

Annotated checklist of the land snail fauna from southern Cambodia (Mollusca, Gastropoda)

Chirasak Sutcharit¹, Phanara Thach², Samol Chhuoy², Peng Bun Ngor^{2,3},
Ekgachai Jeratthitikul⁴, Warut Siriwt⁴, Ruttapon Srisonchai⁵, Ting Hui Ng⁶,
Arthit Pholyotha¹, Parin Jirapatrasilp¹, Somsak Panha¹

1 Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand **2** Inland Fisheries Research and Development Institute (IFReDI), Fisheries Administration, No. 86, Norodom Blvd., PO Box 582, Phnom Penh, Cambodia **3** Wonders of the Mekong Project, c/o IFReDI, No. 86, Norodom Blvd., PO Box 582, Phnom Penh, Cambodia **4** Animal Systematics and Molecular Ecology Laboratory, Department of Biology, Faculty of Science, Mahidol University, Bangkok 10400, Thailand **5** Department of Biology, Faculty of Science, Khon Kaen University, Khon Kaen 40002, Thailand **6** Lee Kong Chian Natural History Museum, Faculty of Science, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Republic of Singapore

Corresponding author: Somsak Panha (somsak.panha@chula.ac.th); Parin Jirapatrasilp (parin_ohayo@hotmail.com)

Academic editor: Eike Neubert | Received 3 March 2020 | Accepted 12 May 2020 | Published 13 July 2020

<http://zoobank.org/20E7C613-5771-4F32-8F6C-44A7E84AFA68>

Citation: Sutcharit C, Thach P, Chhuoy S, Ngor PB, Jeratthitikul E, Siriwt W, Srisonchai R, Ng TH, Pholyotha A, Jirapatrasilp P, Panha S (2020) Annotated checklist of the land snail fauna from southern Cambodia (Mollusca, Gastropoda). ZooKeys 948: 1–46. <https://doi.org/10.3897/zookeys.948.51671>

Abstract

Prior to this study, few collections and records were made of the land snails in Cambodia and the historical taxa had never been reviewed. Herein a report on the land snail diversity based on specimens collected recently from karstic and non-karstic areas in southern Cambodia is provided. This checklist presents 36 species of land snails (two Neritimorpha, six Caenogastropoda, and 28 Heterobranchia). Illustrations and brief taxonomic notes/remarks are provided for every species. We also described *Georrisa carinata* Sutcharit & Jirapatrasilp, **sp. nov.** based on some distinct shell morphological characters. Since the first descriptions during the colonial period in the nineteenth century, some land snail species (e.g., *Trichochloritis norodomiana*, *Durgella russeola*, *Anceyoconcha siamensis obesula* **comb. nov.**, *Anceyoconcha chaudiensis* **comb. nov.**, and *Succinea tenuis*) have not been reported subsequently. This probably reflects a lack of knowledge concerning land snail biodiversity in this country. To our knowledge, this is the first comprehensive survey of land snails in southern Cambodia. A need for more field research and systematic revision of the land snails in this interesting region is also highlighted and demonstrated.

Keywords

Biodiversity, conservation, Indochina, limestones, systematics

Introduction

Cambodia forms a part of the Indo-Chinese sub-region of the Indo-Burma biodiversity hotspot (Myers et al. 2000, Wikramanayake et al. 2001, Bain and Hurley 2011, Tordoff et al. 2012). Its terrain mostly consists of low-lying plains and the Mekong Delta and is flanked by the Cardamom Mountains in the west and the Annamite chain in the east (Gupta 2005). As with other parts of Indochina, Cambodia has lost most of its forest areas through changes in land use in the past six decades (Davis et al. 2015, Tsujino et al. 2019), resulting in decreased or irreplaceable losses of biodiversity (Hughes 2017). There is an urgent need to implement conservation action to protect the known fauna and flora of the country, as well as conduct intensive research to reveal species that are not known to science (Sodhi et al. 2010).

The inventory of the Cambodian fauna, primarily for the vertebrates and insects, has been increasing and rapidly improved with field surveys in recent years, e.g., for freshwater fish (Hartmann et al. 2013, So et al. 2019), herpetofauna (Neang et al. 2015, Geissler et al. 2019), dragonflies (Kosterin 2012, Kosterin et al. 2012, Kosterin and Chartier 2014), aquatic Hemiptera (Zettel et al. 2017), beetles (Freitag et al. 2018, Jocque et al. 2019), bees (Ascher et al. 2016), and ants (Hosoishi et al. 2012, 2015). Knowledge of a handful of other invertebrate fauna has also been accumulated, e.g., rotifers (Sor et al. 2015), crustaceans (Naruse et al. 2014), and millipedes (Likhitrakarn et al. 2015). Without doubt, many other major groups of invertebrates remain to be explored including the terrestrial snails (Hun et al. 2019). Malacological research in Cambodia can be traced back to the 19th century, but studies have been temporally and spatially sporadic. However, a small number of local investigations have been undertaken in the past decade (Vermeulen et al. 2007, 2019a, b).

The earliest land snail collections in Cambodia were made by the French naturalist Henri Mouhot from the mountainous areas of eastern and southwestern Cambodia during the mid-1800s (Mouhot 1864a, b). In the colonial period of the late 19th to early 20th century, the most prominent land snail collections were carried out by the well-known French explorer Augustus Pavie. He traveled to most parts of Cambodia and accumulated huge collections of natural history objects (Pavie 1904, see also Inkhavilay et al. 2019). The Pavie collections of land snails were then studied and published by Crosse and Fischer (1876), Morlet (1883, 1885, 1886, 1889, 1890), Rochebrune (1881a, b) and some others. Later, a list of 84 taxa of the land snail fauna of Cambodia was compiled and listed in the “Mission-Pavie”, the significant book series by Fischer and Dautzenberg (1904). Some sixty years later, small collections of land snails from southern Cambodia and Vietnam were collected by the geologist, Edmund Saurin and studied by van Benthem Jutting (1962). The species list of molluscan fauna

from Cambodia was reviewed by Fischer (1973a–c). The endemic and monotypic slug, *Cambodiparmarion doroshenkoi*, was described from the south of Cambodia (Kuznetsov and Kuzminykh 1999) and Vermeulen et al. (2007, 2019a, b) reported land snails from south Cambodia and Vietnam, mainly focusing on Mekong Delta limestone in the southwest and the foothills of the southern Annamite range in the northeast. In addition, Hun et al. (2019) discovered the giant land snail *Bertia cambojiensis* in Cambodia for the first time. It is clear that the land snails in southern Cambodia remain poorly known (Hun et al. 2019, Vermeulen et al. 2019a, b).

Southern Cambodia (Fig. 1) represents an interesting biogeographic transition zone between the Cardamom Mountain Ranges in the west, Mekong Delta limestones in the southwest, and the foothills of the southern Annamite range in the northeast (Bain and Hurley 2011, Geissler et al. 2015). Two ecoregions are recognised within this area: the Cardamom Mountains Rain Forests [IM0106] and the Southern Annamites Montane Rain Forests [IM0152] ecoregions (WWF 2019a, b). The aim of our study was therefore to contribute to the filling of a knowledge gap on more land snails from karstic and associated habitat types. Herein, we present the record of land snails collected in September 2019 in the limestone hills, sandstone forest and reserved forest of Kirirom National Park and Preah Monivong Bokor National Park in southern Cambodia.

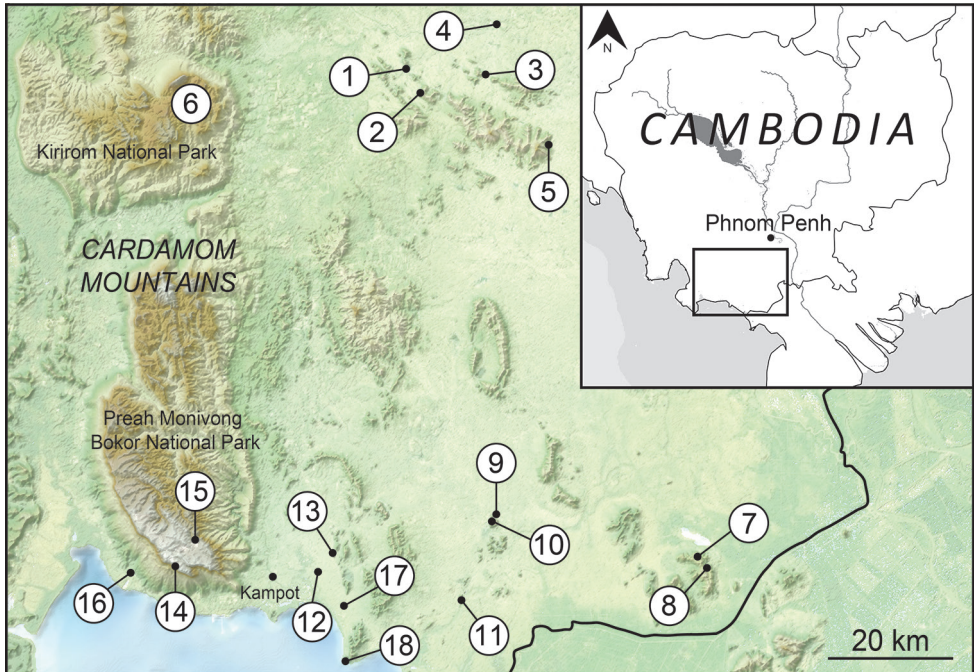


Figure 1. Map of the Kingdom of Cambodia showing the collection localities. The numbers indicate the collection sites which correspond to Table 1 and in the material examined sections.

Materials and methods

Field surveys

The survey sites were chosen to cover the main habitat types and the localities are shown in Figure 1 and Table 1. Field surveys were conducted during the day using the encounter survey technique (Crump and Scott 1994). Empty shells were collected by hand. Living snails were searched for in various habitats/micro-habitats such as tree vegetation, decaying logs and leaf litter on forest floor by CS, PT, EJ, WS, RS, TNG, and AP. Living specimens encountered were photographed prior to euthanasia using the 2-step method (AVMA 2013), and these were subsequently fixed and preserved in 70% ethanol.

All the specimens were identified to genus or species level based on shell characteristics by referring to the historical literature including original descriptions, recent catalogues of land snails from Laos by Inkhavilay et al. (2019), and the collections of the Muséum national d'Histoire naturelle (MNHN, Paris) and The Natural History Museum (NHM, London). The placement of each genus within higher order classification follows MolluscaBase (2020). All specimens were deposited at the Inland Fisheries Research and Development Institute (IFReDI) of the Fisheries Administration, Phnom Penh; Chulalongkorn University Museum of Zoology (CUMZ), Bangkok; Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore (ZRC); The Natural History Museum, London (NHMUK).

Table 1. Locations and geographical coordinates of sampling sites of terrestrial snails within the southern provinces of Cambodia.

No.	Province	Locality code and name	Latitude / Longitude
1	Kampong Speu	C028-Mountain near Phnom Prak Sombo Pagoda, Tang Sya, Phnum Sruoch District	11°23'53.9"N, 104°23'03.8"E
2		C029-Mountain near Phum Krang Ponley, Khum Kiri Voan, Phnum Sruoch District	11°21'43.90"N, 104°24'14.44"E
3		C031-Phnom Cheal Pagoda, Khum Skuh, Samraong Tong District	11°23'11.81"N, 104°30'34.96"E
4		C032-Bridge, Stoeng Prek Thnaot River, Krong Chbar Mon	11°27'40.15"N, 104°31'43.47"E
5		C034-Prasat Neang Khmao Temple, Srang, Kong Pisei	11°16'47.24"N, 104°36'25.50"E
6		C061-Kirirom National Park, Traeng Trayueng, Phnom Sruoch District	11°20'33.81"N, 104°02'9.77"E
7	Takeo	C036-Phnom Bayang, Kiri Vong District	10°38'28.1"N, 104°50'35.8"E
8		C037-Pha-aok Waterfall, Kiri Vong District	10°37'35.3"N, 104°51'30.2"E
9	Kampot	C041-Limestone mountain near To Tong, Dang Tong District	10°41'59.79"N, 104°31'30.14"E
10		C042-Prasat Phnom Totong, Banteay Meas District	10°41'49.6"N, 104°31'20.9"E
11		C043-Phnom Kampong Trach Cave Temple, Kampong Trach District	10°34'1.77"N, 104°28'6.13"E
12		C045-Phnom Kbal Romeas, Tuek Chhou District	10°37'0.08"N, 104°14'37.60"E
13	Kep	C046-Phnom Chhnok Cave, Tuek Chhou District	10°38'34.91"N, 104°16'4.07"E
14		C051-Sampov Pram Pagoda (site 1), Preah Monivong Bokor National Park	10°37'49.07"N, 104°01'3.12"E
15		C052-Popokvil Waterfall (site 2), Preah Monivong Bokor National Park	10°39'31.8"N, 104°03'03.2"E
16		C056-Prek Thnout Eco Park, Tuek Chhou District	10°36'44.29"N, 103°57'16.61"E
17		C047-Phnom Sorsia Temple, Ou Krasar, Krong Kaeb	10°33'53.57"N, 104°17'1.90"E
18		C048-Kep Beach, Prey Thom, Krong Kaeb	10°28'47.1"N, 104°17'32.8"E

Study area

Field surveys were conducted in karstic areas in southwestern Cambodia, Kampot Province. In addition, caves and cave-like chambers which provide appropriate microhabitats for karst-dwelling snails were also surveyed. This area has a monsoonal climate with wet season (May to November) and dry season (December to April). The karst landscape in Kampot is a small, isolated hill rising precipitously from the flat lowlands (Fig. 2A). The forest habitats surrounding the hill area have been degraded because of agricultural encroachment at the base of the hill and is enclosed by highly disturbed scrub vegetation, but the hill itself bears typical limestone vegetation on its cliff. Limestone quarrying is locally widespread.

Lowland habitats of the eastern areas of Kirirom National Park are a conglomerate of hills and a plateau reaching 900 m in elevation, straddling the Kampong Speu and Koh Kong Provinces. The bulk of the plateau is covered with a mosaic of grassland and a reticulated network of pine forest plantations (Fig. 2B). The slopes of the plateau support an evergreen forest interspersed with tracts of mixed deciduous and bamboo forests.

The Preah Monivong Bokor National Park, Kampot Province is in the southeastern portion of the Cardamom Mountain Ranges within a range known as the Elephant Mountains. The plateau reaches an elevation of 1,100 m, and the floral composition of this range is greatly affected by continuous, monsoonal winds arising from the Gulf of Thailand. The climate promotes a mixture of grassland and tropical moist forest that shrouds the upper elevations of the Bokor Plateau in thick fog for much of the year (Stuart and Emmett 2006, Grismer et al. 2008), the condition of which is also present during our time of surveys. The slopes of the area support tracts of primary evergreen forests and steep, fast flowing, rocky streams.

