prolateral view (Tong and Li 2011: figs 2A, 6A)
 ***O. aureola* Tong & Li, 2011**
- 5 (2) Bulb globular; embolus conical, with ventrally swollen base (e.g., Fig. 1K).... **6**
 – Bulb pear-shaped (e.g., Tong and Li 2011: fig. 8A) or globular, but with distal part leading to tube-shaped embolus (e.g., Tong and Li 2011: fig. 9C) **8**
- 6 (5) Palpal tibia distinctly wider than bulb (e.g. Fig. 2E); sperm duct with 1 or 3 loops in prolateral view **7**
 – Palpal tibia narrower than bulb; sperm duct with 2 loops in prolateral view (Xu 1987: fig. 11) ***O. thoracica* Xu, 1987**
- 7 (6) Clypeus with a median projection (Fig. 2H); endites with sub-apical triangular outgrowths (Figs 1H, 2A); sperm duct with 1 loop in prolateral view (Fig. 1I) ***O. zhiwui* Liu, Xu & Henrard, 2019**
 – Clypeus without a median projection; endites without outgrowths (Tong and Li 2011: figs 2B, 7D); sperm duct with 3 loops in prolateral view (Tong and Li 2011: fig. 7A) ***O. clavulata* Tong & Li, 2011**
- 8 (5) Bulb globular **9**
 – Bulb pear-shaped **10**
- 9 (8) Embolus distinctly longer than bulbus; endites with serrula, without modified setae (Liu et al. 2016: figs 1E, 2A, B, 3D, E, 4C, D)
 ***O. apiculata* Liu, Xiao & Xu, 2016**
 – Embolus shorter than bulbus; endites without serrula, with 2–3 strong setae on anterior margin (Tong and Li 2011: figs 2D, 9C).... ***O. tubulata* Tong & Li, 2011**
- 10 (8) Chelicerae with a small apophysis on proximal part; endites unmodified (Tong and Li 2011: figs 2C, 3C, D)..... ***O. truncatula* Tong & Li, 2011**
 – Chelicerae without a small apophysis on proximal part; endites with sharp, hook-shaped distal extension (Liu et al. 2016: figs 8D, 10B)
 ***O. multipunctata* Liu, Xiao & Xu, 2016**
- 11 (1) Carapace without any pattern **12**
 – Carapace with reticulate pattern..... **14**
- 12 (11) Epigaster with an oval mark, posteriorly with 2 nearly parallel, longitudinal deep colored stripes (Xu 1987: fig. 4)..... ***O. sinensis* Xu, 1987**
 – Epigaster without aforementioned character **13**
- 13 (12) Epigaster without a ventral triangular sclerotized plate; anterior part of cylindrical sclerite of endogyne greatly enlarged (Tong and Li 2011: figs 4A, 5D) ***O. aureola* Tong & Li, 2011**
 – Epigaster with a ventral triangular sclerotized plate; anterior part of cylindrical sclerite of endogyne not enlarged (Liu et al. 2016: fig. 5F, G)
 ***O. bialata* Liu, Xiao & Xu, 2016**

- 14 (11) Epigaster with a transverse cuticular fold (Tong and Li 2011: fig. 5I).....
 ***O. zhengi* Tong & Li, 2011**
 – Epigaster without the aforementioned character **15**
- 15 (14) Epigaster with a tubular sclerite visible through the tegument (Tong and Li
 2011: fig. 5F)..... ***O. tubulata* Tong & Li, 2011**
 – Epigaster without the aforementioned character **16**
- 16 (15) Epigaster with large, reddish or dark marks (e.g. Fig. 3E); endogyne with a
 medial cylindrical sclerite (e.g. Fig. 3F) **17**
 – Epigaster without large, reddish or dark marks; endogyne with a circular rather
 than a cylindrical sclerite (e.g. Tong and Li 2011: figs 4D, 5E) **20**
- 17 (16) Abdomen with 3 circumflex-shaped marks ***O. thoracica* Xu, 1987**
 – Abdomen with only 1 circumflex-shaped mark **18**
- 18 (17) Cylindrical sclerite of endogyne greatly enlarged distally (Tong and Li 2011:
 fig. 5D)..... ***O. clavulata* Tong & Li, 2011**
 – Cylindrical sclerite of endogyne not enlarged distally **19**
- 19 (18) Cylindrical sclerite encircled medially by tubular sclerite (Fig. 3F)
 ***O. zhiwui* Liu, Xu & Henrard, 2019**
 – Cylindrical sclerite without the aforementioned character (Liu et al. 2016:
 fig. 2D)..... ***O. apiculata* Liu, Xiao & Xu, 2016**
- 20 (16) Median part of the epigastric furrow with a vaulted, transverse opening (Tong
 and Li 2011: figs 4E, 10A)..... ***O. yinggezui* Tong & Li, 2011**
 – Epigastric furrow without the aforementioned character **21**
- 21 (20) Endogyne with an elongated anterior sclerite (Liu et al. 2019: fig. 10G).....
 ***O. colubrina* Liu, Henrard & Xu, 2019**
 – Endogyne with a very small, chestnut-shaped anterior sclerite (Tong and Li
 2011: fig. 5E)..... ***O. truncatula* Tong & Li, 2011**

***Orchestina zhiwui* Liu, Xu & Henrard, 2019**

Figures 1–4

O. zhiwui Liu, Xu & Henrard in Liu et al. 2019: 250, figs 12A–I, 13A–C, 14A–I, 15A–G.

Material examined. 1♂: CHINA, Liaoning Province, Fengcheng City, Fenghuang Mountain, Cuijiapuzi Village, sifting leaf litter; 26°24'35"N, 124°3'7"E, 130 m; 10.X.2020; Weihua Cheng, Ying Huang, Xiaochen Sun & Yanfeng Tong leg. (SYNU-327); 1♀: same data as previous (SYNU-332); 4♂, same data as previous (SYNU-328-329-330-331); 4♀: same data as previous (SYNU-333-334-335-336); 1♀: same locality; 18.X. 2017; Y.M. Marusik & Bingchuan Zhang leg. (SYNU-337).

Diagnosis. This species is similar to *O. aureola* Tong & Li, 2011 in the shape of the bulb and the short embolus, but can be distinguished by the reticulate carapace pattern (Figs 1A, 3A) in both sexes (vs. uniformly colored (Tong and Li 2011: fig. 1A)). Males can further be recognized by the median projection (Figs 1G, 2H) of the clypeus (vs.

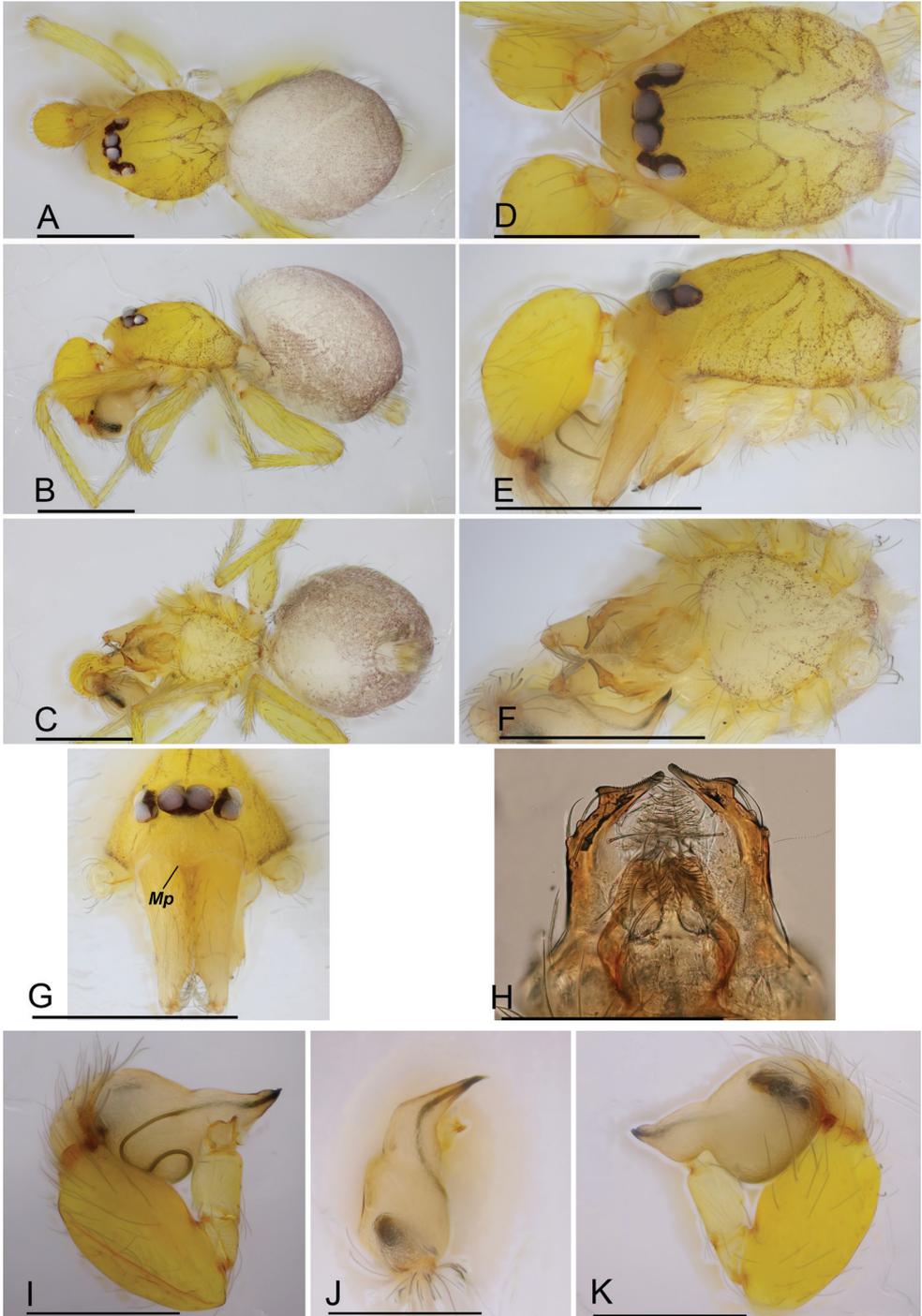


Figure 1. *Orchestina zhiwui* Liu, Xu & Henrard, 2019, male (SYNU-327) **A–C** habitus, dorsal, lateral and ventral views **D–G** prosoma, dorsal, lateral, ventral and anterior views **H** endites and labium, ventral view **I–K** left palp, pro-, dorsal and retrolateral views. Abbreviations: Mp = median projection of clypeus. Scale bars: 0.4 mm (**A–G**); 0.2 mm (**H–K**).

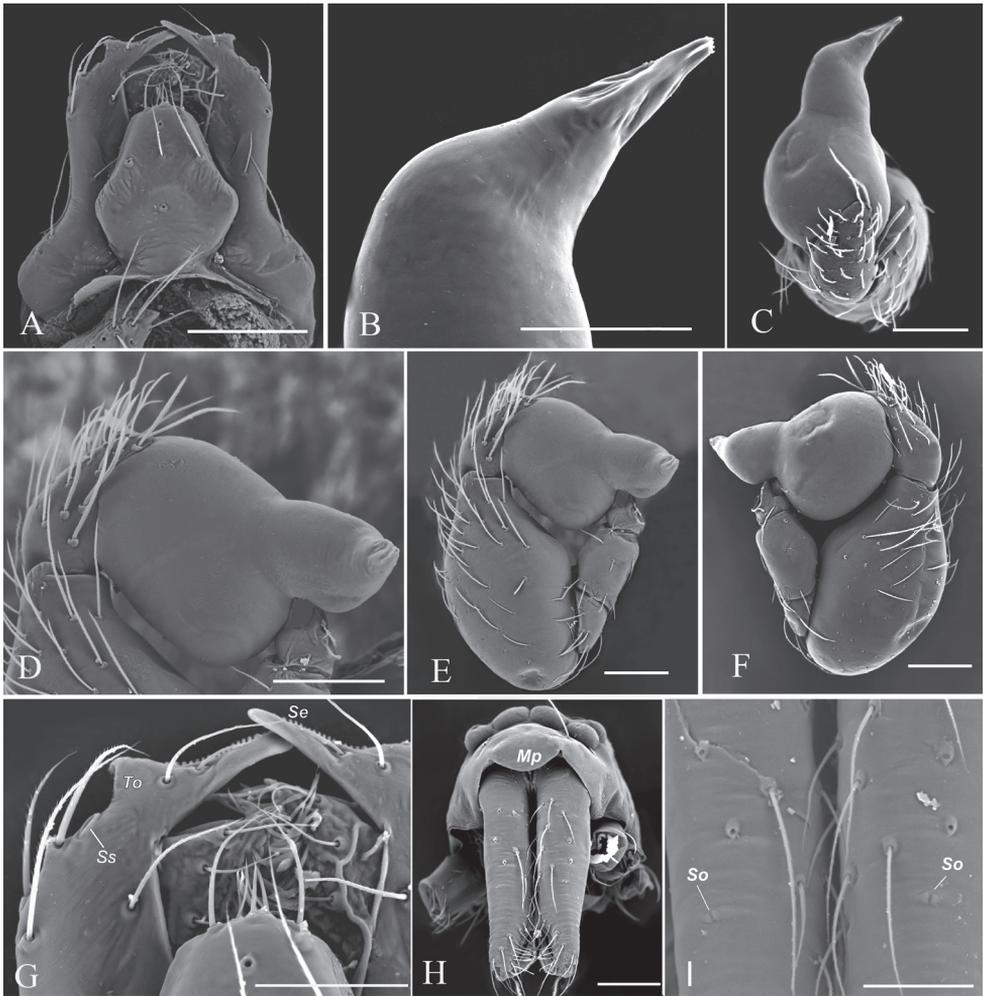


Figure 2. *Orchestina zhiwui* Liu, Xu & Henrard, 2019, male (SYNU-327), SEM **A** labium and endites, ventral views **B** distal part of palpal bulb, dorsal view **C**, **E**, **F** left palp, dorsal, proteral and retrolateral views **D** palpal bulb, proteral view **G** endites, ventral view **H** prosoma, anterior view **I** detail of chelicerae, highlighting slit organs. Abbreviations: Mp = median projection of clypeus; Se = serrula; So = slit organs; Ss = stomate-like structure; To = triangular outgrowth. Scale bars: 0.1 mm (**A**, **C**, **D**–**F**, **H**, **I**); 0.05 mm (**B**, **G**).

with straight anterior margin (Tong and Li 2011: fig. 3A)), the endites with sub-apical triangular outgrowths (Figs 1H, 2A, G) (vs. outgrowths absent (Tong and Li 2011: fig. 2A)) and short sperm duct forming one coil (Fig. 1I) (vs. with several coils (Tong and Li 2011: fig. 6A)). Females can be distinguished by the presence of the tubular sclerite (Fig. 3F) of the endogyne (vs. tubular sclerite absent (Tong and Li 2011: fig. 5A)).

Redescription of male (SYNU-327). *Body*: habitus as in Fig. 1A–C; body length 1.29. *Carapace* (Fig. 1D, E, G): 0.61 long, 0.44 wide; yellow, oval in dorsal view, surface smooth, with net-shaped pattern, with sparse long setae, pars cephalica slightly

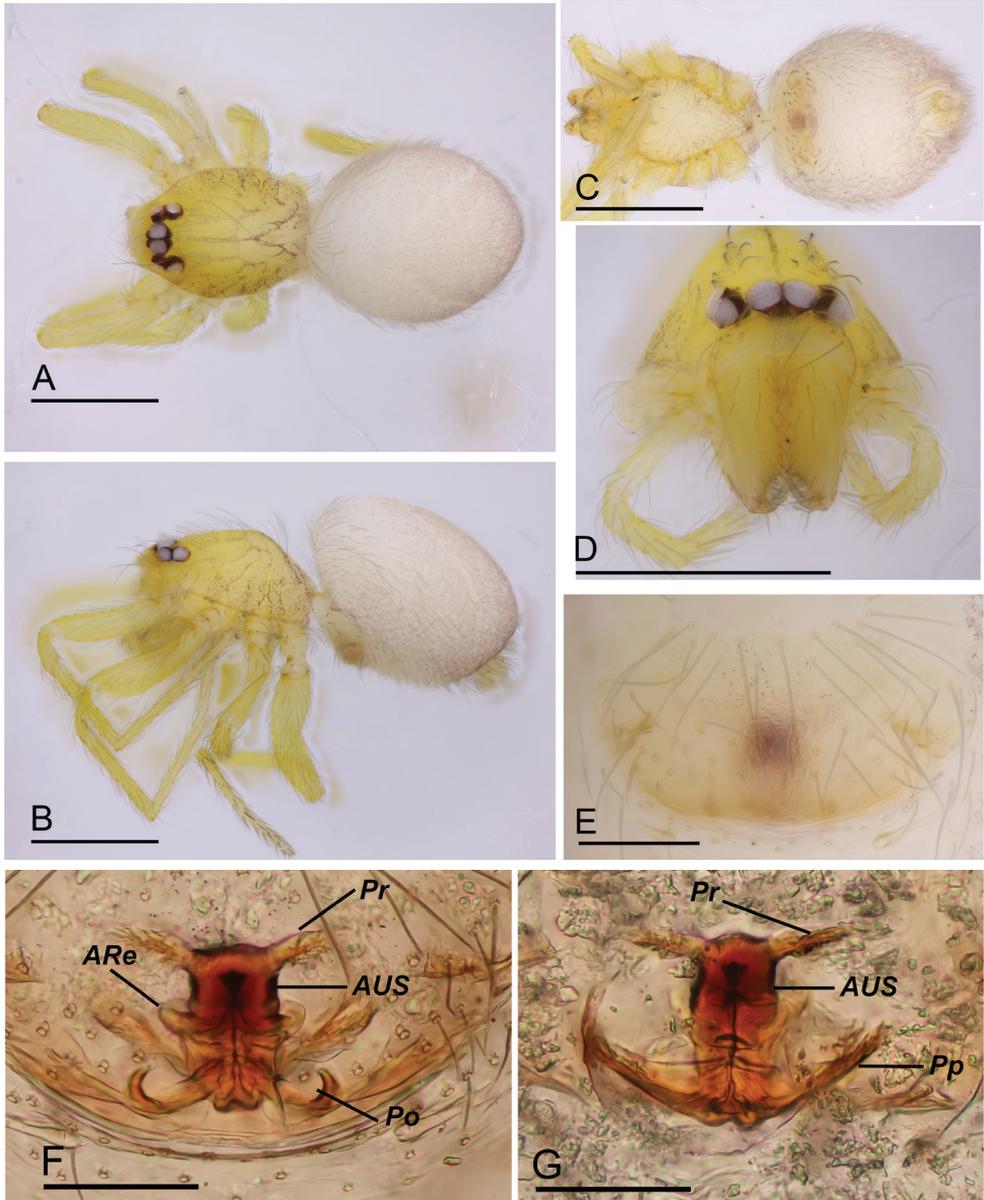


Figure 3. *Orchestina zhiwui* Liu, Xu & Henrard, 2019, female (SYNU-332) **A–C** habitus, dorsal, lateral and ventral views **D** prosoma, anterior view **E** epigaster, ventral view **F, G** endogyne, ventral and dorsal views. Abbreviations: ARE = anterior receptaculum; AUS = anterior uterine sclerite; Po = pore-like structure; Pp = posterior plate; Pr = protrusions. Scale bars: 0.4 mm (**A–D**); 0.1 mm (**E–G**).

elevated in lateral view, anterior margin straight in dorsal view, posterolateral corners rounded. **Eyes** (Fig. 1D, G): well-developed, PME largest; posterior eye row recurved from above; ALE-PLE touching, PLE-PME separated by less than PME radius, PME

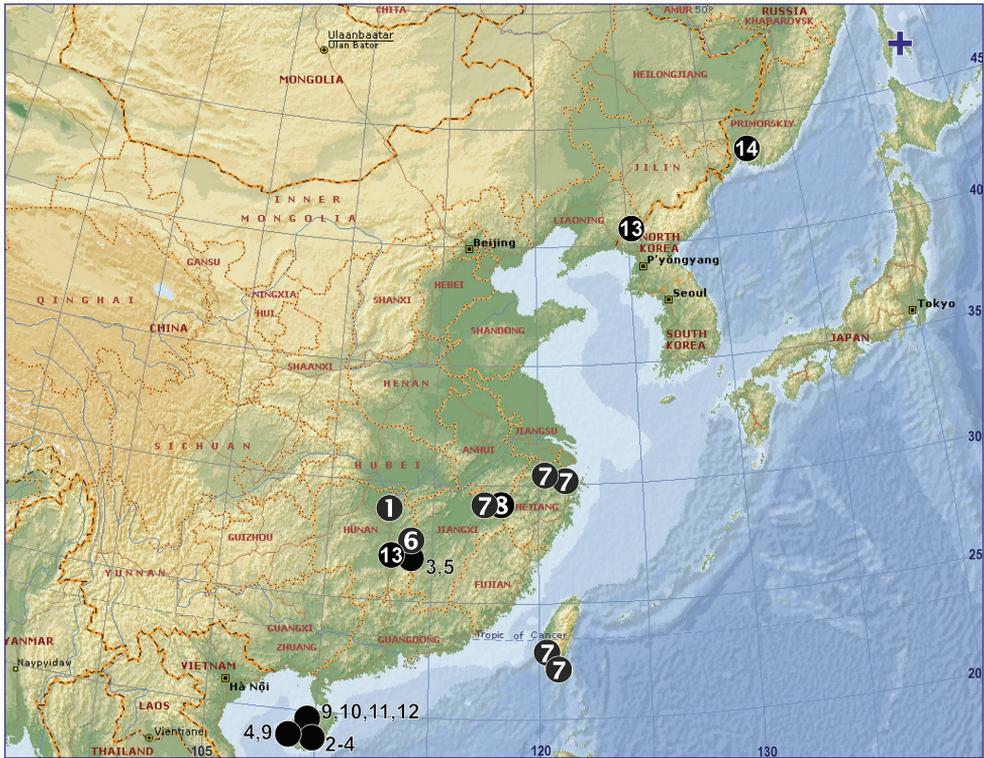


Figure 4. Distribution records of *Orchestina* species from China and the northernmost species in Asia. 1. *O. apiculata* Liu, Xiao & Xu, 2016; 2. *O. aureola* Tong & Li, 2011; 3. *O. bialata* Liu, Xiao & Xu, 2016; 4. *O. clavulata* Tong & Li, 2011; 5. *O. colubrina* Liu, Henrard & Xu, 2019; 6. *O. multipunctata* Liu, Xiao & Xu, 2016; 7. *O. sinensis* Xu, 1987; 8. *O. thoracica* Xu, 1987; 9. *O. truncatula* Tong & Li, 2011; 10. *O. tubulata* Tong & Li, 2011; 11. *O. yinggezui* Tong & Li, 2011; 12. *O. zhengi* Tong & Li, 2011; 13. *O. zhiwui* Liu, Xu & Henrard, 2019; 14. *O. storozhenkoi* (Saaristo & Marusik, 2004); +. *O. sakhalinensis* Marusik, Perkovsky & Eskov, 2018.

touching throughout most of their length. **Clypeus** (Figs 1D, E, G, 2H): with a median projection (Mp) in frontal view, sloping forward in lateral view, high, ALE separated from edge of carapace by 1.7 times their diameter; with pairs of long needle-like setae in front of ALE. **Sternum** (Fig. 1F): longer than wide, yellow, with scattered sepia pigmentation, surface smooth, without radial furrows between coxae; setae sparse, needle-like, evenly scattered, without hair tufts. **Mouthparts** (Figs 1F–H, 2A, G–I): chelicerae straight and long, 4 times longer than wide, with eye-shaped slit organ (So) in medial part; labium as an elongated hexagon, anterior margin not indented at middle; endites strongly sclerotized, except mesal part, basally with shallow diagonal furrow, with elongated extension bearing serrula (Se), sub-apical triangular outgrowth (To) and stomate-like structure (Ss). **Abdomen** (Fig. 1A–C): 0.74 long; grayish, with a pale narrow chevron. **Legs**: yellow, femur IV thickened, wider than femora I–III, without spines. **Palp** (Figs 1I–K, 2B–F): tibia enlarged and strongly swollen, 1.6 times longer than wide and 2 times longer than femur plus patella; cymbium ovoid; bulb stout, ba-

sal part globular, wider than tibia width, with ventral boss proximally; embolus short, conical, with ventrally swollen base; sperm duct with 1 loop on prolateral side, opening of sperm duct small, round, located on tip.

Description of female (SYNU-332). Same as male except as noted. **Body:** habitus as in Fig. 3A–C; body length 1.26. **Carapace:** 0.59 long, 0.42 wide. **Clypeus** (Fig. 3D): anterior margin straight. **Mouthparts:** chelicerae shorter; endites simple, with serrula. **Abdomen:** 0.69 long. **Epigaster** (Fig. 3E, F): without special external features; internal parts visible through integument. **Endogyne** (Fig. 3G): with medial cylindrical sclerite (AUS), encircled medially by tubular sclerite corresponding to anterior receptaculum (ARe), anterior part of cylindrical sclerite (AUS) with pair of lateral protrusions (Pr); posterior part with pair of pore-like structures (Po) on ventral side and posterior plate (Pp) on dorsal side.

Habitats. All specimens were collected in leaf litter in a mountain forest.

Distribution. China (Liaoning and Jiangxi) (Fig. 4).

Discussion

Morphology

While studying the morphology of *O. zhiwui*, we found a character that is undocumented in other *Orchestina* species: slit organs anteromedially on the chelicerae of the male (Fig. 2I). The chelicerae of many *Orchestina* species were quite well illustrated by Henrard and Jocqué (2012) and Izquierdo and Ramírez (2017), but this character does not appear in any descriptions or images. Possibly this character is related to the very long chelicera of the male.

Distribution

Although the record from Liaoning is the northernmost record of this species in China and extends its known distribution limits over 1200 km to the northeast (see Fig. 4), it is not the northernmost species of the genus in Asia. That record belongs to *O. storozhenkoi* (Saaristo & Marusik, 2004) described from the Maritime Province of Russia. It was described in a monotypic genus, *Ferchestina* Saaristo & Marusik, 2004, which was later synonymized by Platnick et al. (2012). This species is found on tree trunks (Saaristo and Marusik 2004) rather than in leaf litter like *O. zhiwui*. There is at least one more northern record of *Orchestina*, *O. sakhalinensis* Marusik, Perkovsky & Eskov, 2018, but it belongs to a fossil species from Sakhalin Island. This species was found in amber deposits near Starodubskoye, ca. 47°24'N (Marusik et al. 2018).

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Morphological and molecular evidence support the taxonomic separation of the medically important Neotropical spiders *Phoneutria depilata* (Strand, 1909) and *P. boliviensis* (F.O. Pickard-Cambridge, 1897) (Araneae, Ctenidae)

Nicolas A. Hazzi^{1,2}, Gustavo Hormiga¹

1 *The George Washington University, Department of Biological Sciences, Washington, D.C. 20052, USA*

2 *Fundación Ecotonos, Cra 72 No. 13^a-56, Cali, Colombia*

Corresponding author: Nicolas A. Hazzi (nicolashazzi@gwu.edu)

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Abstract

The species of the genus *Phoneutria* (Ctenidae), also called banana spiders, are considered amongst the most venomous spiders in the world. In this study we revalidate *P. depilata* (Strand, 1909), which had been synonymized with *P. boliviensis* (F.O. Pickard-Cambridge, 1897), using morphological and nucleotide sequence data (COI and ITS-2) together with species delimitation methods. We synonymized *Ctenus peregrinoides*, Strand, 1910 and *Phoneutria colombiana* Schmidt, 1956 with *P. depilata*. Furthermore, we designated *Ctenus signativenter* Strand, 1910 as a *nomen dubium* because the exact identity of this species cannot be ascertained with immature specimens, but we note that the type locality suggests that the *C. signativenter* syntypes belong to *P. depilata*. We also provide species distribution models for both species of *Phoneutria* and test hypotheses of niche conservatism under an allopatric speciation model. Our phylogenetic analyses support the monophyly of the genus *Phoneutria* and recover *P. boliviensis* and *P. depilata* as sister species, although with low nodal support. In addition, the tree-based species delimitation methods also supported the separate identities of these two species. *Phoneutria boliviensis* and *P. depilata* present allopatric distributions separated by the Andean mountain system. Species distribution models indicate lowland tropical rain forest ecosystems as the most suitable habitat for these two *Phoneutria*

species. In addition, we demonstrate the value of citizen science platforms like iNaturalist in improving species distribution knowledge based on occurrence records. *Phoneutria depilata* and *P. boliviensis* present niche conservatism following the expected neutral model of allopatric speciation. The compiled occurrence records and distribution maps for these two species, together with the morphological diagnosis of both species, will help to identify risk areas of accidental bites and assist health professionals to determine the identity of the species involved in bites, especially for *P. depilata*.

Keywords

Andes, Maxent, niche conservatism, Phylogenetics, species delimitation

Introduction

The species of the genus *Phoneutria* are considered aggressive and amongst the most venomous spiders in the world (Foelix 2010). Currently this genus includes eight large (17–48 mm) nocturnal species that are widely distributed in Central America and South America (Simó and Brescovit 2001; Martins and Bertani 2007). Their venom has a neurotoxic action and many researchers have analyzed its components and the epidemiology of the bites of these species (Gomez et al. 2002; Richardson et al. 2006; Bucaretschi et al. 2008, 2018; Garcia et al. 2008). Most of the clinically relevant bites by this genus are caused by *P. nigriventer* (Keyserling, 1891) and occur in Brazil (around 4,000 cases per year), with only 0.5% being severe (Bucaretschi et al. 2018).

Phoneutria boliviensis (Pickard-Cambridge, 1897) is a widespread species distributed from Central America (Costa Rica) to central South America (Bolivia), found across many types of ecosystems and geographical barriers that commonly divide other taxa (e.g. the Andes mountain system that separates many cis and trans Andean lowland lineages) (Bartoletti et al. 2018; Salgado-Roa et al. 2018). This species was originally described from the “Madre de Dios” Amazonian region in Bolivia and only the male palp was illustrated because the epigynum of the single female was damaged (Schiapelli et al. 1973). Schiapelli et al. (1973) illustrated the epigynum and the male palp based on other specimens identified by F.O. Pickard-Cambridge as *P. boliviensis* (a female from Ecuador and a male from Charaplaga, Bolivia). These authors report that male specimen at The Natural History Museum (at their time known as the British Museum of Natural History) in the vial with the syntypes of *Ctenus boliviensis* was a specimen in good condition of *P. nigriventer* (Keyserling, 1891). Subsequently, Simó and Brescovit (2001) indicated that they were not able to find the type specimens, and therefore they considered them lost.

At that time, *P. boliviensis* was known only to occur in the Amazon region, until Valerio (1983) reported this species in Costa Rica. Later, Simó and Brescovit (2001) revised the genus and synonymized several ctenids with *P. boliviensis*. Simó and Brescovit (2001) acknowledged the large morphological variation of *P. boliviensis* across its distribution range, but they interpreted this variation as intraspecific and diagnosed it by the truncated apex of the male retrolateral tibial apophysis.

During field work in Costa Rica, Panama, Colombia, Ecuador and Peru, and careful examination of museum specimens from these countries, we realize that

P. boliviensis can be separated into two distinct species. One trans-Andean species, *Phoneutria depilata* and the true *P. boliviensis* (cis-Andean) endemic of the Amazon region. Therefore, in this study we revalidated *P. depilata* that was synonymized with *P. boliviensis* by Simo and Brescovit (2001) and we designate a neotype of *P. boliviensis* collected from the Madre de Dios region of Peru. We follow an integrative taxonomic approach using molecular, morphological, and ecological data to support the separation of these two species. We also provided species distribution models (SDMs) for both species of *Phoneutria*. Furthermore, we also tested the hypothesis of niche conservatism under an allopatric speciation model (Wiens 2004; Wiens et al. 2011). This hypothesis states that the tendency of lineages to maintain their ancestral ecological niche, and their failure to colonize and adapt to new environments, separate ancestral taxa promoting speciation (Wiens 2004). Therefore, we expect that *P. depilata* and *P. boliviensis*, separated by the Andean mountain, present niche conservatism. *Phoneutria depilata* has been deeply studied in the literature as *P. boliviensis*, in works regarding its venom composition and toxicity (Estrada-Gomez et al. 2015; Valenzuela-Rojas et al. 2019), natural history (Hazzi 2014; Valenzuela-Rojas et al. 2020), geographic distribution (Valerio 1983; Hazzi et al. 2013), bite accidents to humans (Trejos et al. 1971; Florez et al. 2003) and introductions to Europe through banana shipments (Cathrine and Longhorn 2017; Rozwałka et al. 2017). Unlike *P. depilata*, except for brief field anecdotal mentions (Torres-Sánchez and Gasnier 2010), there is no such information for *P. boliviensis*. We have also provided additional information on the natural history of both species.

Methods

Museum abbreviations

The material examined and/or collected belongs to the following museums:

ICN-AR	Instituto de Ciencias Naturales-Universidad Nacional de Colombia, Bogota (E. Flórez);
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA (G. Giribet and L. Liebensberger);
MPUJ	Museo Pontificia Universidad Javeriana, Bogota (D. Forero);
MUSENUV	Museo Entomológico de la Universidad del Valle, Cali, Colombia (J. Cabra);
MUSM-ENT	Museo de Historia Natural, Lima, Peru (D. Silva);
MZUCR	Museo de Zoología, Escuela de Biología, Universidad de Costa Rica (G. Barrantes);
USNM	National Museum of Natural History, Smithsonian Institution, Washington DC, USA (H. Wood);
ZMB	Museum für Naturkunde der Humboldt Universität, Berlin, Germany (J. Dunlop).

Morphological examination and description of species

Specimens were preserved in 95% ethanol. Descriptions and terminology follows Simó and Brescovit (2001) and Martins and Bertani (2007). All measurements were taken in millimeters using the application of LAS in a Leica M205A stereomicroscope. Epigyna were digested with pancreatin solution (Álvarez-Padilla and Hormiga 2007) to enable study of internal structures. Digital images were taken with a Leica DFC425 camera on a Leica M205A stereomicroscope. Extended focal range images were composed using the software package Helicon Focus (version 6.7.1; www.heliconsoft.com) from Helicon Soft Ltd. The SEM images were taken using a LEO 1430VP scanning electron microscope at the Department of Biology of The George Washington University. For scanning electron microscope preparation, structures were cleaned ultrasonically, transferred to 95% and then to 100% ethanol for 10 min in each immersion before being critically-point-dried. The following abbreviations are used: **C** = conductor, **CD** = copulatory duct, **E** = embolus, **ELA** = epigynal lateral apophysis, **ELF** = epigynal lateral field, **ELG** = epigynal lateral guide, **EMF** = epigynal middle field, **FD** = fertilization duct, **IB** = internal bulge of the embolus, **LP** = lateral projection, **MA** = median apophysis, **RTA** = retrolateral tibial apophysis; **S** = spermatheca, **S** = subtegulum.

DNA-based analysis

Sampling design. Due to the widespread climatic niche of *P. depilata*, we sequenced seven specimens from Costa Rica, Ecuador and Panama that were collected from mountain to lowland areas, and from dry to rain forests ecosystems (Table 1). For *P. boliviensis*, we sequenced six specimens collected in three localities distributed from the north through to the southern part of the Peruvian Amazon, including one specimen from the type locality. In addition, we sequenced a specimen of *Phoneutria fera* Perty, 1833 collected in the Amazon of Ecuador and added two more sequences of the same species from GenBank (HM575999 and KY017637). As an outgroup, we sequenced one specimen of *Spinoctenus escalerete* Hazzi et al., 2018, *Ctenus datus* Strand, 1909, *C. aff. amphora* Mello-Leitão, 1930 and *Kiekie curvipes* (Keyserling, 1881). In addition, we also added a sequence of *Ctenus cruksi* Mello-Leitão, 1930, from GenBank (KY017633.1).

Specimens preserved in 95% ethanol were used for DNA extraction using the Qiagen DNEasy kit. Coxae and femora were used for extractions and the rest of the specimen was preserved as a voucher. Two gene fragments frequently used for species recognition and delimitation in spiders (e.g., Montes de Oca et al. 2016; Ballesteros and Hormiga 2018; Salgado-Roa et al. 2018) were amplified for analysis: the mitochondrial cytochrome c oxidase subunit I (~650 bp, COI) and the nuclear internal transcriber subunit 2 (~300 bp, ITS2). The former was amplified using the primers LCO1490 and HCOout (Folmer et al. 1994; Carpenter and Wheeler 1999) and ITS2 was amplified with the primers FITS and RITS (White et al. 1990; Agnarsson 2010) using the conditions previously reported in Ballesteros and Hormiga (2018).

Table 1. DNA taxon sampling generated in this study. Letters in the haplotype/allele column indicate if individuals have the same sequence in the COI or ITS-2 markers respectively; * indicate that the sequence is unique.

Species	Code	Country	Locality	Latitude / longitude	COI	ITS-2	Haplotype/ allele	Museum code
<i>Kiekie curvipes</i>	GH2776	Costa Rica	Tirimbina Reserve	10.4164, 84.1199	MW598451	MW599260	*/*	MCZ IZ 162190
<i>Ctenus aff. amphora</i>	GH2779	Brazil	Roraima	2.7375, -62.075		MW599262	-/*	MCZ IZ 162193
<i>Ctenus datus</i>	GH2778	Panama	Gamboa	9.1216, -79.7034	MW598452	MW599261	*/*	MCZ IZ 162191
<i>Spinoctenus escalerete</i>	GH2777	Costa Rica	Las Cruces Biological Station	8.7845, -82.9597	MW598442	MW599254	*/*	MCZ IZ 162192
<i>Phoneutria fera</i>	GH2794	Ecuador	Liana Lodge	-1.056, -77.524	MW598443	MW599255	*/A	MCZ IZ 162189
<i>Phoneutria depilata</i>	GH2793	Ecuador	Caimito, Esmeraldas	0.7005, -80.0741	MW598444	MW599256	*/A	MCZ IZ 162184-1
<i>Phoneutria depilata</i>	GH2787	Panama	Gamboa	9.1216, -79.7034	MW598448	MW599256	*/A	MCZ IZ 162179-1
<i>Phoneutria depilata</i>	GH2792	Costa Rica	Tirimbina Reserve	10.4164, -84.1199	MW598445	MW599256	*/A	MCZ IZ 162182-1
<i>Phoneutria depilata</i>	GH2791	Costa Rica	Cirenas	9.7199, -85.2119	MW598446		*/-	MCZ IZ 162181-1
<i>Phoneutria depilata</i>	GH2790	Panama	Puerto Amuelles	8.2841, -82.8691	MW598447		C/-	MCZ IZ 162180-1
<i>Phoneutria depilata</i>	GH2789	Costa Rica	San Isidro	10.0182, -84.0551	MW598447	MW599256	C/A	MCZ IZ 162183-1
<i>Phoneutria depilata</i>	GH2788	Panama	Puerto Amuelles	8.2841, -82.8691	MW598447	MW599256	C/A	MCZ IZ 162180-2
<i>Phoneutria boliviensis</i>	GH2780	Peru	ACP Panguana	-9.6137, -74.9352	MW598450	MW599258	B/C	MCZ IZ 162188-1
<i>Phoneutria boliviensis</i>	GH2781	Peru	Reserva Nacional Allpahuayo Mishana, Biological Station "José Alvarez Alonso"	-3.9663, -73.4368	MW598450	MW599259	B/B	MCZ IZ 162185-1
<i>Phoneutria boliviensis</i>	GH2782	Peru	Reserva Nacional Allpahuayo Mishana, Biological Station "José Alvarez Alonso"	-3.9663, -73.4368	MW598450	MW599259	B/B	MCZ IZ 162185-2
<i>Phoneutria boliviensis</i>	HG2783	Peru	Madre de Dios, Finca Las Piedras	-12.2259, -69.1142	MW598450	MW599258	B/C	MUSM-ENT 54118
<i>Phoneutria boliviensis</i>	HG2784	Peru	ACP Panguana	-9.6137, -74.9352	MW598450	MW599258	B/C	MCZ IZ 162188-2
<i>Phoneutria boliviensis</i>	HG2785	Peru	ACP Panguana	-9.6137, -74.9352	MW598449	MW599259	A/B	MCZ IZ 162188-3
<i>Phoneutria boliviensis</i>	GH2786	Peru	Reserva Nacional Allpahuayo Mishana, Biological Station "José Alvarez Alonso"	-3.9663, -73.4368	MW598449	MW599257	A/*	MCZ IZ 162185-3

Amplified products were sent to Macrogen USA (Rockville, Maryland) for sequencing. Contigs were formed using GENEIOUS 6.0.6 (<http://www.geneious.com>; Kearse et al. 2012) and COI sequences were checked for stop codon position, then queried against NCBI BLAST nucleotide database to check for contamination. Multiple sequence alignments were completed using the Q-INS-I search strategy using MAFFT. Gaps were treated as missing data for the phylogenetic analysis.