Results

A total of 180 voucher specimen lots was collected over the survey. The total of 36 species (two Neritimorpha (Fig. 6A, B), six Caenogastropoda (Figs 3A–C, 6C–F, 7A–C), and 28 Heterobranchia) fell within 25 genera and 13 families, including two non-native species (*Lissachatina fulica* and *Allopeas gracile*). The distribution data given under each species was retrieved from the past records.

Subclass Neritimorpha

Family Hydrocenidae Troschel, 1847

Georissa Blanford, 1864

Georissa monterosatiana Godwin-Austen & Neville, 1879

Fig. 6A

Georissa monterosatiana Godwin-Austen & Nevill, 1879: 739, 740, pl. 59, fig. 6. Type locality: Perak [Perak State, Malaysia]. Foon et al. 2017: 43, fig. 16c.

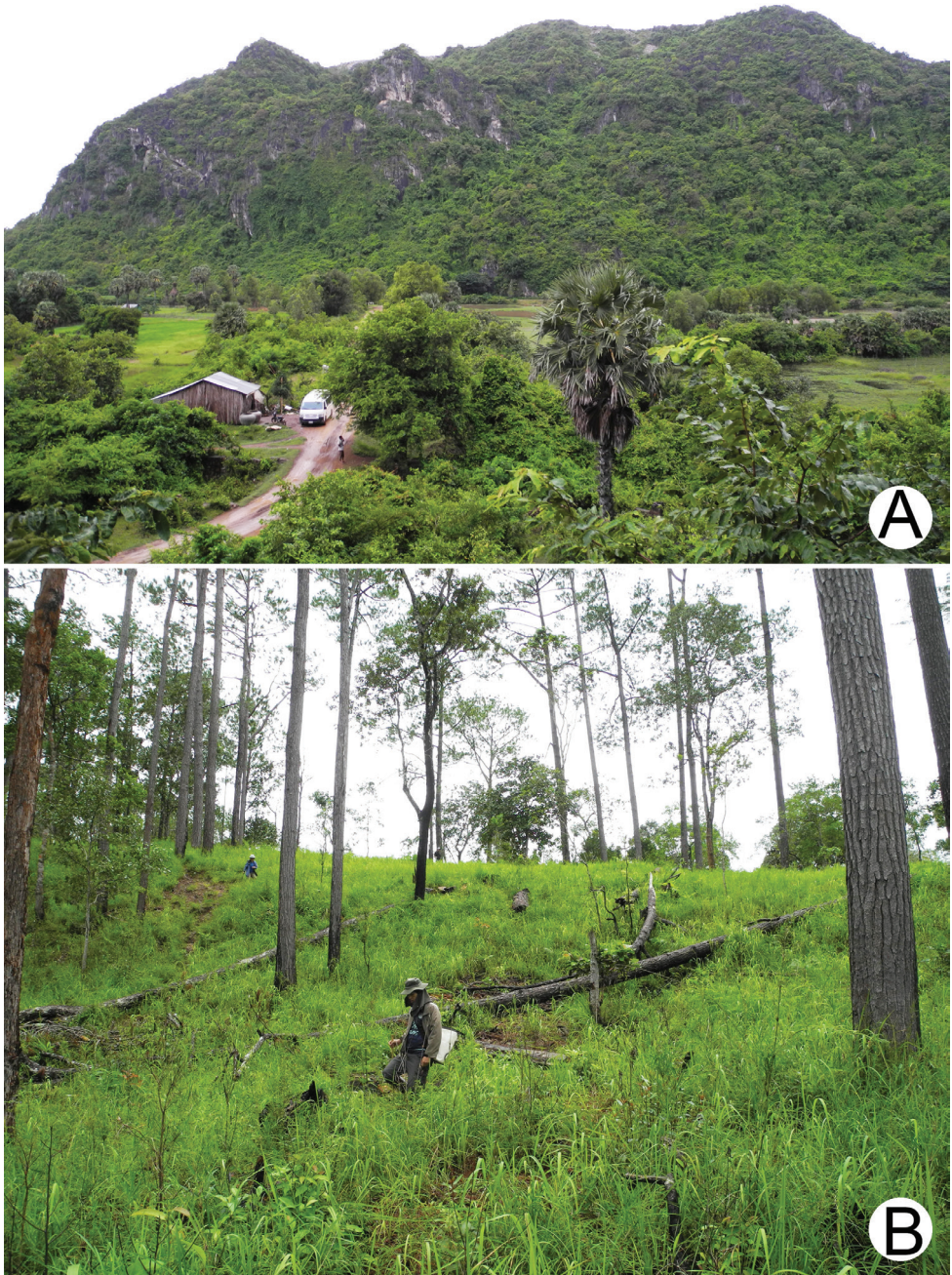


Figure 2. Collecting sites representing two main habitat types. **A** Limestone karsts with dry evergreen forest (September 2019; locality no. 10) **B** sandstones with grassland and coniferous forest (September 2019; locality no. 6).

Material examined. Locality no. 11: CUMZ-CM114 (10 shells; Fig. 6A). The snails were found to live on limestone wall syntopically with other *Hypselostoma* spp.

Distribution. Thailand and Malaysia (Foon et al. 2017).

Remarks. This species was described from “Perak” [Perak State, Malaysia]. The characters of this minute shell are elongate conic, yellowish to pale orange with darker colour on apex. The shell has four to five well-rounded whorls, with wide and impressed suture. Protoconch surface is smooth, with the following whorls sculptured with strong, regularly spaced spiral ribs and with ca. 9–11 spiral ribs on the last whorl (more thin spiral ribs at basal part of the last whorl). The aperture is round to slightly ovate, with a closed umbilicus. Although the specimens from Perak have denser spiral striation (Godwin-Austen and Nevill 1879, Foon et al. 2017), without a comprehensive revision of this genus the specimens from Cambodia were hereby identified as *G. monterosiana*.

This species differs from *G. decora* Möllendorff, 1900 and *G. chrysacme* Möllendorff, 1900 both of which were described from “Touranne” [Da Nang, Vietnam], by having a conic shell with ca. ten strong spiral ribs on the last whorl. However, *G. decora* has an ovate conic shape with fine radial ribs on the last whorl, and *G. chrysacme* has an elongate conic shape with a deep and narrow suture. In addition, the shell shape of *G. monterosiana* approaches the shape of *G. insulae* Khalik et al., 2019 from Borneo, but the former species has stronger and more undulated spiral ridges than the Bornean species (see Khalik et al. 2019).

***Georissa carinata* Sutcharit & Jirapatrasilp, sp. nov.**

<http://zoobank.org/CA891381-B719-4A88-B4A9-B0E36BAB121E>

Fig. 6B

Type material. Holotype CUMZ-CM094/1 (Fig. 6B) from locality no. 11. Measurement: shell height 2.1 mm, shell width 1.5 mm and 4¼ whorls. Paratypes CUMZ-CM094/2 (9 shells) from locality no. 11; CUMZ-CM042 (21 shells), IFRDI (10 shells), ZRC (10 shells) and NHMUK (10 shells) from locality no. 9.

Type locality. Phnom Kampong Trach Cave Temple, Kampong Trach District, Kampot Province, Cambodia, Locality no. 11 (10°34'1.77"N, 104°28'6.13"E).

Other material examined. Locality no. 12: CUMZ-CM086 (23 shells). Locality no. 17: CUMZ-CM102 (18 shells).

Description. Shell minute (shell height up to 2.1 mm, shell width up to 1.5 mm), conic, solid, translucent, yellowish to pale orange with darker colour on apex. Whorls 4¼, last whorl large ca. two-thirds of shell height. Protoconch ca. one whorl; sculpture nearly smooth and discontinuous spiral appearing immediately after protoconch. Following whorls slightly keeled, sculptured with thin and uneven growth lines; upper periphery with irregular and strong sculpture; below periphery with discontinuous spiral ribs. Sutures angular and impressed. Aperture round to slightly ovate. Umbilicus closed. Operculum unknown.

Etymology. The Latin specific name *carinata* represents its keeled whorls of this new species.

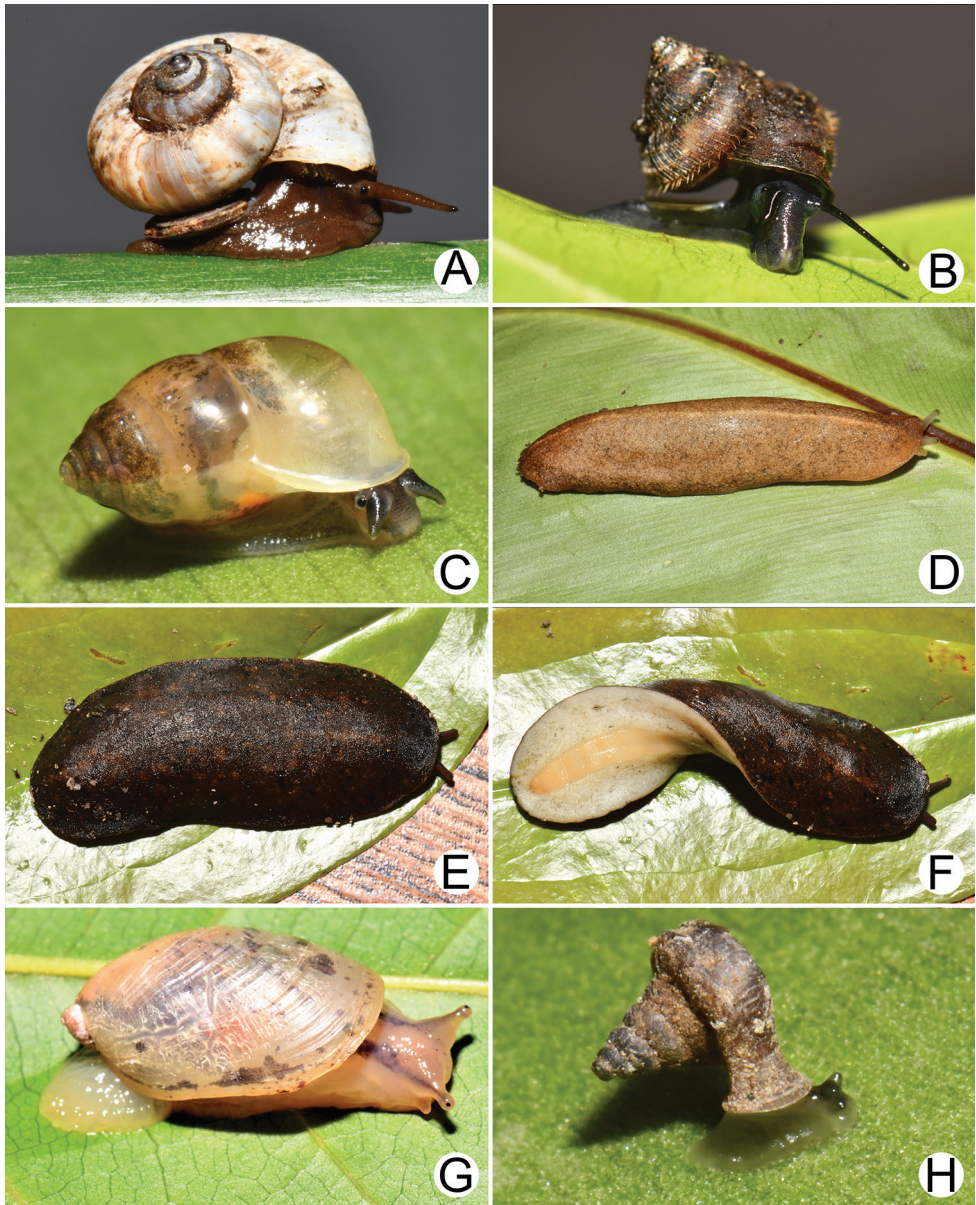


Figure 3. Living snails of **A** *Lugocheilus klobukowskii* (Morlet, 1885) **B** *Lugocheilus landesi* (Morlet, 1885) **C** *Pupina crosseana* Morlet, 1883 **D** *Valiguna siamensis* (Martens, 1867) **E, F** *Valiguna* sp. **E** notum or dorsal view and **F** hyponotum or ventral view **G** *Succinea tenuis* Morelet, 1865 and **H** *Hypselostoma cambodjense* Benthem Jutting, 1962. All not to scale.

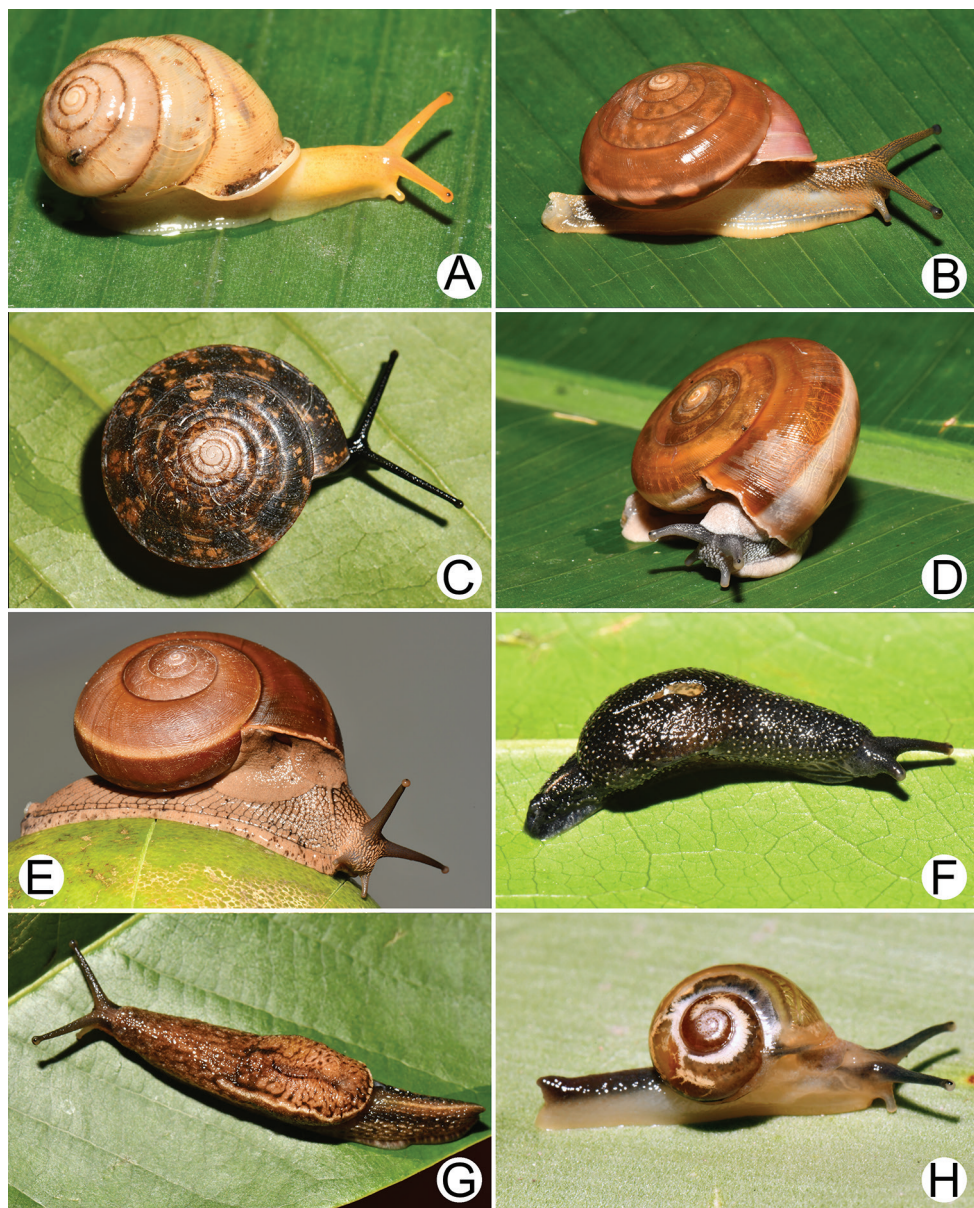


Figure 4. Living snails of **A** *Haploptychius* sp. **B** *Quantula weinkauffiana* (Crosse & Fischer, 1863) **C** *Trochomorpha paviei* (Morlet, 1885) **D** *Cryptozonia siamensis* (Pfeiffer, 1856) **E** *Hemiplecta distincta* (Pfeiffer, 1850) **F** *Cambodiparmarion doroshenkoi* Kuznetsov & Kuzminykh, 1999 **G** *Parmarion martensi* Simroth, 1893 and **H** *Durgella russeola* (Morelet, 1865). All not to scale.