The best partitioning scheme and substitution models were explored using PartitionFinder 2.1.1 using the "greedy" search strategy and the correction of the Akaike information criterion (AICc). Four partition schemes were used as input data: first, second and third codon position for COI, and ITS-2 as a whole. Phylogenetic analyses

were performed using parsimony (MP), maximum likelihood (ML) and Bayesian inferences (BI). The parsimony analyses were carried out in TNT v. 1.5 (Goloboff et al. 2008; Goloboff and Catalano 2016) using 100 random addition sequences followed by TBR branch swapping algorithm and retaining 10 trees per replicate. Branch support was assessed using 1000 replicates of jackknife resampling (Farris et al. 1996). The Bayesian analyses were performed in MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) running 20 million generations from four Markov Chain Monte Carlo chains (MCMC). Trees and parameters were sampled every 1000 generations, 25% of the trees were discarded as burn-in and the remainder were used to calculate posterior probabilities. To check that the run was long enough for the chains to converge, the probabilities of the marginal parameters were observed in Tracer v. 1.5 (Rambaut et al. 2014b). The maximum likelihood analyses were performed with the package IQ-TREE 1.4.2 (Nguyen et al. 2015) and ultrafast bootstrap (UFBoot) were used as support measure (Minh et al. 2013).

To measure relationships between haplotypes, we constructed haplotype median-joining networks for each marker using PopArt v1.7 (Leigh and Bryant 2015). Due to the small genetic variation found in the allele network of the nDNA, we only calculated genetic distances for the mDNA. Uncorrected genetic distances (uncorrected p-distance) were calculated within and among *Phoneutria* species pairs using MEGA v.10 (Kumar et al. 2018). We performed both genetic distance and tree-based species delimitation methods in order to distinguish species of *Phoneutria*. The Automatic Barcoding Gap Discovery (ABGD) method (Puillandre et al. 2012) was used to identify breaks between the intraspecific and interspecific diversity (this is known as the barcode gap). This method relies on just pairwise genetic distances and therefore does not use phylogenetic information. Because ABGD was designed for single locus analysis, we only used this method with the COI sequences data. The analysis was performed through the web-server (<https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html>) using default settings and the uncorrected p-distances option.

The three remaining methods used are tree-based. First, we applied the general mixed Yule coalescent model (GMYC, Pons et al. 2006; Fujisawa and Barraclough 2013) using GMYC web server (<https://species.h-its.org/gmyc/>). This method models the Yule and coalescent processes on an ultrametric tree to determine the transition between intra and interspecific divergences. The ultrametric tree was estimated in BEAST 2.6.0 (Bouckaert et al. 2014) using a coalescent constant population as a tree prior. An uncorrelated relaxed clock with log normal distribution and GTR+Gamma substitution model for each codon was applied. We ran the analysis with 20 million generations of MCMC. Trees and parameters were sampled every 1000 generations, 25% of the trees were discarded as burn-in and the remainder were used to calculate posterior probabilities. To check that the run was long enough for the chains to converge, the probabilities of the marginal parameters were observed in Tracer v.1.5 (Rambaut et al. 2014b). TreeAnnotator version 2.6.0 (BEAST package) was used to build maximum clade credibility trees. For the second method, we applied a Bayesian framework of the multi-rate Poisson tree process (mPTP, Kapli et al. 2017). This

approach differs from GMYC in modelling coalescent and speciation events as relative to numbers of substitutions rather than time (Kapli et al. 2017). The minimum branch length was calculated and used as an input together with a likelihood tree (estimated as above). We ran the alignment with 2 independent replicates of MCMC of 5,000,000 generations, sampling every 1000 with a burn-in of 10% of the total length of the chain. GMYC and mPTP were designed to model single locus data, and because ITS-2 market lumped the three morphologically diagnosable species in one, we only show the results with COI.

Finally, we applied the Bayesian Phylogenetics and Phylogeography software (BPP, Yang 2015), a species delimitation approach based on the Multi Species Coalescent Model. This method uses a Bayesian modelling framework to estimate posterior probabilities of species assignment's multilocus gene trees, considering uncertainties in the coalescent process. We carried out joint species delimitation and species tree estimation (A11 analysis), assigning individuals *a priori* to a species based on the phylogeny and morphology. For the root age of the tree (τ) and the ancestral population size (θ), four combinations of priors were used. Combinations were among deep divergence times ($\tau = G(1, 10)$) and shallow divergence times ($\tau = G(2, 2000)$), and large populations sizes ($\theta = G(1, 10)$) and small populations sizes ($\theta = G(2, 2000)$). We performed 100,000 iterations, sampling every 2, using the 10% of the chain as burn-in. Because mtDNA has a different mutation rate and effective population size than nDNA, we did analysis with mtDNA+nDNA and mtDNA alone. As mtDNA obtained similar results, we only provide the results of the multilocus dataset. Currently, all species delimitation methods differentiate simplifying assumptions on the potential real parameter space relevant to species delimitation. Therefore, any of these assumptions could be violated easily in a particular empirical system, consequently only congruently delimited lineages across the different methods were considered as species (Carstens et al. 2013).

Species model distributions and niche comparisons

We estimated the distribution of *P. boliviensis* and *P. depilata* using the Maxent algorithm (Phillips et al. 2006; Elith et al. 2011). We used occurrence records from the literature, fieldwork and museum specimens examined by us (herein after LIFIMU database). In addition, we used iNaturalist (<https://www.inaturalist.org/>) as a novel procedure in spiders to obtain more distribution records for these species. iNaturalist is a citizen science platform that provides unprecedented access to documenting species diversity and distribution across the world (Hochmair et al. 2020). Users upload media (mostly images) of biological findings to the iNaturalist data portal that are later identified to some taxonomic level by the iNaturalist community. Because in most cases, spiders can only reliably be identified by examining their genitalia under the stereoscope, these new apps that rely on images for species identification have not been used on spiders, to our knowledge. However, for these medically relevant spiders, it is possible to identify them using only images (Fig. 1A–D). In the case of *P. depilata*, after extensive fieldwork and the study of museum specimens, we have been able to conclude that this is the only *Phoneutria*

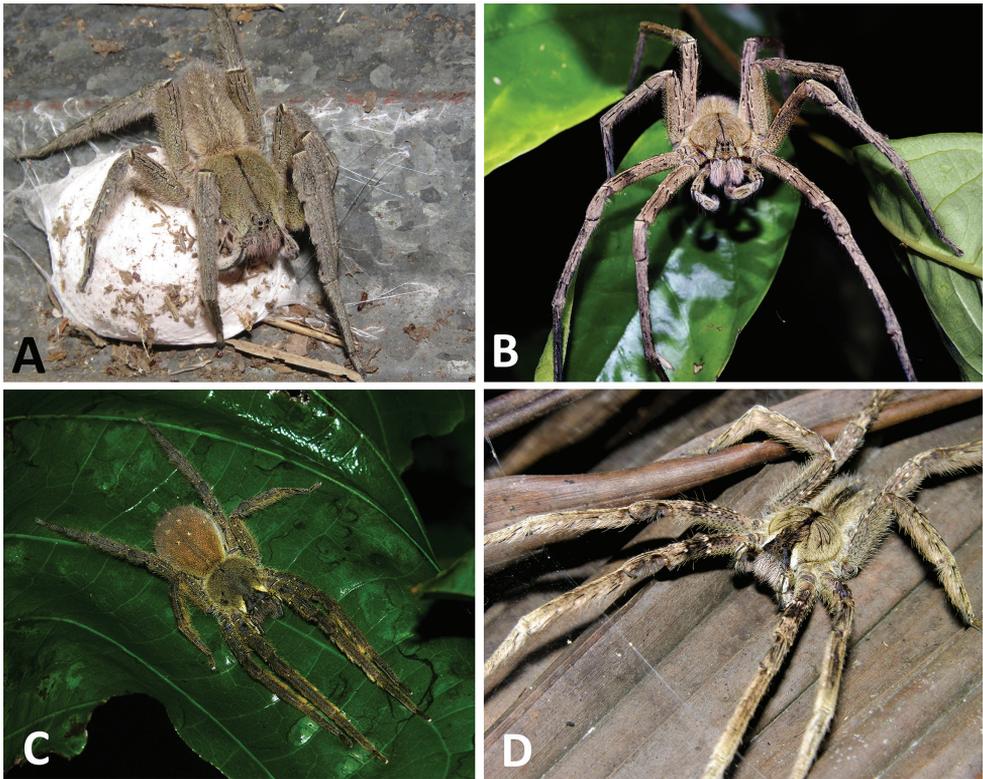


Figure 1. **A–D** Habitus of *Phoneutria* spp. **A** female of *P. depilata* with eggs sac (from Chiriquí, Panama) **B** female of *P. depilata* (from Barro Colorado Island, Panama) **C** female of *P. boliviensis* (from Madre de Dios, Peru) **D** male of *P. boliviensis* (from Napo, Ecuador).

species distributed in the Trans Andean region reaching Central America (Nicaragua). Thus, we can assign with high certainty *Phoneutria* images from these regions to *P. depilata*. *Phoneutria boliviensis* is endemic to the Amazonian region and it co-occurs with two more species of *Phoneutria*: *P. fera* and *P. reidyi* (F. O. Pickard-Cambridge, 1897). However, *P. boliviensis* is the only species that has two conspicuous lateral white bands in the anterior area of the carapace (Fig. 1C, D, 4A). In addition, males of *P. boliviensis* have dark black grooves in the carapace (Fig. 1D, 4A). Therefore, *Phoneutria* images from the Amazon region with these coloration features were identified as *P. boliviensis*.

To mitigate the impact of uneven sampling in our occurrence data, we applied a distance correction by taking only one point within a radius of 10 km. We obtained 19 bioclimatic predictor layers summarizing annual trends, seasonality and extremes in precipitation and temperature at a spatial resolution of 30 arc-seconds (i.e. 1 km²) from the WorldClim database (Fick and Hijmans 2017). In order to reduce collinearity of the predictor variables, we selected the following variables (Pearson <0.7): annual mean temperature (Bio1), mean diurnal range (Bio2), temperature seasonality (Bio4), annual precipitation (Bio12), precipitation seasonality (Bio15) and precipitation of warmest quarter (Bio18). The modelling area selected for *P. depilata* was the trans-Andean region

until Nicaragua and for *P. boliviensis* the Amazon and Orinoquia basins (cis-Andean region). We selected these regions considering species accessible area M (diagram by Barve et al. 2011) based on the geographical extension of gathered records of both species and the distribution of terrestrial ecoregions (Olson et al. 2001) and biogeographic regions of endemism (Morrone 2014) in the Neotropical Region.

We ran the models selecting a logistic output and random seed, and the maximum number of background points maintained at 10,000. To assess model performance, we applied k-fold cross validation procedure splitting the occurrences into training and testing records (70% and 30%, respectively), and replicating this process 15 times. Models were evaluated using the Area Under the Curve Metric (AUC) that compares model results with null expectations using a threshold-independent measure. We average the AUC values obtained in the replicates and created confidence intervals values to assess model significance from random model expectations (AUC > 0.5). In order to make the binary distribution maps, habitat suitability values were converted in presence and absence using the 5th percentile as the threshold value (Liu et al. 2005, 2013). In addition, areas with high probability of presence, but disjunct from areas where specimens have been recorded, were excluded from the prediction (Helgen et al. 2013).

To test niche conservatism among these two species, we used the niche similarity test (Peterson et al. 1999) and niche equivalency test (Graham et al. 2004) in the R package *Ecospat* (Di Cola et al. 2017). First, we performed an environmental principal component analysis (PCA-env) (Broennimann et al. 2012), calibrated with the accessible areas of the two species. We then created a grid of 100 × 100 cells over the ordination space, and a kernel density function was applied on the occurrence data in order to estimate Schoener's D index (Schoener 1968) with the first to principal components. This metric estimates niche overlap and D values ranging from zero, when niches do not overlap, and one, when niches completely overlap. Finally, the niche equivalence test and the niche similarity test were performed using 1000 simulated replicates in the R package *Ecospat* (Di Cola et al. 2017). Both metrics assess the statistical significance of a measured niche similarity against null model niches taken randomly from the modelling area. However, while niche equivalency test is estimated comparing the empirical D value with random relocation of the occurrence records on different distribution ranges (species lineages), the similarity test is estimated through random shifts of the niches within the available conditions of the study area (Warren et al. 2008; Broennimann et al. 2012).

Results

Phylogenetic and species delimitation analyses

The tree topologies of the parsimony, Bayesian and maximum likelihood analyses were congruent in recovering with high support metrics the monophyly of the genus *Phoneutria* and the three morphologically recognized species: *Phoneutria depilata*, *P. fera* and *P. boliviensis*. Therefore, only the likelihood tree is shown (Fig. 2), and the

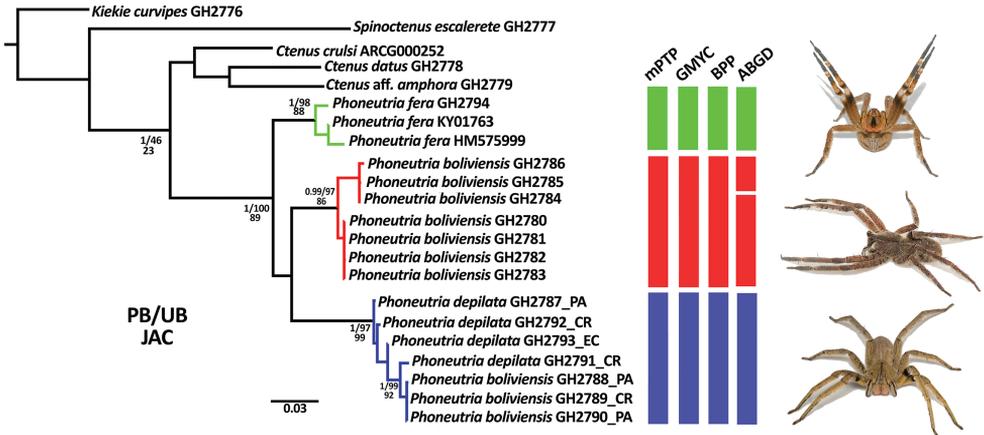


Figure 2. Maximum likelihood phylogenetic tree of the concatenated alignment of COI and ITS-2 markers. PB = posterior probabilities (derived from the Bayesian tree), UB = ultrafast bootstrap (derived from the likelihood tree), and JAC = jackknife (derived from the parsimony tree). Support metrics for nodes with low support (UB and PB < 0.95, and Jac < 70) are not shown. *Phoneutria* images: *P. fera* (top), *P. boliviensis* (center), *P. depilata* (bottom).

main discrepancies amongst analyses relate to the relationships of *Phoneutria* species mentioned below. While the likelihood and parsimony analyses indicated that *P. boliviensis* is the sister species of *P. depilata*, the Bayesian analysis suggests that *P. boliviensis* is the sister species of *P. fera*. The incongruent nodes receive very low support values of jackknife, posterior probabilities, and ultrafast bootstraps.

mtDNA haplotype networks (Fig. 3) revealed three major haplogroups that were congruent with the three species clades found in the phylogenetic analyses. *Phoneutria fera* haplotypes were separated from *P. boliviensis* by 29 mutations, and *P. boliviensis* was separated from *P. depilata* by 39 mutations. However, nDNA network (Fig. 3) shows that *P. depilata* and *P. fera* share alleles, and alleles of *P. boliviensis* are separated from this group just by one mutation (Fig. 3). Average genetic mDNA distance for *P. depilata*-*P. fera* was 8.2%, *P. depilata*-*P. boliviensis* 7.4%, and *P. fera*-*P. boliviensis* 6.1%. For intraspecific variation comparisons, the mean p-distance for *P. depilata* was 2%, *P. fera* 1% and *P. boliviensis* 1%.

The ABGD method indicates four species, separating two specimens of *P. boliviensis* (GH2782 and GH2783) as a separate species. Instead, the mPTP species delimitation analysis indicated with high support (ASV = 0.99) the delimitation of three morphologically recognizable species. In addition, The GMYC analysis produces the same result. The posterior probabilities for the three species in each model tested in BPP were always many times higher than the alternatives scenarios: 0.97 for deep divergence and large population size, 0.33 for deep divergence and small population size (the next most likely scenario was one species with 0.10), 0.71 for shallow divergence and small population size (the next most likely scenario was two species with 0.14) and 1.00 for shallow divergence and large population size. Thus, three parameter combinations suggest the same number of species.

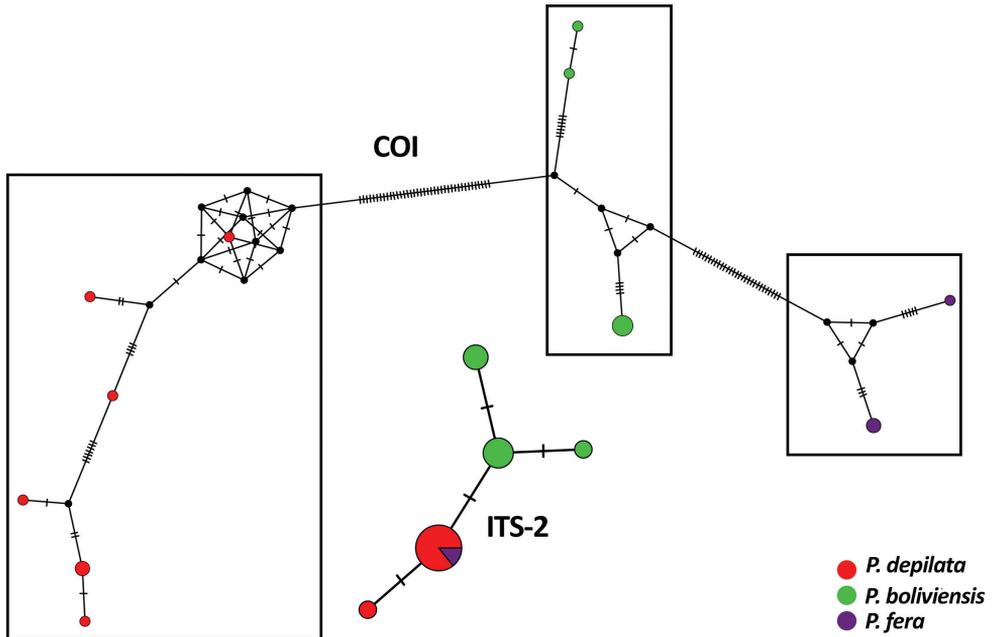


Figure 3. Median joining haplotype network of the COI and ITS-2 markers. Each tick mark on the network branches represents a mutation step and the three black boxes indicate the three haplogroups.

Occurrence records, potential distribution and niche conservatism

The Fig. 11A, B show the compilation of occurrence records for the two species of *Phoneutria* obtained from LIFIMU database and iNaturalist. Qualitatively, iNaturalist records match relatively well with the known distribution range of both species of *Phoneutria*, and the localities where the records came from are the same localities or the same regions of the localities of LIFIMU database. However, it is important to highlight that iNaturalist provided more occurrence records for both species than LIFIMU database. For instance, in *P. depilata* iNaturalist extends its distribution range to Honduras and there is more density of records in the inter-Andean Valley of Magdalena in Colombia, and the Choco region in Ecuador. In the case of *P. boliviensis*, iNaturalist provides more distribution records in the Amazon of Ecuador, where LIFIMU database has only one record.

Distribution models of *P. boliviensis* and *P. depilata* presented high performance compared to random expectations (AUC = 0.84 ± 0.10 SD for *P. boliviensis* and AUC = 0.84 ± 0.06 SD for *P. depilata*). The distribution model of *P. depilata* highlighted areas with different levels of suitability across Central and South America (Fig. 12A), with highest suitability values located in lowland and premontane areas, and from dry to tropical rain forest ecosystems. This species is well distributed in the inter-Andean Valleys of Magdalena and Cauca in Colombia. In addition, *P. depilata* is distributed in many areas of the Choco region of Ecuador and Colombia, and the Caribbean region

reaching to Honduras. For *Phoneutria boliviensis*, the distribution model (Fig. 12B) indicated suitable values in lowland ecosystems of the West Amazon including Brazil, Bolivia, Colombia, Ecuador, Peru and small portion of Venezuela (although without a confirmed occurrence record). The Fig. 13A, B depicts the binary maps of the predicted distribution range of both species of *Phoneutria*.

In the niche comparison analysis, the 1st and 2nd axis of the PCA-env explained 53.49% and 14.19% of the variance, respectively (Fig 14B). Niche overlap among *P. depilata* and *P. boliviensis* was moderate ($D = 0.31$, Fig. 14A). In addition, *P. depilata* presented a larger climatic niche area than *P. boliviensis*. The niche equivalency test indicated that climatic niche of these two species are more equivalent than expected by chance (Fig. 14C). Similarity tests also reject the null expectation between the two species (although the p-value of the similarity test *boliviensis-depilata* was marginal) (Fig. 14C). Thus, there is more significant climatic niche conservatism than expected by a null models between the two species of *Phoneutria*.

Taxonomy

Family Ctenidae Keyserling, 1877

Phoneutria Perty, 1833

Type species. *Phoneutria fera* Perty, 1833.

Phoneutria boliviensis (F. O. Pickard-Cambridge, 1897)

Figs 1C, D, 4A, B, 5A, C, 6A, B, 9A, D, 10A, B

Ctenus boliviensis: F. O. Pickard-Cambridge, 1897: 80, pl. 3, (female holotype from Madre de Dios, Bolivia, fig. 3a-c (male), The Natural History Museum, London not found; see Schiapelli and Gerschman de Pikelin 1973: 36, and Simó and Brescovit 2001: 74.

Ctenus nigriventroides Strand, 1907: 426 (female holotype from Bolivia, Museum für Natur und Umwelt der Hansestadt, Lübeck presumed lost; see Eickstedt 1979: 111, and Simó and Brescovit 2001: 74).

Ctenus valdehirsutulus Strand, 1910: 318 (syntypes: female from Sara, W. Bolivia, 60 m, 14 March 1907, J. Steinbach leg., in ZMB 30615; female from Sara, Dpto. Sta. Cruz de la Sierra, Bolivia, 500 m, Steinbach, in ZMB 30616, see Simó and Brescovit 2001: 74).

Ctenus nigriventroides: Petrunkevitch, 1911: 475 (only citation of Strand 1907), 735.

Ctenus chilesicus Strand, 1915: 128 (female holotype from Chile, 1902, O. Hohenemser leg., in SMF-4557).

Phoneutria boliviensis: Schmidt, 1954: 414; 1956: 28; Bücherl 1968: 188; 1969a: 49; Schiapelli and Gerschman de Pikelin 1973: 31, 33–38 (redescription male and female).

Phoneutria nigriventroides: Bonnet, 1958: 3621 (in part, only material from Bolivia); Eickstedt 1979: 111.



Figure 4. **A, B** dorsal view of the carapace and ventral view of the abdomen of *P. boliviensis* (male from Finca Las Piedras, Madre de Dios, Peru) **C, D** dorsal view of the carapace and ventral view of the abdomen of *P. depilata* (male from Chiriquí, Panama). Scale bars: 2.00 mm.

Neotype (herein designated; see comments below). Peru: Male from Madre de Dios, Puerto Maldonado, Finca Las Piedras (12.2259°S, 69.1142°W, 260 m), 20.IX.2019, N. Hazzi coll. (MUSM-ENT 54118).

Justification of the neotype designation. We have designated a neotype for *P. boliviensis* in accordance with Article 75 of the International Code of Zoological Nomenclature (ICZN 1999). The type material of *Ctenus boliviensis* was considered lost after examination of the spider material at the Natural History Museum, London (Simó and Brescovit 2001). The epigynum of the syntype female was reported to be damaged by Schiapelli and Gerschman (1973). In absence of type material, we consider necessary to designate a neotype to clarify the taxonomic status of *P. boliviensis*. Although the original type locality of *P. boliviensis* is the Madre de Dios area of Bolivia (F.O. Pickard-Cambridge 1897), the locality of the neotype (in Peru) belongs to the same region. The region takes its name from the Madre de Dios river, which is part of the Amazon river watershed. The Madre de Dios basin spreads across Bolivia and Peru. This area is called Inambari and is considered as a single biogeographic area because of its unique composition of species (Da Silva et al. 2005). In addition, the neotype locality is very close to the Bolivian border (30 km in linear distance).

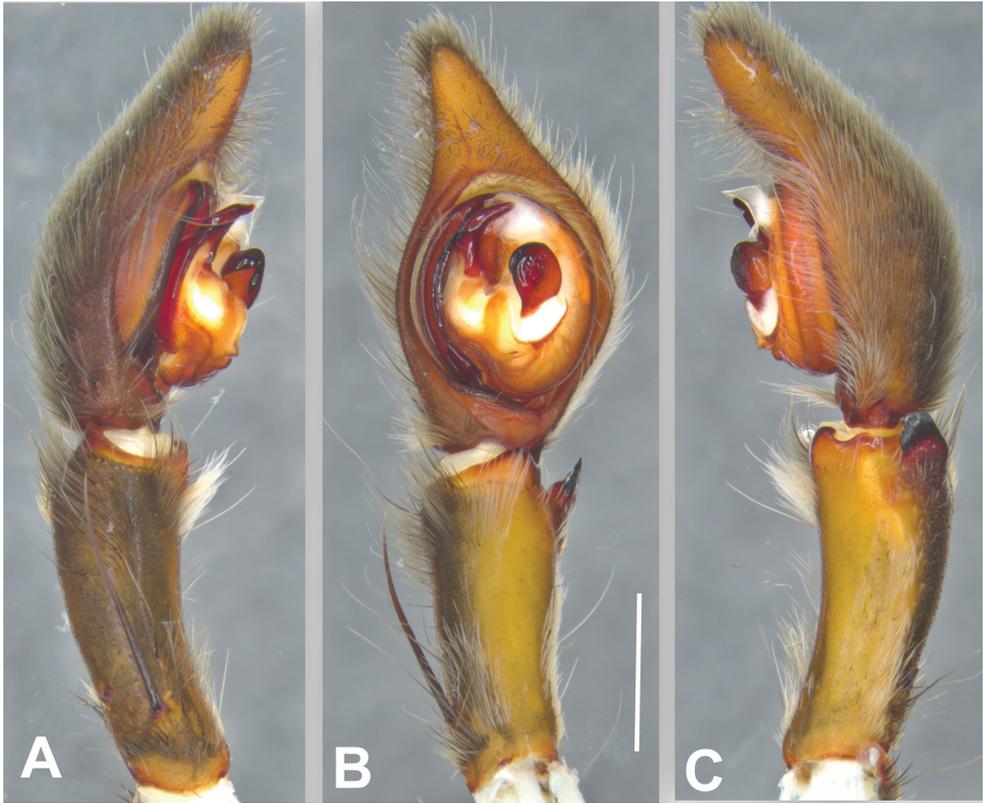


Figure 5. *Phoneutria boliviensis* (from Finca Las Piedras, Madre de Dios, Peru), left male palp **A** prolateral view **B** ventral view **C** retrolateral view. Scale bar: 2.00 mm.

Comments. The syntypes of *Ctenus valdehirsutulus* were revised by Simó and Brescovit (2001) and this species was deemed to be a junior synonym of *Phoneutria boliviensis*. The syntype localities of *valdehirsutulus* (the Sara Province of Bolivia, in the Santa Cruz Department) are within the distribution area of *boliviensis* which corroborates the synonymy proposed by Simo and Brescovit (2001). The type of *Ctenus chilesicus* comes from an undisclosed locality in Chile and was deemed to be conspecific with *Phoneutria boliviensis* by Simó and Brescovit (2001). The records of *Phoneutria* from Chile are of introductions of *P. fera* (Zapfe 1963; Canals et al. 2004). Although we have no reason to question the synonymy of *chilesicus* with *Phoneutria boliviensis*, which was based on the examination of type specimens, future work should revise the type of *chilesicus*. We suspect that the only specimen of *chilesicus* is an introduction of an already described species (as suggested by Simó & Brescovit) or the result of labeling error.

Other material examined. Colombia: Caqueta: two males, Universidad de la Amazonia (1.4998°N, 75.6632°W, 240 m) Florencia, 30.VII.2019, N. Hazzi, L. Martínez, and E. Across-Valencia (MUSENUV); Amazonas: Comunidad Monifue Amena (4.1128°N, 69.9311°W, 70 m) 03.X.2005 (MPUJ). **Peru:** Loreto: two males and two females, Reserva Nacional Allpahuayo Mishana, Biological Station “José Alvarez Alonso” (3.9663°S, 73.4368°W, 120 m) Iquitos, 02.IX.2019, N. Hazzi, E.

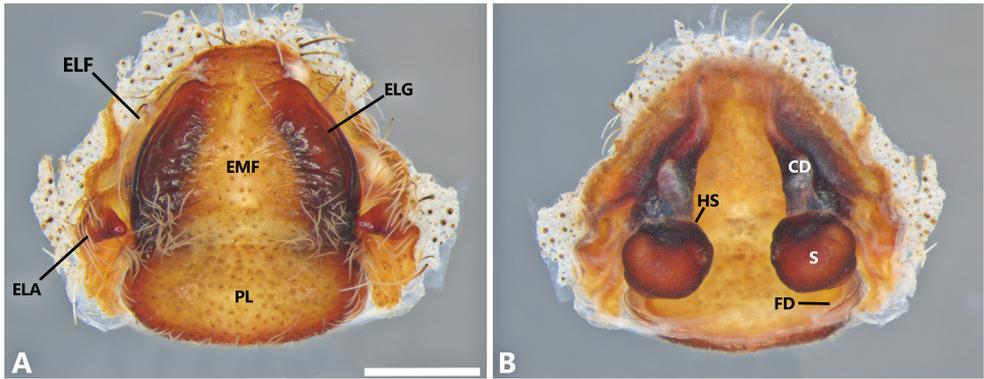


Figure 6. *Phoneutria boliviensis* (Finca Las Piedras, Madre de Dios, Peru), female genitalia **A** epigynum, ventral view **B** vulva, dorsal view. CD = copulatory duct, ELA = epigynal lateral apophysis, ELF = epigynal lateral field, ELG = epigynal lateral guide, EMF = epigynal middle field, FD = fertilization duct, HS = head of spermatheca, PL = posterior lobe, S = spermatheca. Scale bar: 1.00 mm.

Vargas and G. Gagliardi (MCZ IZ 162185); one female and one male, Universidad Nacional de la Amazonia Peruana (3.8466°S, 73.3671°W, 110 m), Puerto Almendras, Iquitos, 01.IX.2019, N. Hazzi and E. Vargas (MCZ IZ 162186?); one female, San Rafael (3.5617°S, 73.1191°W, 90 m), 04.IX.2019, N. Hazzi and E. Vargas (MCZ IZ 162187?); Inahuaya, Cerros Orullana (7.1158°S, 75.2709°W, 150 m), 9.VII.1988, R. Fernandez and P. Hocking (MUSM-ENT 511187); Ucayali: four females and four males, Panguana Biological Research Station (9.6137°S, 74.9352°W, 220 m), 15.IV.2019, N. Hazzi (MCZ IZ 162188); Madre de Dios: one female, same data as neotype (MUSM-ENT 054122); one female Zona Reservada de Manu (11.96°S, 71.30°W, 250 m), 01.X.1987, D. Silva & J. Coddington (USNM); three females and one male, Zona Reservada Tambopata (12.83°S, 69.283°W, 290 m) (MUSM-ENT 507653, 507657, 507658 and 507659); Zona Reservada Pakitza (11.96°S, 71.30°W), 26.V.1987, (MUSM-ENT 509196), one male, Explorers Inn (12.8455°S, 69.2942°W), 19.VI.2009 (MUSM-ENT 500807); Santuario Nacional Pampas del Heath (12.042°S, 71.7248°W), 27.VI.1987, V. Morales (MUSM-ENT 509147); Huánuco: one female and one male, Dantas la Molina (9.633°S, 75°W, 270 m), SW Puerto Inca, 18.V.1987 (MUSM-ENT 507582, 511349); San Martin: one female, Juanji (7.1669°S, 76.7395°W, 350 m), 16.VIII.1998 (MUSM-ENT 511348); Pasco: one male, Santa Maria, Rio Palcazu (9.9369°S, 75.2471°W), 8.III.1998, P. Hocking (MUSM-ENT 511043); Amazonas: one male, Condorcanqui (4.59841°S, 77.8599°W), 18.VII.1994, M. Ortega (MUSM-ENT 509062).

Diagnosis. Males of *P. boliviensis* resemble those of *P. depilata* by the truncated apex of the RTA (Fig. 9C, D), but differ by the smaller tegulum (Figs 5B, 9A), round median apophysis enlarged at the base (Figs 5B, 9A), locking lobes located posteriorly (Figs 5B, 9A), in contrast with the narrow base of the median apophysis and pronounced lateral locking lobes in *P. depilata*; and embolus without internal bulge (Figs 5B, 9A). Females of *P. boliviensis* also resemble those of *P. depilata* by the general configuration of the epigynum but differ by the wider area of the EMF (Figs 6A, 10A),

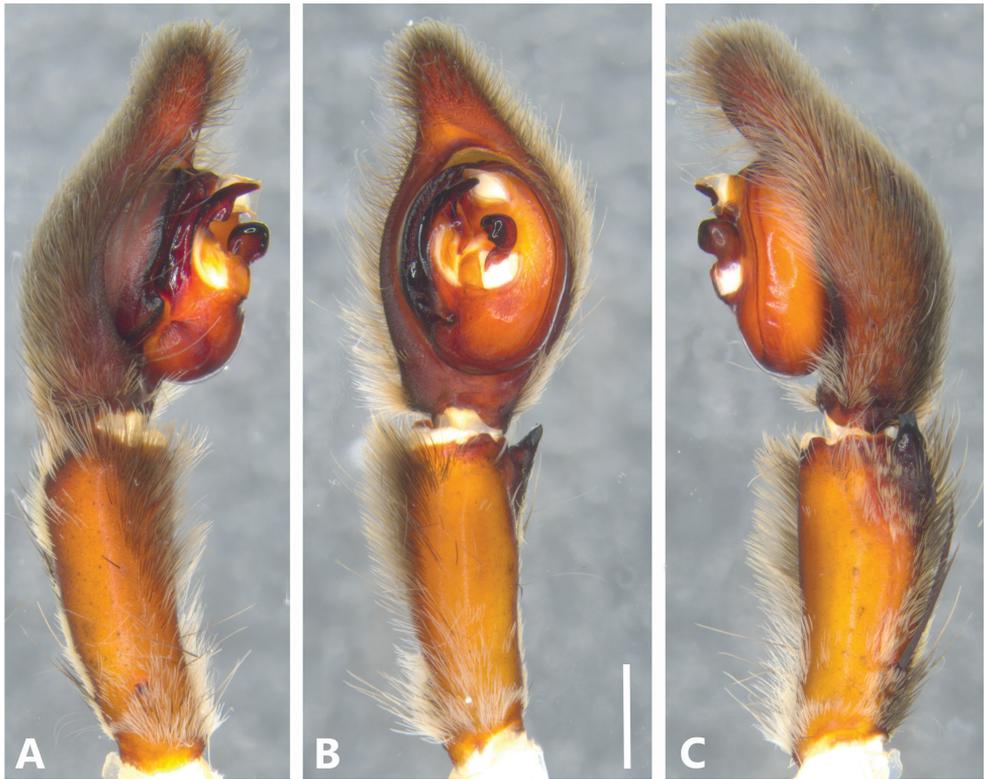


Figure 7. *Phoneutria depilata* (from Puerto Amuelles, Chiriqui, Panama), left male palp **A** prolateral view **B** ventral view **C** retrolateral view. Scale bar: 2.00 mm.

copulatory ducts strongly sclerotized (Figs 6B, 10B), and reduced spermatheca heads (Figs 6B, 10B), in contrast with the less sclerotized copulatory ducts and larger spermatheca heads of *P. depilata*. In addition, both females and males can be distinguished from *P. depilata* and the remaining Amazonian species (*P. perty* and *P. fera*) by the two lateral conspicuous white-yellow bands in the anterior area of the carapace which are also absent in all other congeneric species (Fig. 4A).

Description. Male (from Madre de Dios, Puerto Maldonado, Finca Las Piedras, Peru; MUSM-ENT 54118). Coloration (Figs 1D, 4A, B): Carapace brown with a longitudinal black line, transversal black stripes and two lateral conspicuous white-yellow bands in the anterior area. Ocular area with dark black-blue setae and back oblique band from PLE to anterior dorsal shield of prosoma edge. Chelicerae brown. Sternum, endites and labium yellowish-brown. Dorsal abdomen yellow-brown, with a longitudinal black line reaching to the median region; ventrally dark brown with four series of pale brown dots. Total length 20.93. Carapace 10.91 long and 13.18 wide, eye diameters: AME 0.41, ALE 0.23, PME 0.72, PLE 0.46. Clypeal height 0.26, sternum 4.57 long, 4.00 wide; labium 1.31 long, 0.84 wide. Leg measurements: I: femur 12.20, patella 4.20, tibia 13.52, metatarsus 17.98, tarsus 5.00, total 52.90 ; II: 17.60, 7.49,

18.81, 13.65, 3.94, total 61.49; III, 14.09, 6.62, 12.42, 8.18, 2.43, total 43.74; IV 11.79, 4.42, 10.8, 12.58, 3.42, total 43.01. Leg spination: I tibia v2-2-2-2, d1-1-1, p0-1-0, r1-1-0, metatarsus v2-2-2, p1-0-0 r1-0-0, II tibia v-2-2-2-2, d1-1-1, p1-1-0, r1-1-0, metatarsus v2-2-2, p1-0-0 r1-0-0, III v2-2-2, d1-1-1, p1-0-1-0, r1-0-1-0, metatarsus v2-2-2-2, p1-1-2, r1-1-2, IV tibia v2-2-2, d1-1-1, p1-0-1-0, r1-0-1-0, metatarsus v2-2-2-2, d0-1-0, p1-1-2, r1-1-2. Palp. RTA small and truncated at the apex (Figs 5C, 9C); embolus curve without internal bulge (Figs 5B, 9A); cup-shaped median apophysis constrained at the base (Figs 5B, 9A); conductor membranous, hyaline and C-shaped (Figs 5B, 9A); tegulum with probasal rounded projection (Figs 5B, 9A).

Female (from Madre de Dios, Puerto Maldonado, Finca Las Piedras, Peru; MUSM-ENT 054122). Coloration (Figs 1C, 4A, B): Carapace brown with a longitudinal black line and two lateral conspicuous white-yellow bands in the anterior area. Ocular area with dark brown setae and back oblique band from PLE to anterior dorsal shield of prosoma edge. Chelicerae brown with red setae. Sternum, endites and labium yellowish-brown. Dorsal abdomen yellow-brown, with a yellow dot; ventrally dark brown with four series of pale brown dots. Total length 20.19. Carapace 9.70 long and 7.57 wide, eye diameter: AME 0.45, ALE 0.29, PME 0.46, PLE 0.53. Clypeal height 0.44, sternum long 3.94 and 3.55 wide, endites 3.89 long and 2.50 wide, labium 1.43 long and 1.25 wide. Leg measurements: I: femur 9.06, patella 3.98, tibia 9.93, metatarsus 8.01, tarsus 2.33, total 33.31; II, 8.45, 4.19, 8.67, 6.90, 2.27, total 30.48; III 6.92, 3.20, 5.97, 5.46, 1.59, total 23.14; IV 8.66, 3.51, 8.06, 9.00, 1.58, total 30.81. Leg spination: tibia I–II v2-2-2-2, metatarsus I–II v2-2-2-2; III tibia v2-2-2, d1-1-1, p1-0-1-0, r1-0-1-0; metatarsus v2-2-2-2, p1-1-2, r1-1-2; IV tibia v2-2-2, d1-1-1, p1-0-1-0, r1-0-1-0, metatarsus v2-2-2-2, d0-1-0, p1-1-2, r1-1-2. Epigynum (Figs 6A, 9A): middle field convex with straight edges, anteriorly divergent and posteriorly convergent; lateral field with lateral apophysis. Vulva (Figs 6B, 9B): copulatory ducts strongly sclerotized and reduced spermatheca heads, fertilization ducts small and posteriorly located.

Variation. Males (n = 6): Total length 9.70–10.60, carapace 4.86–5.90, femur I 5.90–6.72. Females (n = 5): Total length 12.22–15.22, carapace 6.33–6.97, femur I 5.20–5.86.

Distribution. Lowland tropical rain forests of the Amazon (0–1000 m) in Bolivia, Brazil, Colombia, Ecuador and Peru (Figs 11–13).