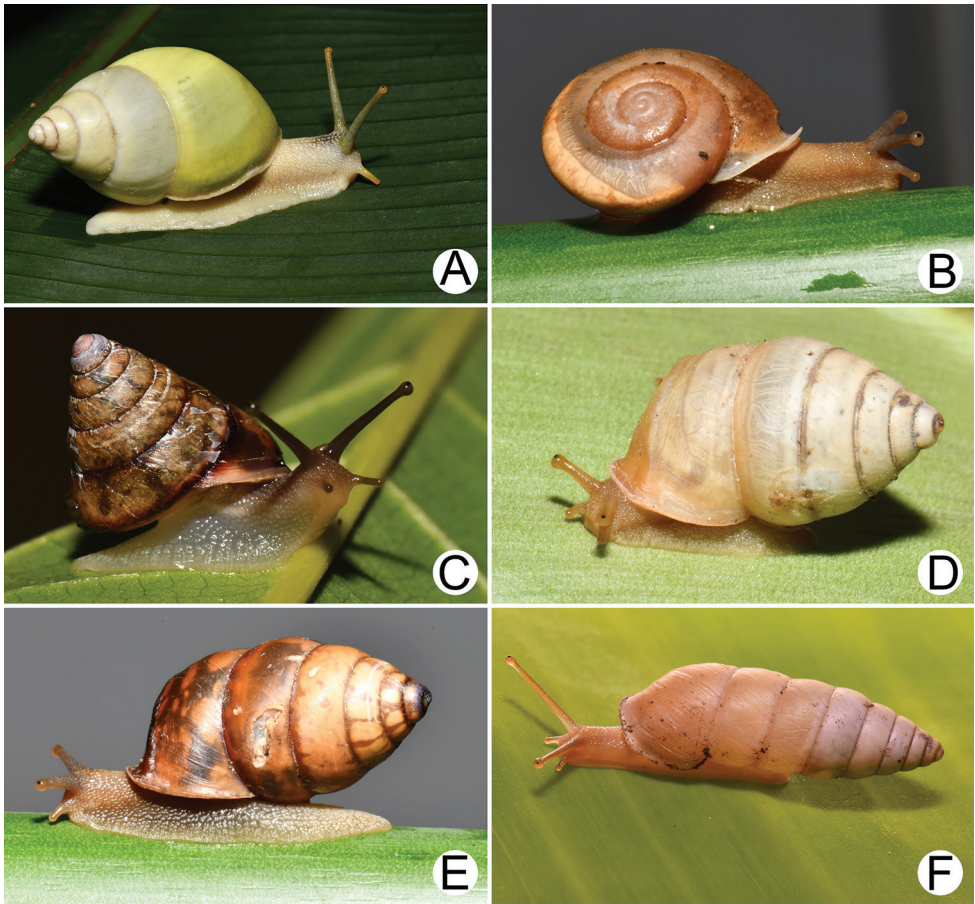


Figure 5. Living snails of **A** *Amphidromus leucoxanthus* (Martens, 1864) **B** *Trichochloritis norodomiana* (Morlet, 1883) **C** *Ganesella perakensis* (Crosse, 1879) **D, E** *Anceyoconcha rhombostoma* (Pfeiffer, 1861) **D** brownish morph and **E** dark brown morph and **F** *Anceyoconcha chaudoensis* (Rochebrune, 1881) comb. nov. All not to scale.

Distribution. This new species is found from Kampot and Kep Provinces. The snails were found to live on limestone wall syntopically with other *Hypselostoma* spp.

Remarks. This new species differs from *G. bocourti* (Rochebrune, 1881) described from “Eaux douces de Preck-Scholl. Haut Mékong” [Chhloung District, Kratié Province, Cambodia], by having a conic shell with $4\frac{1}{4}$ whorls, which are slightly keeled and sculptured with thin and uneven growth lines without conspicuous spiral ribs. However, *G. bocourti* has a turritiform shell with 6–7 whorls and sculptured with conspicuous spiral ribs (Rochebrune 1881a). *Georissa carinata* sp. nov. differs from *G. poirieri* Mabilie, 1887 and *G. conspicua* Mabilie, 1887 described from “Tonkin” [Vietnam] in that the latter two species are larger (shell height 3–5 mm, shell width $2\frac{1}{2}$ –3 mm) and

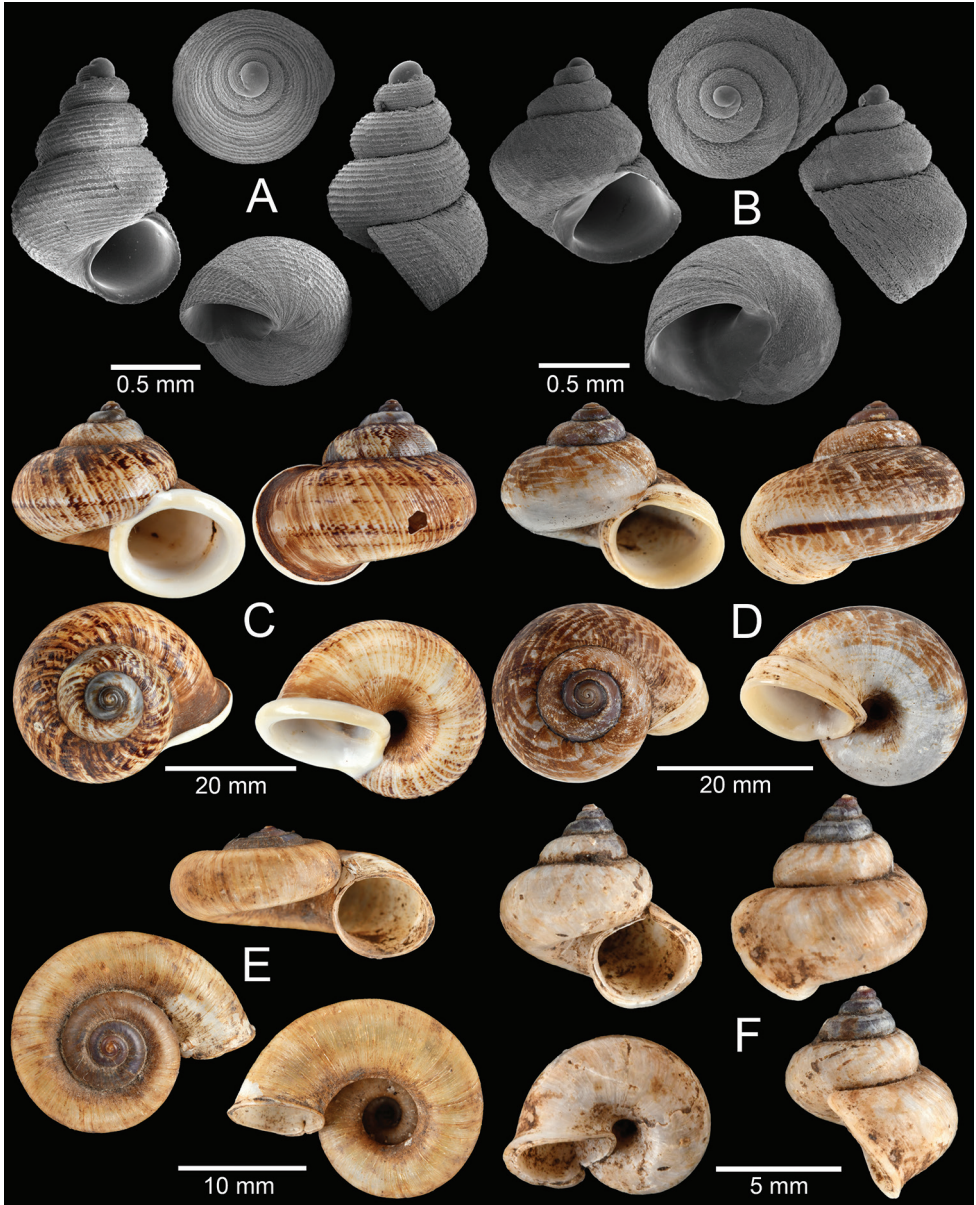


Figure 6. **A** *Georissa monerosatiana* Godwin-Austen & Neville, 1879 **B** *Georissa carinata* Sutcharit & Jirapatrasilp, sp. nov. **C** *Cyclophorus amoenus* (Pfeiffer, 1854) **D** *Cyclophorus paviei* Morlet, 1885 **E** *Opisthoporus bernardii* (Pfeiffer, 1862) and **F** *Lagocheilus landesi* (Morlet, 1885).

has a turriform shell. In addition, *G. poirieri* has very thin, tight, wavy spiral ribs, while *G. conspicua* has uneven spiral ribs with additional protuberances unequally arranged along the longitudinal rows (Mabille 1887a, b).

Subclass Caenogastropoda

Family Cyclophoridae Gray, 1847

Cyclophorus Montfort, 1810

Cyclophorus amoenus (Pfeiffer, 1854)

Fig. 6C

Cyclostoma (*Cyclophorus*) *amoenum* Pfeiffer, 1854[1852]: 62. Type locality: unknown. *Cyclophorus amoenus*: Nantararat et al. 2014a: 4, 5, fig. 3a, b. Nantararat et al. 2014b: 103, table 1, fig. 1b. Do and Do 2019: 6, 7, table 1, figs 1.2, 13b, c.

Material examined. Locality no. 10: CUMZ-CM053 (21 shells), CUMZ-CM054 (1 shell; Fig. 6C). Locality no. 7: CUMZ-CM0110 (1 shell). Locality no. 11: CUMZ-CM071 (2 shells). The empty shells were collected from the ground among leaf litter.

Distribution. Cambodia and Thailand (Nantararat et al. 2014b). The distribution in Vietnam is doubtful (Do and Do 2019).

Remarks. *Cyclophorus* is the genus encompassing highly variable shell morphology of both inter- and intraspecific entities. The demarcation among different species is poorly understood. Thus, both intensive and thorough revision and redescription require more effective taxonomic characters, e.g., morphometric analysis of large series of specimens and perhaps molecular phylogeny to clarify the exact species boundaries (see Nantararat et al. 2019).

This species was described from an unknown type locality. Later, the type specimens were examined and illustrated (Nantararat et al. 2014a) and then subsequently reported from central Thailand (Nantararat et al. 2014b). Do and Do (2019) reported this species from central and southern Vietnam, but it needs revision and confirmation by more studies. The distinguishing characters of this species are a less expanded apertural lip, thickened with multiple layers and with a highly variable colour pattern.

Cyclophorus paviei Morlet, 1885

Fig. 6D

Cyclophorus paviei Morlet, 1885[1884]: 389, 390, pl. 11, fig. 4, 4a. Type locality: Les montagnes de Dey-Crahom (terre rouge) [The mountains of Dey-Crahom (red earth)], sur la rive droite du grand fleuve [on the right bank of the great river (Mekong River)]. Do and Do 2019: 24, figs 9.39, 23c.

Cyclophorus (*Eucyclophorus*) *paviei*: Kobelt 1908: 615, 616, pl. 83, figs 7, 8.

Material examined. Locality no. 13: CUMZ-CM119 (1 shell). Locality no. 6: CUMZ-CM176 (1 shell). Locality no. 9: CUMZ-CM036 (2 shells), CUMZ-C037 (1 shell; Fig. 6D), CUMZ-CM038 (1 specimen in ethanol). Locality no. 12: CUMZ-CM096 (1 shell). Locality no. 16: CUMZ-CM168 (2 shells), CUMZ-CM169 (1 specimen in

ethanol), CUMZ-CM170 (1 specimen in ethanol). The snails were found to live on the ground among leaf litter.

Distribution. Cambodia (Kobelt 1908). The distribution in Vietnam is doubtful (Do and Do 2019).

Remarks. *Cyclophorus pavieri* was described from “Les montagnes de Dey-Crahom”, from Cambodia. It differs from *C. cambodgensis* Morlet, 1885, which was described from the same area in having a smaller (shell width 32 mm) conical shell, with a white-yellowish apertural lip, while *C. cambodgensis* has a larger (shell width 42 mm) and turbinate conic shell, with an orange to reddish apertural lip.

***Opisthoporus* Benson in Pfeiffer, 1851**

***Opisthoporus bernardii* (Pfeiffer, 1862)**

Fig. 6E

Rhiostoma bernardii Pfeiffer, 1862: 45, 46, pl. 6, fig. 5. Type locality: Siam [Thailand].

Kobelt 1911: 761, pl. 111, figs 9, 10.

Cyclotus bernardii: Inkhavilay et al. 2019: 19, fig. 8d, e.

Opisthoporus bernardii: Do et al. 2020: 108, table 3.

Material examined. Locality no. 9: CUMZ-CM043 (8 shells). Locality no. 13: CUMZ-CM127 (2 shells), CUMZ-CM118 (2 shells). Locality no. 10: CUMZ-CM062 (3 shells; Fig. 6E), CM063 (1 shell), CUMZ-CM064 (2 specimens in ethanol). The snails were found to live on the ground among leaf litter.

Distribution. Cambodia, Laos and Thailand (Inkhavilay et al. 2019).

Remarks. *Opisthoporus bernardii* was originally described from “Siam” [Thailand], and it has been reported from Cambodia (Fischer 1973a) and Laos (Inkhavilay et al., 2019). The diagnostic characters of this species are the depressed helicoid shell, with thick or thin periostracum, circular aperture, and a short to long sutural tube (accessory breathing device) located just behind an apertural lip. Pfeiffer (1862) provided details of the operculum, which is calcareous and has a multi-spiral plate-like shape, while the operculum of *Rhiostoma* is thick calcareous and has a multi-spiral cup shape (Egorov 2009).

***Lagocheilus* Blanford, 1864**

***Lagocheilus klobukowskii* (Morlet, 1885)**

Figs 3A, 7A, B

Cyclophorus klobukowskii Morlet, 1885[1884]: 391, 392, pl. 12, fig. 1. Type locality: Near the Kamchay rapids, around the Kébal-Réméas cave (Kampot-Hatien road); commonly found on mountains, in forests, up to Compong-Som, and on the banks of Tap-Chéang. Fischer 1973a: 46, 47.

Lagocheilus klobukowskii: Inkhavilay et al. 2019: 19, 20, figs 9b, c, 18c.

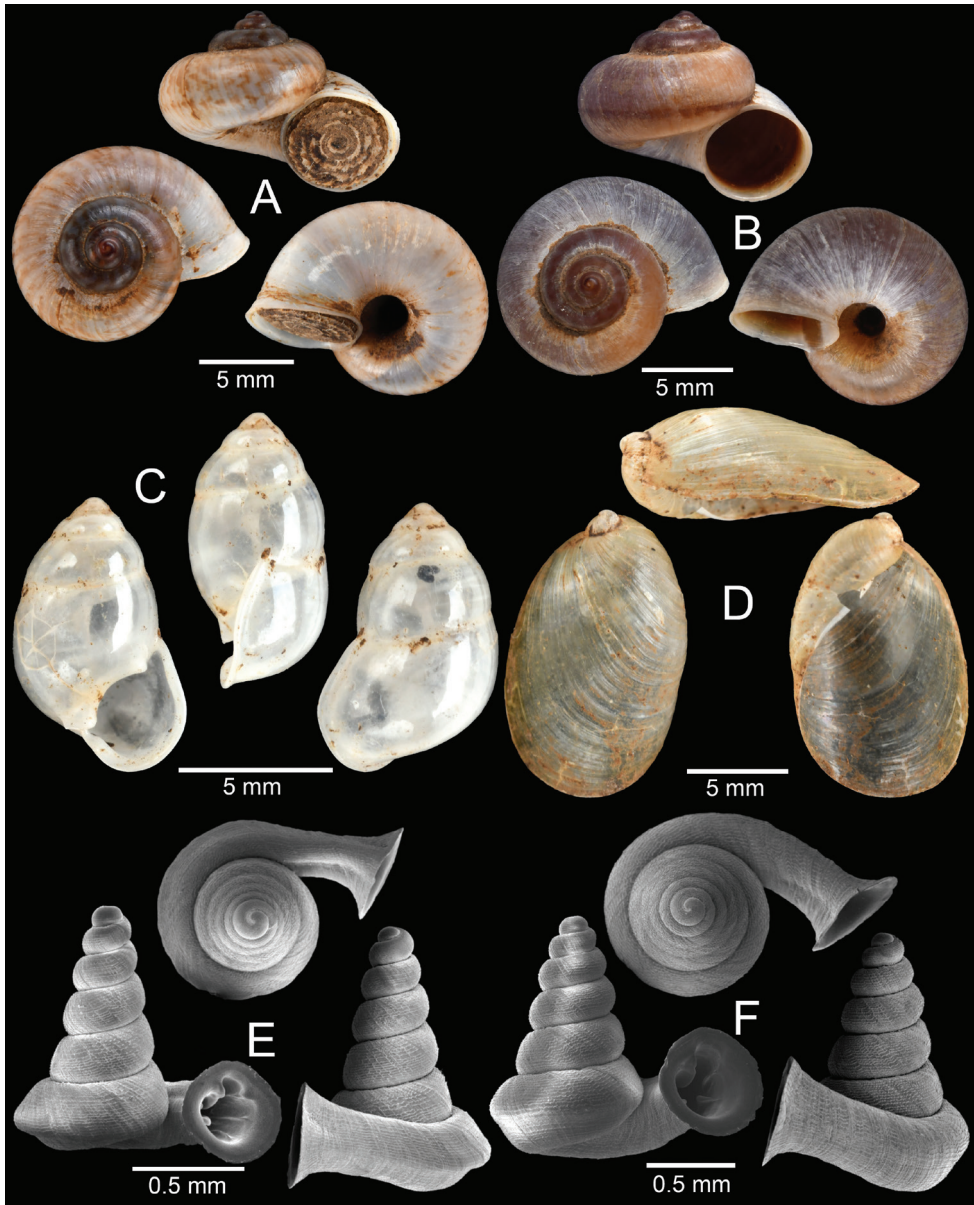


Figure 7. **A, B** *Lagocheilus klobukowskii* (Morlet, 1885) **A** yellowish morph and **B** purplish-black morph **C** *Pupina crosseana* Morlet, 1883 **D** *Succinea tenuis* Morelet, 1865 and **E, F** *Hypselostoma benetuitum* Vermeulen et al., 2019 **E** from locality no. 11 (type locality) and **F** from locality no. 17.

Material examined. Locality no. 9: CUMZ-CM044 (7 shells), CUMZ-CM045 (12 specimens in ethanol). Locality no. 10: CUMZ-CM068 (3 specimens in ethanol). Locality no. 11: CUMZ-CM079 (2 shells). Locality no. 13: CUMZ-CM128 (3 shells),

CM129 (53 specimens in ethanol; Fig. 3A). Locality no. 17: CUMZ-CM137 (18 shells; Fig. 7A, B). The snails were found to live on the ground among leaf litter and decaying wood, on tree trunks and limestone wall.

Distribution. Cambodia and Laos (Inkhavilay et al. 2019).

Remarks. This species was described from “...grotte de Kébal-Réméas (route de Kampot à Hatien) ...”. We collected topotypic specimens that tend to have a variable shell colour from yellowish (Fig. 7A, see fig. 9b in Inkhavilay et al. 2019 for the syntype) to purplish-black (Fig. 7B). This limestone associated species has a wide distribution from southern Cambodia to eastern Laos (Inkhavilay et al. 2019). The snails are commonly found in montane forest, living on decaying wood, on tree trunks and exposed limestone.

Lagocheilus klobukowskii was originally placed in the genus *Cyclophorus* and later was transferred to the genus *Lagocheilus* (see Inkhavilay et al. 2019). The distinguishing characters from the genus *Cyclophorus* are a conic shell, an aperture thickened (not expanded), and a thick calcareous, multispiral and plate-like operculum, whereas *Cyclophorus* has a turbinate shell, a thick and expanded lip, and a corneous multispiral operculum.

Lagocheilus landesi (Morlet, 1885)

Figs 3B, 6F

Cyclophorus landesi Morlet, 1885[1884]: 392, 393, pl. 11, fig. 5, 5a. Type locality: extrémité de la chaîne de l'Éléphant, non loin de la mer [Preah Monivong Bokor National Park, Kampot Province, Cambodia].

Cyclophorus laudesi [sic]: Fischer 1973a: 47.

Lagocheilus landesi: Inkhavilay et al. 2019: 20, fig. 9d.

Material examined. Locality no. 11: CUMZ-CM080 (4 shells; Fig. 6F), CUMZ-CM082 (1 specimen in ethanol). Locality no. 12: CUMZ-CM104 (4 shells). Locality no. 14: CUMZ-CM152 (2 specimens in ethanol; Fig. 3B). The snails were found to live on tree trunks and leaves.

Distribution. Cambodia and Laos (Inkhavilay et al. 2019).

Remarks. This species was originally described from “Elephant Mountains” [Preah Monivong Bokor National Park, Kampot Province]. Both empty shells and living snails were collected from Preah Monivong Bokor National Park showing similar characteristics with the original description and illustration.

Living snails are typical of cyclophorids with a blackish soft body. The shell surface is furnished with thick and regular periostracal hairs. There are three rows of periostracal hairs on the upper periphery and several rows of short periostracal hairs below the periphery. The periostracum usually disappears in old and worn specimens. The species has a conic shell, an aperture thickened (not expanded), and the thick calcareous, multi-spiral and plate-like operculum characteristic of *Lagocheilus*.

Family Pupinidae Pfeiffer, 1853***Pupina* Vignard, 1829*****Pupina crosseana* Morlet, 1883**

Figs 3C, 7C

Pupina crosseana Morlet, 1883: 108, 109, pl. 4, fig. 5. Type locality: Cambodge [Cambodia]. Fischer 1973a: 48.

Material examined. Locality no. 7: CUMZ-CM029 (1 shell). Locality no. 9: CUMZ-CM039 (10 shells). Locality no. 10: CUMZ-CM066 (1 shell), CUMZ-CM067 (57 specimens in ethanol; Fig. 3C). Locality no. 11: CUMZ-CM072 (10 shells; Fig. 7C). Locality no. 12: CUMZ-CM097 (4 shells). Locality no. 13: CUMZ-CM133 (1 specimen in ethanol). Locality no. 17: CUMZ-CM142 (1 specimen in ethanol). The snails were found to live on the ground among leaf litter.

Distribution. Cambodia (Fischer 1973a).

Remarks. This species was originally described from “Cambodge” [Cambodia]. The diagnostic characters of this porcelain shell are a pupoid shell with varying shell colour from brownish to whitish, having a large, ovate last whorl ca. two-thirds of shell height. The shell has a thickened parietal callus, with a small posterior plica that is located some distance from an angular corner of aperture, which possesses a wide posterior canal. The anterior canal is a narrowly transverse slit overhung by a square and thickened columella plica. The aperture is circular with a white, thickened and slightly expanded lip.

Subclass Heterobranchia**Family Veronicellidae Gray, 1840*****Valiguna* Grimpe & Hoffmann, 1925*****Valiguna siamensis* (Martens, 1867)**

Fig. 3D

Vaginulus siamensis Martens, 1867: 68, pl. 5, fig. 3. Type locality: Petshaburi [Petchaburi Province, Thailand].

Valiguna siamensis: Inkhavilay et al. 2019: 48, figs 19b, 55b.

Material examined. Locality no. 12: CUMZ-CM116 (8 specimens in ethanol; Fig. 3D). The slugs were found to live under leaf litter.

Distribution. Laos, Sri Lanka and Thailand (Inkhavilay et al. 2019).

Remarks. This species was recorded from several localities from this survey. They occur in anthropogenic habitats all over Laos and Thailand (Inkhavilay et al. 2019).

This species has an elongate elliptical and flattened body, the notum with light brownish colour and with a pale yellow median stripe.

***Valiguna* sp.**

Fig. 3E, F

Material examined. Locality no. 6: CUMZ-CM178 (1 specimen in ethanol; Fig. 3E, F). The slug was found to live under rotten logs.

Remarks. This slug specimen was collected under rotten logs in grassland mixed with pine forest of Kirirom National Park at ca. an altitude of 660 m. They have a long elliptical and dorsolaterally flattened body. The dorsal side (notum) is thickened, with dark colour and scattered with brownish spots, and without median stripe. The ventral side (hyponotum) is with much lighter, pale creamy colouration, with tiny greyish spots distributed across hyponotum, and a narrow foot sole located in the middle. The foot sole is as long as and slightly narrower than the hyponotum, with pale yellowish brown colour. This slug is different from *V. siamensis* in having a blackish notum without the median stripe.

Family Succineidae Beck, 1837

***Succinea* Draparnaud, 1801**

***Succinea tenuis* Morelet, 1865**

Figs 3G, 7D

Succinea tenuis Morelet, 1865: 225, 226. Type locality: Cochinchina [South Vietnam].

Breure et al. 2018: 450, figs 1129, 1130.

Succinea tenella Morelet, 1875: 244, pl. 12, fig. 5 [unjustified emendation].

Material examined. Locality no. 12: CUMZ-CM106 (2 shells), CUMZ-CM107 (2 specimens in ethanol; Figs 3G, 7D). The snails were found to live on tree trunks and leaves.

Distribution. Cambodia, Thailand and Vietnam (Schileyko 2011).

Remarks. We placed these Cambodian specimens under *S. tenuis* [= *S. tenella* Morelet, 1875] due to their appearance resembling the syntype that was recently figured in Breure et al. (2018: figs 1129, 1130). The diagnostic characters of this species are succiniform with thin and fragile shell, with ca. 3 whorls. The last whorl is very large, greatly expanded with approaching the shell height; the shell surface has strong irregular growth lines.

There is one species, *S. cochinchinensis* Crosse & Fischer, 1863 [= *S. cochinchinensis* Pfeiffer, 1865, junior homonym and junior synonym] reported from this area (Schileyko 2011). This nominal species was described from “Saigon”. However, the original description was very brief, and the type specimens have not been figured. Examination of types of *S. cochinchinensis* may reveal them to be conspecific with *S. tenuis*.

Family Vertiginidae Fitzinger, 1833***Hypselostoma* Benson, 1856*****Hypselostoma benetuitum* Vermeulen et al., 2019**

Fig. 7E, F

Hypselostoma benetuitum Vermeulen et al., 2019b: 32, 33, figs 64, 65. Type locality: Phnom Kampong Trach, Kampong Trach area, Kampot Province, Cambodia.

Material examined. Locality no. 11: CUMZ-CM061 (6 shells; Fig. 7E). Locality no. 17: CUMZ-CM081 (19 shells; Fig. 7F). The snails were found to live on limestone wall syntopically with *Georissa* spp.

Distribution. Kampong Trach area, Kampot Province, Cambodia (Vermeulen et al. 2019b).

Remarks. The specimens from the type locality (locality no. 11; Fig. 7E) agree well with the drawing by Vermeulen et al. (2019b). This species tends to have a much smaller shell size and be less abundant than the syntopic congener *H. cambodjense* Benthem Jutting, 1962.

The specimens from locality no. 17 (Fig. 7F) could be identified to this species by having a smaller size than another congener, *H. cambodjense*. However, they differ slightly from the typical form in having less distinct peripheral ridges on the last whorl, while the protoconch, shell sculpture and major lamellae are identical to the topotype. Therefore, we consider these specimens to come within intraspecific variation.

***Hypselostoma cambodjense* Benthem Jutting, 1962**

Figs 3H, 8A–C

Hypselostoma cambodjense Benthem Jutting, 1962: 3–5, fig. 1. Type locality: Phnom Can Long, à 6 km au Sud de Tuk Méas, Cambodge. Vermeulen et al., 2019b: 33.

Material examined. Locality no. 11: CUMZ-CM004 (77 shells; Fig. 8B). Locality no. 12: CUMZ-CM073 (63 shells). Locality no. 9: CUMZ-CM087 (122 shells; Figs 3H, 8A). Locality no. 17: CUMZ-CM138 (40 shells; Fig. 8C). The snails were found to live on limestone wall syntopically with *Georissa* spp.

Distribution. Kampot Province, Cambodia and Ha Tien Town area, Kien Giang Province, Vietnam (Vermeulen et al. 2019b).

Remarks. This species was originally described from limestone hills near “Tuk Méas”, probably in Banteay Meas area. The specimens collected from locality no. 9 are thus considered as topotypic specimens. These specimens agree well with the illustration in van Benthem Jutting (1962: fig. 1).