Natural history. *Phoneutria boliviensis* is the smallest species of the genus and it inhabits in sympatry with *P. fera* and *P. reidyi*. Torres-Sánchez and Gasnier (2010) indicated that *P. boliviensis* seems to be restricted to periodically inundated forests because they have never been detected in “terra firme” forests. In Peru, this species was also very common in swamp forests (aguajales) dominated by the large, dioecious palm *Mauritia flexuosa*. However, we also found that *boliviensis* is not exclusive to inundated forests but also can be found in “terra firme” forests and even in the Amazonian foothills in Caqueta, Colombia. In these non-inundated ecosystems, *P. boliviensis* is found in secondary forests and forest edges. This species lives in the leaf litter and low vegetation. It is interesting to highlight that in the Amazon of Colombia, Ecuador and Peru, we always found *P. boliviensis* in sympatry with *P. fera* but never with *P. reidyi*.

***Phoneutria depilata* (Strand, 1909) sp. reval.**

Figs 1A, B, 4C, D, 7A–C, 8A, B, 9B, D, 10C, D

Ctenus depilatus Strand, 1910. Holotype male from Colombia (ZMB 30615, examined). Valerio 1983: 101, fig. 2 (female).

Ctenus peregrinoides: Strand, 1910: 318 (syntypes: two females from Guatemala, in ZMB 30717, not examined). New synonymy.

Phoneutria depilata: Schmidt, 1954: 417–418.

Phoneutria colombiana Schmidt, 1956: 418; 1956: 28 (female holotype from Colombia, in SMF, not examined). New synonymy.

Phoneutria boliviensis: Simó & Brescovit, 2001: 74 (as senior synonym of *P. depilata*); Rozwałka, Rutkowski and Bielak-Bielecki 2017: 61, fig. 1b, c (female); Hazzi et al. 2018: 112, fig. 10D (male).

Phoneutria cf. *boliviensis*: Cathrine & Longhorn, 2017: 13, figs 1–6 (female).

Comments. In their revision of *Phoneutria* Simó and Brescovit (2001) distinguished the Amazonian specimens of *Phoneutria boliviensis* from the specimens from Colombia and Central America (which we identify now as *P. depilata*) based on the epigynal morphology: “In specimens from Central America to Colombia it is triangular, with a wide base and a narrow apex, but in specimens from Ecuador to Bolivia the apex is more rounded”. Based on the fact that Simó & Brescovit were able to distinguish these epigynal morphological differences among these two *Phoneutria* species and that the only species of *Phoneutria* in the trans-Andean region is *P. depilata*, we suggest that *Ctenus peregrinoides* (from Guatemala) is a junior synonym of *P. depilata*. Strand described *Ctenus signativenter* in 1909 based on immature syntypes from Paramba, Ecuador (one male and two female syntypes, all immatures, 3500 ft, 28 April 1898, Rosenberg leg., in ZMB 306, not examined). We have designated *Ctenus signativenter* as a *nomen dubium* because the exact identity of this species cannot be ascertained with immature specimens, but we note that the type locality suggests that the *C. signativenter* syntypes belong to *P. depilata*. Based on the epigynal morphology (Schmidt 1956, fig.3), we synonymize *Phoneutria colombiana* with *P. depilata*. Both *peregrinoides* and *colombiana* had been synonymized with *P. boliviensis* by Simó and Brescovit (2001).

Other material examined. **Nicaragua:** Región Autónoma de la Costa Caribe Sur: one female, Escondido River (12.1065°N, 84.0256°W, 10 m), 12.VII.1892, C.W. Richmond (USNM). **Panama:** Panama: one male, Pearls Island, San José (8.270219°N, -79.112038°W, 30 m), 02.IV.1944, J.P. Morrinson (USNM); Bocas del Toro: one female, Changuinola, El Silencio (9.3845°N, 82.5356°W, 20 m), E. Marrango (USNM), one male and one female, Gamboa (9.1176°N, 79.6959°W, 50 m), 05.XIII.2018, N. Hazzi and S. Maneses (MCZ IZ 162179); Chiriquí: one male, one female, Puerto Amuelles (8.2841°N, 82.8691°W, 10 m), 25.VII.2018, N. Hazzi, J. Bernal, T. Rios (MCZ IZ 162180). **Costa Rica:** Alajuela: one male and one female, San Ramón, Muelle San Carlos (10.4335°N, 84.5622°W, 990 m) (MZUCR); one male, Canaleta, Upala (10.8358°N, 85.0437°W, 950 m), 25.XI.1979 (MZUCR), two females and two males, San Carlos, Peje Viejo (9.644°N,

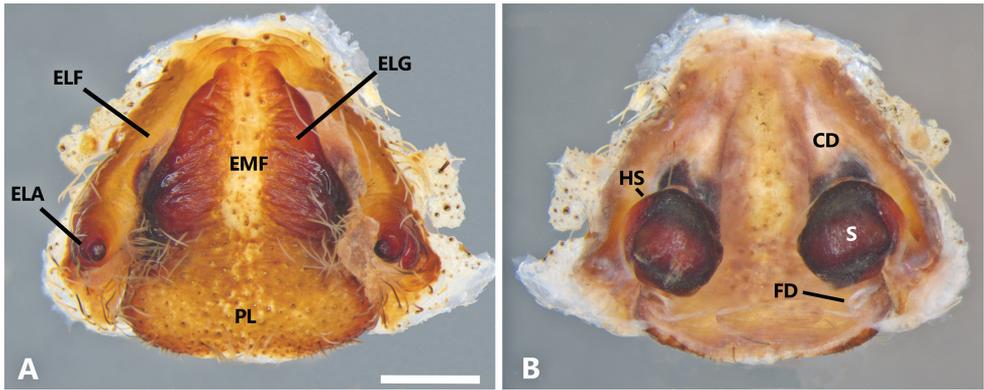


Figure 8. *Phoneutria depilata* (from Puerto Amuelles, Chiriquí, Panama), female genitalia **A** epigynum, ventral view **B** vulva, dorsal view. CD = copulatory duct, ELA = epigynal lateral apophysis, ELF = epigynal lateral field, ELG = epigynal lateral guide, EMF = epigynal middle field, FD = fertilization duct, HS = head of spermatheca, PL = posterior lobe, S = spermatheca. Scale bars: 1.00 mm.

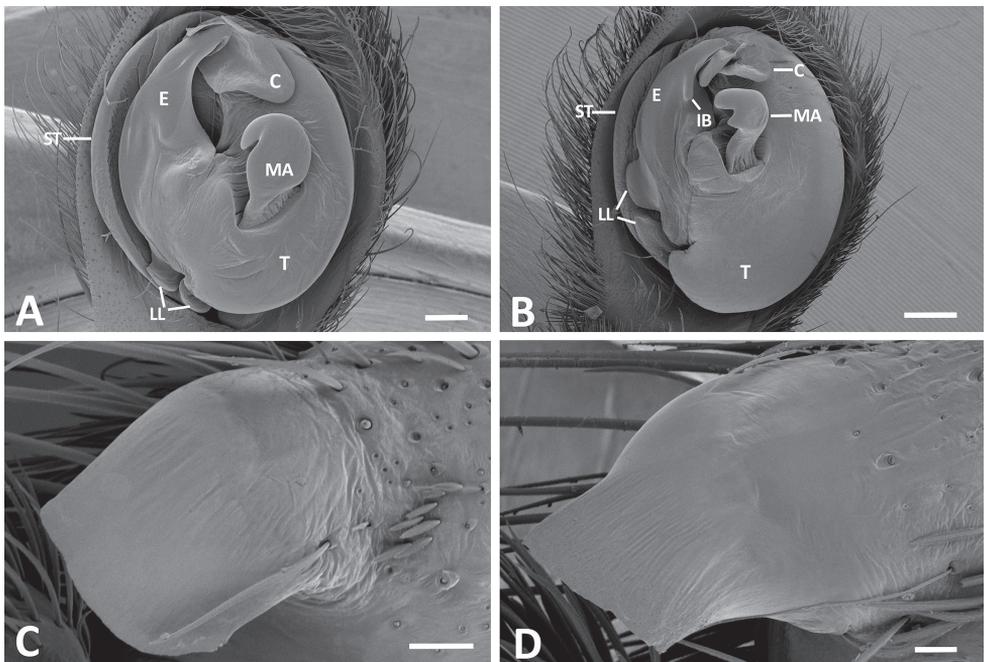


Figure 9. **A, B** ventral view of the male palp of *P. boliviensis* (from Pucallpa, Peru) and *P. depilata* (from Gamboa, Panama), respectively **C, D** retrolateral tibia apophysis of *P. boliviensis* and *P. depilata*, respectively. Scales bars: 0.10 mm (**A**); 0.20 mm (**B**); 0.10 mm (**C**); 0.05 mm (**D**). C = conductor, E = embolus, IB = internal bulge, LL = locking lobes, MA = median apophysis, ST = subtegulum.

82.7516°W), F. Garray (MZUCR), 00.X.1999; Limón: one female, Guapiles (10.2217°N, 83.7705°W, 450 m), 30.IX.1977 (MZUCR); one female, Batán (10.0842°N, 83.3364°W), 12.VIII.1984, Federico Muñoz (MZUCR), Reserva

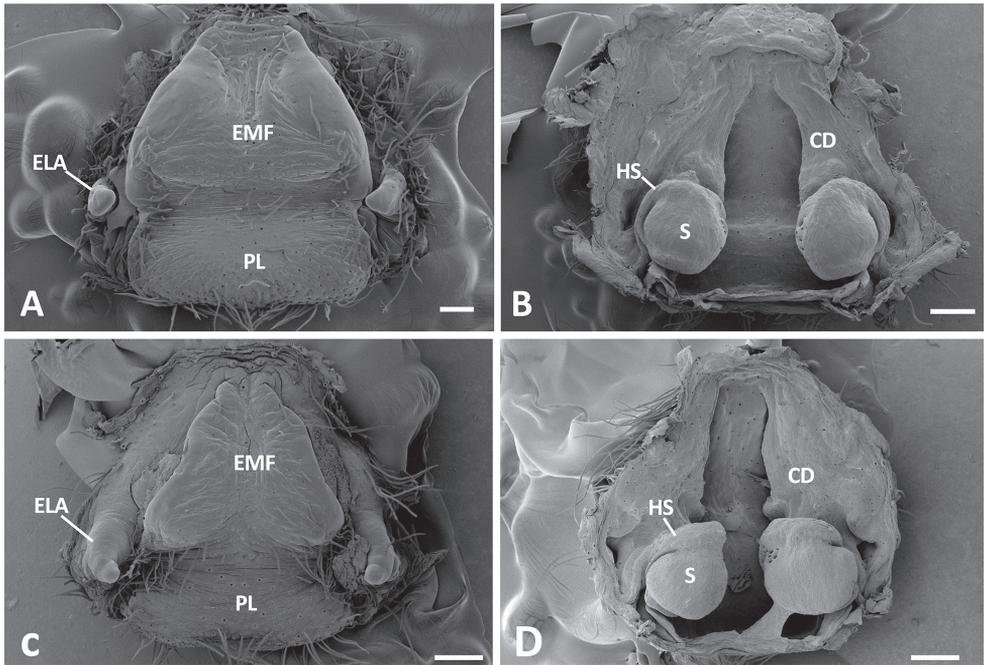


Figure 10. **A, B** epigynum and vulva (dorsal view) of *Phoneutria boliviensis* (from Pucallpa, Peru) **C, D** epigynum and vulva (dorsal view) of *Phoneutria depilata* (from Caimito, Esmeraldas, Ecuador). ELA = epigynal lateral apophysis, EMF = epigynal middle field, FD = fertilization duct, HS = head of spermatheca, PL = posterior lobe, S = spermatheca. Scales bars: 0.20 mm (**A**), 0.20 mm (**B**), 0.30 mm (**C**), 0.30 mm (**D**).

Biológica Hitoy Cerere (9.647°N, 83.0709°W); one female, Talamanca, Amumbri de Bratsi (9.6501°N, 82.7542°W) (MZUCR); Puntarenas: one female, Rincón de Osa (8.6986°N, 83.4876°W, 20 m), 00.III.1967, C. Valerio (MZUCR); one male, Conte, Casa de la Guardia Rural (8.443°N, 83.0401°W, 990 m), 14.VII.1984; one female and one male Cirenas (9.7199°N, 85.2119°W, 10 m), 00.VI.2018, N. Hazzi (MCZ IZ 162181), Cartago: one female, Turrialba, Bajo Pacuare (9.862°N, 83.5203°W, 730 m), 25.IV.1983, F. Calderón (MZUCR); Heredia: one juvenile, Sarapiquí, Reserva Tirimbina (10.4164°N, 84.1199°W, 160 m), 10.VI.2019, N. Hazzi; one male, San Isidro (10.0182°N, 84.0551°W, 1300 m) (MCZ IZ 162183). **Ecuador:** Esmeraldas: Esmeraldas, Caimito (0.7005°N, 80.0741°W, 10 m), 1.10.2019, N. Hazzi (MCZ IZ 162184). **Colombia:** Chocó: one female, Bahía Solano, Ciudad Mutis (6.2186°N, 77.4075°W, 5 m), 5.V.1973 (ICN-AR); one juvenile, Acandí, Capurgana (8.6338°N, 77.3503°W, 15 m), 08.X.2007, C. Duran (MPUJ); Cundinamarca: Fusagasugá (4.3439°N, 74.3678°W, 1600 m), 00.XII.2001 (ICN-AR-5258); Yacupi, vereda La Oscura (5.45°N, 74.35°W, 1190 m), 03.I.2000 (ICN-AR-907); Quipile, Vereda el Trigo (4.7455°N, 74.5341°W, 1300 m); 28.V.2000 (ICN-AR-908); Pandi, vereda El Caucho (4.1911°N, 74.4875°W, 910 m), 20.IX.2000 (ICN-AR-903); La Mesa (4.6333°N, 74.4666°W, 1080 m), 16.VI.1983 (ICN-AR-343); Nilo, Pueblo Nuevo (4.3166°N, 74.6333°W, 480 m), 12.I.1980 (ICN-AR-303); Santander: Chima, El Rodeo (6.3458°N, 73.3736°W, 113 m); 03.I.1970 (ICN-AR-315); one female, Suaita

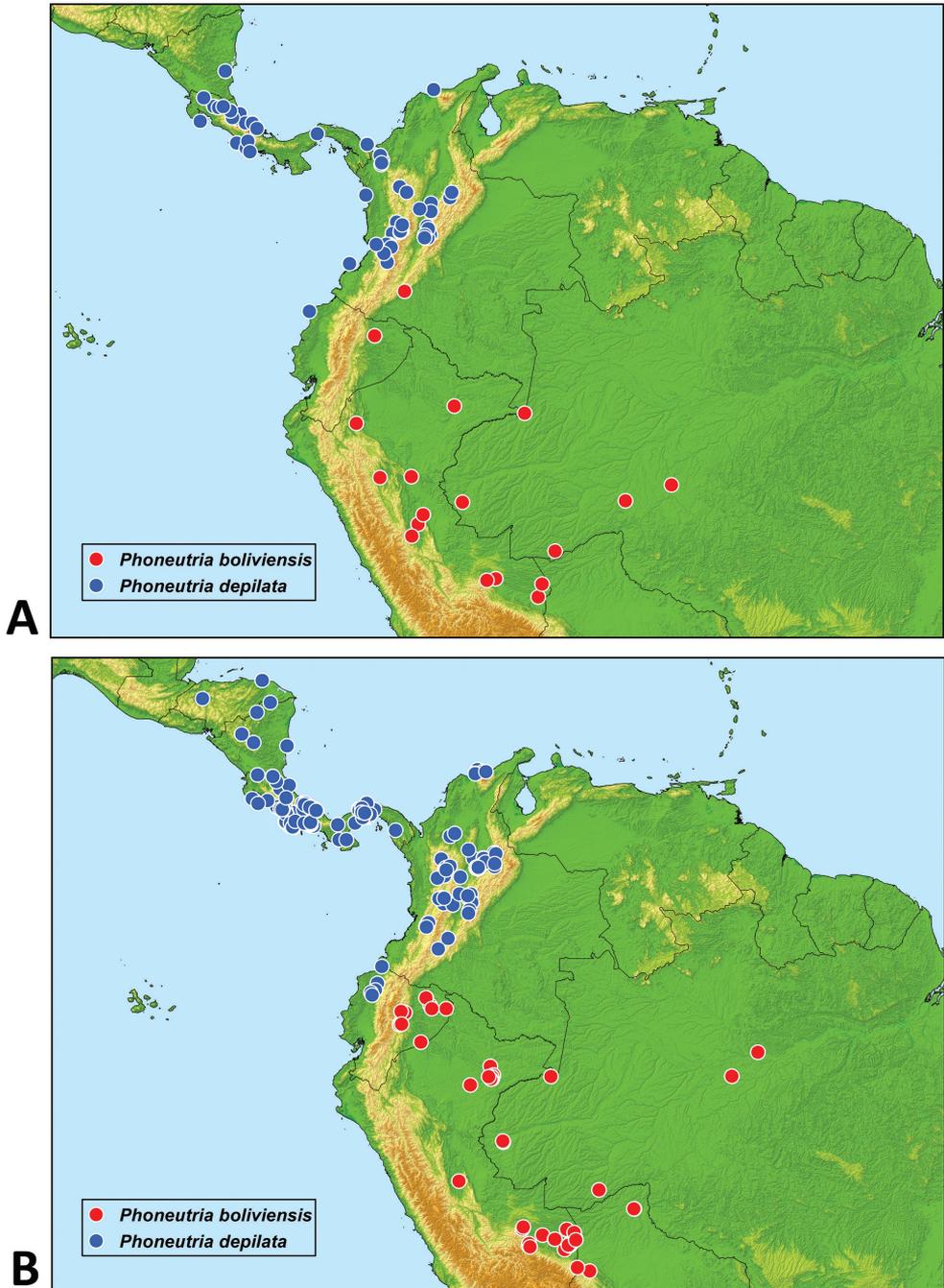


Figure 11. Occurrence records of *P. boliviensis* and *P. depilata* obtained from LIFIMU database (**A**) and iNaturalist (**B**).

(6.10°N, 73.45°W, 1550 m), 10.V.1998 (ICN-AR-5261); Antioquia: one female, Urabá, Apartadó (7.8856°N, 76.6347°W, 20 m), 00.VII.2003 (ICN-AR-5259); one female, Urabá, Turbó (8.0981°N, 76.7317°W, 20 m) (ICN-AR-5260); one female,

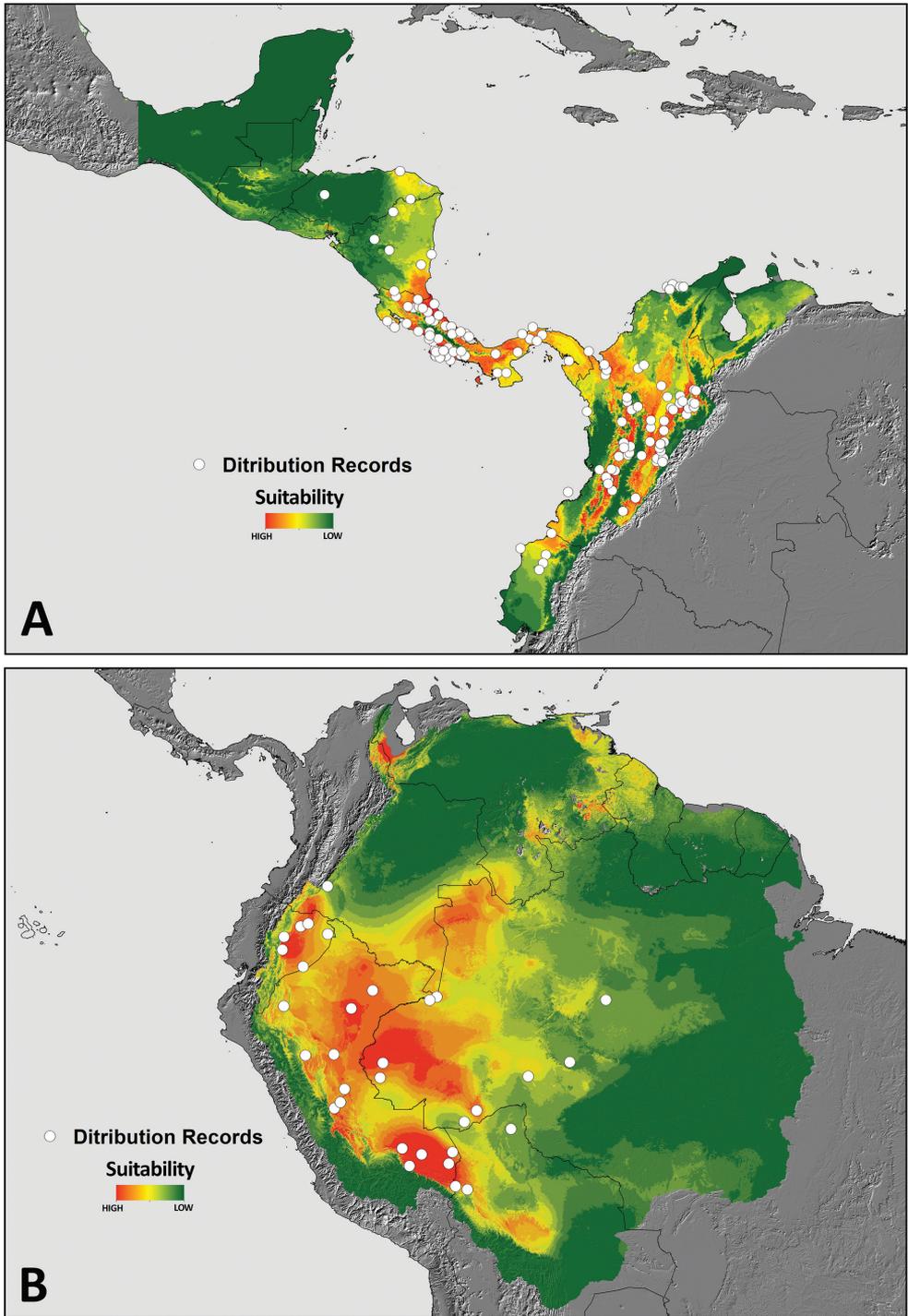


Figure 12. Distribution models **A, B** continuous model of *P. depilata* and *P. boliviensis*, respectively.

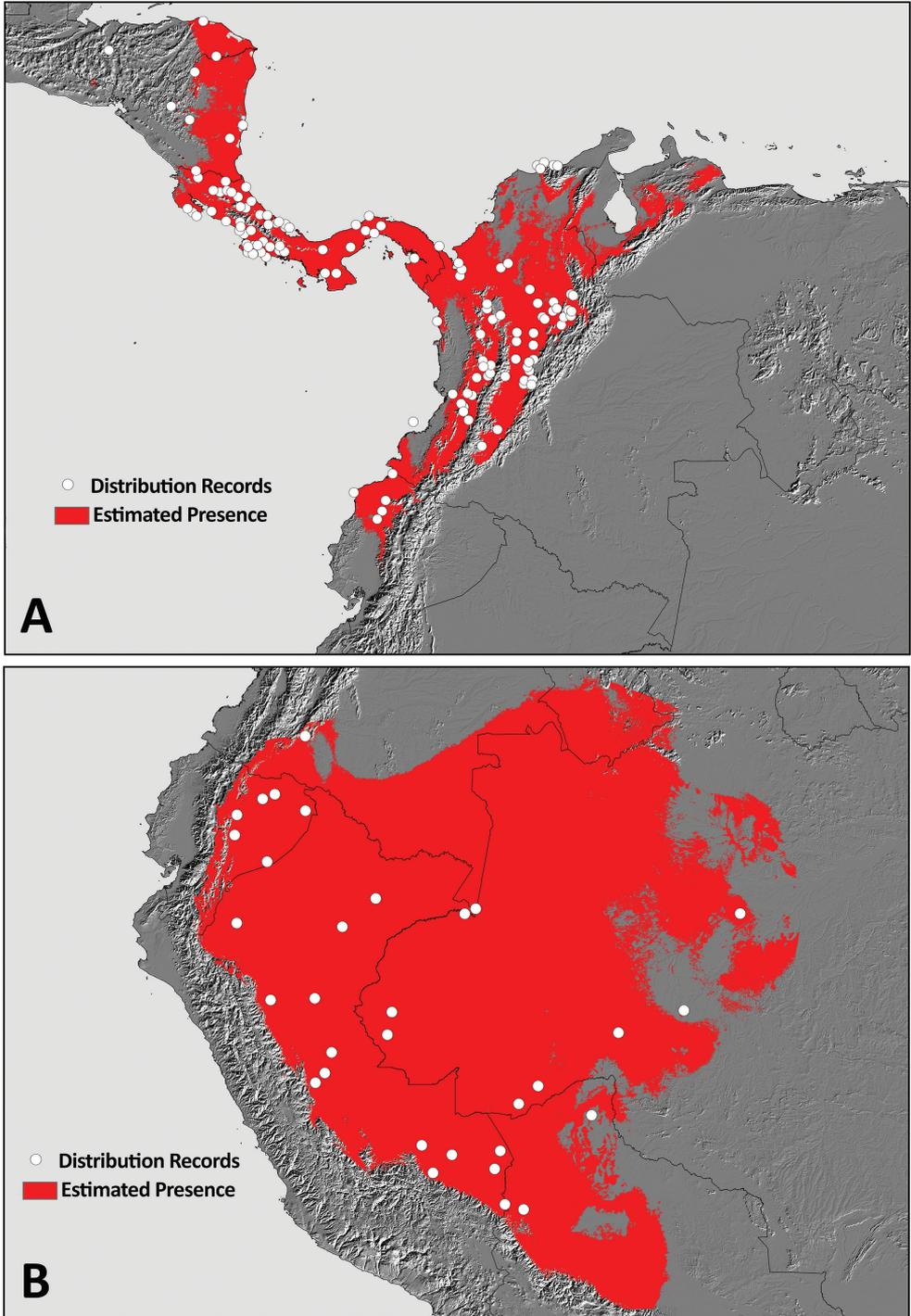


Figure 13. Distribution models **A, B** binary model (5% threshold) of *P. depilata* and *P. boliviensis*, respectively.

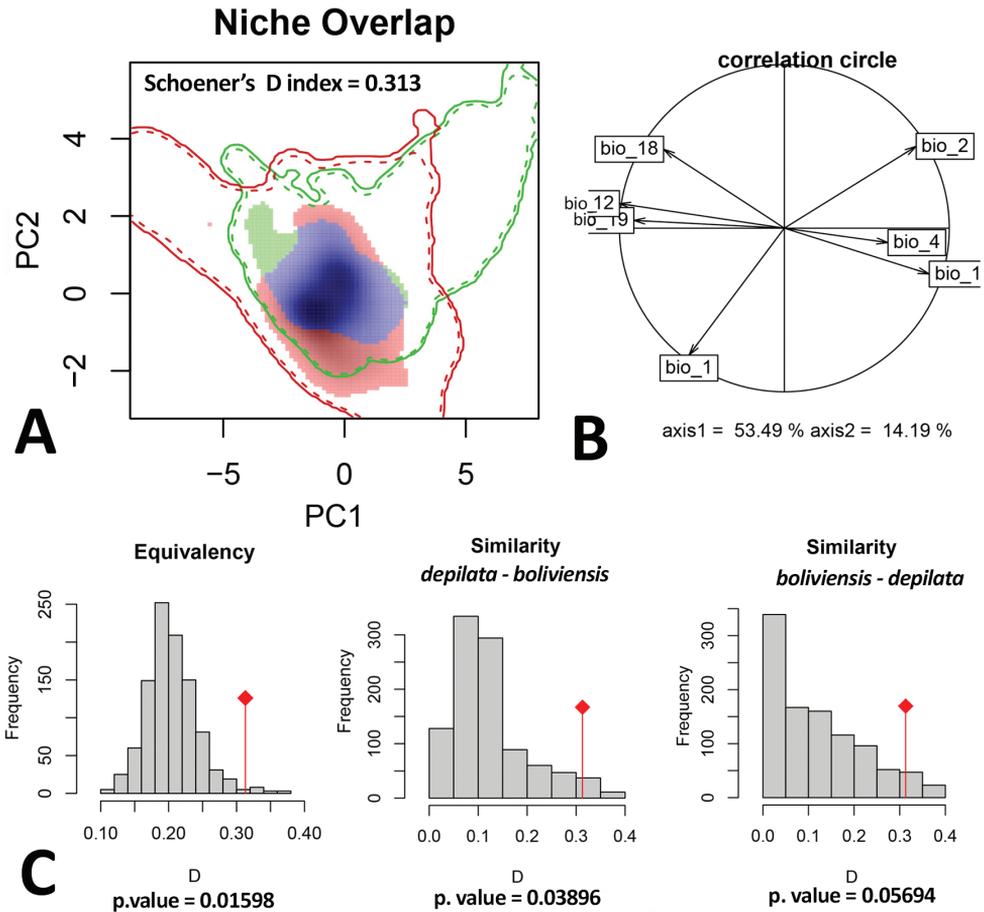


Figure 14. Equivalence and similarity tests in environmental space for *P. boliviensis* and *P. depilata* **A** PCA of ecological climatic **B** the variables contribution to the analyses **C** graphical results of the equivalency and similarity permutation tests comparing the two species of *Phonutria*. Line marks and filled squares are the available environment in each range (M) and occupied space by each species, respectively. Occupied climatic niche by *P. boliviensis*, *P. depilata* and niche overlap (D) are in green, red and blue colors, respectively.

Urabá, Chigorodó (7.6769°N, 76.6864°W, 20 m), 00.IX.2003 (ICN-AR-5262); Cauca: one male, PNN. Gorgona Island (2.98°N, 78.1825°W, 5 m), 00.XII.2003 (ICN-AR-5263); one female and five males, Caloto, vereda Morales (3.0369°N, 76.4116°W, 1100 m), 00.X.2009, N. Muriel (MUSENUV); Valle del Cauca: one female and one male, Cali, El Aguacatal (3.4617°N, 76.5560°W, 1000 m), N.Hazzi (MUSENUV); one female, Cali (3.4616°N, 76.5560°W, 1000 m), 20.X.1982 (MUSENUV); one female, same locality 00.X.1986 (MUSENUV); one male, Cali, Barrio El Refugio (3.4372°N, 76.5225°W, 1000 m), 00.XI.1995(MUSENUV) one female, Dagua, El Palmar (3.6033°N, 76.6463°W, 1300 m), 27.IX.1994 (MUSENUV); one female, Roldanillo (4.4147°N, 76.1547°W, 950 m) (MUSENUV); KM 30, El Carmen

(3.566°N, 76.6475°W, 1400 m); 10.XII.2008, N. Hazzi (MUSENUV); one male, Buga, Liceo de los Andes (3.8833°N, 76.2986°W, 950 m), 12.XII.2009, N. Hazzi (MUSENUV), one female, Buenaventura, Reserva Natural San Cipriano (3.8833°N, 76.9166°W, 180 m), 00.II.2012, N.Hazzi and J. Moreno (MUSENUV); Boyaca: Puerto Boyaca, Puerto Romero, vereda Los Quinchos (5.8375°N, 74.3408°W, 160 m); Risaralda: one female, Pereira (4.8133°N, 75.6961°W, 1400 m) (MUSENUV); one male, Balboa (4.9517°N, 75.9572°W, 1400 m); 10.XI.1998 (ICN-AR-5264); Quindío: one female, Montenegro, La Tebaida (4.5542°N, 75.7181°W, 1200 m), 27.I.2010, N. Hazzi (MUSENUV); one female, Montenegro, Pueblo Tapado (4.5178°N, 75.7847°W, 1250 m), 00.X.2004 (MUSENUV); Caldas: Samaná, Norcasia, Carrisa (5.5666°N, 74.8833°W, 600 m); 10.X.1992 (ICN-AR342).

Diagnosis. Males of *P. depilata* resemble those of *P. boliviensis* by the truncated apex of the RTA (Fig. 9C, D), but differ from this and the remaining *Phoneutria* species by the lateral pronounced projection of the locking lobes visible in ventral view (Fig. 9B). In addition, males present an embolus with an internal bulge which is absent in *P. boliviensis*; and a much larger tegulum (Figs 7B, 9B). Females of *P. boliviensis* also resemble those of *P. depilata* by the general configuration of the epigynum but differ by the narrow area of the EMF (Fig. 8A), copulatory ducts slightly sclerotized (Fig. 8A), and large spermatheca heads (Figs 8B, 10D). In addition, both males and females of *P. depilata* can be distinguished from *P. boliviensis* and the remaining Amazonian species (*P. perty* and *P. fera*) by the four conspicuous series of yellow dots in the ventral side of the abdomen (this character is also present in *Phoneutria eickstedtae* Martins & Bertani, 2007).

Description. Male (from Puerto Amuelles, Chiriquí, Panama, MCZ IZ 162180-1). Coloration (Figs 1B, 4C, D): Carapace brown with a longitudinal black line. Ocular area with brown setae and back oblique band from PLE to anterior dorsal shield of prosoma edge. Chelicerae brown with reddish setae. Sternum, endites and labium yellowish-brown. Abdomen yellow-brown dorsally, with yellow dots; ventrally dark brown with four conspicuous series of yellow dots. Total length 23.21. Carapace 12.38 long and 9.94 wide, eye diameters: AME 0.46, ALE 0.34, PME 0.55, PLE 0.55. Clypeal height 0.45, sternum 5.03 long, 4.65 wide; labium 1.62 long, 1.62 wide. Sternum 2.58 long and 2.50 wide, labium 1.99 long and 2.15 wide, endites 2.93 long and 1.70 wide. Leg measurements: I: femur 14.65, patella 5.77, tibia 15.75, metatarsus 14.31, tarsus 3.93, total 54.41; II: 13.72, 5.19, 13.85, 12.63, 3.30, total 48.69; III, 11.12, 4.95, 10.21, 10.09, 3.17, total 39.54; IV 13.56, 4.86, 13.25, 16.35, 3.96, total 51.98. Leg spination: I tibia v2-2-2-2-2, d1-1-1, p0-1-0, r1-1-0, metatarsus v2-2-2-2, p1-0-0 r1-0-0, II tibia v-2-2-2-2-2, d1-1-1, p1-1-0, r1-1-0, metatarsus v2-2-2-2, p1-0-0 r1-0-0, III v2-2-2, d1-1-1, p1-0-1-0, r1-0-1-0, metatarsus v2-2-2-2, p1-1-2, r1-1-2, IV tibia v2-2-2, d1-1-1, p1-0-1-0, r1-0-1-0, metatarsus v2-2-2-2, d0-1-0, p1-1-2, r1-1-2. Palp: RTA small and truncated at the apex (Figs 7C, 9D); embolus curve with internal bulge (Figs 7B, 9B); cup-shaped median apophysis constrain at the base (Figs 7B, 9B); conductor membranous, hyaline and C-shaped (Figs 7B, 9B); tegulum large with probasal rounded projection (Figs 7B, 9B).

Female (from Puerto Amuelles, Chiriquí, Panama, (MCZ IZ 162180-2). Coloration (Figs 1B, 4C, D): Carapace brown with a longitudinal black line. Ocular area with brown setae and back oblique band from PLE to anterior dorsal shield of prosoma edge. Chelicerae brown with reddish setae. Sternum, endites and labium yellowish-brown. Abdomen yellow-brown dorsally, with yellow dots; ventrally dark brown with four conspicuous series of yellow dots. Total length 25.77. Carapace 12.56 long and 9.82 wide, eye diameter: AME 0.47, ALE 0.36, PME 0.60, PLE 0.65. Clypeal height 0.89, sternum long 5.15 and 4.76 wide, endites 3.89 long and 2.30 wide, labium 1.33 long and 1.59 wide. Leg measurements: I: femur 13.43, patella 5.09, tibia 12.78, metatarsus 9.99, tarsus 3.33, total 44.62; II, 11.22, 5.00, 11.57, 9.30, 3.00, total 40.09; III 7.83, 4.00, 7.89, 7.60, 2.50, total 29.83; IV 12.00, 4.62, 9.83, 12.72, 3.15, total 42.32. Leg spination: tibia I–II v2-2-2-2-2, metatarsus I–II v2-2-2-2-2; III tibia v2-2-2, d1-1-1, p1-0-1-0, r1-0-1-0; metatarsus v2-2-2-2, p1-1-2, r1-1-2; IV tibia v2-2-2, d1-1-1, p1-0-1-0, r1-0-1-0, metatarsus v2-2-2-2, d0-1-0, p1-1-2, r1-1-2. Epigynum (Figs 6A, 10C): middle field convex with straight edges, anteriorly divergent and posteriorly convergent; lateral field with lateral apophysis. Vulva (Figs 6B, 10D): copulatory ducts slightly sclerotized, enlarged spermatheca heads, fertilization ducts small and posteriorly located.

Variation. Males (n = 5): Total length 21.00–26.37, carapace 11.26–13.75, femur I 13.27–15.84. Females (n = 8): Total length 25.77–34.00, carapace 12.56–15.00, femur I 13.43–14.36.

Distribution. Trans-Andean region (0–1700 m) in Ecuador, Colombia, Panama, Costa Rica, Nicaragua, Honduras and Guatemala.

Natural history. This species is found in disturbed habitats associated with both dry and humid tropical forests (0–1700 m), usually on the ground with sparse litter and low vegetation (Hazzi 2014). The range of eggs per egg sac is 430–1300, and spiderlings emerge 28–34 days after the egg sacs are produced. Sexual maturity occurs after 14–17 molts, and spiders mature 300–465 days after emerging from the egg sac (Hazzi 2014). Valenzuela-Rojas et al. (2020) reported that *P. depilata* is an euryphagous predator with a broad diet made up predominantly of arthropods and to a lesser extent of small vertebrates (Gekkonidae, Hylidae, and Sphaerodactylidae). There are human bite records of this species reported in Costa Rica and in banana plantations in Colombia (Flórez et al. 2003). All the cases reported have occurred with adults, and most of them have presented mild to moderate envenomation symptoms, with only one patient presenting severe symptoms such as renal failure (Flórez et al. 2003). Estrada-Gómez et al. (2015) partially characterized the venom of this species, detecting Ctenitoxin-Pb48 and Ctenitoxin-Pb53, which showed a high homology with other Ctenitoxins (family Tx3) from *P. nigriventer*, *P. keyserlingi* and *P. reidyi* affecting voltage-gated calcium receptors (Cav 1, 2.1, 2.2 and 2.3) and NMDA-glutamate receptors. Valenzuela-Rojas et al. (2019) found that the venom of *P. depilata* was significantly more effective on vertebrate (geckos) than invertebrate (spiders) prey in both LD50 and immobilization time. In addition, males had slightly more toxic venom (LD50) to geckos and much more toxic venom to spiders when compared to females (Valenzuela-Rojas et al. 2019). For two periods, March to May and October to November, adult males and females with

egg sacs are always found in homes in the Inter-Andean Cauca Valley of Colombia. This likely indicates two reproductive peaks that coincided with the two rainy seasons during those same periods (N. Hazzi, unpub. data).

Discussion

Despite the medical importance of *Phoneutria*, its taxonomy and systematics have been always debated and there is still disagreement about the exact number of species in the genus. For instance, the last two taxonomic revisions of the genus contradict the boundaries of some species. Simó and Brescovit (2001) lumped several species into the medically relevant species *P. nigriventer* and only recognized five valid species. Martins and Bertani (2007) split *Phoneutria nigriventer* into three species, some of which had been recognized by other previous authors as valid. In the case of *Phoneutria depilata*, this species has been found co-occurring with *P. boliviensis* for several decades and many works on *P. depilata* have been published with the species misidentified as *P. boliviensis* (Valerio 1983; Hazzi et al. 2013; Hazzi 2014; Estrada-Gomez et al. 2015; Valenzuela-Rojas et al. 2019, 2020). The combination of detailed morphological (coloration and genitalia morphology) and molecular data has allowed us to distinguish *P. depilata* from *P. boliviensis*, and therefore reconsider the status *P. depilata* as a valid species.

Previous works of DNA barcoding in Lycosoidea have shown a range of genetic distances among congeneric species of 4–6.9% (Correa-Ramírez et al. 2010; Planas et al. 2013). Our analyses of the three species of *Phoneutria* resulted in interspecific distances between 6.1 to 8.2%, indicating similar genetic divergence to other Lycosoidea congeneric species. In addition, these divergences are also congruent with p-distances reported in other congeneric species of spiders (Barrett and Hebert 2005; Bidegaray-Batista et al. 2014; McHugh et al. 2014; Hormiga 2017; Agnarsson et al. 2018; Montes de Oca et al. 2016; Ballesteros and Hormiga 2018; Valdez-Mondragón 2020). Moreover, interspecific distances among haplotypes were, by far, higher than intraspecific variation between species haplotypes. For instance, the higher number of mutations was 6 between intraspecific haplotypes, compared with the lower number of mutations of interspecific species haplotypes (*P. boliviensis*-*P. fera* = 29). Interestingly, ITS-2 presented few segregating sites, and it was only able to differentiate haplotypes of *P. boliviensis* from the remaining two species just by one mutation step.