Hypselostoma cambodjense tends to be abundant and widely distributed in several karstic hills in southern Cambodia and Vietnam (see Vermeulen et al. 2019b). The

populations from the localities no. 11 (Fig. 8B) and 17 (Fig. 8C) differ from the toptypic specimen (Fig. 8A) by having an obtusely angular to slightly shouldered last whorl, with the presence of minor lamellae, while the protoconch, shell sculpture, and major lamellae (parietal, upper palatal, lower palatal and columellar) are identical. Therefore, we treat them as a morphological variant of the same species.

Family Achatinidae Swainson, 1840

Allopeas Baker, 1935

Allopeas gracile (Hutton, 1834)

Fig. 9A

Bulimus (?) *gracilis* (?) Hutton, 1834: 84, 85, 93. Type locality: Mirzapoor; Futtehpoor Sikra; between Agra and Neemuch [Uttar Pradesh and Madhya Pradesh States, India].

Allopeas gracilis [sic]: Inkhavilay et al. 2019: 50, fig. 21a–c.

Material examined. Locality no. 12: CUMZ-CM105 (1 shell; Fig. 9A). Locality no. 6: CUMZ-CM177 (5 specimens in ethanol). The snails were found to live on the ground among leaf litter.

Distribution. Pantropical and subtropical (Robinson et al. 2009).

Remarks. This is the first official record of the non-native *A. gracile* in Cambodia. This species could be found in both natural and transformed anthropogenic habitats. This widespread and pantropical species has been introduced into many countries, including in greenhouses in temperate regions, and occurs throughout Laos, Thailand and Vietnam (Schileyko 2011, Inkhavilay et al. 2019).

Lissachatina Bequaert, 1950

Lissachatina fulica (Bowdich, 1822)

Fig. 9B

Achatina fulica Bowdich, 1822: pl. 13, fig. 3. Type locality: unknown.

Lissachatina fulica: Inkhavilay et al. 2019: 49, fig. 20a.

Material examined. Locality no. 10: CUMZ-CM065 (1 shell; Fig. 9B). Locality no. 12: CUMZ-CM095 (4 shells). The snails were found to live on tree trunks and on the ground among leaf litter.

Distribution. Pantropical and subtropical (Fontanilla et al. 2014).

Remarks. The likely origin of this species is from East Africa (Bequaert 1950). Currently, it has been introduced to many tropical countries, including all over Indochina (Fontanilla et al. 2014, Inkhavilay et al. 2019). The previous record of this species in Cambodia also indicated that this species is an intermediate host of the rat lungworm *Angiostrongylus cantonensis* (Brumpt et al. 1968).

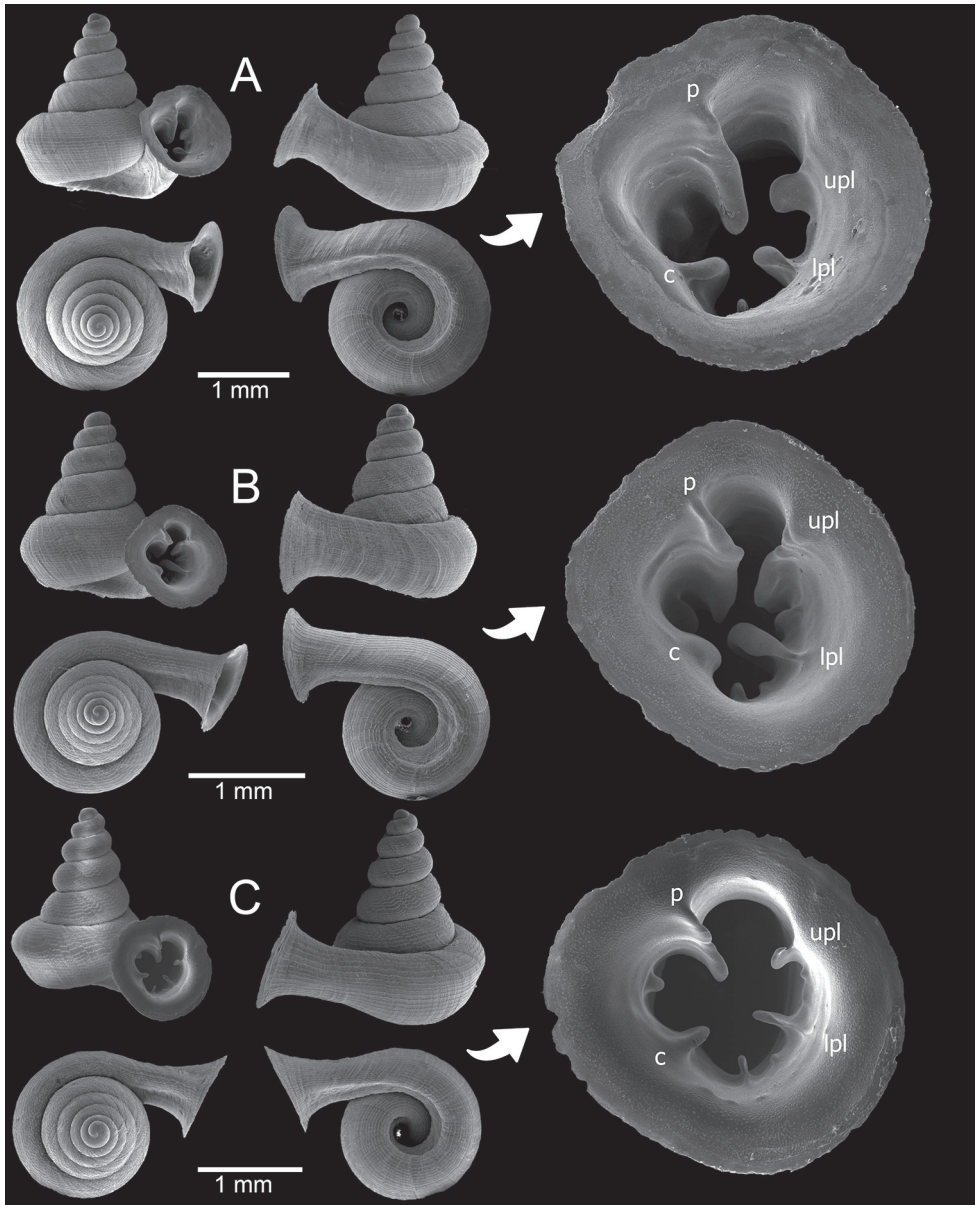


Figure 8. Morphological variation among *Hypselostoma cambodjense* Benthem Jutting, 1962 populations **A** from locality no. 9 (topotype) **B** from locality no. 11 and **C** from locality no. 17. The insets show the apertural dentition. Abbreviation: p, parietal lamella; upl, upper palatal lamella; lpl, lower palatal lamella; c, columellar lamella.

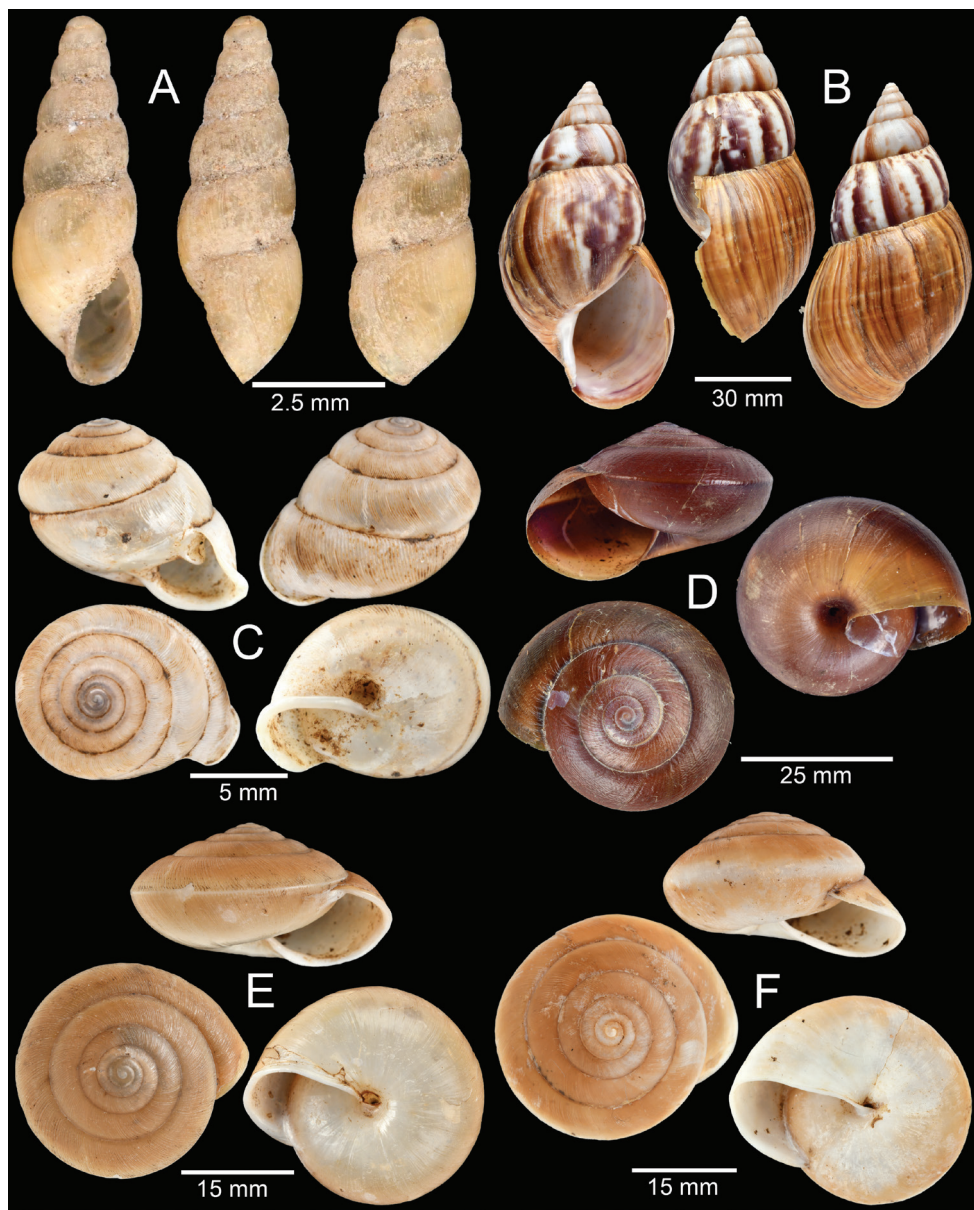


Figure 9. **A** *Allopeas gracile* (Hutton, 1834) **B** *Lissachatina fulica* (Bowdich, 1822) **C** *Haploptychius* sp. **D** *Dyakia* sp. and **E, F** *Quantula weinkauffiana* (Crosse & Fischer, 1863) with **E** angular last whorl and **F** rounded last whorl.

Family Streptaxidae Gray, 1860
***Haploptychius* Möllendorff, 1905**

***Haploptychius* sp.**

Figs 4A, 9C

Material examined. Locality no. 6: CUMZ-CM179 (1 specimen in ethanol). Locality no. 11: CUMZ-CM074 (12 shells; Fig. 9C), CUMZ-CM075 (1 shell), CUMZ-CM076 (14 specimens in ethanol; Fig. 4A). Locality no. 12: CUMZ-CM098 (8 shells), CUMZ-CM099 (1 shell), CUMZ-CM100 (9 specimens in ethanol). Locality no. 13: CUMZ-CM121 (21 shells), CUMZ-CM122 (1 specimen in ethanol). The snails were found to live on the ground among leaf litter in the limestone area.

Remarks. This species is similar to *H. michaui* (Crosse & Fischer, 1863), but the latter is more ovate and less oblique in shell shape. In addition, this species can be distinguished from *H. pellucens* (Pfeiffer, 1863), *H. porrectus* (Pfeiffer, 1863) and *H. perlissus* Vermeulen et al., 2019 by having strong and prominent radial ridges. For comparison, the latter three species have a smooth to nearly smooth shell surface, *H. pellucens* has an oblique-ovate shell shape, *H. porrectus* and *H. perlissus* have an oblique heliciform shell shape (see Inkhavilay et al. 2016, and Vermeulen et al. 2019b for further comparison).

Family Dyakiidae Gude & Woodward, 1921
***Dyakia* Godwin-Austen, 1891**

***Dyakia* sp.**

Fig. 9D

Material examined. Locality no. 15: CUMZ-CM155 (5 shells), CUMZ-CM156 (4 shells), CUMZ-CM157 (1 shell; Fig. 9D), CUMZ-CM158 (3 specimens in ethanol). The snails were found to live on tree trunks and leaves.

Remarks. The large sinistral helicoid shell discriminates this species from most other species known in this region. This species can be distinguished from *Bertia cambodjiensis* (Reeve, 1861) by having a brownish shell, with spirally undulated surfaces, while *B. cambodjiensis* has a smooth surface (see Sutcharit et al. 2019b for further comparison).

The specimens from the Popokvil Waterfall (locality no. 15) located on the plateau of Preah Monivong Bokor National Park may be young individuals, as their shell size is relatively small compared to those of other congeners recorded from peninsular Thailand. It differs from *D. salangana* (Martens, 1883) and *D. retrorsa* (Gould, 1843) by having a dark brown shell, with wide angle of peripheral keels. In contrast, *D. retrorsa* tends to have sharp peripheral keel, *D. salangana* has round periphery and usually with brownish peripheral band, and both species are pale brownish in shell colour (BEDO 2017).

Quantula* Baker, 1941**Quantula weinkauffiana* (Crosse & Fischer, 1863)**

Figs 4B, 9E, F

Helix weinkauffiana Crosse & Fischer, 1863: 350, 351. Type locality: Cochinchine [Southern Vietnam].

Quantula weinkauffiana: Inkhavilay et al. 2019: 71, figs 32b–d, 55h.

Material examined. Locality no. 1: CUMZ-CM002 (8 shells). Locality no. 2: CUMZ-CM006 (10 shells). Locality no. 5: CUMZ-CM011 (2 shells). Locality no. 7: CUMZ-CM013 (82 shells), CUMZ-CM014 (1 shell), CUMZ-CM015 (1 shell + 1 specimen in ethanol; Fig. 4B). Locality no. 9: CUMZ-CM034 (7 shells), CUMZ-CM035 (3 shells). Locality no. 10: CUMZ-CM052 (1 shell). Locality no. 12: CUMZ-CM093 (5 shells). Locality no. 13: CUMZ-CM120 (5 shells). Locality no. 17: CUMZ-CM135 (3 shells). Locality no. 18: CUMZ-CM143 (3 shells), CUMZ-CM144 (1 shell). Locality no. 16: CUMZ-CM166 (4 shells), CUMZ-CM177 (1 shell). Locality no. 6: CUMZ-CM174 (9 shells), CUMZ-CM175 (2 shells; Fig. 9E, F). The small juveniles were found on tree trunks and leaves, while the adults were found to live on the ground among leaf litter.

Distribution. Cambodia, Laos, Thailand and Vietnam (Schileyko 2011, Inkhavilay et al. 2019).

Remarks. This species was originally described from “Cochinchina”. The distinguishing characters are a depressed-conic to conic shell shape and brownish shell colour. The last whorl is round to angular, with upper shell surface sculptured with fine radial ridges, below the periphery the surface is usually smooth. The aperture is sub-circular, with lip thickened in adult specimens. However, this species tends to have a highly variable shell from depressed-conic to dome-shaped shell, and the last whorl rounded (Fig. 9F) to angular (Fig. 9E).

The living snail has reticulated skin, yellowish to pale orange body, usually with dark longitudinal anterior stripes. *Quantula weinkauffiana* is considered to be a common species in Cambodia, where they can be found in both natural and highly disturbed human-modified habitats, such as agricultural plantations. Although Brumpt et al. (1968) reported that *Q. striata* from Cambodia is an intermediate host of the rat lungworm *Angiostrongylus cantonensis*, the land snail species in that study was more likely *Q. weinkauffiana*.

Family Trochomorphidae Möllendorff, 1890***Trochomorpha* Albers, 1850*****Trochomorpha paviei* (Morlet, 1885)**

Figs 4C, 10A

Helix paviei Morlet, 1885[1884]: 386, 387, pl. 11, fig. 1, 1a. Type locality: dans les forêts, entre Kampot et Phnom-Penh, particulièrement près des rapides de Kam-

chay (rivière de Kampot), sur les bois pourris et les petite plantes [In forests, between Kampot and Phnom Penh, especially near the rapids Kamchay (Kampot River), on rotten wood and small plants].

Trochomorpha paviei: Inkhavilay et al. 2019: 72, figs 33a, b, 56a.

Material examined. Locality no. 14: CUMZ-CM153 (3 specimens in ethanol). Locality no. 15: CMZ-CM162 (2 shells), CUMZ-CM163 (14 specimens in ethanol; Figs 4C, 10A), CUMZ-CM164 (6 specimens in ethanol). The snails were found to live on tree trunks and on the ground among leaf litter.

Distribution. Cambodia, Laos and Vietnam (Schileyko 2011, Inkhavilay et al. 2019).

Remarks. This species was originally described from “Dans les forêts, entre Kampot et Phnom-Penh”. The unique characters are a depressed conic shell (shell width 12 mm) with a very strong and sharp peripheral keel, and a widely opened and deep umbilicus. The shell surface has thin and regular radial ridges, and very thin spiral ridges. Based on shell morphology, *T. paviei* closely resembles *T. saigonensis* (Crosse, 1867) that was described from “Poulo-Condor and Saigon, Cochinchine”. The latter species is slightly smaller (shell width 11 mm), having the last whorl with a wide angled peripheral keel and being slightly convex below the periphery. The type specimens of both species were recently figured in Inkhavilay et al. (2019: fig. 33a, c). However, we hesitate to lump them together, as additional information is necessary to further confirm their status.

Trochomorpha sp.

Fig. 10B

Material examined. Locality no. 10: CUMZ-CM057 (2 shells; Fig. 10B), CUMZ-CM058 (1 shell), CUMZ-CM059 (1 specimen in ethanol). Locality no. 13: CUMZ-CM134 (3 shells). The snail was found to live on a tree trunk.

Remarks. The specimens from Prasat Phnom Totong (locality no. 10) have a conic shell with a very strong and sharp peripheral keel, widely opened and deep umbilicus, and slightly convex below the periphery. The shell surface has irregular growth lines and very thin spiral ridges. These specimens tend to differ from *T. paviei* and *T. saigonensis* in having a larger shell (shell width 14 mm), an elevated domed spire, more whorls, and being nearly flat below the periphery. However, the identification is provisional, and further evidence from examination of genitalia or DNA will be necessary to elucidate their status.

Family Ariophantidae Godwin-Austen, 1883

Cryptozona Mörch, 1872

Cryptozona siamensis (Pfeiffer, 1856)

Fig. 4D

Helix siamensis Pfeiffer, 1856: 32. Type locality: Siam [Thailand].

Hemiplecta dichromatica Morlet, 1889: 124, 175, 176, pl. 6, fig. 2. Type locality: de Srakéo à Ang-Son (Siam) [Srakeo Province, Thailand].

Cryptozona siamensis: Inkhavilay et al. 2019: 75, 76, figs 35a, 56b.

Material examined. Locality no. 4: CUMZ-CM147 (1 specimen in ethanol; Fig. 4D). Locality no. 18: CUMZ-CM146 (2 shells). The snails were found to live on the ground among leaf litter.

Distribution. Cambodia, Laos, Malaysia, Singapore and Thailand (Tan et al. 2016, Inkhavilay et al. 2019).

Remarks. This widespread species has recently been recorded from Singapore and Peninsular Malaysia (Tan et al. 2016), Laos (Inkhavilay et al. 2019) and Yunnan, China (C. Sutcharit, pers. obs.). In Thailand, *C. siamensis* is found throughout the country and the allozyme analysis by Prasankok and Panha (2011) indicates a surprisingly high level of genetic homogeneity among populations. This suggests that *C. siamensis* probably occupies almost all habitat types through accidental introduction or horticultural trade activities, and this species is especially abundant in human-modified landscapes.

The historical record of this species from Cambodia was probably under the name “*Hemiplecta dichromatica* Morlet, 1889” which was subsequently considered to be conspecific with this species (Fischer and Dautzenberg 1904). In this survey, *C. siamensis* was found from a suburb of Krong Chhbar Mon (locality no. 4), in which its habitats are associated with human activities. In contrast, *Q. weinkauffiana* could be found commonly in both natural forest and anthropogenic habitats.

Hemiplecta Albers, 1850

Hemiplecta distincta (Pfeiffer, 1850)

Figs 4E, 10C

Helix distincta Pfeiffer, 1850: 69, 70. Type locality: insulis Moluccis [Molucca Islands].

Hemiplecta distincta: Inkhavilay et al. 2019: 76, figs 35b, c, 56c.

Material examined. Locality no. 7: CUMZ-CM021 (6 shells), CUMZ-CM022 (1 specimen in ethanol), CUMZ-CM023 (1 specimen in ethanol). Locality no. 11: CUMZ-CM069 (2 shells), CUMZ-CM070 (1 specimen in ethanol; Fig. 4E). Locality no. 12: CUMZ-CM115 (1 shell). Locality no. 3: CUMZ-CM123 (1 specimen in ethanol). Locality no. 17: CUMZ-CM136 (4 shells). Locality no. 18: CUMZ-CM145 (1 shell). Locality no. 14: CUMZ-CM149 (1 shell). Locality no. 16: CUMZ-CM171 (1 shell; Fig. 10C), CUMZ-CM172 (1 specimen in ethanol). Locality no. 6: CUMZ-CM180 (3 specimens in ethanol). The small juveniles were found on tree trunks and leaves, while the adults were found to live on the ground among leaf litter.

Distribution. Cambodia, Laos, Thailand and Vietnam (Schileyko 2011, Inkhavilay et al. 2019).

Remarks. This is one of the largest land snail species recorded from Indochina. *Hemiplecta distincta* has a wide distribution from Southern Vietnam, throughout

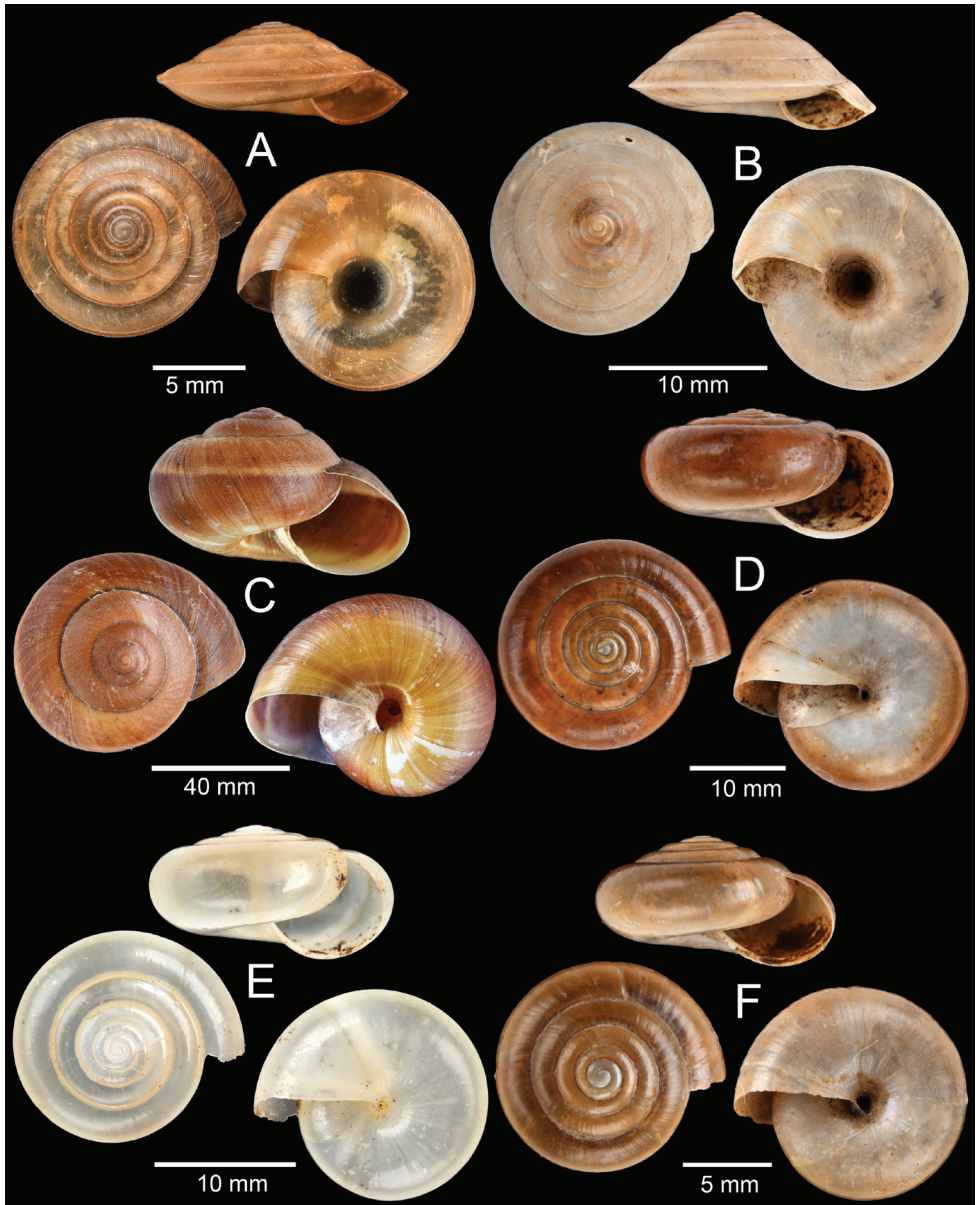


Figure 10. **A** *Trochomorpha paviei* (Morlet, 1885) **B** *Trochomorpha* sp. **C** *Hemiplecta distincta* (Pfeiffer, 1850) **D** *Sarika* sp. 1 **E** *Sarika* sp. 2 and **F** *Sarika* sp. 3.

Cambodia, northeastern Thailand, and throughout Laos (Schileyko 2011, Inkhavilay et al. 2019). The snails are widely used as local food and are gathered for personal consumption or sold in high quantities, especially in Northeastern Thailand and Laos (Panha 1987). This species is an intermediate host of the rat lungworm *Angiostrongylus cantonensis* in Cambodia (Brumpt et al. 1968).

Sarika* Godwin-Austen, 1907**Sarika* sp. 1**

Fig. 10D

Material examined. Locality no. 9: CUMZ-CM032 (12 shells), CUMZ-CM033 (3 shells). Locality no. 10: CUMZ-CM050 (24 shells), CUMZ-CM051 (1 shell; Fig. 10D). The empty shells were collected among leaf litter in the limestone area.

Remarks. The common ground dwelling snail genus *Sarika* is probably restricted to the Indochina region (Godwin-Austen 1907). Identifications at species level in *Sarika* based solely on shells cannot be achieved with confidence because of the limited distinguishing shell characters. Species level distinguishing characters in *Sarika* are based mainly on their reproductive anatomy.

However, this specimen can be discriminated from *S. bocourti* (Morelet, 1875) by having a reddish-brown shell with a wide whitish or creamy area surrounding the umbilicus. *Sarika bocourti*, which is described from “Battambang, Cambodje”, has a uniform brownish shell (see Breure et al. (2018: fig. 135) for the syntype).

***Sarika* sp. 2**

Fig. 10E

Material examined. Locality no. 12: CUMZ-CM089 (4 shells). Locality no. 13: CUMZ-CM117 (2 shells; Fig. 10E). The empty shells were collected among leaf litter in the limestone area.

Remarks. Recently, Vermeulen et al. (2019b) introduced a species *Macrochlamys psyche* Vermeulen et al., 2019 based on the shell alone. However, its generic placement remains uncertain since genitalia data is still lacking. Godwin-Austen (1907) and Pholyotha et al. (2018) stated that most of the species attributed to “*Macrochlamys*” in Southeast Asia belong to the genus *Sarika*.

This species is distinguished from the other known *Sarika* species in Cambodia by having a milky-coloured shell, flattened spire, and a relatively large shell (largest shell diameter 25 mm). These specimens differ from *M. psyche* in having a nearly flattened to slightly elevated spire, with a slightly shouldered last whorl and milky shell colour, while *M. psyche* has a slightly sunken spire, with a well-rounded last whorl and whitish shell colour (see Vermeulen et al. (2019b) for comparison).

***Sarika* sp. 3**

Fig. 10F

Material examined. Locality no. 11: CUMZ-CM088 (10 shells), CUMZ-CM092 (1 shell; Fig. 10F). The empty shells were collected among leaf litter in the limestone area.

Remarks. The specimens from Phnom Kbal Romeas (locality no. 12) have a small shell (diameter ca. 10 mm), which is depressed, slightly thick, translucent, shiny, and pale reddish-brown. The shell surface is smooth with obvious irregular growth lines. The shell has 5 to 6 whorls, with wide and shallow suture. The spire is convex, with an elevated apex. The last whorl has a well-rounded periphery, with an ovate-lunate aperture and a simple lip. An umbilicus is widely open and deep.

These specimens can be distinguished from *Macrochlamys psyche*, *Sarika* sp. 1 and sp. 2 by having a small size and slightly elevated spire. In contrast, *M. psyche* and *Sarika* sp. 1 have a large, whitish shell and a flatten to slightly shrunken spire, while *Sarika* sp. 2 has a larger, reddish-brown shell with whitish area surrounding the umbilicus. Live specimens are required so that the anatomical characters can be used to discriminate among the species.

Family Helicarionidae Bourguignat, 1877

Cambodiparmarion Kuznetsov & Kuzminykh, 1999

Cambodiparmarion doroshenkoi Kuznetsov & Kuzminykh, 1999

Figs 4F, 11A

Cambodiparmarion doroshenkoi Kuznetsov & Kuzminykh, 1999: 113–116, figs 1, 2.