The distance-based method (ABGD) split *P. boliviensis* into two species, one which was not monophyletic. Several species delimitation studies in spiders have also shown that the ABGD method is sensitive to sampling and tends to over-split species when compared with other methods (Hamilton et al. 2014; Ortiz and Francke 2016; Valdez-Mondragón 2020). Instead, the phylogeny-based species delimitation methods employed in this study were congruent in identifying the three species of *Phoneutria*, corresponding completely with the morphological data. However, GMYC and mPTP methods grouped the three *Phoneutria* species into one, when only ITS-2 was used (an

expected result due to the low genetic variation of this marker, as mentioned above). Because these two species delimitation methods were designed for single locus data (Pons et al. 2006; Fujisawa and Barraclough 2013; Kapli et al. 2017), we also implemented the BPP which explicitly models the evolution of multilocus data (Yang 2015; Luo et al. 2018). The results of this analysis also supported the existence of three species of *Phoneutria*. Although the ITS-2 has rarely been used in studies of spiders compared to other nDNA markers (e.g. 28S and histone H3), several studies have started to use it for DNA barcode and species delimitation recently. In *Anelosimus* species (Agnarsson 2010) and *Gasteracantha cancriformis* (Chamberland et al. 2020), this marker has insufficient variation to resolve relationships within species and among closely related species. However, for species of the genus *Theridion*, ITS-2 has shown a perfect match with the morphology-based species delimitation (Domènech et al. 2020). In addition, this marker has also shown to be informative with species of *Loxosceles* (Valdez-Mondragon et al. 2019). Therefore, ITS-2 sometimes can be useful for species identification and delimitation, and it should be used together with COI.

Citizen science platforms have provided unprecedented access to documenting species diversity and distribution across the world (Amano et al. 2016). In the case of iNaturalist, this platform presents more than 46,765,000 observations of more than 291,200 putative species of animals and plants (Horn et al. 2018). Recently, various studies have used this platform to detect disease in red mangroves (Rossi 2017), document biodiversity and distribution of echinoderms and termites (Michonneau and Paulay 2015; Hochmair et al. 2020), the rediscovery of threatened rare species (Wilson et al. 2020), and the discovery and description of new species (Winterton 2020). To our knowledge, this is the first study that has used iNaturalist to gather occurrence records on venomous species to estimate distribution models. For the two species of *Phoneutria* studied here, iNaturalist presented higher and more widely distributed records than our database, compiled using literature, examination of specimens from different museums, and years of personal fieldwork. Thus, our study demonstrated iNaturalist's ability to gather occurrence records and improve distribution knowledge of conspicuous and large, venomous spiders that inhabit synanthropic environments, like species of *Phoneutria*. Unfortunately, for the two remaining Amazonian species of *Phoneutria* (*P. reidyi* and *P. fera*), based on our limited knowledge, it is only possible to distinguish these two species with genitalia images and not with photographs of the habitus at this time. Therefore, we were not able to include the information of iNaturalist to model their potential distribution.

Phoneutria boliviensis and *P. depilata* live in lowland areas, and sometimes premontane ecosystems as well (Valerio 1983; Simó and Brescovit 2001; Hazzi et al. 2013). The distribution models corroborate that suitable areas for both species are lowland rainforest ecosystems. However, the model also indicated dry and premontane tropical ecosystems reaching elevations of 1600 m as suitable areas for *P. depilata*, which is congruent with the occurrence records and previous observations about the wide niche plasticity of this species (Hazzi 2014). It is also important to highlight that the species distribution maps (SDM) indicated that a large area of the Pacific of Colombia is

unsuitable for this species. However, we think that the species may be present along this area but there are no records as this is one of the less explored regions of this country (Arbeláez-Cortés 2013; Arbeláez-Cortés et al. 2017). The compiled occurrence records and SDMs obtained for these two species, together with the morphological diagnosis, could have significant use in identifying risk areas of accidental bites and help health care personnel determine the species involved, especially for *P. depilata* which has been involved in bite accidents (Trejos et al. 1971; Florez et al. 2003).

Phylogenetic niche conservatism has been suggested as one of the potential forces in speciation and species richness patterns in the tropics (e.g., Wiens and Graham 2005; Wiens et al. 2011; Pyron et al. 2015). Under the allopatric speciation model, especially when allopatric lowland taxa are separated by a geographic barrier, one may expect that the tendency of species to maintain their ancestral climatic niche prevents them from adapting to new environments (such as mountains), isolating, and promoting speciation. (Wiens 2004; Pyron et al. 2015; Posso-Terranova and Andrés 2016). *Phoneutria depilata* has an allopatric distribution with respect to the three Amazonian species of *Phoneutria* (*P. fera*, *P. boliviensis* and *P. reidyi*). The Andes works as the geographic barrier that separates *P. depilata* (trans-Andean species) from the Amazonian species (cis-Andean species), a biogeographic pattern commonly seen with many other Neotropical taxa (Albert et al. 2006; Weir and Price 2011; Richardson et al. 2015; Bartoletti et al. 2018; Salgado-Roa et al. 2018). The niche comparison analysis of these two species, using equivalency and similarity tests, indicated that both species presented niche conservatism. However, the phylogenetic analyses using different optimality criteria were not able to support, with high confidence, that *P. depilata* and *P. boliviensis* are sister species. In addition, we did not have samples of *P. reidyi*. Nevertheless, we think that it is still possible to conclude that Amazonian and the trans-Andean species of *Phoneutria* have conserved their climatic niches because the three Amazonian species are sympatric, occupying the same kind of ecosystems (climatic areas). Furthermore, the allopatric species *P. depilata* has a climatic niche similar to the Amazonian species *P. boliviensis*. These results are also congruent with other allopatric lowland cis and trans-Andean taxa that have conserved their climatic niches (Albert 2010; Richardson et al. 2015).

In conclusion, using morphological and molecular data, together with species delimitation methods our study revalidates *Phoneutria depilata* as a valid species separate from *P. boliviensis*. Both species have allopatric distributions separated by the Andean mountains, and species distribution models indicated lowland tropical rain forest ecosystems as the most suitable environments for these species. In addition, this work demonstrated the value of citizen science platforms like iNaturalist for occurrence records and improving species distribution knowledge. *Phoneutria depilata* and the three Amazonian species presented niche conservatism following the expected neutral model of allopatric speciation. Finally, the morphological diagnosis of these two species and the distribution maps provided in this work will be useful for future studies in venom, epidemiology of bites, and systematics of this venomous group of spiders.

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Supplementary material 1

Concatenated alignment

Authors: Nicolas A. Hazzi, Gustavo Hormiga

Data type: DNA alignment

Explanation note: Concatenated DNA Alignment of ITS-2 and COI.

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Link: <https://doi.org/10.3897/zookeys.1022.60571.suppl1>

Supplementary material 2

Curated iNaturalist database for *Phoneutria boliviensis* and *P. depilata*

Authors: Nicolas A. Hazzi, Gustavo Hormiga

Data type: Occurrences

Explanation note: Curated iNaturalist database for *Phoneutria boliviensis* and *P. depilata*. Accessed in July 2020.

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Link: <https://doi.org/10.3897/zookeys.1022.60571.suppl2>

Four new species of the genus *Cratospila* Foerster (Hymenoptera, Braconidae, Alysiinae) from South Korea

JuHyeong Sohn^{1*}, Cornelis van Achterberg^{2*}, Yun Jong Han¹, Hyojoong Kim¹

1 Animal Systematics Lab., Department of Biology, Kunsan National University, Gunsan, 54150, South Korea

2 State Key Laboratory of Rice Biology and Ministry of Agriculture / Key Lab of Agricultural Entomology, Institute of Insect Science, Zhejiang University, Hangzhou, 310058, China

Corresponding author: Hyojoong Kim (hkim@kunsan.ac.kr)

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Abstract

The species of the genus *Cratospila* Foerster, 1863 (Braconidae, Alysiinae) from South Korea are revised, and the genus is recorded for the first time from South Korea. All four species are new to science, and *Cratospila albifera* **sp. nov.**, *C. ejuncida* **sp. nov.**, *C. luteocephala* **sp. nov.**, and *C. syntoma* **sp. nov.** are described and illustrated herein. In addition, COI has been sequenced of three species. A key to the Korean species is provided.

Keywords

Alysiini, COI, Hymenoptera, new record, taxonomy, new species

Introduction

Alysiinae are a large subfamily of the family Braconidae and include two tribes; Alysiini and Dacnusini, with over 100 genera (Yu et al. 2016). Alysiinae occurs worldwide and contains over 2,440 valid species (Yu et al. 2016), of which 180 species in 21 genera are listed in the National Species List of South Korea (NIBR 2019). Alysiinae are known as koinobiont endoparasitoids of dipterous larvae, using their mandible to break open

* The authors contributed equally to this paper.

the puparium of the host. Some species of Alysiinae are commercially utilized for biological control (Abd-Rabou 2006).

The genus *Cratospila* Foerster, 1863, is a small, worldwide genus of Alysiinae, which includes 15 very similar species (Yu et al. 2016). Until now, four species are known from the Oriental region and two others are doubtfully known. Although Yaakop and Aman (2012) reported *C. circe* (Haliday, 1838) from Malaysia, this record most likely represents one of the very similar Oriental species of *Cratospila*. Also questionable is *C. curvabilis* Bhat, 1980 from India because its original description does not fit well with other species of *Cratospila*, and *C. curvabilis* probably belongs to another genus. Two other species occur in India and Bhutan, and Tobias (1990) described one species from Vietnam. In addition, Wharton (2002) described six species from Australia. Wu and Chen (1995) firstly reported a *Cratospila* species from China. Papp (1994) reported *C. circe* from North Korea, but without any details, and its record is doubtful because *C. circe* seems to be a Western Palearctic species. Herein, we report for the first time the genus *Cratospila* from South Korea and include four newly discovered species. We present new morphological characters and the barcode region of the mitochondrial cytochrome c oxidase subunit I gene (COI) data of three of these new species. Descriptions, diagnoses, an identification key, and photographs of the diagnostic characters are provided.

Materials and methods

Samples used in this study were collected at the following localities in South Korea: Inje-Gun, Gangwon (sweep net); National Arboretum of Korea, Gwangneung Forest, Pocheon-si, Soheul-eup, Gyeonggi-do (Malaise traps) and DMZ Botanical Garden, Mandae-ri, Haean-myeon, Yanggu-gun, Gangwon-do (Malaise traps). Sorting and preparation was done at the Department of Biology, Kunsan National University at Gunsan. For the identification of the genus Wharton et al. (1997) and Zhu et al. (2017) were used. The types are deposited in the Department of Biology, Kunsan National University at Gunsan (KSNU).

Morphological characters were observed with a Leica M205C stereo microscope. The Taxapad database (Yu et al. 2016) was used for references. For terminology used, see Wharton (2002) and van Achterberg (1993).

Extraction of DNA was done in ASL, KSNU. Whole genomic DNA was extracted from the specimens by using a DNeasy Blood & Tissue kit (QIAGEN, Inc., Dusseldorf, Germany) following the manufacturer's protocol. In order to have complete voucher specimens after DNA extraction, non-destructive DNA extraction was performed with a slightly modified method from Favret (2005). A tissue lysis buffer with protease K solution was used to treat a leg at 55 °C for 12 h. The primers LCO-1490 (5'-GGT-CAACAAATCATA AAGATATTGG-3') and HCO-2198 (5'-TAAACTTCAGGGT-GACCAAAAAATCA-3') were used to amplify 658 bp as the partial front region of the COI and amplified by using AccuPowerH PCR PreMix (BIONEER, Corp., Daejeon)

in 20 µl reaction mixtures containing 0.4 µM of each primer, 20 µM of the dNTPs, 20 µM of the MgCl₂, and 0.05 µg of the genomic DNA template. The polymerase chain reaction (PCR) amplification was performed using a GS1 thermo-cycler (Gene Technologies, Ltd., U.K.) according to the following procedure: initial denaturation at 95 °C for 5 min, followed by 34 cycles at 94 °C for 35 sec; an annealing temperature of 48 °C for 25 sec; an extension at 72 °C for 45 sec, and a final extension at 72 °C for 5 min. The PCR products were visualized by electrophoresis on a 1.5% agarose gel. A single band was observed, purified using a QIAquick PCR purification kit (QIAGEN, Inc.), and then sequenced directly using an automated sequencer (ABI Prism 3730 XL DNA Analyzer) at Macrogen Inc. (Seoul, South Korea).

Sequence alignment were performed in MEGA version 7 (Kumar et al. 2016) with ClustalW tool. The *P*-distance model was conducted using MEGA version 7.

Results

A total of 605 bp of the COI fragment were sequenced from *Cratospila albifera* sp. nov. (GenBank accession no. MW376064), *C. luteocephala* sp. nov. (GenBank accession no. MW376065) and *C. syntoma* sp. nov. (GenBank accession no. MW376066). A pairwise distance was constructed by using the *P*-distance model with the option for pairwise deletion. As a result, the morphologically very similar *C. albifera* sp. nov. showed to differ genetically from *C. luteocephala* sp. nov. by 10% and from *C. syntoma* sp. nov. by 7%. In addition, *C. luteocephala* sp. nov. differed by 9% from *C. syntoma* sp. nov.

Taxonomy

Cratospila Foerster, 1863

Figures 1–4

Cratospila Foerster, 1863: 265; Shenefelt. 1974: 985; Wharton 1980: 84; Tobias 1990; Belokobylskij 1998: 287; Zhu et al. 2017: 60. Type species (by monotypy): *Alysia circe* Haliday, 1838.

Hedylus Marshall, 1891: 14–15 (not Foerster, 1868); Papp 2009: 29–30 (as synonym of *Cratospila* because of the synonymising of both type species). Type species (by monotypy): *Hedylus habilis* Marshall, 1894 (examined; = *Alysia circe* Haliday, 1838).

Notes. The genus can be identified by using the illustrated key to the Chinese genera of Alysini by Zhu et al. (2017). The *Cratospila* species treated in this paper have the apical half of ♀ antenna with 8–13 white segments (unknown of *C. syntoma* sp. nov., but it has a largely yellowish-brown head, morphologically related to *C. ejuncida* sp. nov., and has according to the COI analysis a derived position compared with the other species); apex of antenna white, if dark brown then antennal white part 2.5–5.0 times as long as apical dark part of antenna. Papp (1994) reported *Cratospila circe* from

North Korea, which is most likely a misidentification because this species is found so far only in the Western Palaearctic, and in the Eastern Palaearctic region there are several similar species. *Cratospila circe* can be separated from the new species described here by having the pale part of the female antenna either absent or present by a few whitish, greyish or ivory segments, and the pale part is 0.7–1.8 times as long as apical dark part of antenna.

Biology. Rather small genus, of which the biology is unknown.

Distribution. Cosmopolitan except Neotropical region.

Key to species of *Cratospila* Foerster from South Korea

- 1 Mesoscutum medio-posteriorly and scutellum reddish brown; head in dorsal view less transverse (Figs 1D, 3D) and yellowish brown; notauli on middle of mesoscutum comparatively coarsely crenulate (Figs 1G, 3G); pterostigma rather slender and narrowly yellow basally (Fig. 1C, 3C); vein r of fore wing 3–5 times longer than wide; vein 1-SR+M of fore wing slightly sinuate (Figs 1C, 3C); mesosoma 1.5–1.6 times longer than high in lateral view and anterior half of propodeum less sloping (Figs 1F, 3F); propodeum less extensively rugose medially (Fig. 1H, 3H); antennal sockets comparatively close to level of inner side of eyes (Figs 1E, 3E) **2**
- Mesoscutum medio-posteriorly and scutellum black; head in dorsal view more transverse (Figs 2D, 4D) and at least posteriorly darkened; notauli on middle of mesoscutum narrowly crenulate (Figs 2G, 4G); pterostigma rather robust and brown basally (Figs 2C, 4C); vein r of fore wing 1–2 times longer than wide; vein 1-SR+M of fore wing nearly straight (Figs 2C, 4C); mesosoma 1.4–1.5 times longer than high in lateral view and anterior half of propodeum largely sloping (Figs 2F, 4F); propodeum more extensively rugose medially (Figs 2H, 4H); antennal sockets more removed from level of inner side of eyes (Figs 2E, 4E) **3**
- 2 Minimum width of face 0.9 times its height (measured from lower rim of antennal socket to upper medio-dorsal margin of clypeus; Fig. 3E); vein r of fore wing ca 3 times longer than wide; first subdiscal cell of fore wing ca 7.5 times longer than wide (Fig. 3C); [colour of apical antennal segments unknown] ...
..... ***C. luteocephala* sp. nov.**
- Minimum width of face 1.2 times its height (Fig. 1E); vein r of fore wing ca 5 times longer than wide; first subdiscal cell of fore wing ca 5.0 times longer than wide (Fig. 1C); [antenna of ♀ with ca 11 white segments, including apical segment] ***C. albifera* sp. nov.**
- 3 Second submarginal cell rather slender (vein 2-SR 1.8–1.9 times longer than vein 3-SR); vein r of fore wing twice as long as wide (Fig. 2C); first subdiscal cell of fore wing ca 8 times longer than wide; pedicellus entirely yellow; eye in dorsal view ca 2.1 times longer than temple (Fig. 2D); width of face 0.95 times its height; head (except posteriorly) yellowish brown (Fig. 2D);

[antenna of ♀ with 10 or 11 white or ivory segments and apical segment dark brown, pale part 4.6 times longer than apical dark brown part]

- *C. ejuncida* sp. nov.
 – Second submarginal cell robust (vein 2-SR 1.4–1.5 times longer than vein 3-SR); vein r of fore wing approx. as long as wide (Fig. 4C); first subdiscal cell of fore wing ca 6 times longer than wide; pedicellus partly infuscated; eye in dorsal view ca 1.6 times longer than temple (Fig. 4D); width of face 1.1 times its height; head black dorsally (Fig. 4D); [colour of apical antennal segments unknown] *C. syntoma* sp. nov.

***Cratospila albifera* Sohn & van Achterberg, sp. nov.**

<http://zoobank.org/8ABF4632-930C-431D-A637-C8A9949590CB>

Figure 1

Type material. *Holotype*, ♀ (NIBR), SOUTH KOREA, National Arboretum of Korea, Gwangneung Forest, Pocheon-si, Soheul-eup, Gyeonggi-do, 37°45'32.2"N, 127°09'42"E, 16–30.IV.2018, Kim, Kim, Jo, Ki. GenBank accession no. MW376064.

Paratype. 1♀, same data as holotype.

Comparative diagnosis. Belongs to the group of *Cratospila* species together with *C. alboapicalis* Tobias, 1990, described from Vietnam in having the apical half of ♀ antenna with 8–13 white segments. However, in *C. alboapicalis* length of eye 4–5 times length of temple in dorsal view (1.9 times in the *C. albifera* sp. nov.) and antenna of ♀ with dark apical segments (only white segments in *C. albifera* sp. nov.). Differs from the very similar *C. Cratospila* sp. nov. by having the minimum width of face 1.2 times its height (0.9 times in *C. luteocephala* sp. nov.), vein r of fore wing ca 5 times longer than wide (ca 3 times), and first subdiscal cell of fore wing ca 5.0 times longer than wide (ca 7.5 times). COI sequence of *C. albifera* sp. nov. differs by 10% from that of *C. luteocephala* sp. nov. (Table 1).

Description. *Holotype*, ♀: length of body in lateral view 3.2 mm, length of antenna 4.6 mm, and length of fore wing 3.1 mm.

Colour: body (Fig. 1A) brown, but head entirely orange-yellow; first tergite and mesonotum entirely reddish brown; antenna yellowish brown basally, medially dark brown, subapically white (11 flagellomeres); mandible pale orange.

Head (Fig. 1D): width 1.3 times median length in dorsal view. Antenna (Fig. 1B) 1.4 times longer than body in female, 32-segmented. First flagellomere 2.0 times longer than second. Compounded eye slightly oval 1.1 times as long as wide in lateral view. Width of face (Fig. 1E) 1.2 times its height from ventral rim of antennal sockets to upper margin of clypeus. Eye in dorsal view 1.9 times as long as temple. Ocello-ocular line (OOL) 2.0 times longer than diameter of anterior ocellus; OOL: antero-posterior ocellar line (AOL) : postero-ocellar line (POL) = 11 : 3 : 6. Stemmaticum concave. Vertex smooth and polish with reddish brown line. Mandible with three teeth; second tooth narrow and sharp with dark brown tip. Maxillary palp approximately as long as mesosoma.

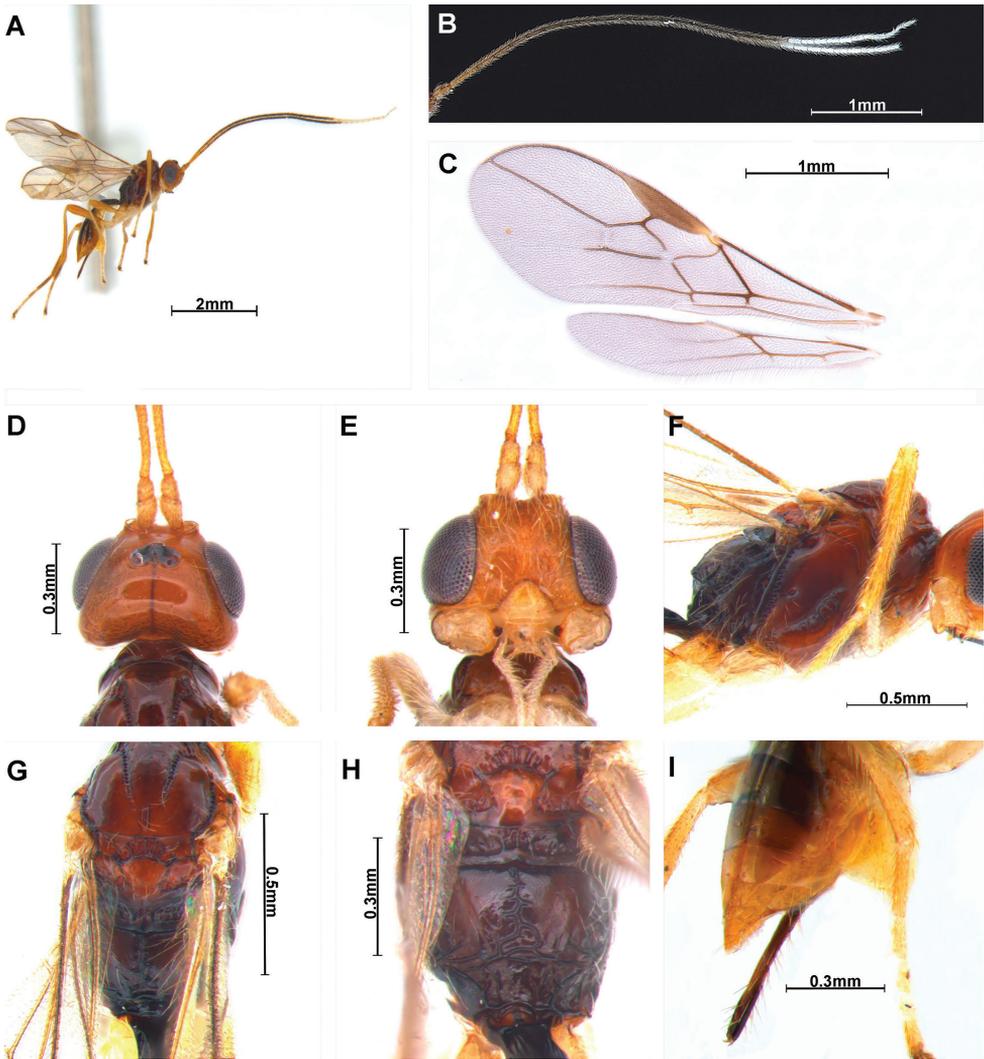


Figure 1. *Cratospila albifera* sp. nov. ♀. **A** body **B** antennae **C** wings **D** head, dorsal **E** head, frontal **F** mesosoma, lateral **G** mesosoma, dorsal **H** propodeum, dorsal **I** ovipositor sheath, lateral.

Table 1. COI pairwise genetic distances between three new *Cratospila* species from South Korea.

	<i>Cratospila albifera</i>	<i>Cratospila luteocephala</i>	<i>Cratospila syntoma</i>
<i>Cratospila albifera</i>	0.000	0.101	0.093
<i>Cratospila luteocephala</i>	0.101	0.000	0.079
<i>Cratospila syntoma</i>	0.079	0.093	0.000

Mesosoma: 1.5 times longer than wide in dorsal view. Mesosoma (Fig. 1G) with medio-posterior depression; notauli chain-shaped, completed but not reaching medio-posterior depression; scutellar sulcus with six carinae; metanotum sculptured; small basal bump on hind coxa. Propodeum (Fig. 1H) 0.5 times longer than wide, anterior half

of propodeum smooth, posterior of median carina strongly wrinkled; precoxal sulcus (Fig. 1F) deep and distinct, consist of about seven grooves, lateral view of propodeum bent. Fore wing (Fig. 1C) 2.5 times as long as wide; pterostigma long and narrow, 3.9 times longer than wide; vein r of fore wing 4.7 times longer than wide; vein 2-SR slightly bent; vein 2-SR+M and r-m not sclerotized; vein 2-SR:vein r : vein 3-SR = 34 : 9 : 24; first subdiscal cell of fore wing ca 5.0 times longer than wide. Hind wing vein M+CU : vein 1-M = 66 : 5

Leg: hind coxa compressed and grooved; hind coxa 2.8 times longer than hind trochanter; hind femur 0.9 times longer than hind tibia; hind tibia 0.8 times longer than hind tarsus.

Metasoma: first tergite striate and narrow, 2.8 times longer than apical width and dark brown, T1:T2 = 59:23. Setose part of ovipositor sheath (Fig. 1I) 0.6 times as long as mesosoma, 0.5 times as long as hind tibia and with long setae.

Male. Unknown.

Variation. Body length of female is 2.9–3.2 mm; length of the fore wing of female is 3.0–3.1 mm; Antenna 1.2–1.4 times longer than body in female, 27–32-segmented. First flagellomere 1.9–2.0 times longer than second; metasoma 2.7–2.8 times longer than apical width; setose part of ovipositor sheath 0.58–0.61 times as long as mesosoma, 0.46–0.51 times as long as hind tibia and with long setae.

Distribution. South Korea.

Etymology. Named after the white apex of the ♀ antenna: “*albifera*” is derived from “*albus*” (Latin for white) and “*fero*” (Latin for carry or bear).

***Cratospila ejuncida* Sohn & van Achterberg, sp. nov.**

<http://zoobank.org/EC085A4F-BA86-4BB9-8442-60B6AA33F24B>

Figure 2

Type material. *Holotype*, ♀ (NIBR), SOUTH KOREA, Inje-Gun, Bukmyeon, Hangyeri, 38°08'46.5"N, 128°15'47.5"E, 9–16. IX. 2017 (Malaise trap), J.H. Sohn.

Comparative diagnosis. Belongs to the group of *Cratospila* species together with *C. alboapicalis* Tobias, 1990, described from Vietnam, in having the apical half of ♀ antenna with 8–13 white segments, and antenna of ♀ with dark apical part. In *Cratospila alboapicalis* length of eye 4–5 times length of temple in dorsal view (1.6 times in *Cratospila ejuncida* sp. nov.), vein m-cu of fore wing subinterstitial (distinctly antefurcal in *C. alboapicalis*), and notauli on middle of mesoscutum narrowly crenulate (coarser crenulate). Differs from the similar *C. syntoma* sp. nov. by having the second submarginal cell rather slender (vein 2-SR 1.8–1.9 times longer than vein 3-SR; 1.4–1.5 times in *C. syntoma* sp. nov.), vein r of fore wing twice as long as wide (approximately as long as wide), first subdiscal cell of fore wing ca 8 times longer than wide (6 times), pedicellus entirely yellow (partly infuscated), and eye in dorsal view ca 1.6 times longer than temple (ca 2.1 times).

Description. *Holotype*, ♀: length of body in lateral view 2.5 mm (Fig. 2A), length of antenna 4.4 mm, and length of fore wing 2.5 mm.

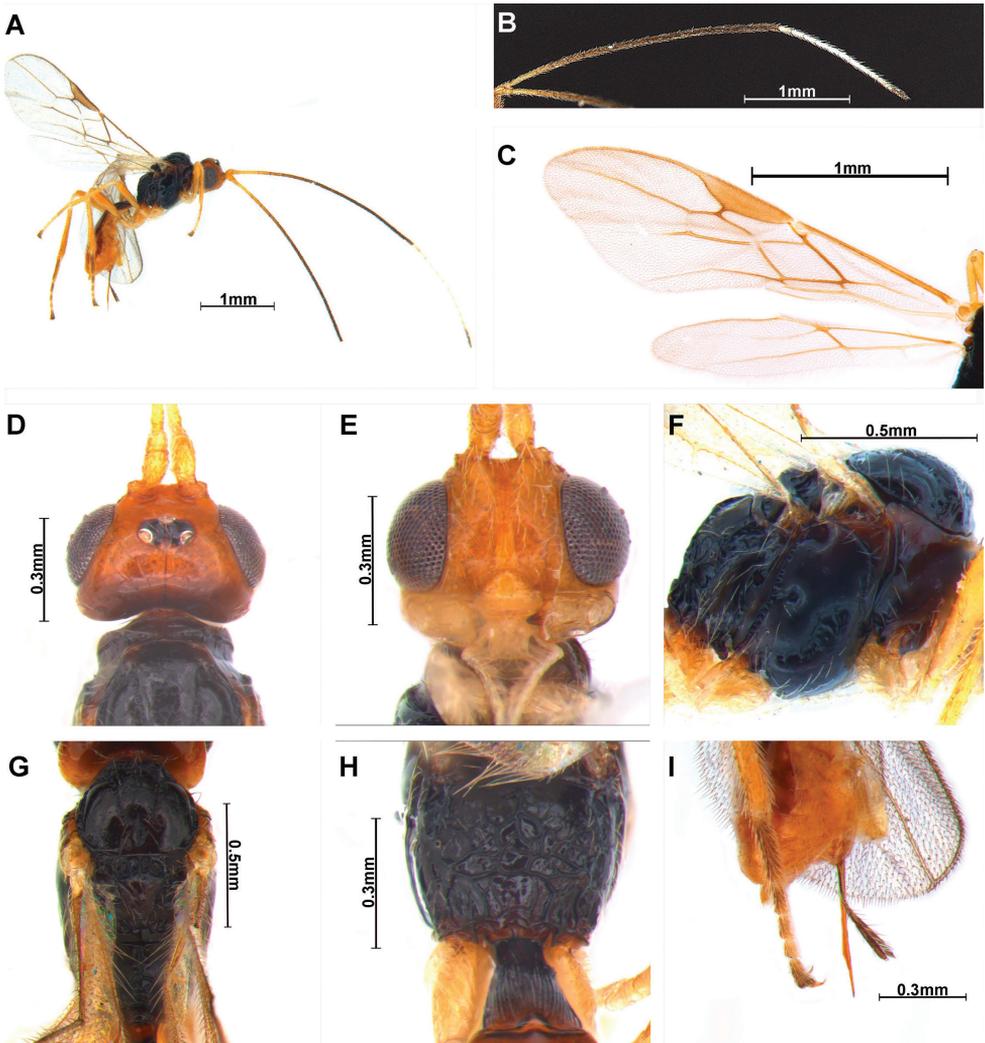


Figure 2. *Cratospila ejuncida* sp. nov. ♀ **A** body **B** antenna **C** wings **D** head, dorsal **E** head, frontal **F** mesosoma, lateral **G** mesosoma, dorsal **H** propodeum, dorsal **I** ovipositor and its sheath, lateral.

Colour: Head orange; antenna (except for two dark apical segments), with 11 flagellomeres white; mandible orange brown and apically dark brown. First tergite dark brown and mesonotum entirely black. Pedicellus entirely yellow.

Head (Fig. 2D): width 1.2 times median length in dorsal view. Antenna (Fig. 2B) twice as long as body in female, 28 segmented. First flagellomere 1.8–1.9 times longer than second flagellomere. Compounded eye slightly oval 1.2 times as long as wide in lateral view. Width of face (Fig. 2E) 0.9–1.0 times its height from ventral rim of antennal sockets to upper margin of clypeus. Eye in dorsal view 1.6 times as long as temple. Ocello-ocular line 2.5 times longer than diameter of anterior ocellus; OOL : AOL :

POL = 11 : 3 : 7. Stemmaticum concave. Vertex smooth and gloss with black line. Mandible with three teeth; first and third teeth smooth.

Mesosoma: Mesosoma (Fig. 2G) 1.5–1.6 times longer than wide in dorsal view. Notauli on middle of mesoscutum narrowly crenulate, not reaching medio-posterior depression; scutellar sulcus with four carinae; metanotum sculptured; small bump in hind coxa adjacent to metapleuron. Propodeum (Fig. 2H) 0.6 times longer than width, more extensively rugose medially, lateral view of propodeum not bent; precoxal sulcus (Fig. 2F) is shallow and incomplete. Fore wing (Fig. 2C) 2.5 times as long as wide; pterostigma long and narrow, 4.2 times longer than wide; vein r of fore wing 1.9 times longer than wide; vein 2-SR slightly bent; vein 2-SR+M and r-m not sclerotized; vein 2-SR : vein r : vein 3-SR = 33 : 5 : 17; first subdiscal cell of fore wing ca 7.3 times longer than wide. Hind wing vein M+CU : vein 1-M = 69 : 4

Leg: hind coxa compressed and grooved; hind coxa 1.5 times longer than hind trochanter; hind femur 0.6 times longer than hind tibia; hind tibia 1.01 times longer than hind tarsus.

Metasoma: first tergite striate and narrow, brown, 2.5 times longer than apical width; T1:T2 = 41:23. Setose part of ovipositor sheath (Fig. 2I) 0.7 times as long as mesosoma, 0.5 times as long as hind tibia and with setae.

Male. Unknown.

Distribution. South Korea.

Etymology. Named after the relatively slender second submarginal cell of the fore wing: “*ejuncidus*” is Latin for slender.

***Cratospila luteocephala* Sohn & van Achterberg, sp. nov.**

<http://zoobank.org/3055D636-AFE8-456A-A6FA-B40570050C00>

Figure 3

Type material. *Holotype*, ♀ (NIBR), SOUTH KOREA, Inje-Gun, Bukmyeon, Hangyeri, 38°08'46.5"N, 128°15'47.5"E, 9–16. IX. 2017 (Malaise trap), J.H. Sohn. GenBank accession no. MW376065.

Comparative diagnosis. Differs from other species of *Cratospila* by having the apical half of ♀ antenna with 8–13 white segments combined with a relatively wide face (1.2 times its height; 0.9–1.1 times in other species). Closely related to *C. albifera* sp. nov.; for differences, see they key above.

Description. *Holotype*, ♀; length of body in lateral view 3.2 mm (Fig. 3A), length of antenna 4.2 mm (apex of antenna missing) and length of fore wing 2.9 mm.

Colour: head (Fig. 3D) orange-yellow; with at least 4 flagellomeres of antenna white (apex of antenna missing); mandible whitish orange. First tergite dark brown and mesonotum entirely reddish brown.

Head: width 1.4 times median length in dorsal view. Antenna (Fig. 3B) twice as long as body in female, 24 segmented (but apex of antenna missing). First flagellomere 1.8 times longer than second. Compounded eye slightly oval, 1.1 times as long as wide

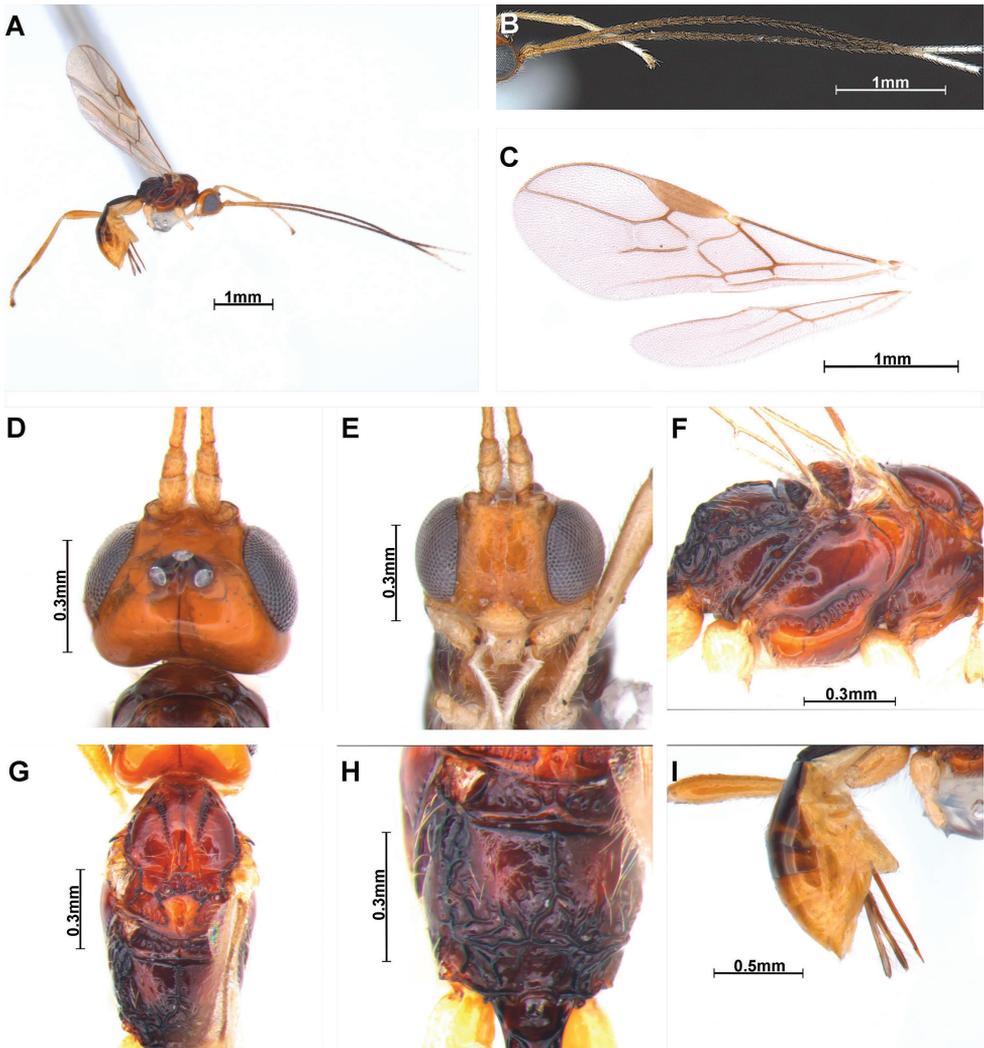


Figure 3. *Cratospila luteocephala* sp. nov. ♀ **A** body **B** antennae **C** wings **D** head, dorsal **E** head, frontal **F** mesosoma, lateral **G** mesosoma, dorsal **H** propodeum, dorsal **I** ovipositor and ovipositor sheath, lateral.

in lateral view. Width of face (Fig. 3E) 0.9 times its height from ventral rim of antennal sockets to upper margin of clypeus. Eye in dorsal view 1.7 times as long as temple. Ocello-ocular line 1.8 times longer than diameter of anterior ocellus; OOL : AOL : POL = 10 : 3 : 8. Stemmaticum concave. Vertex smooth, glossy, and with brown line. Mandible with three teeth; second tooth prominent, with black tip. Maxillary palp about equal length of mesosoma.

Mesosoma (Fig. 3G): 1.5 times longer than wide in dorsal view. Mesoscutum with medio-posterior depression and setae near it; notauli on middle of mesoscutum, comparatively coarsely crenulate, not reaching medio-posterior depression; scutellar

sulcus with six carinae; metanotum sculptured; small bump in hind coxa adjacent to metapleuron. Propodeum (Fig. 3H) 0.8 times longer than width, anterior half of propodeum less sloping; lateral view of propodeum is bent; precoxal sulcus (Fig. 3F) deep and distinct, consist of about nine grooves. Fore wing (Fig. 3C) 2.5 times as long as wide; pterostigma long and narrow, 4.1 times longer than wide; vein r of fore wing 3.2 times longer than wide; vein 2-SR slightly bent; vein 2-SR+M and r-m not sclerotized; vein 2-SR : vein r : vein 3-SR = 33 : 9 : 23; first subdiscal cell of fore wing ca 7.5 times longer than wide Hind wing vein M+CU : vein 1-M = 66 : 7

Leg: hind coxa compressed and grooved; hind coxa 1.7 times longer than hind trochanter; hind femur 0.9 times longer than hind tibia; hind tibia 1.1 times longer than hind tarsus.

Metasoma: first tergite striate and narrow, reddish brown, 2.8 times longer than apical width; T1:T2 = 59:24. Setose part of ovipositor sheath (Fig. 3I) 0.4 times as long as mesosoma, 0.5 times as long as hind tibia and with long setae (Fig. 2F).

Male. Unknown.

Distribution. South Korea.

Etymology. Named after its yellowish head: “*luteocephala*” is derived from “luteus” (Latin for yellow) and “cephalus” (Latin for head).

***Cratospila syntoma* Sohn & van Achterberg, sp. nov.**

<http://zoobank.org/4F72B2F8-D2FD-4D00-BBDA-224067368CD5>

Figure 4

Type material. *Holotype*, ♀ (NIBR), SOUTH KOREA, DMZ Botanical Garden, Mandae-ri, Haean-myeon, Yanggu-gun, Gangwon-do, 38°15'09.3"N, 128°06'40.6"E, 20.VI.–4.VII.2017, H.T. Shin, S.J. Kim. GenBank accession no. MW376066.

Comparative diagnosis. Differs from other new species herein by the short vein r of the fore wing (ca as long as wide; 2–5 times in other species). Unfortunately, the antenna is incomplete but the COI analysis places it in the group of derived *Cratospila* species having the apical half of the ♀ antenna with 8–13 white segments (Table 1). Closely related to *C. ejuncida* sp. nov.; for differences, see the key above.

Description. *Holotype*, ♀; length of body in lateral view 2.5 mm (Fig. 4A), length of antenna 2.8 mm (but apex of antenna missing) and length of fore wing 2.4 mm.

Colour: head (Fig. 4D) entirely black; mandible yellowish brown. Antenna entirely dark brown (but apical segments missing). First tergite dark brown and mesonotum entirely black.

Head: width 1.6 times median length in dorsal view. Antenna (Fig. 4B) 1.1 times longer than body in female, 23-segmented (apex of antenna missing). First flagellomere 1.7 times longer than second. Compound eye slightly oval, 1.2 times as long as wide in lateral view. Width of face (Fig. 4E) 1.1 times its height from ventral rim of antennal sockets to upper margin of clypeus. Face with dense setae. Eye in dorsal view 1.9 times as long as temple. Ocello-ocular line 2.0 times longer than diameter of

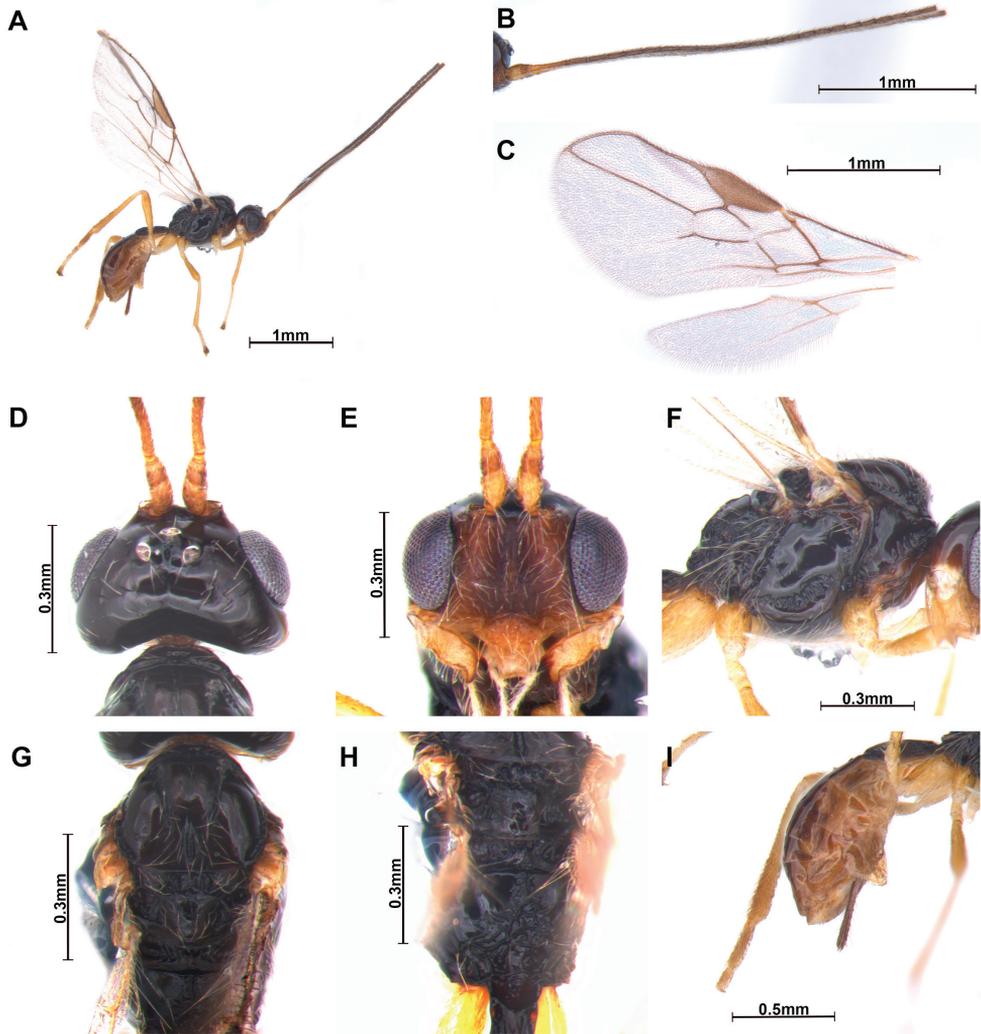


Figure 4. *Cratospila syntoma* sp. nov. ♀ **A** body **B** antennae **C** wings **D** head, dorsal **E** head, frontal **F** mesosoma, lateral **G** mesosoma, dorsal **H** propodeum, dorsal **I** metasoma and ovipositor sheath, lateral.

anterior ocellus; OOL : AOL : POL = 5 : 3 : 7. Stemmaticum concave. Mandible with three teeth; third tooth bent outside.

Mesosoma (Fig. 4G): 1.9 times longer than wide in dorsal view with medio-posterior depression and setae near it; notauli on middle of mesoscutum narrowly crenulate, not reaching medio-posterior depression; scutellar sulcus with six carinae; metanotum sculptured; small bump in hind coxa adjacent to metapleuron; metapleuron with long setae. Propodeum (Fig. 4H) 0.8 times longer than width, more extensively rugose medially; lateral view of propodeum not bent; precoxal sulcus (Fig. 4F) completed with 10 grooves; scutellum with setae partially. Fore wing (Fig. 4C) 2.9 times as long as wide; pterostigma long and narrow, 3.2 times longer than wide; vein r of fore wing 1.5 times

longer than wide; vein 2-SR slightly bent; vein 2-SR+M and r-m not sclerotized; vein 2-SR : vein r : vein 3-SR = 27 : 5 : 20; first subdiscal cell of fore wing ca 6 times longer than wide; second submarginal cell robust. Hind wing vein M+CU : vein 1-M = 39 : 4.

Leg: hind coxa compressed and grooved; hind coxa 1.4 times longer than hind trochanter; hind femur 0.6 times longer than hind tibia; hind tibia 1.2 times longer than hind tarsus.

Metasoma: first tergite striate and narrow, reddish brown, 2.7 times longer than apical width; T1:T2 = 45:19. Setose part of ovipositor sheath (Fig. 4I) 0.3 times as long as mesosoma, 0.4 times as long as hind tibia and with long setae.

Male. Unknown.

Distribution. South Korea

Etymology. Named after the short second submarginal cell of the fore wing: “*syn-tomus*” is Greek for shortened.

Acknowledgements

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Description of a new species of *Megischus* Brullé (Hymenoptera, Stephanidae), with a key to the species from China

Si-Xun Ge¹, Hong-Liang Shi¹, Li-Li Ren¹, Jiang-Li Tan²

1 College of Forestry, Beijing Forestry University, Beijing 100083, China **2** Shaanxi Key Laboratory for Animal Conservation / Key Laboratory of Resource Biology and Biotechnology in Western China, College of Life Sciences, Northwest University, 229 North Taibai Road, Xi'an, Shaanxi 710069, China

Corresponding author: Li-Li Ren (lily_ren@bjfu.edu.cn); Jiang-Li Tan (tanjl@nwu.edu.cn)

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Abstract

A new species of the genus *Megischus* Brullé, 1846, *Megischus kuafu* Ge & Tan, **sp. nov.**, is described and illustrated from Guizhou Province, China. The key to all four species from China is included. A distribution map of the Chinese species is added.

Keywords

Distribution, largest Stephanidae, parasitoids, taxonomy, wasp

Introduction

The small family Stephanidae Leach, 1815, consisting of 364 extant species, is cosmopolitan but mainly restricted to the subtropical and tropical areas (van Achterberg 2002; Aguiar 2004, 2006; Aguiar and Jennings 2005; van Achterberg and Quicke 2006; Aguiar et al. 2010; Hong et al. 2010, 2011; Tan et al. 2015a, b, 2018; Chen et al. 2016; Moghaddam et al. 2019; Binoy et al. 2020; Gupta and Gawas 2020). Species of Stephanidae are generally parasitoids of coleopterous larvae, including species of Buprestidae, Cerambycidae, and even Curculionidae, but also hymenopterous larvae

of Siricidae (Chao 1964; Taylor 1967; Kirk 1975; Königsmann 1978; van Achterberg 2002; Aguiar 2004). The stephanids which are conspicuous by the five tubercles on the head (thus the name *stephanos*, Greek for crown), are considered to be rare and nearly 95% of all the species are described from a single specimen (Aguiar 2001; van Achterberg 2002). Among them, *Megischus* Brullé, 1846 is a large genus of Stephanidae with 87 species worldwide and 30 species from the Oriental region (van Achterberg 2002; van Achterberg and Yang 2004; Hong et al. 2010, 2011; Binoy et al. 2020). However, there are only three species known from China up to date (Hong et al. 2010, 2011). *Megischus* contains the largest known species of Stephanidae with a body length up to 35 mm, excluding the ovipositor (Hong et al. 2011). Here we report the fourth species of the genus from the Oriental part of China with a body length of 39 mm.

Materials and methods

The holotype was collected by sweep net and directly preserved in 70% alcohol. For identification of the family Stephanidae and genera, van Achterberg (2002) and Hong et al. (2011) were used.

The descriptions, measurements, and figures were made using a Leica M205A microscope with a Leica Microsystem DFC550 digital camera. Photographs were combined using the Leica Application Suite (Version 4.5.0). Morphological nomenclature follows van Achterberg (2002) including the abbreviations for the wing venation. The holotype is deposited in the College of Forest Protection, Beijing Forestry University (BFU), China.

Taxonomy

Genus *Megischus* Brullé, 1846

Megischus Brullé, 1846: 537. Type species (designated by Viereck 1914): *M. annulator* Brullé, 1846 [= *M. furcatus* (Lepeletier & Serville, 1825)].

Megischus Brullé, 1846: van Achterberg 2002: 53–168; Aguiar and Johnson 2003: 469–482.

Bothriocerus Sichel, 1860: 759. Type species: *Bothriocerus europaeus* Sichel, 1860 (by monotypy) (= *Stephanus anomalipes* Foerster, 1855, according to Madl 1991).

Diagnosis. Medium to large size. Temple without pale yellowish streak behind eye. Pronotum robust without transverse protuberance. First subdiscal cell of fore wing comparatively narrow basally, approximately as wide as first discal cell or narrower; vein 1-SR of fore wing differentiated with first discal cell present because of presence of vein 1-SR+M; vein 1-M and vein 2-SR straight or nearly so. Hind wing without trace of vein cu-a. Hind coxa without dorsal tooth; hind femur with two distinct teeth; hind tibia narrowed basally and inner side usually with wide sub-medical depression, evenly

rounded ventrally and without oblique striae or rugae on the outer sides; hind tarsus with three tarsomeres. Sternite I not differentiated from tergite I. Tergite I $4.2\text{--}17.6 \times$ as long as its apical width, cylindrical, distinctly longer than tergite II; tergite II more or less petiolate and sculptured basally. Ovipositor sheath with ivory subapical band.

Distribution. Cosmopolitan. The distribution of Chinese species is illustrated in Fig. 20.

Note. *Megischus* specimens are still poorly collected. The known diversity in China compared with the diversity outside China is low and higher numbers of species can be expected.

Key to Chinese species of the genus *Megischus* Brullé

- 1 Head orange brown, temple distinctly convex behind eye; neck rather short and robust, anteriorly rather shallowly concave; middle pronotum steeply rises from neck postero-dorsally; vein 1-M of fore wing ca $2.2 \times$ as long as vein 1-SR; widest part of hind tibia of male nearly straight ventrally. [Pronotal fold absent; vein 1-M of fore wing $0.9 \times$ vein m-cu; hind basitarsus ca $3.5 \times$ as long as wide. Female unknown] (Hubei).....
..... ***M. applicatus* Hong, van Achterberg & Xu, 2010**
- Head dark brown or reddish brown, temple slightly convex or narrowed behind eye; neck elongate and anteriorly distinctly concave (in some specimens of *M. ptosimae* shallowly emarginate); neck at same or lower level than middle part of pronotum postero-dorsally; vein 1-M of fore wing more than $4 \times$ as long as vein 1-SR; widest part of hind tibia weakly to distinctly concave ventrally. **2**
- 2 Head brown, temple narrowly rounded medially behind eye in dorsal view; pronotal fold and concavity absent; medially middle part of pronotum at same level with posterior part postero-dorsally. [vein 1-M of fore wing ca $5.0 \times$ as long as vein 1-SR and $1.2 \times$ vein m-cu.] (Fujian)
..... ***M. chaoi* van Achterberg, 2004**
- Head dark brown or reddish brown, temple slightly convex behind eye in dorsal view; pronotal fold distinct and with a cavity below it; neck at lower level than middle pronotum postero-dorsally. [vein 1-M of fore wing ca $4.2\text{--}5.9 \times$ as long as vein 1-SR and $0.7\text{--}1.3 \times$ vein m-cu]..... **3**
- 3 Head dark brown and malar space pale yellowish; vein 1-M of fore wing ca $4.2\text{--}5.5 \times$ as long as vein 1-SR and $1.1\text{--}1.3 \times$ vein m-cu; widest part of hind tibia distinctly concave ventrally; hind basitarsus $3.0\text{--}3.5 \times$ as long as wide; ivory part of ovipositor sheath $0.7\text{--}2.0 \times$ as long as dark apical part (Guangdong, Shaanxi, Sichuan, Zhejiang, Fujian)..... ***M. ptosimae* Chao, 1964**
- Head completely dark reddish brown (red in alive specimen; Fig. 19); vein 1-M of fore wing ca $5.9 \times$ as long as vein 1-SR and $0.8 \times$ vein m-cu; widest part of hind tibia weakly concave ventrally; hind basitarsus ca $7.4 \times$ as long as wide; ivory part of ovipositor sheath ca $2.0 \times$ as long as dark apical part (Guizhou) ***M. kuafu* Ge & Tan, sp. nov.**

***Megischus kuafu* Ge & Tan, sp. nov.**

<http://zoobank.org/3CDF81C0-D859-45F8-8E57-E3A77CBC9615>

Figures 1–19

Material examined. *Holotype*, ♀ (BFU), CHINA: Guizhou, Libo, Maolan National Nature Reserve; Wuyanqiao; 108°6.065'E, 25°17.598'N, 541 m, 26.V.2020, leg. Si-Xun Ge.

Diagnosis. Head completely dark reddish brown (red in alive specimen; Fig. 19), temples slightly bulging behind eyes; ocellar area (Fig. 2) transversely rugose; vertex reticulate-rugose medially, followed by weakly transverse rugae posteriorly almost reaching occipital carina; pronotum (Fig. 4) subparallel anteriorly and with distinct pronotal fold; apical median portion of neck shiny (before pronotal fold); medio-anterior pronotum moderately wide (in dorsal view) and strong transverse rugae; scutellum (Fig. 6) almost glabrous and with foveolae laterally; vein 1-M ca 5.9 × as long as vein 1-SR; hind basitarsus densely setose and parallel-sided, ventral length 7.4 × maximum width.

Description. *Holotype. Female.* Length of body 39.1 mm; forewing 21.3 mm; ovipositor sheath 59 mm.

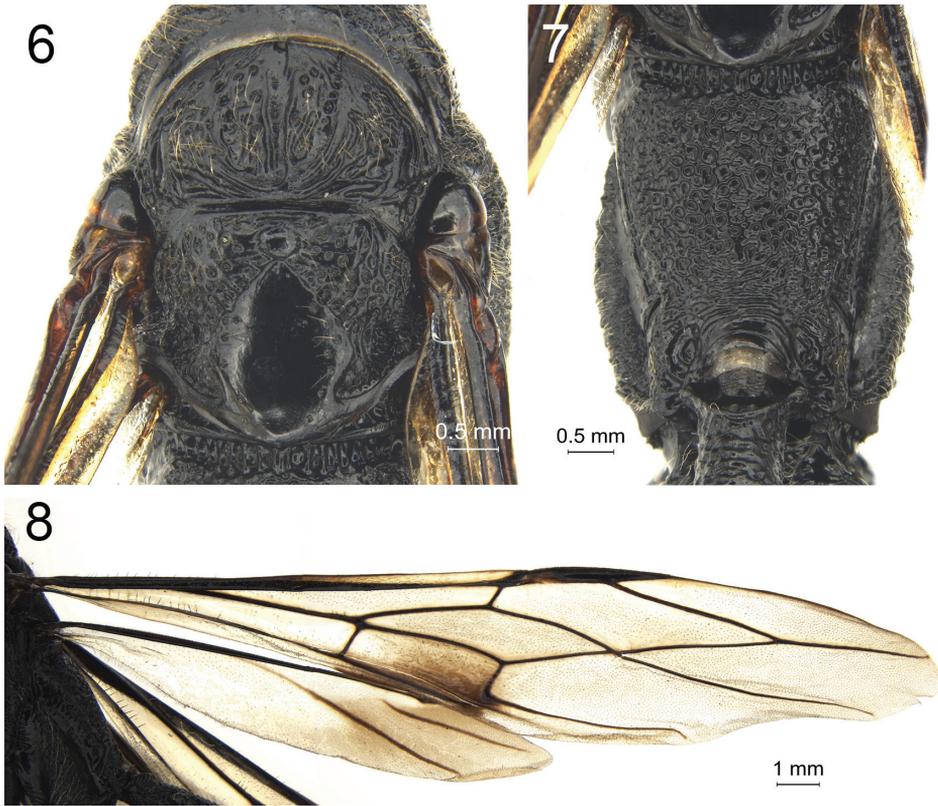
Head. Antenna with 39 flagellomeres; the first flagellomere slender, length 3.4 × its maximum width, and length of second flagellomere 1.2 × its width; frons coarsely and transversely rugose (Fig. 1); three anterior coronal teeth large and lobe-shaped, both posterior ones smaller and wider; vertex transversely rugose anteriorly and reticulate-rugose medially, followed by coarsely and slightly curved rugosities reaching occipital carina; temple slightly bulging, smooth and shiny (Fig. 2), except for some fine punctures laterally; occipital carina strongly developed and connected to hypostomal carina; hypostomal carina large and without distinct rugae, only some punctures (Fig. 3).

Mesosoma. Neck robust and anteriorly distinctly concave (Fig. 4), with several weak incomplete carina anteriorly and three interrupted and rather strong carina, at lower level than middle part of pronotum postero-dorsally (Fig. 5), and with large smooth and shiny area before pronotal fold; pronotal fold strong, weakly sinuate and below it with rather deep concavity (Fig. 4); middle part of pronotum with nine weak and irregular transverse carinae (as laterally) and with distinct oblique lateral groove; no median carina anteriorly; middle part of pronotum weakly differentiated from posterior part (Fig. 5), and latero-posteriorly rather weakly convex; posterior part of pronotum generally with rather sparse setosity, latero-ventrally densely setose but dorso-posteriorly glabrous, with several coarse punctures and latero-posteriorly with some crenulae; propleuron coriaceous and setose; prosternum densely foveolate, foveolae circular and setose; convex part of mesopleuron strongly foveolate and with dense short whitish setosity (Fig. 5); mesosternum largely smooth (except some fine punctures); scutellum smooth and with foveolae laterally (Fig. 6); propodeum dorsally almost glabrous (Fig. 7), completely with shallow, circular foveolae, most foveolae are separated and some of them coalescent.



Figures 1–5. *Megischus kuafu* Ge & Tan, sp. nov. Holotype ♀ **1** head, frontal view **2** head, dorsal view **3** head, lateral view **4** pronotum, dorsal view **5** mesosoma, lateral view.

Wings. Fore wing: wing membrane largely subhyaline (Fig. 8), and surface evenly bristly; vein M+CU1 with four short, erect, equidistant spiny setae; vein 1-M $5.9 \times$ as long as vein 1-SR and $0.8 \times$ vein m-cu; vein 2-SR $0.9 \times$ as long as vein r; vein r ends



Figures 6–8. *Megischus kuafu* Ge & Tan, sp. nov. Holotype ♀ **6** mesoscutum and scutellum, dorsal view **7** propodeum, dorsal view **8** wings.

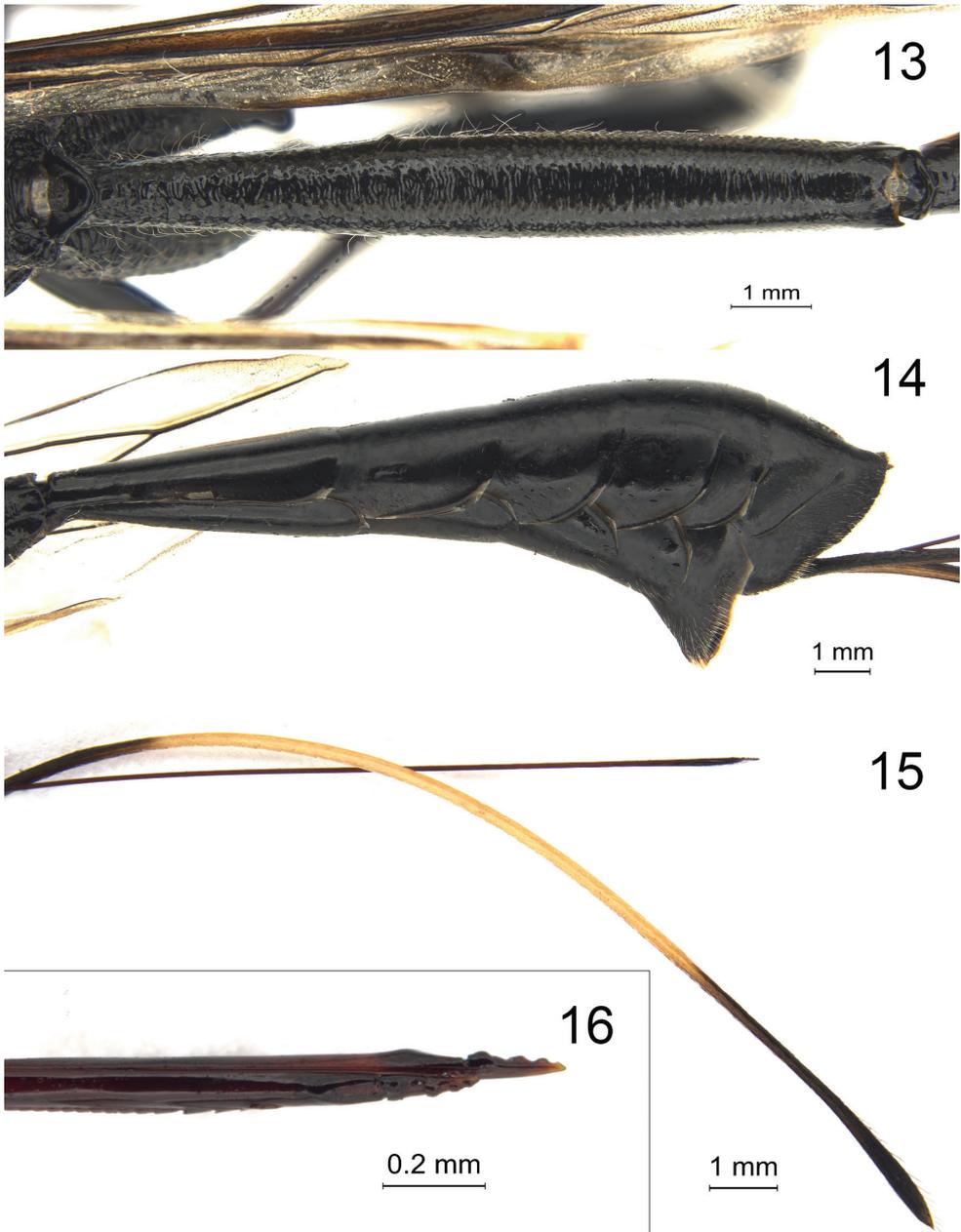
0.5 × length of pterostigma behind the level of apex of pterostigma; vein 1-SR 1.1 × as long as parastigmal vein; vein 3-CU1 distinct and curved apically.

Legs. Hind coxa rather strong, annular, largely transversely striate, with long whitish setosity strongly inclined towards (Fig. 9); hind femur robust, with scattered punctures and largely smooth and shiny interspaces (Fig. 10), hind femur ventrally with two large teeth and ten minute teeth in between and one small tooth behind large posterior tooth; hind tibia distinctly curved basally (Fig. 11), elongate and 1.2 × longer than hind femur, densely setose and mostly sparsely punctate, basal narrow part of hind tibia 0.5 × as wide as widest part, lateral view of hind tibia below depression nearly parallel-sided and slender, inner side rather convex basally, densely setose; hind basitarsus slender and parallel-sided, bristly setose ventrally, ventral length 7.4 × its maximum width (Fig. 12).

Metasoma. Tergite I transversely striate-rugose (Fig. 13), ca 6.9 × as long as its maximum width and 10.4 × its apical width, 1.9 × as tergite II and 0.7 × as remainder of metasoma; basal 0.1 of tergite II rugose, remainder smooth and glabrous; remainder of tergites (Fig. 14) shiny and with sparse and short setae (except tergite VII densely

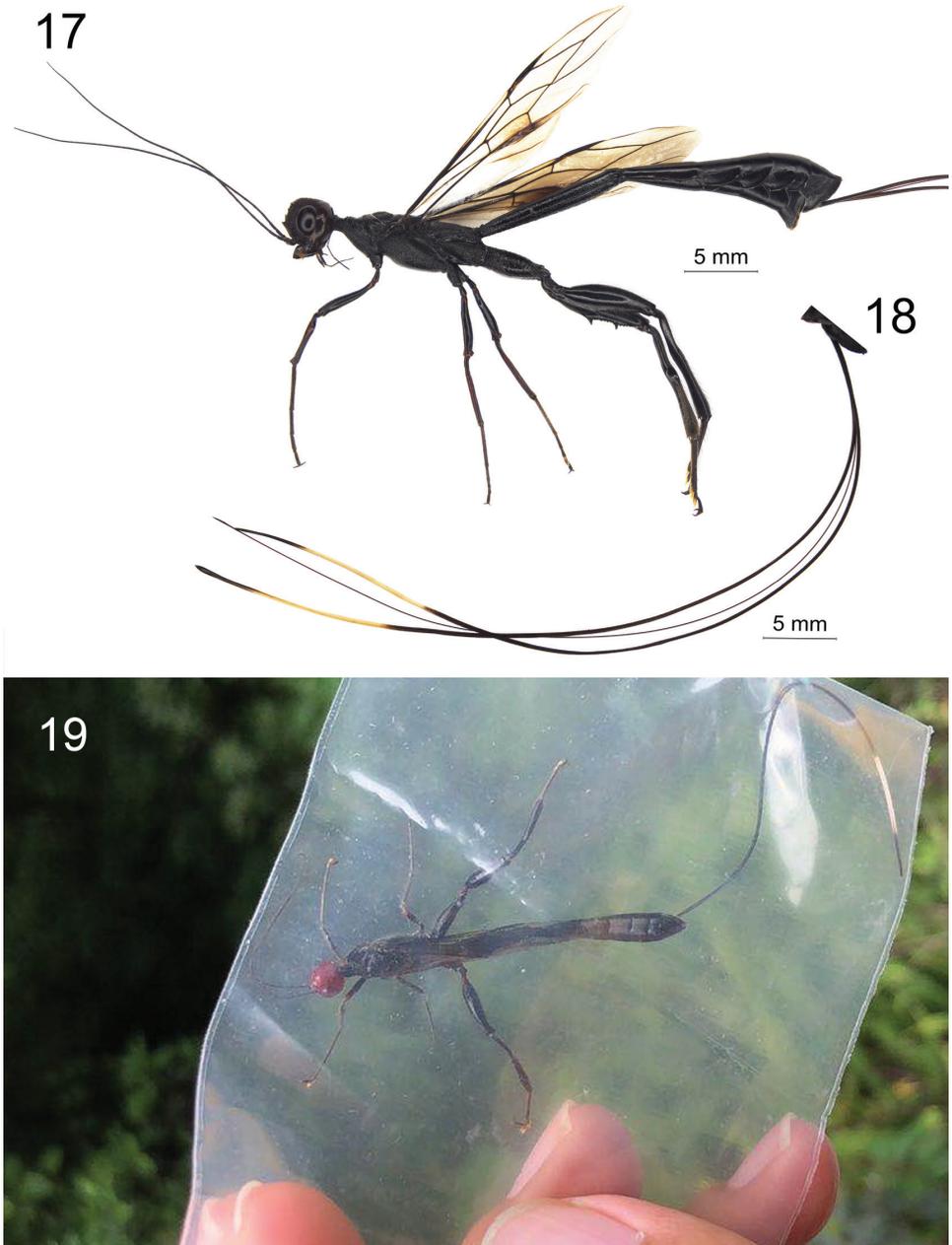


Figures 9–12. *Megischus kuafu* Ge & Tan, sp. nov. Holotype ♀ **9** hind coxa, lateral view **10** hind femur, lateral view **11** hind tibia, lateral view **12** hind tarsi, lateral view.



Figures 13–16. *Megischus kuafu* Ge & Tan, sp. nov. Holotype ♀ **13** tergite I, dorsal view **14** metasoma (except tergite I), lateral view **15** distal part of ovipositor and sheath, lateral view **16** apex of ovipositor, lateral view.

setose medially); pygidial area coriaceous, medially moderately convex and distinctly punctate medially and anteriorly, with long straight setae; length of ovipositor sheath ca $1.5 \times$ as long as body and ca $2.8 \times$ as long as forewing, length of subapical whitish band (Fig. 15) twice as long as dark apical part. Ovipositor tip laterally compressed, with minute teeth apically (Fig. 16).



Figures 17–19. 17 habitus of holotype. ♀ *Megischus kuafu* Ge & Tan, sp. nov. (except ovipositor and ovipositor sheath) 18 ovipositor and ovipositor sheath 19 collecting living specimen.

Colour. Mostly black; mesosoma, metasoma, antennae, and hind legs black or blackish; head dark reddish brown; tergite II brownish bilaterally; wing membrane light brownish, hyaline, except most of hind portion of first subdiscal cell and apical part of hind wing brown; veins and pterostigma brown or dark brown; fore and mid-

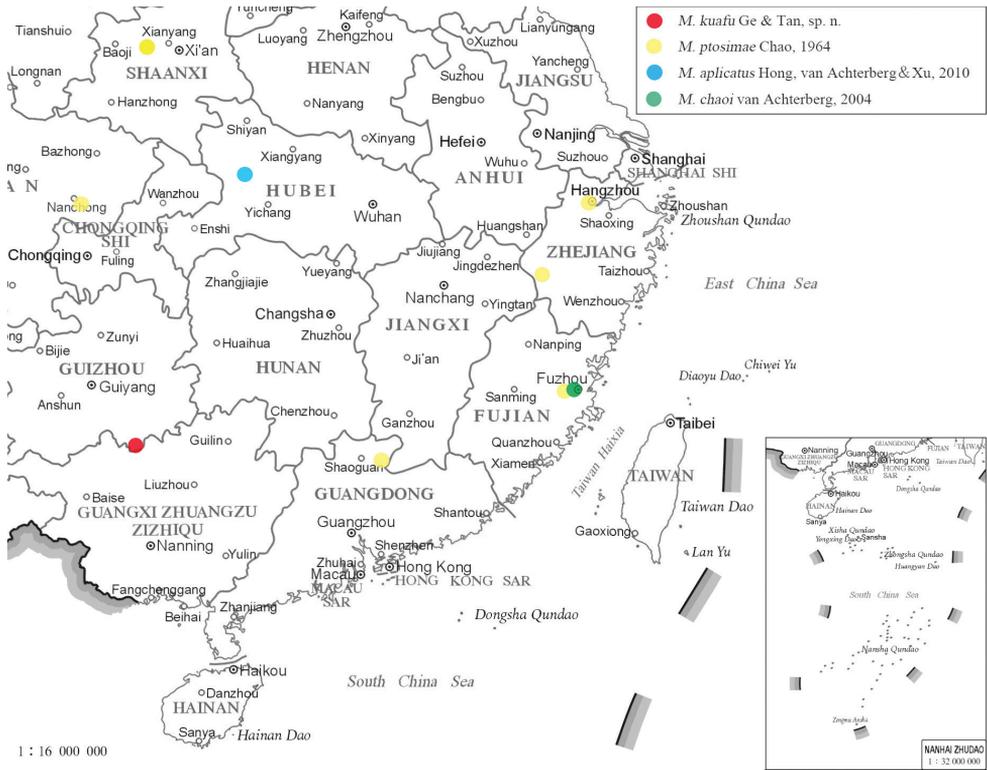


Figure 20. Distribution map of *Megischus* species from China (map of China from: <http://bzdt.ch.mnr.gov.cn/>).

dle legs dark brown (except for coxae black); ovipositor sheath largely black and with whitish subapical band.

Male. Unknown.

Etymology. The species name is derived from the name of a giant chasing the sun in Chinese mythology, as an analogy of its exclusively large size and a dark reddish-brown head.

Distribution. China (Guizhou).

Biology. Collected in May. Host is unknown.

Note. The description is based on the pinned holotype. The colour of the head changed from bright red into dark reddish brown after it died (Fig. 19). The genus *Megischus* contains the largest known stephanids and some of them can be up to 35 mm (Binoy et al. 2020). Although the size of parasitoids varies among specimens of the same species due to the nutritional conditions of the host and other factors, the body length of 39 mm makes *M. kuafu* the largest known *Megischus* specimen, and also the largest Stephanidae.

The large size and general colour pattern more or less resemble *M. ducaloides* van Achterberg, 2004, but it can be easily distinguished from it by the distinct pronotal fold and the rounded shape of the posterior part of the pronotum. The new species

runs to *M. ptosimae* in the key to Chinese species by Hong et al. (2011) in having the temple slightly convex behind eye, a distinct pronotal fold and cavity below it, and vein 1-M of fore wing ca $5.5 \times$ as long as vein 1-SR. However, the new species differs from *M. ptosimae* in lacking a pale yellowish malar space, vein 1-M $0.8 \times$ as long as vein m-cu of the fore wing, less sculptured scutellum, posterior half of the hind tibia weakly concave ventrally and the hind basitarsus ca $7.4 \times$ as long as wide. This new species runs to *M. rubripes* (Kieffer, 1916) in the key to Old World *Megischus* by van Achterberg (2002), but it differs from *M. rubripes* in having a more irregular sculpture of the vertex, a large, smooth, and shiny concavity before the pronotal fold, blackish hind tibia and hind basitarsus and tergite I ca $6.9 \times$ as long as its maximum width.

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A review of the introduced herpetofauna of Mexico and Central America, with comments on the effects of invasive species and biosecurity methodology

Víctor Hugo González-Sánchez¹, Jerry D. Johnson², David González-Solís¹,
Lydia Allison Fucsko³, Larry David Wilson^{4,5}

1 *El Colegio de la Frontera Sur (ECOSUR), Chetumal, Quintana Roo, Mexico* **2** *Department of Biological Sciences, The University of Texas at El Paso, El Paso, 79968-0500, TX, USA* **3** *Department of Humanities and Social Sciences, Swinburne University of Technology, Melbourne, Victoria, Australia* **4** *Centro Zamorano de Biodiversidad, Escuela Agrícola Panamericana Zamorano, Departamento de Francisco Morazán, Honduras;* **5** *1350 Pelican Court, Homestead, 33035-1031, FL, USA*

Corresponding author: Larry David Wilson (bufodoc@aol.com)

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Abstract

Among the principal causes producing detrimental effects on global biodiversity are introductions of alien species. Very few attempts to control introduced amphibians and reptiles in Middle America (Mexico and Central America) can be identified, so listings are provided for 24 exotic species, 16 translocated species, and 11 species that were removed from the introduced species listing because of lack of substantiating evidence that they are from established populations. Biosecurity methods are also identified that can be applied for preventing, controlling, and managing introduced and especially invasive species.

Resumen

Entre las principales causas que producen efectos perjudiciales sobre la biodiversidad mundial se encuentran la introducción de especies exóticas. Se pueden identificar muy pocos intentos de controlar anfibios y reptiles introducidos en América Central (México y América Central), por lo que proporcionamos listas de 24 especies exóticas, 16 especies translocadas y 11 especies que eliminamos de la lista de especies introducidas debido a la falta de evidencia que corrobore que provienen de poblaciones establecidas. También identificamos métodos de bioseguridad que se pueden aplicar para prevenir, controlar y gestionar especies introducidas y especialmente invasoras.

Keywords

Biological invasion, exotic species, herpetofauna, introduced species, Middle America, translocated species

Palabras claves

Especies ex́ticas, especies introducidas, especies translocadas, herpetofauna, invasion biol3gica, mesoam3rica

Introduction

Among the most important drivers for biotic extinctions are introduced invasive species (Mack et al. 2000; Simberloff 2005). This phenomenon is not new, since human-mediated biological invasions or translocations of non-native species (e.g., goats, pigs, cats, dogs, and rats, among various mammals) by humans have been occurring for at least 20,000 years (Hofman and Rick 2018). Geographic scope, frequency, and number of species involved, however, have increased as a direct consequence of growths in transportation and commercial activities, so few habitats on Earth remain devoid of species introduced by humans (Mack et al. 2000). Among others, the main pathways for introducing amphibians and reptiles are accidental transport in cargo shipments on land and over water; intentional and accidental release via pet trade; as biocontrol agents; those associated with human food consumption, as well as for aesthetic purposes (Kraus 2003). Among many other effects, invasive non-native species can have negative impacts at all biological levels, including genetic pollution and hybridization (Cedeño-Vázquez et al. 2008), competition and depredation (Sakai et al. 2001), introducing parasites (Williams et al. 2013), epizootics (Garner et al. 2006), zoonoses (Hulme 2014), habitat modification, by altering nutrient and energy cycles and biomass structure (Beard et al. 2002; Crooks 2002), shifting water cycles (Gallardo et al. 2015), and triggering trophic cascades (Zavaleta et al. 2001). The impact of invasive species, such as the anurans *Lithobates catesbeianus* and *Rhinella horribilis*, as two well-known examples, on human economics and human well-being is considered collateral damage, because of the loss and alterations to goods (agricultural crops, animal husbandry, forest products, fisheries) and services (clean water, climate stabilization, pollination, human culture, recreation), as identified by Pejchar and Mooney (2009) and Walsh et al. (2016).

A common misbelief is that the ecology of invasive species and the ecosystem alterations they produce are extensively documented (Cadotte 2006). This is only partially true, since most research on ecology of alien species involves significant taxonomic and geographical biases (Pyšek et al. 2008; MacIsaac et al. 2010). This situation is relevant since historically introduced amphibians and reptiles have received less attention in Mesoamerica than have other groups, such as mammals, vascular plants, and insects (Reed and Kraus 2010). This deficiency has led to an omission of the status of introduced and invasive species in several herpetofaunal inventories. Therefore, listings of exotic and invasive herpetofaunal species in Middle America

(Mexico and Central America) have been comprised of only a few species, including members of the genus *Boa*, Morelet's Crocodile (*Crocodylus moreletii*), the Pond Slider (*Trachemys scripta*), and the American Bullfrog (*Lithobates catesbeianus*). Gekkonid lizards are found frequently in listings of introduced species, but their ecology and potential impacts have received little attention. Presently, 78 amphibian and 198 recognized reptile species have become established outside their native ranges around the world (Capinha et al. 2017). The goal of this paper is to review and assess the current knowledge and status of members of the introduced herpetofauna in Middle America, their history of colonization, their impacts on ecosystems, and their current geographic distributions.

Materials and methods

We compiled a list of the introduced reptiles and amphibians in Middle America by examining relevant literature for the region, complemented with records obtained from GBIF (GBIF.org 2018), iNaturalist (inaturalist.org 2018), Amphibian Species of the World (Frost 2020), Reptile Database (Uetz et al. 2020), International Union for Conservation of Nature (2020), and VertNet (vertnet.org, 2018) platforms. In addition to these sources, for Mexico we considered only records with acceptable confirmation, properly georeferenced, and found in the literature and databases of the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO 2018) and Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT 2017). Scientific names are based on Wilson et al. (2013a, b) and Johnson et al. (2015b), along with the most recent lists at Uetz et al. (2020) and Frost (2020), with full understanding that nomenclatural changes will occur regularly during future taxonomic revisions. Common names, when appropriate, follow Liner and Casas-Andreu (2008) for Mexico and adjacent Central America when species are shared between the two regions. Common names of species occurring only outside of Mexico and adjacent areas are those found in the literature and websites listed above. For convenience, we use the term “reptiles” to name taxonomic groups traditionally considered orders of the class Reptilia as listed by Uetz et al. (2020) (i.e., Testudines – turtles; Crocodylia – crocodiles; Squamata – snakes and lizards), so we use the term herpetofauna when generally referring to the amphibians, turtles, crocodiles, snakes, and lizards occurring within Middle America. For more on our taxonomic positions, see the section below and especially Johnson et al. (2015b).