Type locality: In tropical forest between Motel Lomherkay and Hotel Koh Pos, SW end of Kompong Som [= Sihanoukville], Kompong Som district, Kampot province, Cambodia.

Material examined. Locality no. 12: CUMZ-CM108 (4 shells). Locality no. 13: CUMZ-CM130 (2 shells), CUMZ-CM131 (1 specimen in ethanol; Fig. 4F). Locality no. 11: CUMZ-CM083 (1 shell; Fig. 11A), CUMZ-CM084 (9 shells). The semi-slug was found to live on tree trunks and leaves in the limestone area.

Distribution. Known only from the type locality (Kuznetsov and Kuzminykh 1999).

Remarks. This monotypic genus was recently described. It differs from the genus *Microparmarion* Simroth, 1893 in having an enlarged and long cylindrical gametolytic sac, while the latter has a short and globular gametolytic sac. When *C. doroshenkoi* was described, the authors did not mention the characters used to discriminate this species from *Parmarion martensi* Simroth, 1893. Here, we provide supplementary distinguishing characters as *C. doroshenkoi* has a solid, ear-shape shell with ca. 2 whorls, a blackish body and mantle, and a long flagellum, while *P. martensi* has a thin nail-shape shell with a trace of shell coiling, a greyish to blackish body and a short flagellum (Simroth 1893, Kuznetsov and Kuzminykh 1999).

Breure et al. (2018: figs 1196, 1197) illustrated the syntype of *Vitrina unguiculus* Morelet, 1865 described from “Cochinchina”. The syntypes are very similar in all characters to the shells of *C. doroshenkoi* examined herein. Further collections are needed to generate anatomical and molecular data to confirm whether they are conspecific or not.

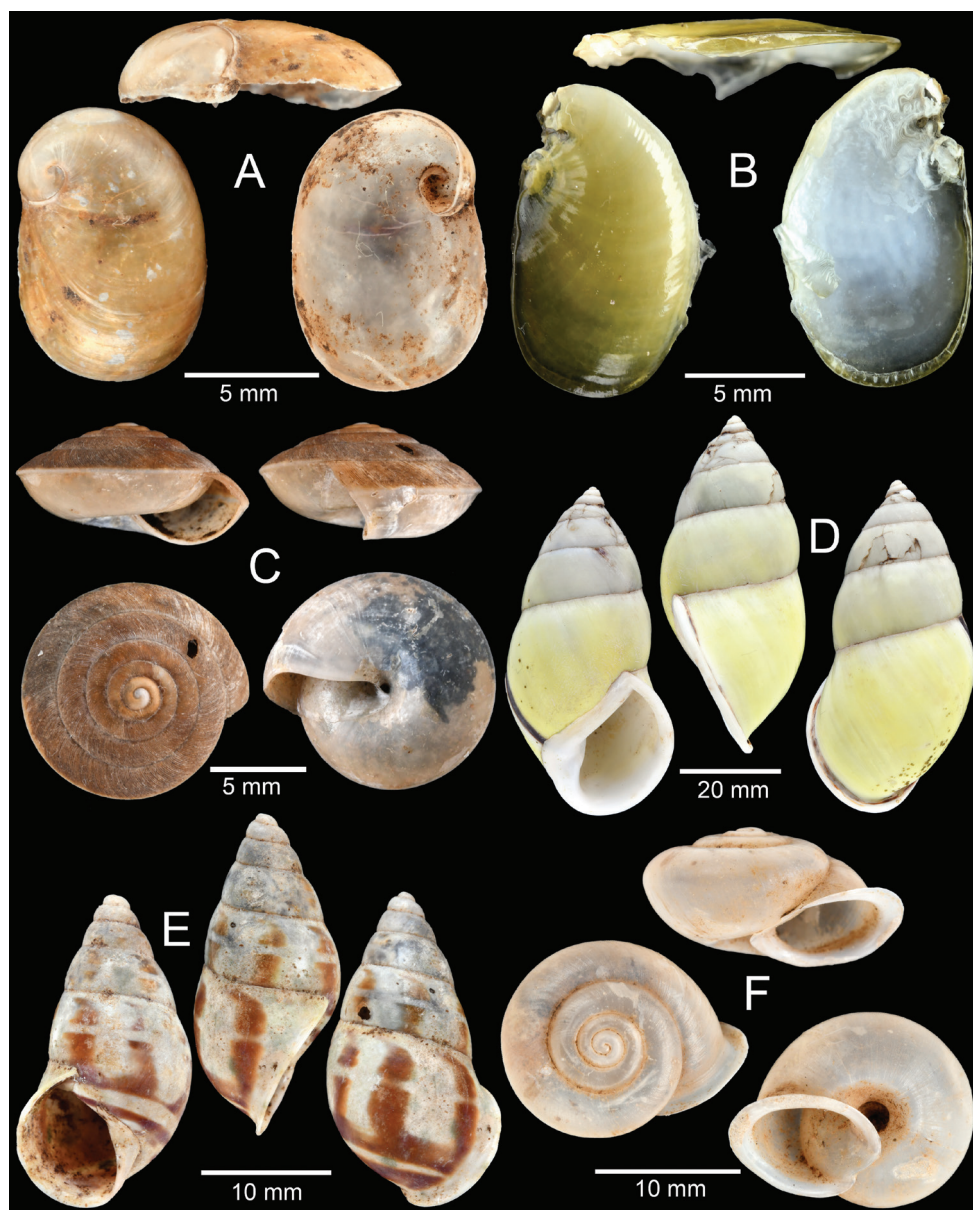


Figure 11. **A** *Cambodiparmarion doroshenkoi* Kuznetsov & Kuzminykh, 1999 **B** *Parmarion martensi* Simroth, 1893 **C** *Sesara* sp. **D** *Amphidromus leucoxanthus* (Martens, 1864) **E** *Amphidromus semitessellatus* (Morlet, 1885) and **F** *Trichochloritis norodomiana* (Morlet, 1883).

Parmarion* Fischer, 1855**Parmarion martensi* Simroth, 1893**

Figs 4G, 11B

Parmarion martensi Simroth, 1893: 107, 108, pl. 7, fig. 8, pl. 8, figs 20–22. Type locality: Cambodia [Cambodia]. Inkhavilay et al. 2019: 81, figs 19g, 57d.

Material examined. Locality no. 14: CUMZ-CM150 (1 shell), CUMZ-CM151 (6 specimens in ethanol; Figs 4G, 11B). Locality no. 15: CUMZ-CM165 (3 specimens in ethanol). The semi-slugs were found to live on tree trunks and leaves.

Distribution. Cambodia, Laos, Malaysia and Singapore (Maassen 2001, Inkhavilay et al. 2019).

Remarks. This semi-slug bears a small shell (plate or nail-like without a trace of shell coiling), in which the shell is usually entirely covered with movable mantle lobes. *Parmarion martensi* has also been reported as an introduced species to Samoa and Hawaii (Cowie et al. 2018).

Durgella* Blanford, 1863**Durgella russeola* (Morelet, 1865)**

Fig. 4H

Vitrina russeola Morelet, 1865: 225. Type locality: Cochinchina. Breure et al. 2018: 416, figs 980, 981.

Megaustenia russeola: Schileyko 2011: 32.

Material examined. Locality no. 7: CUMZ-CM030 (3 specimens in ethanol; Fig. 4H). The snails were found to live on tree trunks and leaves.

Distribution. Vietnam (Schileyko 2011).

Remarks. A syntype of *Durgella russeola* (Morelet, 1865) was figured in Breure et al. (2018: figs 980, 981); the type locality is “Cochinchina”. The shell of this species is globose, very thin (leather like or membranous) with a few calcareous elements, transparent, ovate conic. The shell has approximately 3 to 4 whorls, with an expanded last whorl, ovate aperture and closed umbilicus. Although there is no anatomical information at the moment, the distinct shell characteristics suggest that this species belongs to the semi-slug genus *Durgella*. Further additional anatomical examination is necessary since the shell morphology is insufficient for species identification.

Sesara* Albers, 1860**Sesara* sp.**

Fig. 11C

Material examined. Locality no. 7: CUMZ-CM031 (1 shell; Fig. 11C). The empty shell was collected among leaf litter in the limestone area.

Remarks. The single shell was collected from Phnom Bayang (locality no. 7). It is distinguished from *Sesara polita* Vermeulen et al., 2019 and *S. sesarella* Vermeulen et al., 2019, which were recently described from Kampot Province, Cambodia, in having strong and prominent radial ridges continuously covering the entire teleconch and last whorl, and without any apertural lamella. *Sesara polita* possesses a smooth shell surface usually with one small basal and one transverse palato-basal lamellae, while *S. sesarella* has strong radial ridges on the teleconch, with a smooth last whorl, and has one thick and transverse parietal, one small palato-basal lamella and one small palatal lamella (Vermeulen et al. 2019b).

Family Camaenidae Pilsbry, 1895***Amphidromus* Albers, 1850*****Amphidromus leucoxanthus* (Martens, 1864)**

Figs 5A, 11D

Bulimus leucoxanthus Martens, 1864: 526. Type locality: unknown.

Amphidromus (*Amphidromus*) *atricallosus leucoxanthus*: Sutcharit and Panha 2006: 20, 21, figs 3p, 4a–e, 10d–f, 12b, 14c, d, 15c.

Material examined. Locality no. 7: CUMZ-CM018 (2 shells; Fig. 11D), CUMZ-CM020 (2 specimens in ethanol; Fig. 5A). The snails were found to live on tree trunks and leaves.

Distribution. Eastern Thailand (Sutcharit and Panha 2006).

Remarks. This species has been formerly treated as a subspecies within *A. atricallosus* (Sutcharit and Panha 2006). However, this species differs from *A. atricallosus* by having an elongate conic shell with thick or thin and whitish parietal callus, while *A. atricallosus* usually has a more ovate shell, with thickened and black parietal callus. In addition, *A. leucoxanthus* tends to be distributed in the eastern part of Thailand and in Cambodia, while *A. atricallosus* occurs in eastern and southern Thailand along the Tenasserim ranges and in southern Myanmar. Moreover, molecular phylogenetic data suggested a distinct lineage between *A. leucoxanthus* and *A. atricallosus* (Sutcharit et al. 2007).

***Amphidromus semitessellatus* (Morlet, 1885)**

Fig. 11E

Bulimus (*Amphidromus*) *semitessellatus* Morlet, 1885[1884]: 387, 388, pl. 11, fig. 2, 2a.

Type locality: les montagnes qui bordent le grand fleuve au delà de Stung-Treng.

Les forêts et les montagnes de Kampot à Compong-Som [Mountains and forest in Stung Treng, Kampot and Sihanoukville Provinces, Cambodia].

Amphidromus (*Syndromus*) *semitessellatus*: Inkhavilay et al. 2017: 27, 28, fig. 10l, m.*Amphidromus semitessellatus*: Inkhavilay et al. 2019: 94.

Material examined. Locality no. 9: CUMZ-CM040 (2 shells). Locality no. 10: CUMZ-CM055 (1 shell). Locality no. 12: CUMZ-CM101 (2 shells; Fig. 11E). Locality no. 13: CUMZ-CM124 (2 shells). The empty shells were collected from the ground, and the living snails probably live on tree trunks and leaves.

Distribution. Cambodia, Laos, Thailand and probably in Vietnam (Schileyko 2011, Inkhavilay et al. 2017, 2019).

Remarks. This species was described based on specimens collected from the area of Kampong Som [Sihanoukville] and Kampot (Morlet 1885). Inkhavilay et al. (2017: fig. 10l) illustrated the lectotype of this species, which has a larger shell (height 35 mm) and the last whorl has only a blackish subsutural band (without any other bands on the last whorl) compared with the single worn shell that we collected from limestone near Kampot (height 23 mm), with brownish supra-peripheral and sub-peripheral bands. Thus, we provisionally identified these specimens as *A. semitessellatus* due to the similarity of both brown supra-peripheral and sub-peripheral bands on the penultimate whorls and the geographical proximity. The subgenus *Syndromus* typically has a small shell which exhibits high variation on shell size, colour, and pattern (see Inkhavilay et al. 2017).

Trichochloritis* Pilsbry, 1891**Trichochloritis norodomiana* (Morlet, 1883)**

Figs 5B, 11F

Helix norodomiana Morlet, 1883: 106, 107, pl. 4, fig. 3, 3a, b. Type locality: Khamchay [Cambodia].*Chloritis norodomiana*: Inkhavilay et al. 2019: 102, 103, fig. 52c.

Material examined. Locality no. 7: CUMZ-CM024 (2 shells). Locality no. 9: CUMZ-CM041 (35 shells). Locality no. 10: CUMZ-CM056 (1 shell). Locality no. 11: CUMZ-CM077 (4 shells; Fig. 11F), CUMZ-CM078 (1 shell). Locality no. 12: CUMZ-CM103 (1 shell). Locality no. 13: CUMZ-CM125 (4 shells), CUMZ-CM126 (1 specimen in ethanol). Locality no. 16: CUMZ-CM173 (3 specimens in ethanol; Fig. 5B). The snails were found to live on tree trunks and leaves.

Distribution. Cambodia, Thailand, and Vietnam (Schileyko 2011). Schileyko (2011) reported this species from “Soutem Mt. near Xieng-Moi” as from Eastern Laos. However, “Xieng-Moi” currently refers to Chiang Mai Province in Northern Thailand.

Remarks. This species was described from “Kamchay” which probably refers to Kamchay Mear, Prey Veng Province in southeastern Cambodia. The distinguishing characters of this species include a small to medium discoidal shell, periostracum thickened with short fibrous hair covering the entire shell. The spire is flat to somewhat curved with an impressed suture. The last whorl descends approaching the aperture. The peristome is circular and oblique, with narrow and thin parietal callus. The aperture opens sub-ventrally, with an expanded and whitish lip.

***Ganesella* Blanford, 1863**

***Ganesella perakensis* (Crosse, 1879)**

Figs 5C, 12A

Helix (Geotrochus) perakensis Crosse, 1879: 199, 200, pl. 8, fig. 4. Type locality: Perak [Perak State, Malaysia].

Ganesella perakensis: Richardson 1985: 130. Sutcharit et al. 2019a: fig. 4d.

Material examined. Locality no. 15: CUMZ-CM159 (3 shells; Fig. 12A), CUMZ-CM160 (2 shells), CUMZ-CM161 (3 specimens in ethanol; Fig. 5C). The snails were found to live on tree trunks and leaves.

Distribution. Peninsula Malaysia (Sutcharit et al. 2019a).

Remarks. This species was originally described from Perak, Peninsula Malaysia, and a syntype was recently figured in Sutcharit et al. (2019a: fig. 4d). Characteristics of this species are its small shell size and trochoid shape. The whorls are slightly convex, with wide and shallow suture. The shell surface exhibits thin growth lines and thin corneous periostracum. The last whorl is with well-developed peripheral keel and blunt at lower periphery. The shell colour is pale yellow to brownish, with dark brown spiral bands on peripheral keel. The apertural lip is expanded, whitish, and angled.