Our study area comprises Mexico and all Central American countries (Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, and Panama), ordered by latitude. Our use of the term “Middle America” refers to the Central American countries plus Mexico. We do not use the term “Mesoamerica,” since this label is generally considered more relevant in an anthropological and historical context (Romero-Contreras and Ávila-Ramos 1999), even though it is a commonly used synonym for Middle America.

In this paper, we consider introduced species to be populations whose presence in an area is attributed to human activities that enabled them to overcome biogeographical barriers that they otherwise could not cross and become established. We prefer introduced as the universal term over some others, such as exotic, non-native, alien, or non-indigenous, since the word “introduced” is more easily associated with human intervention (Young and Larson 2011). We will use the terms exotic and translocated most often, however, to describe the two major groupings of introduced species, and use other synonymous terms occasionally to lessen redundancy. This idea is clearly opposite to the concept of “native species,” to designate those that have evolved in a given area without human involvement, or that have arrived there by natural means without intentional or unintentional intervention of humans, from areas in which they are also native (Pyšek and Richardson 2010).

Introduced species are not all-encompassing on temporal and geographical bases, because not all introduced organisms manage to become “established;” i.e., surviving long enough to produce descendant lineages (Davis 2009). We also understand that some species occasionally can be “naturalized,” which are those introduced species sustaining self-replacing populations for several life cycles without, or despite, direct intervention by humans (Richardson et al. 2011). In this sense, “population persistence” is the ongoing accumulation of establishment successes by individuals arising within an area (Davis 2009). Non-native species do not have to be introduced necessarily within the totality of a region, but transported to areas within the same area outside their native range; these will be referred to as “translocated species” (Shine et al. 2000). Countries are good examples of useful geographic units for qualifying which type of introduction a population exemplifies (exotic versus translocated), although sometimes adjustments need to be made to meet criteria, such as between islands and the mainland belonging to the same country, or a slightly disconnected mainland from a large peninsula belonging to the same country (e.g., Baja California peninsula and mainland Mexico). A closely related concept is “invasive species,” here defined as those well-established introduced species having deleterious effects on native ecosystems as the result of increasing their population numbers. In addition, invasive species can have deleterious effects on native populations, even if their populations are not increasing, e.g., through the introduction of new diseases, which can then kill native species.

The “impact” of an introduced invasive species, either exotic or translocated, refers to how an introduced species distresses the physical, chemical, or biological environment, the effect of which might be evident at the genetic, individual, population, community, ecosystem, landscape, regional, or global levels (Parker et al. 1999; Mack et al. 2000; Richardson et al. 2011). Of course, we do not overlook the fact that impacts and the reasons for them might be controversial (Parker et al. 1999; Young and Larson 2011), and that many invasive species can have negative influences on cultural, economic, and social issues relating to alleged human welfare (McNeely 2001; Perrings et al. 2005; Pejchar and Mooney 2009). Those topics remain unexplored in the field of invasive species in the herpetological literature, so some of the invasive species covered

herein will focus our discussions on known impacts affecting ecological components. Finally, we adopt the term “biosecurity,” as defined by Pyšek and Richardson (2010), as the management of risks posed by organisms to the economy, environment, and human health through exclusion (prevention of initial introduction), mitigation, adaptation, control, and eradication.

Our taxonomic positions follow those discussed in Johnson et al. (2010), Porras et al. (2013), and expanded upon by Johnson et al. (2015b), which are predicated on modern phylogenetic principles. We regard species as separate evolutionary lineages and consider them the lowest evolutionary lineage segment placed on a phylogeny in a formal phylogenetically based taxonomy. We also consider the subspecies category to be a taxonomic anachronism that should not be used in a formal classification hierarchy because subspecies merely represent geographic variations in populations of the same species that are connected by gene flow (intergradation) and not separate evolutionary lineages. We do, however, concede that officially classifying subspecies had much influence in the past, so we reference them in a historical perspective in a few taxa discussed below. In those cases, the taxonomy reverts to the binomial.

Results and discussion

Status of the exotic and translocated herpetofauna of Middle America

Currently, 40 species of herpetofaunal species are considered introduced to a region of Middle America, or indigenous to a region, but translocated to non-native areas. Of these, 24 are exotics (Tables 1, 2), whereas 16 are translocated (Tables 1, 3). Most are reptiles (30 [18 exotics and 12 translocations]), and ten are anuran amphibians [six exotics and four translocations]). Three species are listed among the 100 worst invasive alien species of the world (Lowe et al. 2000): the American Bullfrog (*Lithobates catesbeianus*), the Puerto Rican Coqui (*Eleutherodactylus coqui*), and the Pond Turtle (*Trachemys scripta*). Twenty-six species are listed in the IUCN Red List of Threatened Species (IUCN 2014), with most of those, as expected, in the Least Concern category. Two, however, are under risk categories: The Spiny Chuckwalla (*Sauromalus hispidus*) as Near Threatened, and the Mexican Giant Musk Turtle (*Staurotypus triporcatus*) as Lower Risk/Near Threatened. Mexico has the largest number of introduced species (24; 13 exotics and 11 translocations), whereas El Salvador only has two species, both exotic. In addition to Mexico, Honduras also has translocated species, such as *Ctenosaura similis* on Isla Roatán (Table 1).

Herpetofaunal introductions in Middle America can be traced back to colonial times and were associated with commercial routes between the Philippines and New Spain (mainly Acapulco, Mexico), or through the slave trade from Western Africa to the Caribbean and Antillean islands, and from there into Central America. More recent events involved the opening of the Panama Canal in 1914, the expansion of the irrigation infrastructure after the 1950's in northern Mexico, and throughout Middle

Table 1. List of introduced and translocated herpetofauna in the countries from Middle America. Introduced herpetofauna in Middle America (Right total = number of countries in which the species has “exotic” or “translocated” status; Bottom total = number of exotic and translocated species in that country). Parentheses enclose the number of exotic and translocated species for that taxon.

Taxa	Exotic (E) or translocated (T)	Mexico	Guatemala	Belize	Honduras	El Salvador	Nicaragua	Costa Rica	Panamá	Total	Main references	
Amphibians (10)												
Anurans (10)												
Eleutherodactylidae (4)												
<i>Eleutherodactylus antillensis</i>	E								+	1	de Sousa et al. (1989), Barker and Rodríguez-Robles (2017)	
<i>Eleutherodactylus coqui</i>	E								+		Barrantes-Madrigal (2017), Barrantes-Madrigal et al. (2019)	
<i>Eleutherodactylus johnstonei</i>	E								+	1	Ibañez and Rand (1990), McCranie and Valdez-Orellana (2014)	
<i>Eleutherodactylus planirostris</i>	E	+			+			+	+	5	Crawford et al. (2011), McCranie and Gutsche (2014), Barquero and Araya (2016), Cedeño-Vázquez et al. (2014), Alvarez-Romero et al. (2008)	
Hylidae (2)												
<i>Osteopilus septentrionalis</i>	E								+	1	Savage (2002)	
<i>Smilisca baudinii</i>	T	+								1	Recuero et al. (2004)	
Pipidae (1)												
<i>Xenopus laevis</i>	E	+								1	Murphy (1983) Álvarez-Romero (2008), Peralta-García et al. (2014)	
Ranidae (3)												
<i>Lithobates berlandieri</i>	T	+								1	Rorabaugh and Servoss (2006)	
<i>Lithobates catesbeianus</i>	T	+								1	Casas-Andreu et al. (2001), Lemos-Espinal and Smith (2016), Grismer (2002)	
<i>Lithobates forreri</i>	T	+								1	Grismer (2002)	
Reptiles (31)												
Crocodylia (1)												
Crocodylidae (1)												
<i>Crocodylus moreletii</i>	T	+								1	Alvarez-Romero (2008)	
Squamata (23)												
Dactyloidae (4)												
<i>Anolis allisoni</i>	E	+		+	+					3	Charruau et al. (2015), Schmidt (1941), McCranie and Köhler (2015), Glor et al. (2005)	
<i>Anolis carolinensis</i>	E	+								1	Terán-Juárez et al. (2015)	
<i>Crenonotus cristatellus</i>	E								+	1	Savage (2002), Mayer (2010)	
<i>Norops sagrei</i>	E	+	+	+	+				+	+	6	Lee (1996), Sexton and Brown (1977), Stuart (1955), Savage and Bolaños-Vives (2005), Batista et al. (2019)
Gekkonidae (9)												
<i>Gehyra mutilata</i>	E	+								1	Álvarez-Romero (2008) Cruz-Sáenz et al. (2017), Reynoso (1990a), Lemos-Espinal and Dixon (2013)	
<i>Gekko gecko</i>	E			+						1	Meerman and Garel (2002)	
<i>Hemidactylus frenatus</i>	E	+	+	+	+	+	+	+	+	8	Weterings and Vetter (2017)	
<i>Hemidactylus garnotii</i>	E		+						+	2	Savage (2002), Morales et al. (2017)	
<i>Hemidactylus haitianus</i>	E				+					2	McCranie (2015), Auth (1994)	
<i>Hemidactylus mabouia</i>	E	+			+				+	+	4	Álvarez-Romero (2008), Gutsche and McCranie (2009), Abarca and Monge (2007), Auth (1994)
<i>Hemidactylus turcicus</i>	E	+							+	2	Martínez-Hernández et al., (2017), McCoy (1970), Lee (1996)	
<i>Lepidodactylus lugubris</i>	E	+					+	+	+	4	Smith and Grant (1961), Savage (2002), Hoogmoed and Avila-Peres (2015)	
<i>Tarentola mauritanica</i>	E	+									Ortiz-Mena et al. (2019)	
Iguanidae (5)												
<i>Ctenosaura conspicuosa</i>	T	+								1	Grismer (2002)	
<i>Ctenosaura pectinata</i>	T	+								1	Aguirre-Léon and Matías-Ferrer (2017)	

Taxa	Exotic (E) or translocated (T)										Total	Main references
		Mexico	Guatemala	Belize	Honduras	El Salvador	Nicaragua	Costa Rica	Panamá			
<i>Ctenosaura similis</i>	T				+						1	McCranie and Valdés-Orellana (2014)
<i>Sauromalus hispidus</i>	T	+									1	Grismer (2002), Petren and Case (1997)
<i>Sauromalus varius</i>	T	+									1	Hollingsworth et al. (1997)
Leiocephalidae (1)												
<i>Leiocephalus varius</i>	E				+						1	Schwartz and Thomas (1975), McCranie (2018)
Phrynosomatidae (1)												
<i>Uta stansburiana</i>	T	+									1	Upton and Murphy (1997)
Sphaerodactylidae (1)												
<i>Sphaerodactylus argus</i>	E	+						+		+	3	Harris and Kluge (1984), Lee (1996), Sunyer et al. (2013), Thomas (1975)
Boidae (1)												
<i>Boa imperator</i>	T	+									1	López-González (1991)
Typhlopidae (1)												
<i>Indotyphlops braminus</i>	E	+	+	+	+	+	+				6	Wallach et al. (2014), Leets-Rodríguez et al. (2019)
Testudines (7)												
Chelydridae (1)												
<i>Cheylra serpentina</i>	E	+									1	Dixon (2013), Powell et al. (2016), Terán-Juárez et al. (2016)
Emydidae (1)												
<i>Trachemys scripta</i>	T	+									1	Lavín et al. (2014)
Kinosternidae (1)												
<i>Kinosternon integrum</i>	T	+									1	Iverson et al. (1998)
Staurotypidae (1)												
<i>Staurotypus triporcatus</i>	T	+									1	Terán-Juárez et al. (2015)
Testudinidae (1)												
<i>Chelonoidis carbonarius</i>	E							+				Salazar-Savecedra et al. (2015), Villa et al. (1988)
Trionychidae (1)												
<i>Apalone spinifera</i>	T	+									1	Grismer (2002), McGaugh and Janzen (2008)
Totals	24E/16T	29	4	5	9	2	6	9	10	–		

America due to the highly popular pet trade and agricultural practices. On the other hand, translocations have more obscure origins, and certainly some of those could have occurred in pre-Columbian times, like translocations of iguanid lizards onto several islands in the Sea of Cortes (also called the Gulf of California, or Mar de Cortés in Spanish) by the Seri society. Whereas it is often accepted in invasive species biology that 1492 is the cutoff date for delineation between native and non-native species, we are concerned at this point with translocated species, not non-native species. In addition, it is our opinion that the year 1492, as the time when Christopher Columbus “discovered” the New World, is of disputable significance from a biological point of view. The matter of most significant concern, we think, is to what extent humans, whether from Spain or elsewhere, have had a hand in the movement of creatures around the world.

We recognize six major Middle American sites as “hotspots” for herpetofaunal invasions (four of which are depicted on Fig. 1): 1) Northwestern Baja California and nearby Río Colorado delta in the Mexicali Valley, where hydrological systems and agricultural channels most likely served as pathways for the invasion of several introduced species already established in California, Arizona, and New Mexico; 2) The Panama Canal, where concentrated traffic of cargo shipping has been an important source of

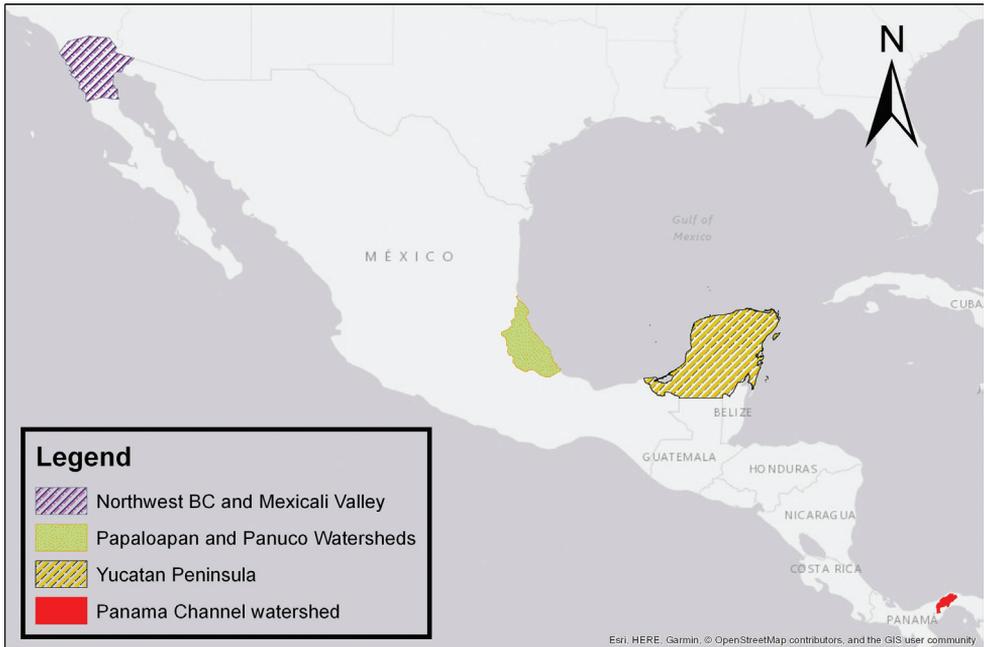


Figure 1. The four main Middle American sites considered as “hotspots” for herpetofaunal invasions: Northwestern Baja California and nearby Río Colorado delta in the Mexicali Valley, the Panama Canal, the Mexican Yucatan Peninsula, and The Papaloapan and Panuco basins in the Mexican state of Veracruz. The airports and seaports are not depicted due their ubiquity.

invaders; 3) The Mexican Yucatan Peninsula, a tropical region with flat topography and low elevation, with its highest point around 300 m, containing extensive communication and tourism infrastructures; 4) The State of Veracruz, historically having the largest and most important Mexican sea port, as well as being a main logistic center for Mexico’s economy; 5) Major airports and seaports of each Middle American country; and 6) Insular systems within the Sea of Cortes and Pacific Ocean in northwestern Mexico, where distributional patterns of several species can be explained only by natural or translocated dispersal overwater and island hopping; some translocations could have occurred there during pre-Columbian or even prehistoric times.

Finally, we recognize the following four major causes of introductions: 1) accidentals, mainly small species transported inadvertently by cargo vehicles, most frequently gekkonid lizards and anurans; 2) intentional releases, principally associated with pet trade and as food resources; most significantly chelonians and iguanid lizards, respectively; 3) escapees from the farming industry; mainly crocodiles and anurans, such as Morelet’s Crocodiles and American Bullfrogs; and 4) expanding invasion fronts when introduced naturalized species with high reproduction potential are well adapted to altered habitats. This fourth mechanism is especially relevant in anurans, such as those within the genus *Eleutherodactylus* and other species of original dispersers along invasion fronts.

The exotic herpetofauna of Middle America

Amphibia – Anura – Frogs

Family Eleutherodactylidae

Eleutherodactylus antillensis (Reinhardt & Lütken, 1863)

The Antilles Robber Frog is native to Puerto Rico, the Virgin Islands, and several associated islands and cays in that region. Numerous individuals apparently were introduced in the late 1950's or early 1960's into Panama City, probably through ornamental plants or intentionally released by a family after returning from a trip to Puerto Rico (Barker and Rodríguez-Robles 2017). Since then, this frog has spread throughout suburban and rural gardens, abandoned parcels, and pastures in the Panama City metropolitan area (Barker and Rodríguez-Robles 2017) (Table 2, Map 1).

Eleutherodactylus coqui (Thomas, 1966)

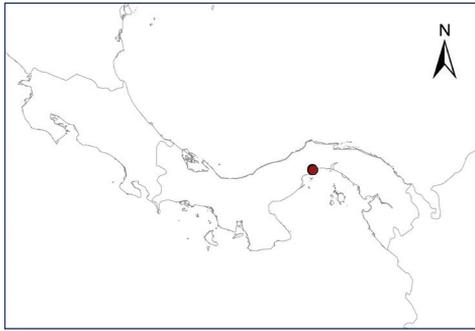
Fig. 2

The Puerto Rican Coqui was first reported in Costa Rica by García-Rodríguez et al. (2010). According to them, it was a recent introduction, probably around the end of the 1990's by a pet trader who carried six individuals from Puerto Rico and released

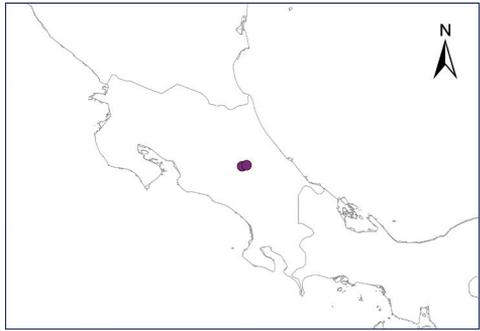


Figure 2. *Eleutherodactylus coqui*. Southern Florida. Photograph by Louis Porras.

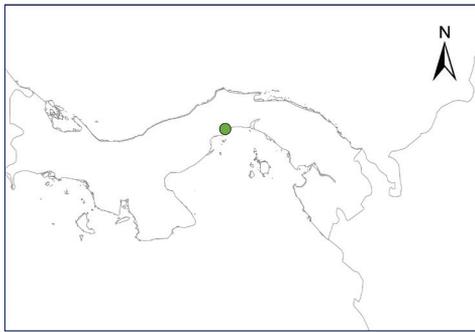
Table 2. Distribution of introduced amphibians and reptiles in Mexico and Central American countries.



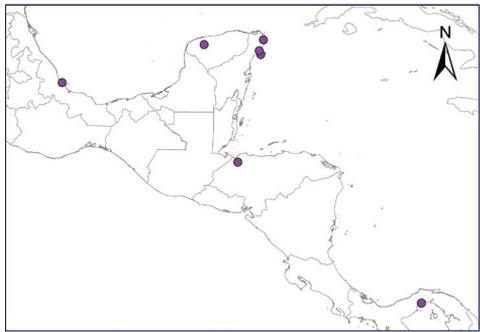
Map 1. *Eleutherodactylus antillensis*.



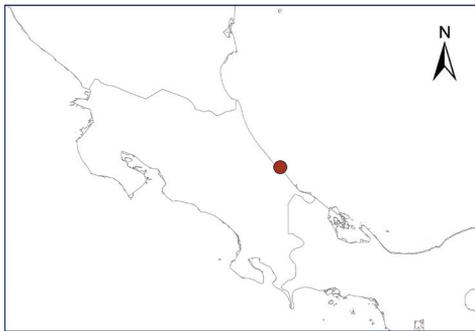
Map 2. *Eleutherodactylus coqui*.



Map 3. *Eleutherodactylus johnstonei*.



Map 4. *Eleutherodactylus planirostris*.



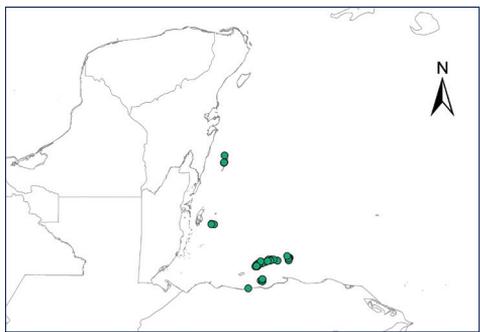
Map 5. *Osteopilus septentrionalis*.



Map 6. *Xenopus laevis*.

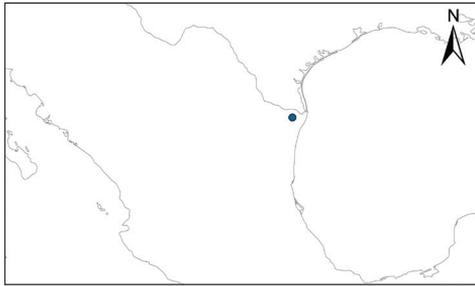


Map 7. *Chelonoidis carbonarius*.

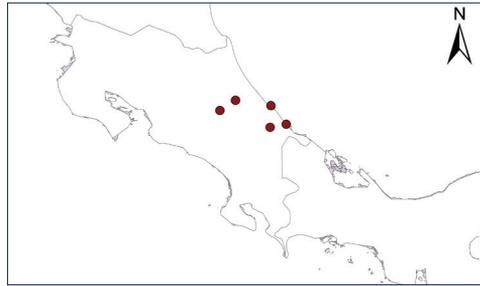


Map 8. *Anolis allisoni*.

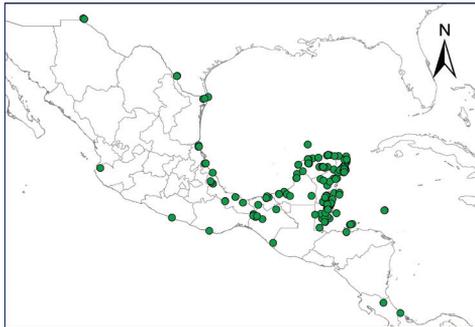
Table 2. Continued.



Map 9. *Anolis carolinensis*.



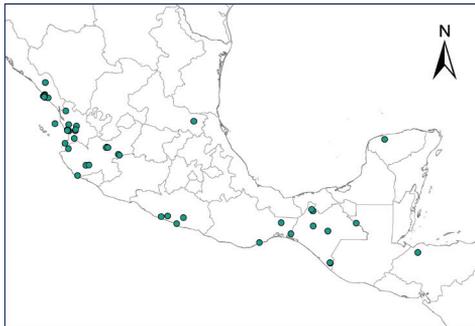
Map 10. *Ctenonotus cristatellus*.



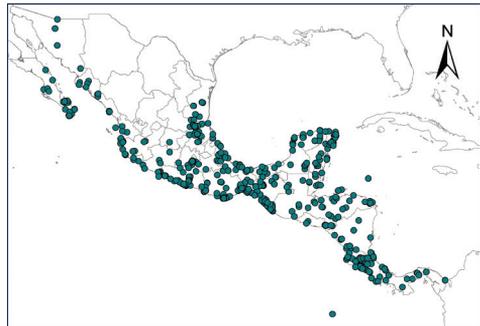
Map 11. *Norops sagrei*.



Map 12. *Gekko gekko*.



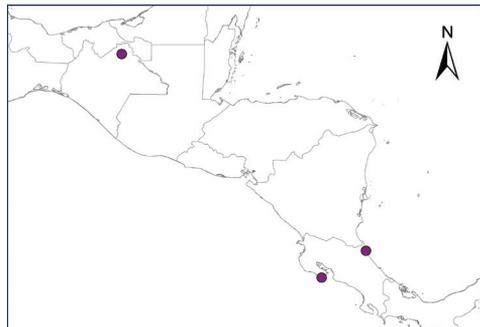
Map 13. *Gebyra mutilata*.



Map 14. *Hemidactylus frenatus*.

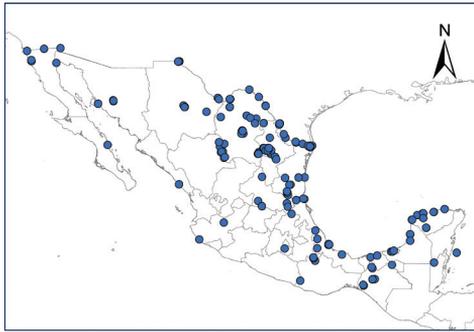


Map 15. *Hemidactylus mabouia*.

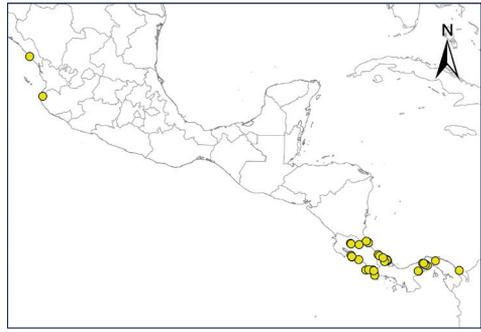


Map 16. *Hemidactylus garnotii*.

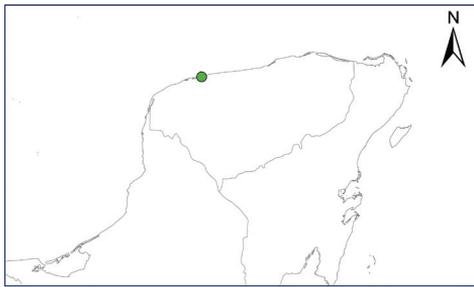
Table 2. Continued.



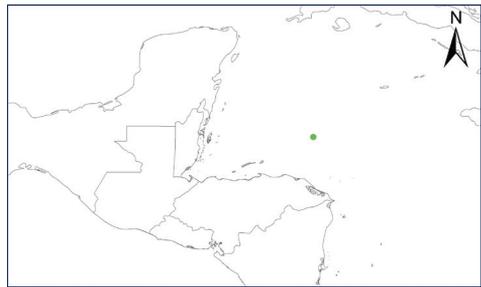
Map 17. *Hemidactylus turcicus*



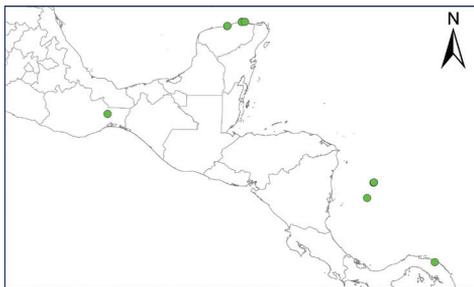
Map 18. *Lepidodactylus lugubris*



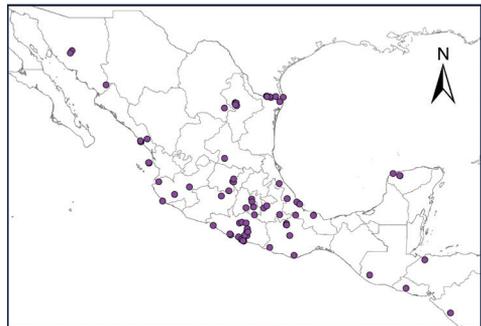
Map 19. *Tarentola mauritanica*.



Map 20. *Leiocephalus varius*.



Map 21. *Sphaerodactylus argus*.



Map 22. *Indotyphlops braminus*.

them in Turrialba, where their descendants invaded surrounding localities despite attempts to exterminate them with poison; afterwards, survivors were sold as pets in other parts of Costa Rica. Besides Turrialba, however, the only other known established Costa Rican population is in nearby Juan Viñas (Barrantes-Madrigal 2017; Barrantes-Madrigal et al. 2019) (Table 2, Map 2). This is especially troubling since it has had extensive documented negative impacts on the native biota of Hawaii (Beard et al. 2002; Beard et al. 2009), and is listed as one of the 100 world’s worst invasive introduced species (Lowe et al. 2000). The control or eradication of this species is still possible, since its distribution apparently is still restricted to a few localities in Costa Rica (Barrantes-Madrigal 2017).

***Eleutherodactylus johnstonei* (Barbour, 1914)**

Johnstone's Whistling Frog is native to the Lesser Antilles and has been introduced into several Caribbean areas, South America, the United States, and Europe (Savage 2002). This frog is a particularly proficient invader since it easily establishes breeding sites and males vocalize almost immediately after being released into the wild, thereby out competing native frogs (Kaiser and Henderson 1994). In Central America, it currently occurs in residential suburbs of Panama City, where it was believed to have been introduced in the mid-1980's, together with introduced plants (Ibañez and Rand 1990) (Table 2, Map 3). Savage (2002) reported a single specimen collected in a city park in San José, Costa Rica, but it apparently was alone and failed to establish a viable population (Savage and Bolaños-Vives 2005). Due to the lack of more records, Sasa et al. (2010) omitted this frog in their account of the Costa Rican herpetofauna. We agree with their opinion.

***Eleutherodactylus planirostris* (Cope, 1862)**

Fig. 3

The Greenhouse Frog is extremely small-sized (adults < 30 mm in length), is native to Cuba, Bahamas, and Cayman Islands (Crawford et al. 2011; Olson et al. 2012), and currently is found in Honduras in San Pedro Sula, La Paz, and Isla Guanaja, Islas de la Bahía (McCranie and Gutsche 2014). This frog has also been introduced into Puerto Limón, Costa Rica (Barquero and Araya 2016), the Miskito Cays of Nicaragua, in Panama, the Mexican Yucatan Peninsula (Cedeño-Vázquez et al. 2014; García-Balderas



Figure 3. *Eleutherodactylus planirostris*. Southern Florida. Photograph by Louis Porras.

et al. 2016; Ortz-Medina et al. 2017), and Veracruz, Mexico (lvarez-Romero et al. 2008); the last authors noted that this species was first reported there in 1974; no other record existed from Veracruz until the phylogenetic analysis of Contreras-Calvario et al. (2018) concluded that the Greenhouse Frog population of the Gulf versant is related to Cuban populations, thus inferring a different colonization event from the *E. planirostris* on the Yucatan Peninsula, which is closer to Panama and Philippines populations (Cedeno-Vzquez et al. 2014). Recent reports, however, are found for Veracruz and Morelos in the iNaturalist platform (inaturalist.org 2018) (Table 2, Map 4). Environmental impacts produced by the diminutive Greenhouse Frogs need to be determined, since there has been no direct evidence for it being particularly harmful. Still, possible negative impacts include: predation on native invertebrates, competition for food with other insectivorous vertebrates, vulnerability to depredation that could limit its dispersal, but paradoxically it could become an abundant food source for other introduced species, thus facilitating their establishment and pending impacts (Olson et al. 2012).

Family Hylidae

Osteopilus septentrionalis (Dumril & Bibron, 1841)

The Cuban Tree Frog is native to Cuba, Bahamas, and the Cayman Islands (Duellman 2001). In Central America, it is only known from Puerto Limn, Costa Rica, where it arrived in the mid 1980’s as an accidental introduction from cargo ships (Savage 2002) (Table 2, Map 5). Due to high adaptability to humid disturbed areas and its explosive breeding behavior, it has a high potential to spread quickly to other populated areas (Savage 2002).

Family Pipidae

Xenopus laevis (Daudin, 1802)

Fig. 4

The African Clawed Frog is native to “extreme southern Angola...south to Cape Region of Rep. South Africa thence east and north in savanna habitats through Zimbabwe and southeastern Zambia to Malawi” (Frost 2020). This frog is now a widespread invader in lentic waters, and its accidental or deliberate introductions are associated with uses as a laboratory animal or pet (lvarez-Romero et al. 2008; Measey et al. 2012). Although we know now that *Batrachochytrium* is native to Asia (O’Hanlon et al. 2018), the earliest known presence of *Batrachochytrium dendrobatidis* fungal infection outside its native range came from *X. laevis* populations in Africa (Weldon et al. 2004). Thus, the association with global trade markets and frequent releasing of this frog into the wild was credited for initiating the chytridiomycosis epidemics (Kraus 2009). The frog’s presence in Mexico was documented first in the 1980’s from a single observation (Murphy 1983), probably a result of dispersing individuals from established populations in southern California (Peralta-Garca et al. 2014). Today, it is confined to the Tijuana and



Figure 4. *Xenopus laevis*. Rosarito, Baja California, Mexico. Photograph by Anny Peralta.

Ensenada region in northwestern Baja California (Lavín et al. 2014), with large populations reported at sites near Rosarito (Peralta-García et al. 2014) (Table 2, Map 6). Further range expansion of this species is highly probable, since the landscapes all along northern Baja California and northern Mexican Plateau contain suitable habitats (Measey et al. 2012). It is not clear, however, if by “Baja” Measey et al. (2012) meant the total Baja California peninsula or only the Mexican state of Baja California.

Reptiles – Testudines – Turtles

Family Chelydridae

Chelydra serpentina (Linnaeus, 1758)

The Eastern Snapping Turtle is mentioned in the “Lista de las Especies Exóticas Invasoras para México” as present in the northern Mexican states of Coahuila and Chihuahua

(SEMARNAT 2017), based on a distribution terminating at the Rio Grande as mapped by Stebbins (2003), who didn't identify any verified records for Mexico. Several publications, including Lemos-Espinal and Smith (2007a, b), Lemos-Espinal and Smith (2016), Lemos-Espinal et al. (2017), and several chapters in Lemos-Espinal (2015) covering the US-Mexico border states alongside the Rio Grande, did not list *C. serpentina* as having substantiated records from Mexico. Tern-Jurez et al. (2016) discussed the probable presence of this species in the Ro Grande basin across the border from Hidalgo County, Texas, and came to the conclusion that Eastern Snapping Turtles most likely inhabit the border region of south Texas and adjacent Mexico. Michael J. Forstner (personal communication) observed them in Tamaulipas, but didn't take any voucher specimens. Dixon (2013) thought that the Hidalgo, Texas, and adjacent Tamaulipas turtles were introduced from allopatric native populations farther northeast in Texas, a pattern depicted on the map by Powell et al. (2016). Even though we do not have a map showing this species' range in Mexico, we are under the impression that enough evidence now exists to consider Eastern Snapping Turtles in Tamaulipas as exotic in Mexico, being introduced originally from native Texas populations to the north.

Cupul-Magana and Rubio-Delgado (2003) reported an Eastern Snapping Turtle from Puerto Vallarta, Jalisco, which they considered either a released individual or an escaped pet. Cruz-Senz et al. (2017) apparently did not think that the Puerto Vallarta individual was a member of an established population and did not list this species for Jalisco; we agree with that evaluation.

Family Testudinidae

Chelonoidis carbonarius (Spix, 1824)

The Red-footed Tortoise's original distribution range extends from central Panama, through Colombia and the Atlantic versant of the Amazonas in Brazil, as far south as Paraguay and northern Argentina (Kohler 2008). This species was listed originally as part of the Nicaraguan herpetofauna by Villa et al. (1988), who indicated that J. Villa found a single individual on Big Corn Island in 1964. They also mentioned the testimony of a local inhabitant who claimed to have owned a specimen of this species in her childhood, 50 years prior to the interview. If this testimony is true, the red-footed tortoise would have been on Big Corn Island by the end of the 1930's. Thus, this tortoise was known on Great Corn Island by the second half of the 20th century, but since the other known specimens were individuals held in captivity or kept as pets, the Red-footed Tortoise was omitted from the Nicaraguan herpetofauna by subsequent listings (e.g., Kohler 1999, 2001; Ruız-Perez 1996). Salazar-Saveedra et al. (2015), however, reported a breeding wild population on Great Corn Island, and pointed out that this population could be of exotic origin (Table 2, Map 7). They also stated that the known records of *C. carbonarius* on mainland Nicaragua (departments of Nueva Segovia and Masaya) might have originated from the Corn Islands. Sunyer and Martınez-Fonseca (2015) accepted the Red-footed tortoise as a member of the Nicaraguan herpetofauna and remarked that this species is alien in the country.

Reptiles – Squamata – Lizards

Family Dactyloidae

The anole family Dactyloidae contains the second highest number of introduced species (four species) in Middle America, and has exotic members distributed in all countries except El Salvador and Nicaragua. *Norops sagrei* is the most widespread anole in Middle America.

Anolis allisoni (Barbour, 1928)

Fig. 5

Allison's Anole is listed by Álvarez-Romero et al. (2008) as being exotic in Mexico. Lee (1996) considered its occurrence on Cozumel Island doubtful, and González-Sánchez et al. (2017) reported that the only populations of this species in Mexico occur on the cays of Banco Chinchorro, Quintana Roo. *Anolis allisoni* also can be found on other Caribbean islands, such as Half Moon Cay, Belize (Schmidt 1941) and on Islas de Barbareta,



Figure 5. *Anolis allisoni*. Banco Chinchorro Atoll, Mexico. Photograph by Víctor H. González-Sánchez.

Guanaja, Morat, Roatán, Utila, and Cayos Cochinos within the Islas de la Bahía complex in Honduras, as well as near the northern coastal regions, such as in La Ceiba, Atlántida (McCranie and Gutsche 2009), on the Honduran mainland; populations from Utila and La Ceiba might be recent introductions (McCranie and Köhler 2015) (Table 2, Map 8).

Recent evidence (Glor et al. 2005) indicated that *A. allisoni* is native to Cuba. The Mexican and Honduran populations have little variation in genetic distances when compared to Cuban populations, which suggests recent introductions onto the off-shore islands of Mexico and Central America, as well as mainland areas of Honduras. In addition, McCranie and Gutsche (2009) indicated that the *A. allisoni* population (first mainland record for Honduras) in the Caribbean port of La Ceiba is a recent introduction from the Islas de la Bahía.

***Anolis carolinensis* (Voigt, 1832)**

Presence of the Green Anole in Mexico was suggested by Conant and Collins (1998), because of a supposed record from Tamaulipas, but no evidence was provided. Álvarez-Romero et al. (2008) advocated that at least one population in Tamaulipas might be native, but they did not provide any specific locality or give any justification for that reasoning. Farr (2015) did not list the Green Anole from Tamaulipas. The occurrence of this species in Tamaulipas remained controversial until Terán-Juárez et al. (2015) reported photographic records from a courtyard in Ciudad Valle Hermoso where *A. carolinensis* had been observed for at least ten years; they also indicated its presence in the city of Matamoros. We consider *A. carolinensis* an exotic species in Mexico, based on Dixon's (2013) assertion that records from Texas border counties were probable introductions and that its known allopatric native distribution lies to the north of the border region in Texas (Powell et al. 2016; map only) (Table 2, Map 9).

In Belize, the Green Anole is only known from a single specimen collected in 1966 on Half-Moon Cay (UF 23924); no other records were reported thereafter (Lee 1996), although some lizards sighted in 1996 resembled *A. carolinensis* (Platt et al. 1999). This last claim should be treated with caution, as the very similar-looking *A. allisoni* also occurs on that cay, and can be easily misidentified. Lee (1996) hinted that if the Green Anole ever occurred on Half-Moon Cay, it might be extirpated now due to displacement by *A. allisoni*. Stafford et al. (2010) did not list *A. carolinensis* for Belize, so we adopt this view by not recognizing this species as presently having an established population in that country.

***Ctenonotus cristatellus* (Duméril & Bibron, 1837)**

Fig. 6

The Crested Anole is native to Puerto Rico and the Virgin Islands (Köhler 2008). In Central America, it has been established only in Costa Rica, where it has been observed



Figure 6. *Ctenonotus cristatellus*. Southern Florida. Photograph by Louis Porras.

in Puerto Limón (Savage 2002), Cahuita (Mayer 2010), Guayacán, and Valle de Rosas, Limón province, and in Turrialba, Cartago province (Savage 2002). This anole was first recorded in 1970 from Limón (Mayer 2010) and Fitch (1975) noted an explosive population increase of these anoles in a Limón city park and wondered if colonization by *C. cristatellus* might have caused the extirpation of *Gonatodes albogularis* in that park (Table 2, Map 10).

In Mexico, *C. cristatellus* was reported from states on the Yucatan Peninsula, first by a single record from Cozumel, Quintana Roo, although Lee (1996) considered its presence there doubtful. Colston et al. (2015) reported *Norops cristatellus* from Calakmul, Campeche, but González-Sánchez et al. (2017) did not list it for the region because they thought the record needed verification, especially since Calakmul is a popular study site for working herpetologists and no other records are known from there. We concur that this species does not have an established population on Cozumel or Calakmul, so we remove it from the list of introduced species in Mexico.

***Norops sagrei* (Duméril & Bibron, 1837)**

The Cuban Brown Anole is native to Cuba, the Bahamas, and Cayman Islands, but it is unclear if all populations in Jamaica were introduced, or if some were native (McCranie and Köhler 2015). It is important to note that the taxonomic status and identity of this species remain unclear for many populations in Mexico and northern Central America, since the validity of the “native” subspecies *N. s. mayensis* seriously has been questioned (González-Sánchez et al. 2017). Moreover, the description of this subspecies was made from a single population from Isla Polao, in the region of Laguna de Términos, Campeche, and supported only by morphological characters (Smith and

Burger 1949). Anoles as a group can have much geographic variability in morphology, as exemplified by McCranie and Köhler's (2015: 169) statement, "using dewlap color as a diagnostic character for any *N. sagrei* complex population (including isolated island populations) might not be informative." In any case, considering the unlikelihood that *N. s. mayensis* is a valid taxonomic lineage (see our taxonomic positions above in the methods section), and because of the long history of *N. sagrei* colonizing Mexico and Central America, any defining characteristics of a separate evolutionary lineage (=species) were probably eliminated by genetic intergradation with other alien *N. sagrei* populations. Because of this and the close association of this species with human mediated disturbed habitats, we regard the *N. sagrei* complex, with one exception, as a single exotic species within the region. The exception was the recent resurrection by McCranie and Köhler (2015) of *N. nelsoni*, an allopatric *N. sagrei* complex species from the Islas del Cisne, Honduras.

The naturalized distributional range in Mexico of *N. sagrei* comprises all the inland regions and several insular systems off the Yucatan Peninsula (González-Sánchez et al. 2017; Lee 1996), Tabasco (Lee 1996), Ciudad Altamira, Tamaulipas (Terán-Juárez et al. 2015), and Minatitlán and Catemaco, Veracruz (Zamora-Abrego et al. 2006). Specimens labeled *Anolis sagrei* in the Zoological Collection of El Colegio de la Frontera Sur (ECOSUR), in San Cristóbal de las Casas, Chiapas (Muñoz-Alonso 2006), are from Ocozocoautla de Espinosa (Coita), Chiapas, which is located in the semi-arid Central Depression region. Johnson et al. (2010, 2015a) did not report that locality and no other records are known to exist in Chiapas.

In Central America, the Cuban Brown Anole occurs throughout Belize (Lee 1996) and adjacent Caribbean lowlands of Guatemala (Stuart 1955). In Honduras, this species is known to occur at Puerto Cortés and San Pedro Sula, Cortés, and at La Ceiba and Tela, Atlántida, on the northern mainland and on the islands of Roatán and Utila (McCranie and Köhler 2015). An introduced population also exists in the vicinity of Limón, Costa Rica (Savage and Bolaños-Vives 2005). Batista et al. (2019) reported established populations of *N. sagrei* at several sites within and around Panama City. They also mentioned that those populations might have become established approximately five years ago, and arrived there as released pets, or more probably, from shipments arriving at the port of Balboa (Table 2, Map 11).

Family Gekkonidae

Not surprisingly, the geckos contain the highest number of introduced species (10 species) for the region, distributed among two families (i.e., Gekkonidae and Sphaerodactylidae) in Middle America (Table 1). Because of their notorious colonization ability, geckos are frequently referred to as "weedy" species (Kluge 1969).

Hemidactylus is the most speciose genus, comprising five introduced species (*H. frenatus*, *H. garnotii*, *H. haitianus*, *H. mabouia*, and *H. turcicus*). At least one of these species occurs in each country of Middle America, but only *H. frenatus* is present in all seven (Table 2). *Hemidactylus* is a species-rich genus (167 species; Uetz et al. 2020), native to tropical areas of Asia and Africa and the Mediterranean region, most of which



Figure 7. *Gekko gecko*. Southern Florida. Photograph by Louis Porras.

species have small native distributional ranges. A few species, however, can be found almost worldwide in tropical and subtropical areas due to either human intervention or possibly by having undertaken long transmarine journeys (Carranza and Arnold 2006).

***Gekko gecko* (Linnaeus, 1758)**

Fig. 7

The Tokay Gecko is very well known due to its use in scientific research (Roesler et al. 2011), and popularity in the pet trade (Kraus 2009). It was originally native to eastern India, Nepal, Southeast Asia, China, and the Malayan Archipelago (Roesler et al. 2011). Stafford et al. (2010) listed this species as exotic in Belize. The population was reported from South Water Caye, a small sandy caye measuring 8.2 ha on the Belizean barrier reef (Meerman and Garel 2002) (Table 2, Map 12). Apparently, the introduction of the Tokay Gecko occurred around 1994, when a tourism industry worker brought several individuals to South Water Caye and intentionally released them. The introduction of *G. gecko* and the declining numbers of *Aristelliger georgeensis* and *Phyllodactylus tuberculosis* on that island might be related (Meerman and Garel 2002).

***Gehyra mutilata* (Wiegmann, 1834)**

The Stump-toed Gecko is native to the Pacific basin region of Southeast Asia, where it has dispersed among Indian and Oceanic islands since the times of pre-Polynesian

navigators (Fisher 1997). Rocha et al. (2009) suggested that *G. mutilata* is a complex of two cryptic lineages, one of them involving the resurrection of *G. insulensis* for several, if not all, Pacific islands, which includes the former Mexican, but now French Isla Clipperton (Isla de la Pasión). Lorvelec and Pascal (2006) hypothesized that the time and source of invasion on that atoll could have been during the 1950's from Mexican Pacific ports in Nayarit or Sinaloa, but that allegation was merely speculation. If true, however, Mexican populations on the Pacific side would correspond to *G. insulensis*. Since Rocha et al. (2009) did not include Mexican samples in their study, we retain the name *G. mutilata* until more evidence is provided.

The date for the introduction of *G. mutilata* into Mexico is unknown, although Lemos-Espinal and Dixon (2013) remarked that before the advent of aviation, this species was restricted almost exclusively to the Philippines, although specimens collected in Nayarit by the end of the 19th century already existed (GBIF.org 2018). In addition, Ineich and Blanc (1987) hypothesized that it could have been present in Mexico during the 18th Century by way of maritime trade between New Spain and the Philippines. In Mexico, it is now known from the Pacific versant in Sinaloa, Nayarit, Guerrero, and Chiapas (Álvarez-Romero et al. 2008), Jalisco (Cruz-Sáenz et al. 2017), and Baja California Sur (Reynoso 1990a; Lovich et al. 2009), and some Pacific Islands, such as Isabel (Quijada-Mascareñas and Canseco-Márquez 2007). On the Atlantic versant, established populations have been reported only from Veracruz (Álvarez-Romero et al. 2008) and Ciudad Valles, San Luis Potosí (Lemos-Espinal and Dixon 2013) (Table 2, Map 13).

***Hemidactylus frenatus* (Duméril & Bibron, 1836)**

Fig. 8

The Common House Gecko is a well-known successful colonizer of urban environments (Lee 1996). Even though its native range is uncertain, it probably can be restricted to southern India, Sri Lanka, Burma, southern China, Malayan Peninsula, and Philippines (Savage 2002). As an introduction in the Americas, it occurs on both versants from Florida and California through Mexico and Central America to Brazil (Weterings and Vetter 2017), from sea level to 1,545 m elevation (Mata-Silva et al. 2013). Introductions of this gecko possibly could lead to competitive exclusion of native gecko populations and to extinction of insular endemics (Cole et al. 2005).

It is believed that *H. frenatus* arrived on the North American continent around the 16th century by means of maritime commerce between the Philippines and Acapulco, Mexico (Álvarez-Romero et al. 2008). Farr (2011), however, argued that the first records of this species date to the end of the 19th century or even as late as the 1930's. If so, colonization during the colonial period, by an introduced lizard common in hotels of Acapulco today, should have been recorded early on by the first collectors visiting Mexico, but since there are no records from then, introductions into Central American countries might have been even more recent. For example, in Costa Rica



Figure 8. *Hemidactylus frenatus*. León, Nicaragua. Photograph by Javier Sunyer.

the first reports of *H. frenatus* were made after 1990, according to Savage (2002). This exotic species also has been reported from all other Central American countries and many states in Mexico (Uetz et al. 2020). *Hemidactylus frenatus* first was recorded from peninsular Baja California Sur, Mexico, by Reynoso (1990b) from the city of La Paz; Grismer (2002) also observed an established population in Loreto, located north of La Paz on the peninsula. Most recently, the species was reported for the first time from any island in the Sea of Cortes (Isla El Pardito) by Dayton et al. (2020) (Table 2, Map 14). Mata-Silva et al. (2013) found this species to be very common in Oaxaca City, Oaxaca at an elevation of 1,545 m.

***Hemidactylus garnotii* (Duméril & Bibron, 1836)**

The Indo-Pacific or Garnot's House Gecko, is native to the Indo-Pacific basin, and is widespread on several islands in Oceania, Asia, and the Pacific Ocean. In Middle America, it was introduced at several ports and urban centers in Costa Rica (Savage 2002; Köhler 2008) and in Guatemala, Guatemala (Morales et al. 2017). This species is a parthenogenetic all-female species and, therefore, it seems to have no social hierarchy (Frankenberg 1982); it is a territorial and aggressive species (Frankenberg 1984), and successful colonizer of urban and other anthropogenic habitats, with high potential for expansion (Savage 2002). The first record in Middle America was from San José, Costa Rica, in 1992 (Savage 2002), whereas in Guatemala its introduction seems to be more recent, but from an unknown source (Morales et al. 2017) (Table 2, Map 16).

***Hemidactylus haitianus* (Meerwarth, 1901)**

The Haitian House Gecko has had a complex and unclear taxonomic history. Traditionally, it was considered two different taxa: the Middle American and West Indian populations of *H. brooki haitianus*, type locality marked as “Haítí, Port-au-Prince” (Powell and Maxey 1990), and *H. angulatus*, type locality “West Coast of Africa” (Hallowell 1854). Powell et al. (1996) considered *H. brooki haitianus* a full species (*H. haitianus*) for lizards native to the West Indies, including Cuba and Puerto Rico. Further revisions revealed *H. haitianus* as nested inside a larger clade that includes the African populations of *H. brooki* along with *H. angulatus* (Carranza and Arnold 2006; Weiss and Hedges 2007; Bauer et al. 2010; Rösler and Glaw 2010). Weiss and Hedges (2007) and Gamble et al. (2011) reported virtually no genetic divergence among the populations of this complex in the Greater Antilles, and clustered them with African populations, thus corroborating the introductory origin of *H. haitianus* for the Antilles. The source of invasion to the New World might have been through the slave trade between western Africa and the West Indies (Weiss and Hedges 2007). Consequently, the populations of *H. brooki* in Honduras (McCranie 2015) and Panama (Auth 1994) and those of *H. angulatus* in South America might have had their origins by following colonial trade routes between the Antilles and Middle America, although a date has not been suggested. Even if the *H. angulatus-brooki* complex is not fully resolved, the name *H. haitianus*, as suggested by Bauer et al. (2010), is used herein for individuals occurring throughout the Western Hemisphere.

***Hemidactylus mabouia* (Moreau De Jonnès, 1818)**

Moreau’s Tropical House Gecko has no clear-cut geographic origin. The type locality is marked as “Antilles,” and restricted to St. Vincent Island by Stejneger (1904). Nonetheless, its actual origin was without doubt on the African continent, where it is widespread, ranging from southern Africa northward to Liberia and Ethiopia (Álvarez-Romero et al. 2008). An interesting hypothesis suggests arrival of this species in the New World by accidental transport on slave ships along routes from Africa to the West Indies and South America. There is no full concordance, however, between slave ship routes and the distribution of *H. mabouia* (Kluge 1969). Based on the long history of maritime trade between Africa and the Antilles and the 1818 description of the species, it can surely be said that the type specimen from the Antilles represents an introduced population. Moreover, the introductions in Mexico and Central America might be the result of maritime trade from the West Indies (Álvarez-Romero et al. 2008). Currently, introduced populations of *H. mabouia* are found in Veracruz (Ochoa-Ochoa et al. 2006; Álvarez-Romero et al. 2008), and Tamaulipas, Mexico (Sosa-Tovar, et al. 2019), Islas de la Bahía, Honduras (Gutsche and McCranie 2009), San José, Costa Rica (Abarca and Monge 2007), and Panama (Auth 1994) (Table 2, Map 15).

***Hemidactylus turcicus* (Linnaeus, 1758)**

The Mediterranean House Gecko is native to coastal areas of the Mediterranean, where it is widespread across southern Europe, the Levant, and more sporadically in North Africa (Martínez-Hernández et al. 2017). In Mexico, it is known from many states and places, including: Yucatan Peninsula, Baja California, Sonora, Sinaloa, Chihuahua, Coahuila, Durango, San Luis Potosí, Aguascalientes, Ciudad de Mexico, Morelos, Nuevo León, Puebla, Tamaulipas, Oaxaca, Chiapas (Martínez-Hernández et al. 2017), and Querétaro (Tepos-Ramírez, 2019). Its first introduction probably occurred around Acapulco, from colonial-period trade with inhabitants of the Pacific islands (Álvarez-Romero et al. 2008), although another possible source was from Veracruz, where *H. turcicus* was recorded in 1895. Subsequently, *H. exsul* was described in 1906 from Progreso, Yucatán, which in fact was based on a specimen of *H. turcicus* (McCoy 1970). In Panama, it is known from the Canal Zone (McCoy 1970), where the introduction took place after the opening of the Panama Canal in 1914. Stafford et al. (2010) suggested the possible presence of this species in Belize, but we were unable to find records on GBIF.org (2018), or in the available literature, so it is not recognized herein for that country (Table 2, Map 17).

***Lepidodactylus lugubris* (Duméril & Bibron, 1836)**

Fig. 9

The Mourning Gecko is native to southeast Asian and Indo-Australian regions, and currently is distributed worldwide in the tropics from sea level up to 700 m elevation (Köhler 2008). Probably much of its dispersal potential comes from being a complex of parthenogenetic lineages that includes diploid and triploid forms because of hybridization between *L. moestus* and an undescribed species (Fujita and Moritz 2009). In the Americas, it was first reported in the mid 1950's at Ft. Clayton, in the Canal Zone, Panama (Smith and Grant 1961). Even though prior collected specimens exist from the 1910's in that area, it is also known from Bocas del Toro, Panamá (Hoogmoed and Avila-Pires 2015), Golfo Dulce, and Peninsula de Osa and Punta Arenas departments, both from the Pacific versant of Costa Rica (Savage 2002). This species is known also in Costa Rica from the Gandoca-Manzanillo Wildlife Refuge, Talamanca, Limón, and from Tirimbina Biological Reserve and La Virgen of Sarapiquí, Heredia (Jiménez and Abarca 2014). This gecko is established in Nicaragua on the southeastern Caribbean coast at elevations lower than 10 m (Hoogmoed and Avila-Pires 2015), and on the Corn Islands (Sunyer et al. 2013), where individuals probably arrived on cargo ships sometime around 1975 at Bluefields and/or Great Corn Island (Henderson et al. 1976). Hoogmoed and Avila-Pires (2015) thought that the Mourning Gecko should not be listed for Mexico because of inconsistencies in the literature and lack of vouchered museum specimens. A recent (November 2017) photographic record for



Figure 9. *Lepidodactylus lugubris*. Big Corn Island, Nicaragua. Photograph by Javier Sunyer.

the port of Mazatlán, Sinaloa, however, exists in the iNaturalist platform (GBIF.org 2018). In addition, Ahumada-Carrillo and Weatherman (2018) found a recent established population in Puerto Vallarta, Jalisco, Mexico (Table 2, Map 18).

***Tarentola mauritanica* (Linnaeus, 1758)**

Fig. 10

The Moorish Gecko is native to the European and North African Mediterranean basin (Rato et al. 2015). Ortíz-Medina et al. (2019) recently reported this species from cargo containers stored in a warehouse in Progreso, Yucatan, Mexico. They mentioned that six to eight “unusual-looking lizards” were sighted there in early 2017, but only two specimens were captured and identified as *T. mauritanica*. The population in Progreso, however, was supposedly established, which is most likely factual, considering the number of individuals observed at the site, in addition to the well-known success of gekkonid lizards for becoming established species. Another record is known from Guadalajara, Mexico, through a photographic entry in inaturalist.org (2018), but no other records of the Moorish Gecko exist for Mexico, and no validating museum vouchers could be found for Guadalajara (Table 2, Map 19). We have not overlooked the recent evidence suggesting that *T. mauritanica* constitutes a species complex (Rato et al. 2016), but choose to maintain the traditional nomenclature while awaiting full resolution of the group.



Figure 10. *Tarentola mauritanica*. Progreso, Yucatan, Mexico. Photograph by Javier Ortíz-Medina.

Family Leiocephalidae:

***Leiocephalus varius* (Garman, 1887)**

The Cayman Curly-tailed Lizard is native to the Grand Cayman Islands (Garman 1887; Echternacht et al. 2011) and was first reported on the Swan Islands, Honduras, in the mid 1970's (Schwartz and Thomas 1975), where it was conspicuous on human buildings and other places on Big Swan Island (McCranie et al. 2017). While some authors listed it as native to Honduras (Townsend and Wilson 2010; Solís et al. 2014), McCranie et al. (2017) suggested that this lizard was introduced recently to the Swan Islands, although circumstances or the date of the introduction were not provided. We note that McCranie (2018) recently elevated *L. varius* to a full species from *L. carinatus varius*, therefore, *L. varius* replaces *L. carinatus* as the exotic species on the Swan Islands (Table 2, Map 20).

Family Sphaerodactylidae

***Sphaerodactylus argus* (Gosse, 1850)**

The Ocellated Dwarf Gecko is native to Jamaica, Cuba, and adjacent islands in the Bahamas and Antilles, including the Colombian Isla de San Andrés (Harris and

Kluge 1984). It was introduced into the northern Yucatan Peninsula of Mexico (Lee 1996), Isla del Maíz Grande (Corn islands), Nicaragua (Thomas 1975; Sunyer et al. 2013), and on several islands on the Bocas del Toro and San Blas Archipelagos in Panama (Harris and Kluge 1984; Savage 2002). Approximate dates of introductions on the islands of Central America are unknown, but before Thomas (1975) no previous record for Middle America was available.

Records of *S. argus* from the northern coast of Yucatan (Lee 1996) might be the result of active maritime commerce in the region. Furthermore, this gecko was mentioned as occurring on the insular systems of Costa Rica (Lee 1996), but no evidence or citation was provided. *Sphaerodactylus argus* has not been reported on mainland Costa Rica (Savage 2002; Savage and Bolaños-Vives 2005; Köhler 2008; Sasa et al. 2010), although its close proximity to the Bocas del Toro islands could lead to future colonization of mainland areas adjacent to those islands (Savage 2002). *Sphaerodactylus argus* should not be confused with what was formerly known as *S. argus continentalis* (now *S. continentalis*), which ranges from the Isthmus of Tehuantepec, Mexico, into central Honduras (McCranie and Hedges 2012) (Table 2, Map 21).

Reptiles – Squamata – Snakes

Family Typhlopidae

Indotyphlops braminus (Daudin, 1803)

Fig. 11

The Brahminy Blindsnake is the most widespread alien reptile in the world (Capinha et al. 2017). This snake is a small-sized (mean total length < 130 mm) brown to black-colored species (Wallach 2009), with a secretive fossorial lifestyle occupying soil and leaf litter (lvarez-Romero et al. 2008), and can easily be confused with earthworms (Wallach 2009). The wide distributional range of this snake can be explained by the ease with which this snake is carried inadvertently within root masses of potted plants being shipped world-wide by the garden industry (lvarez-Romero et al. 2008). The reproductive characteristics of this species (unisexual, triploid, and parthenogenetic) also allows a single individual to establish a new population (Vitt and Caldwell 2014).

The type locality is reportedly the region of Coromandel, southeast India (Wallach et al. 2014). The center of origin of *I. braminus* is difficult to discern with precision, however, due to its almost cosmopolitan distribution (Wallach et al. 2014; Capinha et al. 2017), previous unclear taxonomy, frequent misidentifications (Wallach 2009), and a long history of exceptional dispersal ability. The only certain location for the center of origin is that it should be an undetermined site in the Old-World tropics (lvarez-Romero et al. 2008). This snake also has a hybrid origin with the parental species still undetermined (Vitt and Caldwell 2014). Currently, it is widespread in Mexico, Guatemala, Belize, Honduras, and El Salvador (Wallach et al. 2014; Lee 1996). In



Figure 11. *Indotyphlops braminus*. Ixil, Yucatan, Mexico. Photograph by Luis Díaz-Gamboa.

Nicaragua, it is known from a recent record (Leets-Rodríguez et al. 2019) from a locality near Managua. Due to the nature of the record (five specimens found accidentally in a suburban backyard), it is probable that the Brahminy Blindsnake is widespread in urban and suburban areas of Managua. Arrival in Mexico was most likely sometime during the 16th century via maritime trade between the Philippines and New Spain at the Acapulco port (Álvarez-Romero et al. 2008). Care should be taken not to confuse *I. braminus* with other local members of Typhlopidae inhabiting the American tropics (Table 2, Map 22).

The translocated herpetofauna of Middle America

Several species of amphibians and reptiles found in a region are translocated when introduced into areas of the same region outside their native ranges. We will consider only those with sound evidence of having been translocated by human activities and that have established populations (Table 1).

Amphibia – Anura – Frogs

Family Hylidae

Smilisca baudinii (Duméril & Bibron, 1841)

The Mexican Treefrog ranges from “Extreme southern Texas (USA) and southern Sonora and southwestern Chihuahua (Mexico) south (including the Balsas Depression of Mexico) in tropical lowlands to Costa Rica on the Pacific slope; including the Tres Marias Islands off the coast of Nayarit, Mexico” (Frost, 2020). This species also can be found on other Mexican Pacific Islands (Woolrich-Piña et al. 2016), but historically was unknown on the Baja California Peninsula (Grismer 2002; Lovich et al. 2009). Records of *S. baudinii* exist from near the village of Todos Santos, Baja California Sur, which could represent an unlikely relictual population, or a more reasonably explained accidental translocation from any of the mainland ferry ports where this frog naturally occurs (Recuero et al. 2004) (Table 3, Map 23).

Family Ranidae

Lithobates berlandieri (Baird, 1859)

The native range of the Rio Grande Leopard Frog extends from southeastern New Mexico and central Texas southward into Mexico (Stebbins 2003) along the Gulf lowlands into the northern half of Veracruz (Zaldívar-Riverón et al. 2004). It is unclear what the status is for populations in the Mexican portion of the lower Colorado Basin, where Grismer (2002) reported a sighting of what he believed to be an individual *L. berlandieri* at the confluence of the Hardy and Colorado rivers in the Mexicali Valley, Baja California. Photographic evidence of this species near San Luis Río Colorado, Sonora, Mexico, was reported by Rorabaugh and Servoss (2006) from a concrete-lined ditch passing through an agricultural field. The invasion front originated somewhere in southwestern Arizona where the Colorado and Gila rivers meet, which is the same area where *L. berlandieri* was collected in a survey in 1981 (Platz et al. 1990). The most probable act of introduction into Mexico was not a single event, but rather a secondary effect of several fish transplant operations into the Yuma, Arizona region from New Mexico in the late 1960’s or early 1970’s (Platz et al. 1990). It is likely that the Mexican populations, if they are established, originated as an expansion of the invasion front, using the Colorado and Gila River systems, and adjacent agricultural canals as dispersal routes (Rorabaugh et al. 2002). It is unknown what the impact of *L. berlandieri* is on the biodiversity of Baja California, but it has been associated with historical declines of populations of other native leopard frogs, such *L. yavapaiensis*, in areas of the lower Rio Colorado basin in Arizona (Rorabaugh et al. 2002) (Table 3, Map 24).

Table 3. Non-native distribution of translocated amphibians and reptiles in Mexico and Central America.

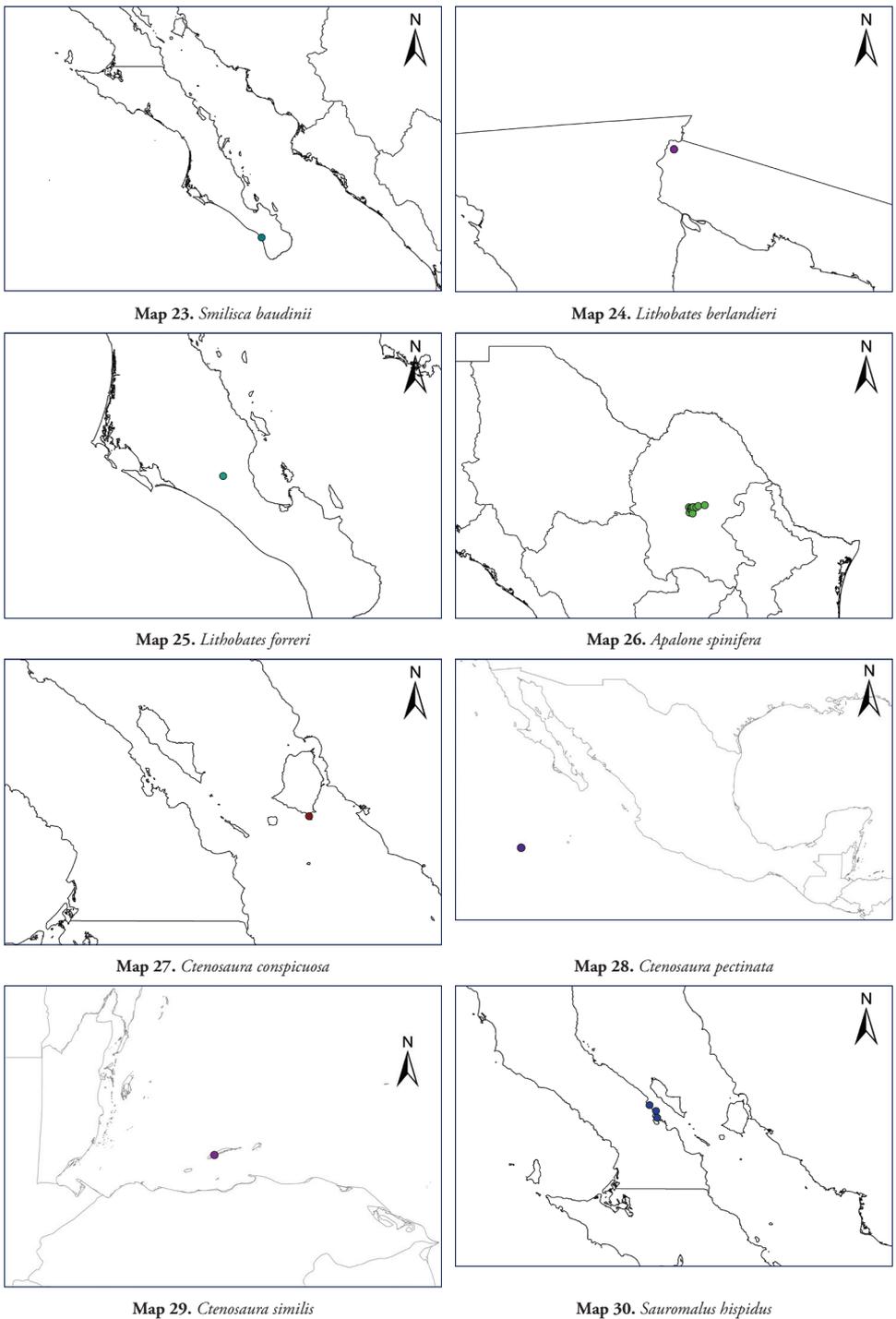


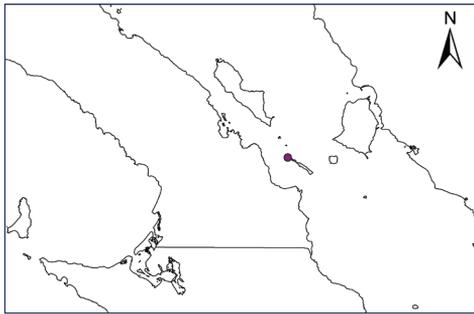
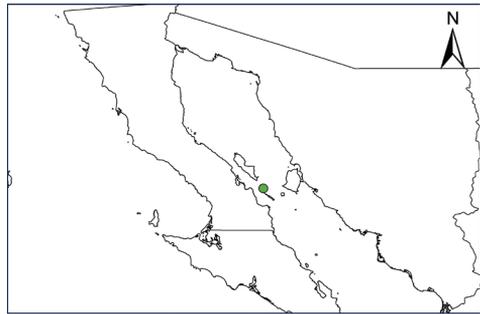
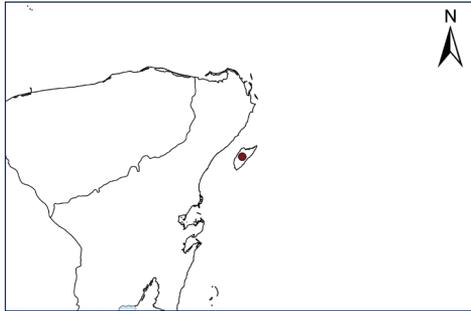
Table 3. Continued.**Map 31.** *Sauromalus varius***Map 32.** *Uta stansburiana***Map 33.** *Boa imperator****Lithobates catesbeianus* (Shaw, 1802)**

Fig. 12

The American Bullfrog originally ranged from southeastern Canada and central and eastern United States into northeastern Mexico (Conant and Collins 1998). It has a long and extensive history of introductions into Mexico, with first reports made near Cadereyta, Nuevo Le3n, in 1853 (Ramos-Guerra and Gatica 2014). Since then, feral populations have been established in many Mexican states and places, including Chihuahua, Durango, and San Luis Potos3 (Lemos-Espinal and Smith 2016), Sinaloa, Sonora, Morelos, Ciudad de Mexico, Puebla, San Luis Potos3 (Casas-Andreu et al. 2001), Aguascalientes (Avila-Villegas et al. 2007), Baja California (Grismer 2002) and Hidalgo (Ram3rez-Bautista et al. 2014), where it is probably linked to the extirpation of *L. yavapaiensis* and *Incilius alvarius*, and declines in *Hylliola cadaverina* (as *Hyla regilla*) and *Thamnophis hammondi* in several oases on the Baja California Peninsula (Grismer 2002). Apparently, American Bullfrogs were introduced intentionally in Costa Rica (Savage and Bola3os-Vives 2005), although the previously known population in La Garita is now thought to be nonexistent (IUCN 2015) (Table 3, Map 25).

Due to a high reproductive rate and generally destructive behaviors, *L. catesbeianus* has great potential for being harmful to native species, and has already been associated



Figure 12. *Lithobates catesbeianus*. Near Chihuahua International Airport, Chihuahua, Mexico. Photograph by Rubén A. Carbajal-Márquez.

with declining and disappearing populations of native amphibians around the world (Casas-Andreu et al. 2001). This frog is considered one of the 100 world's worst invasive introduced species (Lowe et al. 2000). Also of special concern is the relationship of American Bullfrogs with deadly pathogens, such as *Batrachochytrium dendrobatidis* and *Ranavirus* (Schloegel et al. 2009; Kolby et al. 2014). Recently, an outbreak of *Ranavirus* was reported in captive American Bullfrogs from a farm in Guasave, Sinaloa, in northwestern Mexico (Saucedo et al. 2019). Presently, this pathogen seems not to have spread into wild amphibian populations in Sinaloa, but the risk of *Ranavirus* becoming widespread is high, since there are several susceptible frog species in that area (Saucedo et al. 2019).

***Lithobates forreri* (Boulenger, 1883)**

Forrer's Leopard Frog's native distribution was considered to be on the mainland Pacific versant of Mexico from Sonora (Zaldívar-Riverón et al. 2004) into Costa Rica (Savage 2002). Grismer (2002) reported an introduced population in the water systems near Rancho San Juanito within the La Presa region, 100 km north of La Paz, Baja California Sur, suggesting to us a probable intentional translocation from mainland ferry ports across the Sea of Cortes from 1991 to 1993. Those dates were based on personal correspondence between a local rancher and L. L. Grismer (Table 3, Map 25).

Reptiles – Crocodylia – Crocodiles

Family Crocodylidae

Crocodylus moreletii (Duméril & Bibron, 1851)

Fig. 13

Morelet's Crocodile originally ranged only along the Atlantic lowlands of Middle America, from Tamaulipas, Mexico, to northern Guatemala and adjacent Belize (Cedeño-Vázquez et al. 2012). This crocodile formerly was considered an endangered species and subject to strict conservations measures. Fortunately, in the last few decades, significant recovery of populations has occurred within its native range. There has been an increase in the number of sites dedicated to its conservation by captive breeding, but also for exploiting the animals for food and hides; unfortunately, these farms are mainly found on the Pacific versant of Mexico outside its native range (Álvarez-Romero et al. 2008). As a negative side issue, in Mexico there have been several incidences of *C. moreletii* escaping from these farms into the wild, with populations being established primarily in the states of Oaxaca (Lagunas de Chacahua), Sinaloa, and Colima (Laguna de Alcuzahue) (Álvarez-Romero et al. 2008; Lavín et al. 2014). The first documented case took place during the 1970's when several Morelet's Crocodiles were taken from Tabasco to Lagunas de Chacahua, Oaxaca, in order to establish a hide factory there, but after a few years, the project was abandoned and several individuals escaped into the wild (Serrano-Gómez et al. 2016). In addition, the population near Villa Flores in the Central Depression of Chiapas could be an intentional translocation from areas to the north of there (Álvarez-Romero et al. 2008), although that locality is higher up on the Gulf versant with potential riverine access to the lowlands, at least in the past.

The invasion of aquatic habitats by *C. moreletii* might have serious consequences for native biotic communities, since it is a large top predator (Álvarez-Romero et al. 2008). Although *C. moreletii* and *C. acutus* (American Crocodile) are sympatric in some areas of their native ranges, in places where *C. moreletii* had been translocated it tended to out-compete and displace *C. acutus* (Lavín et al. 2014). Several cases of hybridization between the two species have been documented from the Mexican Yucatan Peninsula (Cedeño-Vázquez et al. 2008; Rodríguez et al. 2008), Oaxaca (Serrano-Gómez et al. 2016), and Belize (Ray et al. 2004), which is particularly critical for *C. acutus* (Serrano-Gómez et al. 2016), since the genome of *C. moreletii* seems to have a higher fitness value (Lavín et al. 2014). This apparently is true on the Yucatan Peninsula, given the rarity of *C. acutus* in areas where *C. moreletii* is much more abundant. Actions to prevent genomic pollution of American Crocodiles should be encouraged (Cedeño-Vázquez et al. 2008). Furthermore, undocumented crocodiles could become vectors for infectious diseases, such the West Nile Virus (González-Sánchez et al. 2017).

Lazcano-Barrero (1993) acknowledged several intentional releases of *C. moreletii* on Isla Contoy from 1981 to 1991. The individuals came from zoos and from seizures at regional fairs. Very likely, however, those crocodiles emigrated or failed to establish there, since Morelet's crocodiles are not listed as part of the Contoy herpetofauna (Ariaga y Ramírez-Bautista 2008; González-Sánchez et al. 2017). Also, it is unknown if



Figure 13. *Crocodylus acutus*. Hybrid pattern (see tail) with *C. moreletii*. APFF Yum Balam, Quintana Roo, Mexico. Photograph by Julio César Gutiérrez-Ramírez.

those released crocodiles contributed to genetic pollution of *C. acutus* populations on Contoy, since studies on hybridization between *C. moreletii* and *C. acutus* on the Mexican Yucatan Peninsula did not include samples from that island (Cedeño-Vázquez et al. 2008; Rodríguez et al. 2008; Machkour-M'Rabet et al. 2009) (Fig. 13).

Reptiles – Testudines – Turtles

Family Emydidae

Trachemys scripta (Thunberg in Schoepff, 1792)

Fig. 14

A common misbelief in Mexico is that the Pond Slider is native to Japan, thus the common name “Tortugas japonesas” (Japanese turtles) is used frequently. The species’



Figure 14. *Trachemys scripta elegans* (Elegans pattern class of *T. scripta*). Xcunya, Yucatan, Mexico. Photograph by Luis Díaz-Gamboa.

native geographic range, as presently understood, includes the southeastern United States and adjacent lowlands of northeastern Mexico (Rhodin et al. 2017), but due to their intensive husbandry and commercialization as pets, this turtle has become the most widespread chelonian in the world (Standfuss et al. 2016). It is almost impossible to determine exact invasion routes or dates of introduction, since these turtles have been subjected to extensive illegal trafficking, and can easily be purchased in pet stores and markets throughout Mexico (Yáñez-Arenas et al. 2016). Still, it seems highly probable that most introductions in Mexico occurred during the 1980's through 1990's, when “Japanese Turtles” gained immense popularity among pet owners.

Any review of literature covering the distribution of this introduced turtle should be made with special care, since the name *Trachemys scripta*, until recently, included almost every Pond Turtle population ranging throughout Middle America, unfortunately, listed as subspecies of *T. scripta* (Campbell 1998; Köhler 2008). Perhaps this is the reason why *T. scripta* appears in the Reptile Database as being introduced into all countries of Central America (Uetz et al. 2020). Johnson et al. (2015b) gave an account of the taxonomic and nomenclatural history of many taxa being considered up until that time, but some of that information has changed. Many subspecies of Pond Turtles recently have been rightly elevated to full species, thereby making them native populations to their inclusive ranges throughout Middle America (e.g., Seidel 2002; Fritz et al. 2012; McCranie et al. 2013; Parham et al. 2013, 2015). According to Parham et al. (2015), the native species in Middle America that occurs geographically closest to *T. scripta* is *T. venusta* in northeastern Mexico, which in itself has gone

through taxonomic reorganization, so today its range is primarily restricted to the Atlantic versant of Middle America into northern South America.

Our review of introduced species will only cover what has been called the Red-eared Slider, *T. scripta elegans* (Wied, 1838), which is listed among the 100 most dangerous invasive species, according to the Invasive Species Specialist Group (Lowe et al. 2000), although we herein do not consider subspecies as a legitimate formal taxonomic category (see Johnson et al. 2015b), but only “pattern classes” of geographic variants exhibited within a single species (Grismer 2002). The Elegans pattern class individuals of *T. scripta* are of special concern due to their deleterious tendencies to outcompete other turtles for basking sites, and as possible vectors for spreading diseases (Lavín et al. 2014).

Established introduced populations of the Elegans pattern class of *T. scripta* are disconnectedly distributed in several parts of Mexico, such as in Baja California, within several northern states, along the southern Pacific slopes, and on the Yucatan Peninsula (Lavín et al. 2014). We must clarify that the latest revision of the herpetofauna of the Mexican Yucatan Peninsula (González-Sánchez et al. 2017) failed to mention *T. scripta*, since it was thought that distributional records at that time from the peninsula corresponded to its close relative, *T. venusta*. These authors did overlook the report published by Böehm (2013), however, for some turtles from populations living within cenotes on the Yucatan Peninsula that clearly resembled the Elegans pattern class of *T. scripta*.

In Honduras, *T. scripta* has been observed in Río Llanitos, Santa Bárbara, and Isla Guanaja in the Islas de la Bahía (= Bay Islands) (McCranie et al. 2005; Solís et al. 2014). McCranie and Valdés-Orellana (2014), however, did not know whether the few known specimens from Guanaja were part of an established population, or merely individual escaped pets. McCranie and Valdés-Orellana (2014) also specifically mentioned a female from Isla de Guanaja at Savannah Bight (FMNH 283584) that was suspected to be an escaped pet because both *T. scripta* and *T. ornata* (= *T. venusta*; Parham et al. 2013, 2015) are regularly kept as pets by local citizens. Another report was published by McCranie and Valdés-Orellana (2014) of a vouchered, but supposedly uncatalogued *T. scripta* in the collection of UNAH from 11.9 km north of Cofradía, Cortés, on the mainland, located 290 km southwest of Savanna Bight on Isla Guanaja.

Kraus (2009) listed the red-eared slider (Elegans pattern class of *T. scripta*) as introduced in Panama, citing Moll (1995), but that reference was an editorial letter in which the author only mentioned having collected specimens in Panama; thus, he didn't provide any specific locality, date, or voucher specimen. Jaramillo et al. (2010) did not list *T. scripta* as an introduced species in Panama. Therefore, we have found no verified report for any established populations in Panama (Figure 14).

***Trachemys venusta* (Gray, 1855)**

The Mesoamerican Slider, as discussed elsewhere, was involved in the taxonomic dispute associated with *T. ornata* (Fritz et al. 2012; Parham et al. 2015). Presently,

T. ornata and *T. venusta* are considered as separate species, with *T. ornata* ranging along the Pacific lowlands of Mexico from Sinaloa to at least southeastern Guerrero, and *T. venusta* ranging from Tamaulipas, Mexico, on the Atlantic lowlands into South America (Parham et al. 2015; Legler and Vogt 2013). Much of the taxonomic controversy involved slider turtles sampled from the vicinity of Acapulco, Guerrero, which Parham et al. (2015) showed to be translocated *T. venusta*. We agree with their conclusion.

Family Kinosternidae

Kinosternon integrum (Le Conte, 1854)

A single individual of the Mexican Mud Turtle was captured 29 March 2007 in a perennial pool at the bottom of a rocky canyon in the Sierra La Laguna, Baja California Sur (Luja et al. 2007). Apparently, this was one of a pair mentioned by a local settler as being released into the pool by someone else, most likely in the second half of the 1980's; the other turtle was found dead at the site approximately ten years after its original release. Luja et al. (2007) made no mention about where the turtles originated. We assume the turtles were translocated by someone from the mainland on the Pacific versant of northwestern Mexico. Ferryboats regularly carry people across the Sea of Cortes from the Port of Pichilínque, near La Paz, Baja California Sur, to ports in Sinaloa at Topolobampo (near Los Mochis) in the northwest and Mazatlán in southwestern portion of the state. For now, we assume an established translocated population is probable at this site.

Iverson et al. (1998) stated that *K. integrum* populations in the Valley of Mexico were introduced, but they did not provide arguments to support that idea. It was also suggested that the probable extinction of *K. hirtipes hirtipes*, a supposed endemic subspecies of mud turtle known only from three to five localities in the Valley of Mexico (Legler and Vogt 2013; Rhodin et al. 2017), “may or may not be associated with the introduction of *K. integrum*, which has become very common there” (van Dijk et al. 2007); no evidence or explanation was given to confirm that assessment. Ramírez-Bautista et al. (2009) indicated that *K. integrum* and *K. hirtipes* are sympatric in Lago de Xochimilco (Distrito Federal), but they did not indicate if *K. integrum* was introduced or that *K. hirtipes* had become extinct there. *Kinosternon integrum* also inhabits Canal de Chalco, in the state of Mexico, and *K. hirtipes* also occurs in Lago de Tlahuac. We assume for now that both species have established populations in the Valley of Mexico, and that *K. integrum* was introduced there.

Family Trionychidae

Apalone spinifera (Le Sueur, 1827)

The Spiny Softshell has a limited native range in Mexico, principally in drainage systems associated with the Rio Grande, which is the border with Texas and a very small

segment of New Mexico near El Paso, with neighboring states in Mexico (Chihuahua, Coahuila, Nuevo León, and Tamaulipas), then continuing along the Gulf lowlands to approximately Soto la Marina, Tamaulipas (Legler and Vogt 2013). Farr (2015) apparently considered this turtle native throughout Tamaulipas, as did Lemos-Espinal and Dixon (2013) for the record of *A. spinifera* in San Luis Potosí. This turtle has been reported four times from translocated populations in northwestern Mexico (Rorabaugh and Lemos-Espinal 2016), once in the lower basin of Río Colorado and its drainages in the Mexicali Valley, Baja California (Grismer 2002), and three times in Sonora, twice from the Welton Canal area in the southeastern Río Colorado Valley (Rorabaugh et al. 2008) and once from the Río San Rafael in the Municipality of Cananea, 449 km to the east-southeast (Rorabaugh and King 2013). The introductions in Sonora are probably the result of expansion of an invasion front that might have originated by intentional introductions of Spiny Softshell turtles (together with fishes and frogs) by ranchers along the Gila River early in the 20th century. From there, the range expanded until reaching the lower Colorado Basin and Mexicali Valley (Miller 1946), where reportedly they were once plentiful, but now in decline due to hunting pressures (Melink and Ferreira-Bartrina 2000); Spiny Softshell meat has been served frequently in Chinese restaurants in Mexicali (Grismer 2002) (Table 3, Map 26).

In the Cuatro Ciénegas area of Coahuila, Mexico, *A. spinifera* arrived at some local water sources when irrigation channels were opened from the northeast in the 1880's (McGaugh and Janzen 2008). It has been linked to the impending extinction of the endemic Black Softshell (*A. atra*) due to hybridization, although this claim is yet to be fully confirmed, since "pure" individuals of *A. atra* could still be found during the 1970's and 1980's (Webb 1973; Legler and Vogt 2013), especially at the type locality. McGaugh and Janzen (2008) thought that there was insufficient molecular evidence to differentiate the two turtles and concluded they were conspecific, but Bonin et al. (2006) and Legler and Vogt (2013) regarded them as separate species. Wilson and Johnson (2010) reviewed the evidence and decided to continue recognizing *A. atra* until a study showing complete genetic introgression between all populations of the two species refutes the claim that they are separate evolutionary lineages. We agree with that conclusion because of historical genetic isolation and the reasons enunciated by Wilson and Johnson (2010). If it turns out to be true that a translocated invasive population of *A. spinifera* has hybridized to the point of full genetic introgression with *A. atra*, then, unfortunately, this situation will become a prime example of genetic extinction of a formerly endemic species by hybridization with a non-endemic species.

Outside of northern Mexico, a single record exists for *A. spinifera* from Jalisco in an artificial pond in Puerto Vallarta (Cupul-Magaña 2012), but nothing was said about it being from an established population. According to F. G. Cupul-Magaña (pers. comm.), the turtle was still alive as of August 2018 and living in an open-air aquarium in Puerto Vallarta, but he does not know the original date of translocation or where it originated. Cruz-Sáenz et al. (2017) did not list *A. spinifera* as a member of the Jalisco herpetofauna, presumably because they did not consider it an established population; we agree with that conclusion.

There are, however, documented localities in Guerrero for *A. spinifera* from along the Ŕo Balsas drainage, one from the vicinity of Colonia Valerio Trujano, near the Mezcala Bridge, Municipality of Eduardo Neri, that seems to be from an established population. Local residents indicated that it had been present there since the 1950's (Lemos-Espinal et al. 1999). Two turtles were taken from that area and according to the authors, were deposited in the Herpetology Collection, Unidad de Bioloǵa, Tecnoloǵa y Prototipos, UNAM, Campus Iztacala, Tlalnepantla, Estado de Ḿxico. The other locality that allegedly has an established population is from the Municipality of Copalillo, 5 km northeast of Papalutla at the edge of Ŕo Atoyac; a specimen from there was deposited in the Colecció del Laboratorio de Herpetoloǵa Vivario, Facultad de Estudios Superiores Iztacala, UNAM (CLHV 4462-E) (Jiménez-Arcos et al. 2009).

Castro-Franco and Zagal (2004) reported an adult female *A. spinifera* captured 17 October 1999 in the Ŕo Amacuzac on the Sierra de Huautla Natural Protected Area near Las Huertas Spa, Municipality of Tlaquiltenango, Morelos, which was deposited in the Herpetological Collection of the Universidad Aut́noma del Estado de Morelos (EBUM 2898). Another turtle was observed previously in that same Protected Area in Cruz Pintado Pond, but was not captured. Those turtles indicate a probable established population, and were thought to have been released pets.

García-Vázquez et al. (2009) first reported *A. spinifera* as occurring in Puebla, Mexico, without commenting about it being introduced to the state or not. Most recently, Woolrich et al. (2017) considered the Puebla record as an introduction, a determination with which we agree.

Reptiles – Squamata – Lizards

Family Iguanidae

Ctenosaura conspicuosa (Dickerson, 1919)

The Isla San Esteban Spiny-tailed Iguana only exists on Cholludo and San Esteban islands, in the Sea of Cortes, located in close proximity to the coast of Sonora, Mexico. The cultural evidence suggests that *C. conspicuosa* populations on both islands could be due to a prehistoric introduction of *C. nolascensis* from Isla San Pedro Nolasco by the Seri culture (Grismer 2002; Nabhan 2002). The divergence time between those two lineages, however, is much older (~890, 000 years), which coincides with the detachment of Isla San Esteban from mainland Sonora (Edwards et al. 2005). Even so, there seems to be enough molecular and cultural evidence to indicate that the population of *C. conspicuosa* present on Isla Cholludo was introduced indeed from Isla San Esteban by the Seri culture (Buckley et al. 2016) (Table 3, Map 27).

Ctenosaura pectinata (Wiegmann, 1834)

The Western Spiny-tailed Iguana naturally occurs in low to intermediate elevations primarily on the Pacific versant of Mexico from Sinaloa into Chiapas, including subhu-

mid interior basins and valleys and offshore islands (Uetz et al. 2020). This iguana was introduced on the remote Isla Clarion sometime in the mid-1990's (Aguirre-Léon and Matías-Ferrer 2017; CONANP 2018), although the path of introduction is unknown. We can be sure that they were introduced, since spiny-tailed iguanas are conspicuous animals, and not shy around human presence; thus, they should be noted easily, but were not reported in previous herpetofaunistic listings for that island (Townsend 1890; Brattstrom 1955, 1990). Whether there is an impact of *C. pectinata* on native species, such as the endemic *Urosaurus clarionensis* is unknown (Table 3, Map 28).

Ctenosaura similis (Gray, 1831)

Fig. 15

The Black Iguana naturally occurs on the Atlantic and Pacific versants from Mexico, below the Isthmus of Tehuantepec, through all countries in Central America (McCranie et al. 2005; Köhler 2008; Buckley et al. 2016). This lizard was reported as introduced to Isla Roatán, Honduras, where it was detected in 2012 (Pasachnik 2013); apparently, the site of initial translocation was on a small island off the south coast of Roatán near Coxen Hole. The Black Iguana could be an immediate threat to native *C. oedirhina*, since it might compete for resources and/or hybridize (McCranie and Valdés-Orellana 2014). Probably other insular populations of *C. similis* in the Caribbean waters of Mexico and Central America are intentional introductions, as exemplified by Sunyer et al. (2013), who mentioned probable translocations of *C. similis* and *Iguana iguana* as food sources for residents of the Corn Islands, Nicaragua, although this opinion was not based on empirical fact. A Mexican Navy cadet told one of us (VHGS) that both the Black Iguana and Green Iguana were introduced several dec-



Figure 15. *Ctenosaura similis*. A juvenile specimen from Little Corn Island, Nicaragua. Photograph by Javier Sunyer.

ades ago as ornamental species by navy cadets in Banco Chinchorro, Quintana Roo, Mexico, but there is no way to verify that claim. Thus, except for the Black Iguana population on Roatán, we do not consider the other locations as having confirmed translocations (Table 3, Map 29).

***Sauromalus hispidus* (Stejneger, 1891)**

The Spiny Chuckwalla inhabits several islands within the Gulf of California, including: Angel de La Guarda, Alcatraz, Cabeza de Caballo, Flecha, Granito, Mejía, Piojo, Pond, San Lorenzo Norte, San Lorenzo Sur, and numerous islands in Bahía de Los Ángeles (Grismer 2002; Buckley et al. 2016); a single individual also was reported from Isla Rasa (Velarde et al. 2008). The Spiny Chuckwalla was probably introduced from Ángel de la Guarda onto La Ventana and Smith islands, since individuals from both populations have “a nearly identical cytochrome b sequence as some Ángel de la Guarda *S. hispidus*.” The species also could have been translocated to San Lorenzo Sur, but the possibility exists that there was a previous land bridge involved (Petren and Case 1997). The Spiny Chuckwalla population on Isla Alcatraz might encompass introduced hybrids (Grismer 2002), since hybridization and genetic introgression have been suggested among *S. hispidus*, *S. varius*, and *S. obesus* (Robinson 1972). Kraus (2009) indicated a date of introduction to be around 1920, but he didn’t give concrete reasons for that estimation, and overlooked the much earlier cultural evidence of insular translocations by Seri navigators (Nabhan 2000, 2002). Shaw (1946) pointed out that some introductions probably occurred naturally due to Ospreys (*Pandion haliaetus*) inadvertently dropping live chuckwallas into their nests; he also was aware of translocations of individuals by the Seri culture as food sources (Table 3, Map 30).

***Sauromalus varius* (Dickerson, 1919)**

The Piebald Chuckwalla is only known from the islands of San Esteban and Roca Lobos in the Sea of Cortes (Grismer 2002). Hollingsworth et al. (1997) reported the first record for Roca Lobos, which they considered an introduced population based on the lack of morphological divergence between that population and the one on San Esteban. They also thought that natural colonization seemed unlikely since Isla Sal-sipuedes, with no *S. varius*, lies between the two islands and would have represented a barrier to direct overwater dispersal. Hollingsworth et al. (1997) also pointed out that the *S. varius* population on Roca Lobos could have been an intentional introduction by researchers attempting an experiment on the effects of colonization and evolution of insular populations. Considering the decades of studies they quoted, the introduction might have occurred in the midpoint or end of the 1970’s. A decade after the initial report, the Isla San Esteban Chuckwalla population was reported as being “healthy and reproducing” (Lovich and Mahrdt 2007) (Table 3, Map 31).

Family Phrynosomatidae

Uta stansburiana (Baird & Girard, 1852)

The Side-blotched Lizard is a common widespread generalist, occurring in the western United States, northern Mexico, and along the Baja California Peninsula and many of its associated islands (Grismer 2002). Interestingly, *U. stansburiana* is present on islands in the Sea of Cortes and Pacific Ocean, and on those with both continental and oceanic origins (Murphy and Aguirre-León 2002), some of which also are associated with endemic species of *Uta* (Grismer 2002). Certainly, many of those populations are natural overwater dispersal colonizers and, taking into account the anthropological evidence of translocations, some insular populations, assuredly, could be introduced (Murphy and Aguirre-León 2002). This assertion seems to be supported at least by the *Uta* populations on Isla La Raza, a tiny volcanic island in the Sea of Cortes, where molecular evidence suggests colonization from the north, from Ángel de la Guarda and/or Isla Mejía populations, something that Murphy and Aguirre-León (2002) considered unlikely by natural over water current dispersal, since the severe upwellings in that area should impede that movement. Additionally, the anthropological evidence of human occupancy on Isla La Raza and the lack of genetic differentiation points to accidental introduction, probably during prehistoric times (Upton and Murphy 1997) (Table 3, Map 32).

Reptiles – Squamata – Snakes

Family Boidae

Boa imperator (Daudin, 1803)

The Central American Boa Constrictor, formerly a subspecies of *Boa constrictor* (Reynolds et al. 2014), is widespread in Middle America, ranging on the Atlantic versant of Mexico to the Isthmus of Tehuantepec and on both Atlantic and Pacific sides below the Isthmus to northwestern Colombia (Card et al. 2016; Suárez-Atilano et al. 2017). Despite being native on the mainland Caribbean versant of Mexico, including the Yucatan Peninsula and several offshore islands, it was considered an introduced invasive species on Cozumel Island, Quintana Roo (Martínez-Morales and Cuarón 1999; González-Sánchez et al. 2017), although reasons for its distributional status were controversial as late as 2008 (Álvarez-Romero et al. 2008). It is clear now that *B. imperator* was unknown on Cozumel until 1971, when according to local independent informants, cinematographers filming the movie “El Jardín de la Tía Isabel” released several boas of various sizes in order to create a more “exotic” atmosphere (González-Sánchez et al. 2017). This conclusion was reinforced by the fact boas had not appeared in any biological listing until the inventory made by López-González (1991). A molecular study by Vázquez-Domínguez et al. (2012) documented the existence of a founder effect in the genome of Cozumel’s *B. imperator* and close phylogenetic ties with populations on the adjacent mainland.

Mart́nez-Morales and Cuarón (1999) suggested a possible link between the arrival of *B. imperator* on Cozumel with the decline of several native species, such as the Cozumel Thrasher (*Toxostoma guttatum*), Central American Agouti (*Dasyprocta punctata*), Cozumel Raccoon (*Procyon pygmaeus*), Cozumel Coati (*Nasua narica*), and the Cozumel Curassow (*Crax rubra*), among others. Of those, the Cozumel Raccoon is under a highly critical extinction risk (de Villa-Meza et al. 2011). Thus, it is imperative that a plan should begin now to eliminate or tightly manage this invasive snake species that is threatening Cozumel's wildlife. We are unaware of any attempted *B. imperator* control program on Cozumel Island, however, beyond surveys or ecological studies.

Charruau et al. (2015) suggested that *B. imperator* might be alien to Cayo Centro (Banco Chinchorro, Quintana Roo), since it is a large reptile and not seen previously by local anglers, although the management program for that reserve already listed this snake as occurring there. A molecular analysis, however, should be done in order to clarify the origin of the Cayo Centro population (Table 3, Map 33).

Reported introduced species not on our list of established populations in Middle America

Taricha torosa (Rathke, 1833)

Murphy and Méndez de la Cruz (2010) listed the California Newt (Salamandridae) as introduced into Baja California, but they did not provide any details or explanations. Grismer (2002) considered it a species that probably occurs in northern Baja California. Kuchta (2005) listed it based on supposed records for northwestern Baja California by Slevin (1928), Smith and Taylor (1948), and others, but all of those records need verification. *Taricha torosa* definitely occurs naturally in San Diego County, California, a few kilometers from the Mexican border (Kuchta 2005), therefore, the most probable scenario of potential extant Mexican populations reflects natural range expansions from the San Diego populations. Thus, at this time, we do not consider it a native or an introduced species in Mexico.

Gopherus agassizii (Cooper, 1861)

The taxonomic history of the *G. agassizii* species complex of Desert Tortoises (Testudiniidae) generally had been unresolved (Murphy et al. 2011). Until recently, only *G. agassizii* was officially recognized and naturally resided in the Mojave and Sonoran Deserts in the USA and Mexico, southward in Sonora (including Tiburón Island) into areas of Sonoran desertscrub, Sinaloan thornscrub, and tropical deciduous forest to around Alamos, Sinaloa. Reported populations in Baja California and Baja California Sur were mostly associated with introductions (Bury et al. 2002; Murphy et al. 2011; Legler and Vogt 2013). The species complex has undergone recent taxonomic revisions (Murphy et al. 2011; Edwards et al. 2016) and future studies might well lead to additional taxonomic modifications.

Murphy et al. (2011) removed *G. agassizii* (Agassiz's Desert Tortoise) from the herpetofauna of Mexico by formally describing *G. morafkai* (Morafka's Desert Tortoise). *Gopherus morafkai* also ranges into the USA, primarily in Sonoran Desert areas in Arizona south and east of the Colorado River. *Gopherus agassizii* is now considered native to the Mojave Desert of California, Nevada, Utah, small areas in northwestern and southwestern Arizona, and a small section of the Sonoran Desert in southeastern California. Edwards et al. (2016) further divided the Mexican populations into *G. morafkai* and a new species, *G. evgoodei* (Goode's Desert Tortoise), which is endemic to Mexico and native to primarily Sinaloan thornscrub and tropical deciduous forests in east-central and southern Sonora and northern Sinaloa. The two species occasionally hybridize in the ecotone between Sonoran desertscrub (*G. morafkai* preferred habitat) and Sinaloan thornscrub (*G. evgoodei* preferred habitat); no hybrids were observed from tropical deciduous forest habitats.

Ottley and Velazquez-Solís (1989) described a new species of tortoise (as *Xerobates lepidcephalus*), based on one live individual and shell remains of another, from the Cape region of Baja California Sur, specifically from the Sierra San Vicente, 1.5 km north of the Buena Mujer Dam, 20 km south of La Paz. Crumly and Grismer (1994) noted that its morphological variation fell within that expected for individuals from Sonoran populations, thus they considered *X. lepidcephalus* as a junior synonym of *G. agassizii*; they further opined that the population was a probable introduction. Grismer (2002), however, considered the possibility of a native relict population existing in the Cape region that later was reduced considerably when goat grazing was allowed. To us, it also seems plausible that the construction of Buena Mujer Dam in the 1980's would have destroyed a large area of suitable tortoise habitat, leaving only a few survivors. Murphy et al. (2011) inconclusively pointed out that the holotype of *X. lepidcephalus* might correspond to a hybrid, so if this is the case, it supports the hypothesis of an introduced population, since hybrid lineages are common in non-native species (Edwards et al. 2010). The hybrids most likely would be between *G. morafkai* and *G. evgoodei* that originated as pets taken to the La Paz area. On the other hand, if a population of native tortoises exists in the La Paz region, then they certainly should be considered a separate evolutionary species (Murphy et al. 2011), because of its allopatric distribution compared to that of *G. agassizii*, *G. morafkai*, and *G. evgoodei*. In that case, measures to guarantee the population's protection should be made available as soon as possible (Murphy and Mendez de la Cruz 2010).

At this point, we do not think that the population around La Paz has been identified definitively as being *G. morafkai*, *G. evgoodei*, *G. agassizii*, or one of hybrid origin. We also consider any inhabitants that will be found in northeastern Baja California will probably fall within the native range of *G. morafkai*, unless they can be shown positively to be part of translocated *G. agassizii*, *G. evgoodei*, or hybrid populations. Thus, it will not be appropriate at this time to list any population of the *G. agassizii* species group of Desert Tortoises as being introductions within northwestern Mexico.

***Gopherus berlandieri* (Agassiz, 1857)**

A single specimen of the Texas Tortoise (Testudinidae) was found in a city park at Puerto Vallarta, Jalisco, Mexico (Cupul-Magaña 2012). Cruz-Sáenz et al. (2017) did not consider it as part of the Jalisco herpetofauna, nor is there any other record for this species outside its native range in northeastern Mexico, so we concur that it was not part of an established population.

***Staurotypus triporcatus* (Wiegmann, 1828)**

Until recently, the Mexican Giant Musk Turtle (Staurotypidae) was considered native to the Atlantic lowlands from central Veracruz, Mexico, through the southern Yucatan Peninsula, and on to the western Caribbean lowlands of Honduras (Legler and Vogt 2013; Rhodin et al. 2017). Terán-Juárez et al. (2015) reported this turtle near Ocampo, Tamaulipas, Mexico, ca. 524 km to the north of the closest known locality in central Veracruz. They considered this record the result of an introduction due to the large hiatus between those localities. Terán-Juárez et al. (2016), however, later regarded the population as native because there was no empirical evidence to support its translocation by human activities from farther down the Gulf Coastal Plain. Our experience with *S. triporcatus* indicates that individuals rarely leave water sources and cross roads like other kinosternid turtles, especially those in the genus *Kinosternon* and even *Claudius*. Legler and Vogt (2013) also mentioned that *S. triporcatus* in Belize never were observed on land during its activity season. Crossing roads could be a good source for translocating turtles along roadways, but if that rarely happens with *S. triporcatus*, the capability of being translocated is diminished. Until additional information indicates otherwise, we agree with Terán-Juárez et al. (2015) that the records came from a marginal area of its native range in northeastern Mexico.

***Trachemys ornata* (Gray, 1831)**

The *Trachemys scripta* species group (Emydidae) has had a confusing taxonomic history in Middle America, especially those populations occurring in tropical latitudes (Johnson et al. 2015a), so more work is required to properly determine native species boundaries (Parham et al. 2013, 2015). The Ornate Slider is presently considered a Mexican endemic ranging on the Pacific lowlands of Mexico below 300 m elevation from Sinaloa to 4 km northwest of Ixtapa, Guerrero, which is ca. 220 km northwest of the Acapulco, Guerrero area (Mertz et al. 2015). This turtle also was reported to occur in several lagoons around Acapulco and sold for food in local markets (Legler and Vogt 2013). According to Parham et al. (2015), however, all samples they evaluated near Acapulco were *T. venusta*, which they considered translocations from the Atlantic lowlands of Mexico. Rhodin et al. (2017) alleged that an isolated record of *T. scripta*

(= *T. ornata*?) in Michoacán and other remote records on the Pacific lowlands in Guerrero might have been introduced as well. A connection between the coastal lagoon systems on the Pacific lowlands, however, might have existed in the past (Legler and Vogt 2013), and possibly still does, so it seems likely to us that the range of *T. ornata* might extend even farther down the Pacific lowlands past the Acapulco region. We will not include *T. ornata* as anything other than native until the origins and taxonomic status of those Pacific lowland populations are fully resolved.

***Cnemidophorus ruatanus* (Barbour, 1928)**

The Ruatan Whiptail (Teiidae) was reported (as *Cnemidophorus lemniscatus*) by Stafford and Meyer (2000) from Monkey River town, Toledo District, Belize; Stafford et al. (2010), without comment, considered it as an introduced species. McCranie and Hedges (2013) elevated *C. ruatanus* to species level from its previous status as a subspecies of *C. lemniscatus*. Due to the proximity of this record to other known localities, however, and for maintaining consistency in a coastal scheme of distribution (McCranie and Hedges 2013), we consider this population as being a marginal natural expansion of its total distributional range.

***Gonatodes albogularis* (Duméril & Bibron, 1836)**

Fig. 16

Identifying the native distribution of the Yellow-headed Gecko (Sphaerodactylidae) is problematical because of its wide range in parts of Middle America, northern South America, and on many islands in the West Indies (Uetz et al. 2020). A pertinent question is whether its native range is restricted to Middle and South America and it is introduced in the West Indies, or vice versa. Stuart (1963) was under the impression that all West Indian records were introductions. Villa et al. (1988) and Köhler (2008) did not mention it ranging into the West Indies, which we infer to mean that those individuals were not considered native to that area. Others have apparently included the West Indies as part of the natural range (e.g., Lee 2000; Savage 2002; McCranie et al. 2006; Johnson et al. 2010); most of those sources also reported *G. albogularis* as being introduced into Florida, without referring to its possible origin.

On the mainland, *G. albogularis* occurs from the Pacific slopes of the Soconusco and Sierra Madre regions in Chiapas, Mexico, through Central America into northern Colombia and Venezuela (Johnson et al. 2015a), at elevations lower than 1,000 m. Its northernmost locality on the Atlantic versant of Mexico recently was reported as Minatitlán, Veracruz, by Guzmán-Guzmán and Palma-Martínez (2016). It was discovered in Belize City in 1996 (Lee 2000) and Stafford et al. (2010) thought it had been introduced recently into that country, but with no substantiated evidence. Until new information demonstrates otherwise, we regard *G. albogularis* as being native to Middle and South America and exotic in the West Indies and Florida.



Figure 16. *Gonatodes albobularis*. Ometepe island. Nicaragua. Photograph by Javier Sunyer.

Phyllodactylus nocticolus (Dixon, 1964)

The occurrence of Peninsular Leaf-toed Gecko (Phyllodactylidae) on Isla Tiburón could be due to natural over-water island hopping, accidental introduction (Murphy and Aguirre-León 2002), ancient historical translocation from other islands in the Sea of Cortes (Nabhan 2000), or even by paleotectonic activity (Blair et al. 2009). Without specific evidence to support any of the above-mentioned scenarios, we elect not to list this species as introduced at this time, but it is certainly a candidate worth further investigation.

Phyllodactylus xanti (Cope, 1863)

Mellink (2002), citing Nabhan (2002), indicated that the Cabo Peninsular Leaf-toed Gecko (Phyllodactylidae) was introduced involuntarily from mainland Baja California onto San Lorenzo, San Esteban, Tiburón, and Alcatraz islands, probably by boats. We could not find any corroborating reference or study suggesting that scenario. Thus, because we could not specifically determine if the *P. xanti* population on Tiburón Island originated there by natural dispersal or by some sort of human-mediated introduction process (see *P. nocticolus* account above), we decided not to include this species on our list of introductions at this time.

***Sauromalus obesus* (Baird, 1859)**

A chance exists that the Western Chuckwalla (Iguanidae) might have been translocated to several islands in the Sea of Cortes, based on the same reasons as those for *S. hispidus* and *S. varius* (Nabhan 2002), but not enough evidence was presented to support that contention. Therefore, we are awaiting more verification before deciding to place it on our list of species introduced into Mexico.

***Varanus exanthematicus* (Bosc, 1792)**

The Savanna Monitor (Varanidae) is known in Mexico from a single record in Puerto Vallarta, Jalisco (Cupul-Magaña 2012). This record probably corresponds to an escaped pet or intentional release. We know of no other record from anywhere else in Middle America, so we do not consider the lizard as coming from an established population.

Considerations for management and control measures for introduced species

The main difficulty for management and control of the introduced invasive herpetofauna of Middle America is the lack of documentation. Most conservation managers or agencies have little to no tradition of publishing in the refereed scientific literature, so, for the most part, successes and failures of invasive species are found in grey literature sources (Simberloff 2009). Even more daunting is the fact that among known eradication/management programs cited in the literature, few concern reptiles (Campbell III et al. 1999; Toda et al. 2010) or amphibians (Miller 2006; Greenlees et al. 2018), and hardly any evaluate effectiveness of their control techniques (Rodda et al. 1999; Davis et al. 2015; Haramura et al. 2017; Muller and Schwarzkopf 2017). The main consequence of this “nothing can be done” approach is the lack of evidence for successful programs (Simberloff 2009). Therefore, the first challenge must be to encourage managers to publish their results in the scientific literature.

A key component of any successful control or eradication program is early detection of an invasion and a quick response (Simberloff 2009). Unfortunately, only in limited cases are introductions detected early, so usually dates are merely approximations or suppositions. The true origins of many species are often uncertain, especially if they are common, and times and places of the introduction are unknown; many are commonly considered native even though their true place of origin is unresolved. Those instances refer to the “cryptogenic species” of Carlton (1996), a good example of which is the status of *A. allisoni* being listed as native to the Yucatan Peninsula of Mexico (González-Sánchez et al. 2017), Belize (Stafford et al. 2010), and Honduras (Solís et al. 2014; McCranie 2015), even though others consider them introductions,

including Glor et al. (2005) and lvarez-Romero et al. (2008). Additionally, in some situations, some apparent “endemic” species might be, in fact, the result of an ancient anthropogenic introduction of an alien species; this situation can occur particularly in insular ecosystems after thousands of years of isolation, and are referred to as “ethnospecies” (Hofman and Rick 2018). This explanation could apply to some endemic iguanids (such as *Sauromalus* and *Ctenosaura*) on islands in the Sea of Cortes; there has been speculation about the origin of the population of *C. conspicuosa* on San Esteban island, which is believed to have originated from translocated individuals of *C. nolascentis* from San Pedro Nolasco Islands by the Seri people (Grismer 2002). Davy et al. (2011), however, refuted this notion and specified that *C. nolascentis* and *C. conspicuosa* diverged thousands of years before human colonization of the Sea of Cortes. Still, the idea should not be discarded, as some iguanid endemic lineages on those islands might be ethnospecies.

Another key component of control and eradication programs involves the correct identification of the presumed introduced species by qualified specialists and their training of non-expert volunteers so to avoid misidentification of native species as introduced ones. These specialists also need to participate in the removal programs. These lessons have come from the work of Rick Shine and his colleagues on the Cane Toad or Marine Toad (*Rhinella marina*) in Australia, as reported in numerous publications, including the book *Cane Toad Wars* (Shine 2018). Nonetheless, the work of Shine and his colleagues has demonstrated that simple, physical removal of adult toads is ineffective in reducing their numbers or in curtailing their spread through Australia and that what is more promising is an approach using integrated pest control (Shine 2015). Shine (2015: 312) indicated that “Cane toads are formidable invasion machines, and it is unlikely that any single method will ever eradicate them. Even with a combination of methods, landscape-scale extirpation is vanishingly unlikely. However, the new weapons developed out of recent ecological research on this high-profile invasive anuran provide great encouragement.” Shine (2015: 314) further noted that the release of “juvenile (and thus, non-lethal) toads at the current invasion front [can be employed] to train native predators to avoid toads as prey” and that “funnel-traps baited with toad toxins can eradicate toad tadpoles from natural water bodies.” In general, he concluded that “cane toads in Australia provide a clear example that [one needs] to understand an invasive species if [one wants] to control it.” This “whole-biology” approach also is stressed by Tyler (2006) in his discussion of the potential use of pheromones of both tadpoles and adults in the control of invasive populations of this toad.

A common challenging situation emerges in cases where some translocated species are under legal protection, but are exotic or even invasive in other parts of the country. This situation keeps conservation managers from performing effective eradication or control measures on those invasive populations (Lazcano et al. 2010). For example, Morelet’s Crocodile and *Boa imperator* (as *Boa constrictor*) appear under the categories of “subject to special protection” and “threatened,” respectively, by Mexican legislation (D.O.F. 2015). Obviously, when describing an invasive species, its location of controlling action should be strictly identified (Richardson et al. 2011), or an accurate deline-

ation of both the native areas where the species resides and where it is invasive be given (Ochoa-Ochoa et al. 2017).

The first obvious method for controlling introduced species of amphibians and reptiles is direct capture/sacrifice and trapping methodology. Some biologists, however, are opposed to the sacrificing such introduced creatures, for ethical reasons. This position is entirely understandable and is complex enough to require adequate discussion elsewhere. Several capture techniques include using nooses, pitfall traps, funnel traps, sticky traps, rubber bands, firearms, blowguns, and road cruising, among others, whose effectiveness are well known to herpetologists, thus we will not detail them here. Less common, but potentially successful procedures are discussed below.

Chemical control has a long tradition for managing invasive mammals, but its use has been employed infrequently for herpetofaunal control. The most publicized instances involved Brown Tree Snakes (*Boiga irregularis*) on Guam, where Brooks et al. (1998) tested lethality of dermal and oral drugs. Clark and Savarie (2012) and Clark et al. (2012) used and evaluated bait poisoning techniques. We are unaware of similar techniques being applied on invasive snakes in Middle America, but evaluating drug toxicity and establishing bait-poisoning plots for controlling *B. imperator* on Cozumel Island should be evaluated seriously for a long-term control or eradication program.

Invasive anuran control programs in Australia included spraying lethal chemicals in water sources (Kelehear et al. 2012). In the USA, Witmer et al. (2015) evaluated toxicity of different compounds on American Bullfrogs (*Lithobates catesbeianus*). Several species of anurans and other amphibians have evolved species-specific embryogenic suppression pheromones to reduce intraspecific competition, whereby older larvae produce substances that inhibit development of younger conspecifics (Tingley et al. 2017). The feasibility of using these embryogenic inhibitors for controlling invasive anurans in water sources has received recent attention, with some promising results (Clarke et al. 2016).

A key aspect for the success of some invasive anurans are potent chemical defenses that most vertebrate predators cannot tolerate. Nonetheless, several invertebrate groups are immune to those toxins, and many of them, such as dragonfly nymphs, fishing spiders, water beetles, ants, crabs, and crayfish, voraciously consume tadpoles or early stage metamorphs. Thus, introducing native invertebrate predators can be a biological control option when the only species in the water source is an alien anuran (Cabrera-Guzmán et al. 2012; Cabrera-Guzmán et al. 2015).

A major advantage for invasive species when reaching a new area is access to a parasite-free space (Torchin et al. 2003). With this notion in mind, it makes sense to introduce the relevant parasite into the area in order to diminish the fitness of the invasive population (Torchin et al. 2003; Finnerty et al. 2018). Even if the invasive species does not develop a parasitic disease, accumulation of sub-lethal effects can have significant consequences on overall performance, growth rates, and reproduction potential of infected toads, as reported by Finnerty et al. (2018). Another example of biological control used in Hawaii on the invasive *Eleutherodactylus coqui* was infecting them with the lungworm *Rhabdias elegans* (Marr et al. 2010).

A successful molecular tool for early detection and monitoring aquatic and semi-aquatic invader species is testing water sources for their waterborne environmental DNA (eDNA), as described by Jerde et al. (2011) and Bohmann et al. (2014). So far, however, this technique has been used mainly for detecting rare or elusive species, although it was used to detect invasive amphibians (Dejean et al. 2012) and reptiles (Piaggio et al. 2014; Hunter et al. 2015). The advantage of eDNA is appealing because it can improve chances for detecting hard to observe species or to identify species displaying crypsis (Jerde et al. 2011; Piaggio et al. 2014). This method also allows conservation monitors to identify key amphibian breeding sites, and could be a valuable tool for locating strategic invasion places, such as those near airports, maritime ports, and plant nurseries (Tingley et al. 2017). In addition, it can be a complementary tool for post-eradication confirmation surveys.

A key feature for managing introduced species, especially in large areas, is to identify important sites to focus control and eradication efforts, as well as to prevent invasions and/or reinvasions before they occur. Environmental niche modelling (ENM) has been a helpful tool for identifying potential corridors among the sources and areas vulnerable to invasions (Peterson 2003; van Wilgen et al. 2009). In fact, the use of ENM for managing and controlling introduced herpetofaunal species recently has been increasing, with several examples originating in Middle America (Rodder et al. 2008; van Wilgen et al. 2009; Lira-Noriega and Ramrez 2016; Ynez-Arenas et al. 2016).

Decision makers often require methods that help them justify and decide where, when, and on which species to target conservation and/or control programs. For these reasons, there exist protocols that can be used to determine if a species is potentially at risk and deserves attention. Generally, these protocols consist of a questionnaire that must be answered by a specialist or by a panel of experts; examples are revealed in “Mtodo de Evaluacin Rpida de Invasividad (MERI) para Especies Exticas en Mxico” (Gonzlez-Martnez et al. 2017), and in the Harmonia+ and Pandora+ protocols for invasive species and invasive pathogens, respectively (D’hondt et al. 2015).

Finally, and most important of all, is the human component, which is pivotal for the success of any management program governing actions associated with invasive species (McNeely 2001; Garca-Llorente et al. 2008). The most obvious reason is that humans are often the determining factor when they transport species into new areas voluntarily or involuntarily, thereby enabling individual animals to cross biogeographical barriers (Vitousek et al. 1997; Mack et al. 2000). Personal attitudes of people relating to introduced species also strongly influence management preferences by giving more support to non-intervention approaches when they think animals have equal rights of existence versus control program when they consider human intervention acceptable for maintaining ecosystem integrity (Sharp et al. 2011). In addition, how urgent or harmful people perceive the risk of invasive species to be can directly reflect a potential willingness to help provide funding or other support for developing strategic management or control programs (Garca-Llorente et al. 2011). Therefore, any management policy should include serious sociological decisions, together with effective proclamation and educational campaigns incorporating biosecurity as a real value for local citizens.

Conclusions

As noted previously, interest in introduced invasive species is taxonomically skewed toward other vertebrates, such as mammals, birds, or fishes. Thus, with a few exceptions, the ecological influences and damages caused by introduced invasive amphibians and reptiles are unknown. This lack of knowledge can have ominous consequences, such as taxonomic uncertainty, causing voids in legislation, and omissions of reptiles and amphibians in many biosecurity protocols or practices. Additionally, a great proportion of the literature on monitoring or control programs corresponds to technical reports not easily accessible to other researchers and/or managers. A first barrier to overcome is to encourage managers and researchers to identify results of monitoring and control programs on the invasive herpetofauna and to have that information published in accredited journals.

For conservationists to influence protocols, it is imperative that they promote stricter legislation on damaging practices, such as the pet trade, which should be discouraged, especially in those species with high potential of being harmful to Middle American ecosystems, even if they are already present, like *Trachemys* spp., or those that are common in the pet trade of a region, but not yet reported in the wild, such as *Varanus exanthematicus* and *Python molurus*. Stricter legislation should not be limited to vertebrate species, but also extended to pathogens associated with amphibians (or reptiles), such as *Batrachochytrium dendrobatidis*, *Saprolegnia parasitica*, and *Ranavirus* spp. We are aware that such listing of potential harmful pathogens exists for Mexico (D.O.F. 2016), but it is unknown to us if any equivalent legislation exists in other Middle American countries.

Finally, the ever-growing trade of goods on a global scale, the increasing interest by people for keeping exotic pets, and the human persistence for environmental degradation will continue to favor arrival and settlement of invasive species. Regrettably, the frequency, scope, and intensity of biological invasions are expected to increase during the ensuing decades. Thus, the study and management of introduced amphibians and reptiles in Middle America is a topic that offers a wide spectrum of opportunities for career development associated with young researchers, conservationists, and other professionals dealing in ecological restoration.

We consider biological conservation as a human value, which includes a series of moral codes and behaviors that transcend time and culture and define us as a species. In this way, and like other values, it contributes to building prosperity and free coexistence among societies. It is also obvious that invasive species control and management is controversial, since many people put a high value on any single living organism, independent of its origin. If they accept invasive species to be a legitimate part of our ecological footprint, however, it is clear that we have a moral and ethical responsibility to educate them on the negative impacts invasive species have on the overall well-being of our biosphere. At the same time, it is also our responsibility to help maintain biosecurity and ecological restoration measures as advocates to prevent, mitigate, and remediate damages caused by invasive species until the majority of humanity accepts the fact that being good stewards of our living spaces is the right thing to do. Conservation professionals also must understand what motivates people's different attitudes

towards invasive species (e.g., why they transport them, whether they perceive them as harmful or not, or whether they are willing to accept control methods or not) in order to develop meaningful programs that discourage harmful behaviors and promote more responsible attitudes. Therefore, integration of the human and technical component is fundamental for accepting biosecurity as one more principle guiding societal behavior.

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Supplementary material I

Multipoint shapefiles, occurrence records for introduced and translocated reptiles and amphibians in Mexico and Central American Countries

Authors: Víctor Hugo González-Sánchez, Jerry D. Johnson, Larry David Wilson

Data type: species data

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