Ganesella perakensis belongs to the *G. acris* (Benson, 1859) species complex which is composed of 11 nominal species and widely distributed from Western Ghats of India to Indochina and the Greater Sunda Islands (see Richardson 1985: 129, 130). However, *G. perakensis* differs from all species known in Indochina. It differs from *G. subperakensis* (Pilsbry, 1891) from “Tonquin” and *G. vatheleti* (Bavay & Dautzenberg, 1899) from “Van Bu, Tonkin” by having a strong peripheral keel. For comparison, *G. subperakensis* is convex below periphery, with less strong peripheral keel and without brownish spiral band (Pilsbry 1891), while *G. vatheleti* exhibits a round last whorl and is more convex at base (Bavay and Dautzenberg 1899).

This species is very similar to *G. lantenoisi* (Dautzenberg & Fischer, 1906), which was described from Ha-Giang (Northern Vietnam) and Siam [Thailand]. The descrip-

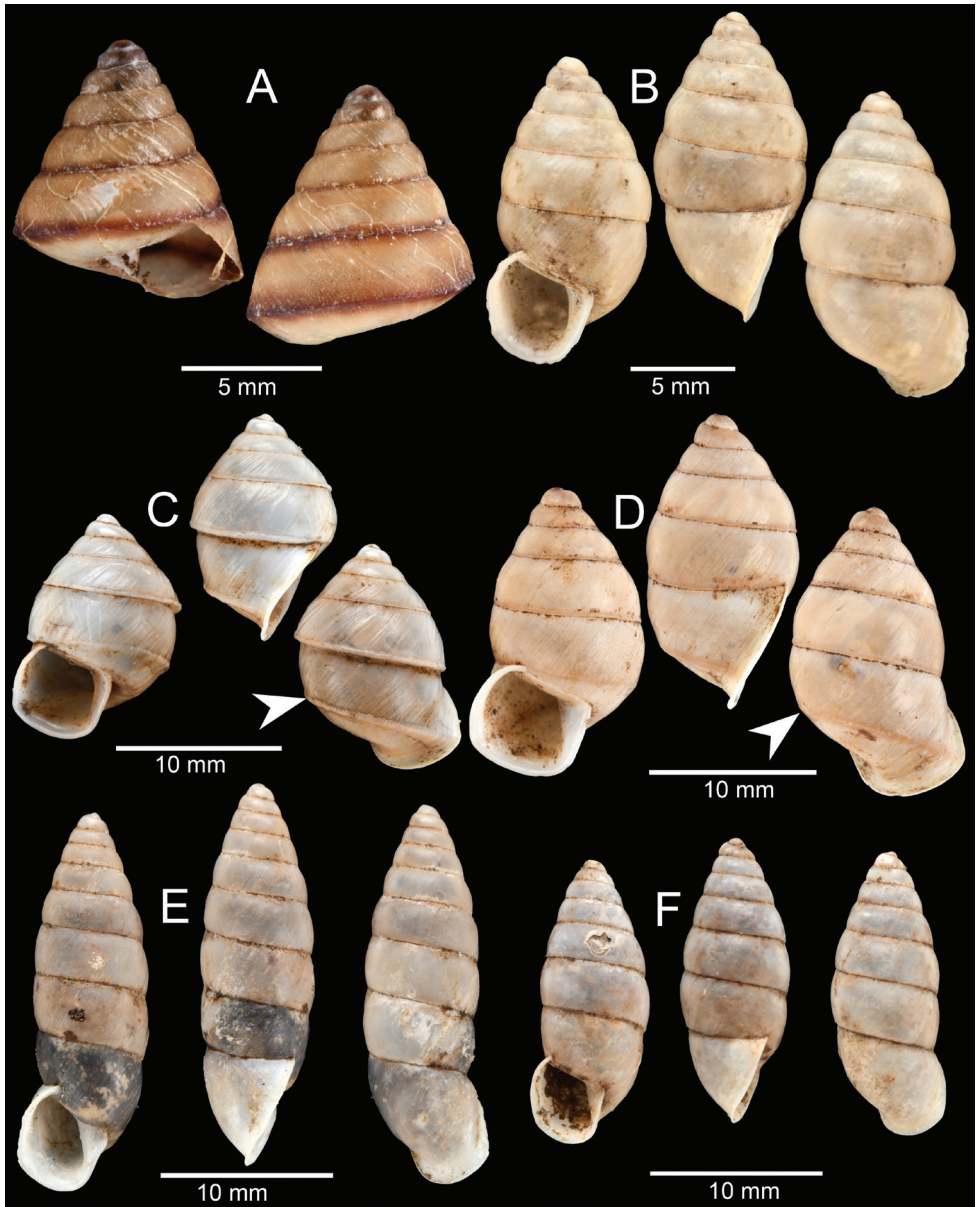


Figure 12. **A** *Ganesella perakensis* (Crosse, 1879) **B** *Ancयोconcha siamensis obesula* (Ancey, 1888) comb. nov. **C, D** *Ancयोconcha rhombostoma* (Pfeiffer, 1861). A white arrowhead indicates strong peripheral keel on the last whorl, the distinguished character of this species and **E, F** *Ancयोconcha chauldoensis* (Rochebrune, 1881) comb. nov.

tion itself was based mainly on the Ha-Giang specimen (Dautzenberg and Fischer 1906: pl. 9, fig. 10) while the Siamese specimen (Dautzenberg and Fischer 1906: pl. 9, fig. 11) is more similar to *G. perakensis*. Thus, the type series of this species seems to comprise

of two separate species, one from northern Vietnam and one from Thailand. *Ganesella perakensis* differs from *G. lantenoisi* (specimen from Ha-Giang) in having a smaller shell (shell height up to 13 mm), shallow suture with 6 to 7 convex whorls, while *G. lantenoisi* performs an elongate trochoid, larger shell (shell height up to 18 mm), suture flattened and smooth 9 to 10 whorls. However, further investigations with both genitalia and DNA analysis will be necessary to elucidate the exact relationship between them.

***Anceyoconcha* S. Tumpeesuwan & C. Tumpeesuwan, 2020**

Ganesella (*Giardia*) Ancey, 1907: 195, 203 (Mollusca: Eupulmonata: Camaenidae).

Preoccupied by Künstler, 1882: (Metamonada: Diplomonadida: Hexamitidae).

Pseudobuliminus (*Giardia*): Zilch 1960: 639.

Pseudobuliminus (*Girardius*) Richardson, 1983: 94. [incorrect subsequent spelling]

Giardia: Schileyko 2003: 1519, fig. 1930. Wood and Gallichan 2008: 48.

Anceyoconcha Tumpeesuwan & Tumpeesuwan in Nahok et al., 2020: 81. New replacement name.

Remarks. The distinguished shell character of this genus is sinistral, elongate cylindrical to more or less conical, with 6–10 convex whorls. The last whorl is rounded (not keeled), with the aperture ovate to slightly trapezoid and the apertural lip expanded. The columella is vertical, with the umbilicus narrowly opened.

Ancey (1907) established *Giardia* as the subgenus of *Ganesella* Blanford, 1863 to include two Indochinese sinistral species: *Bulimus siamensis* Redfield, 1853 and *Bulimus rhombostomus* Pfeiffer, 1861. Subsequently, this nominal name was used as a subgeneric level of *Buliminopsis* Heude, 1890 (family Fruticicolidae) by Thiele (1931: 693). Zilch (1960: 639) transferred this nominal name to the Bradybaenidae as the subgenus of *Pseudobuliminus* Gredler, 1886, and also designated *Bulimus siamensis* Redfield, 1853 as the type species. Zilch's classification was subsequently accepted and used by later authors (Richardson 1983, Vaught 1989). Recently, *Giardia* was treated as a valid genus under the Camaenidae (Schileyko 2003, 2011, Inkhavilay et al. 2019). However, the name *Giardia* Ancey, 1907 is a junior homonym being preoccupied by *Giardia* Künstler, 1882, a genus of anaerobic flagellated protozoan (Phylum Metamonada).

While cataloguing the land snail family Bradybaenidae, Richardson (1983) erroneously introduced the name “*Girardius*”, accompanied by diagnostic characters and attributed *Bulimus siamensis* Redfield, 1853 as the type species. However, this name is considered incorrect subsequent spelling (Schileyko 2003) and thus is not available (ICZN 1999: Art. 33.3). Nahok et al. (2020) thus proposed *Anceyoconcha* S. Tumpeesuwan & C. Tumpeesuwan, 2020 as a new name to replace *Giardia* Ancey, 1907, and included two species, *A. siamensis* and *A. rhombostoma*.

Anceyoconcha comprises around 15 nominal species and/or subspecies but there is an urgent need to clarify the boundary of this genus. Species and sub-

species included in the genus as defined herein are: *A. chauldoensis* (Rochebrune, 1881) comb. nov., *A. maestratii* (Thach, 2017) comb. nov., *A. mantongensis* (Kobelt, 1899) comb. nov., *A. obesa* (Thach & Huber, 2018) comb. nov., *A. ovoideus* (Thach & Huber, 2018) comb. nov., *A. pharangensis* (Dautzenberg & H. Fischer, 1905) comb. nov., *A. rhombostoma pupoidea* (Dautzenberg & Fischer, 1905) comb. nov., *A. rhombostoma rhombostoma*, *A. siamensis maxima* (Ancey, 1888) comb. nov., *A. siamensis nobilis* (Ancey, 1888) comb. nov., *A. siamensis obesula* (Ancey, 1888) comb. nov., *A. siamensis pervariabilis* (Dohrn, 1863) comb. nov., *A. siamensis siamensis*, *A. siamensis zonifera* (Ancey, 1888) comb. nov. and *A. vignei* (Rochebrune, 1882) comb. nov.

The distribution of *Anceyoconcha* is probably within the Indochinese region of Cambodia, Laos, Thailand, and Vietnam (Schileyko 2011, Thach 2017, 2018, Inkhavilay et al. 2019, Nahok et al. 2020).

***Anceyoconcha rhombostoma* (Pfeiffer, 1861)**

Figs 5D, E, 12C, D

Bulimus rhombostomus Pfeiffer, 1861: 194, 195. Type locality: Camboja [Cambodia].

Ganesella rhombostoma: Sutcharit et al. 2019a: 61–63, figs 1c, 3c–i, 5e–g, 7d–f.

Anceyoconcha rhombostoma: Nahok et al. 2020: 82–84, figs 2b, 3c, d, 4b, 6, 7b.

Material examined. Locality no. 9: CUMZ-CM047 (66 shells), CUMZ-CM048 (5 shells; Fig. 12C), CUMZ-CM049 (9 specimens in ethanol; Fig. 5D). Locality no. 10: CUMZ-CM060 (4 shells). Locality no. 11: CUMZ-CM085 (8 shells; Fig. 12D). Locality no. 12: CUMZ-CM113 (5 shells). Locality no. 13: CUMZ-CM132 (3 shells). Locality no. 17: CUMZ-CM139 (5 shells), CUMZ-CM140 (2 specimens in ethanol; Fig. 5E). The snails were found to live on tree trunks and leaves.

Distribution. Cambodia, Thailand and Vietnam (Sutcharit et al. 2019a).

Remarks. This species was originally described from Cambodia based on the Mouhot collection and was recently revised by Sutcharit et al. (2019a) and Nahok et al. (2020) based on Thai and Cambodian specimens. These recent specimens were collected from Kampot area, southern Cambodia and tend to be variable in size and shape compared to the type specimens (see Sutcharit et al. (2019a: fig. 3c, d) for the lectotype and paralectotype, respectively). They have smaller shell size and an ovate trochoid shell, with a large last whorl which is well-rounded and keeled on the periphery for nearly the entire last whorl (Fig. 12C, D indicated by an arrowhead). The aperture shape is trapezoid.

There is one subspecies “*Buliminus rhombostomus* var. *pupoidea* Dautzenberg & Fischer, 1905” described from “Cochinchine: Hong-Chon” [probably in the area of south Vietnam and Cambodia]. Unfortunately, the original description was brief, without measurements and illustrations, and the type specimen could not be located. Therefore, we could not assign the southern Cambodian specimens with certainty to this subspecific entity.

***Anceyoconcha siamensis obesula* (Ancey, 1888)**

Fig. 12B

Buliminus siamensis var. *obesula* Ancey, 1888: 352. Type locality: Saigon, dans le jardin du gouverneur. Wood and Gallichan 2008: 71, pl. 6, figs 6, vi.

Material examined. Locality no. 7: CUMZ-CM027 (14 shells), CUMZ-CM028 (3 shells; Fig. 12B). The empty shells were collected from the ground among leaf litter.

Distribution. Known only from the type locality (Wood and Gallichan 2008).

Remarks. This nominal subspecies was described from “Saigon” (see Wood and Gallichan (2008: pl. 6, fig. 6) for syntype). This species has a sinistral, ovate conic shell, having 6 to 7 whorls. The whorl is convex, having a wide and impressed suture. The shell surface is nearly smooth, with thin and brownish periostracum. The last whorl has a smaller diameter than penultimate whorl, well-rounded with weak keel near aperture. The shell colour is light brownish (becomes whitish when worn) and translucent. The aperture is subovate, with expanded and whitish lip, and thin parietal callus or thickened and whitish. The columella is straight and dilated, with a rimate umbilicus.

Anceyoconcha siamensis obesula differs from the nominotypical subspecies in having a much smaller shell size (shell height ranged from 15 to 20 mm), ovate shell and lower number of whorls. For comparison, *A. siamensis siamensis* (see Inkhavilay et al. 2019: fig. 53d, e) has a larger and elongate conic shell (shell height ranged from 20 to 25 mm), and with a weak keel near the aperture.

***Anceyoconcha chauldoensis* (Rochebrune, 1881)**

Figs 5F, 12E, F

Petraeus chauldoensis Rochebrune, 1881a: 70. Type locality: Montagnes de Chauldoe Cambodge [Chau Doc, An Giang Province, Vietnam].

Ena chauldocensis [sic]: Fischer 1973b: 90.

Material examined. Locality no. 1: CUMZ-CM003 (20 shells; Fig. 12E, F), CUMZ-CM005 (1 specimen in ethanol; Fig. 5F). Locality no. 2: CUMZ-CM007 (9 shells). Locality no. 3: CUMZ-CM010 (1 specimen in ethanol). The snails were found to live on tree trunks and leaves.

Distribution. Cambodia (Fischer 1973b).

Remarks. This species was originally described from “Montagnes de Chauldoe Cambodge” [Chau Doc, An Giang Province, Vietnam] probably in the area bordering Cambodia and Vietnam. The original description of this species was brief and without illustration. This species has a sinistral elongate conic to slightly ovate conic shell, with 7 to 9 whorls, which increase regularly; cylindrical, having convex whorl and wide and impressed suture. The shell surface possesses fine growth lines, and the periostracum is thin and brownish. The last whorl is well rounded and without keel near aperture and has a similar diameter to the penultimate whorl. The shell colour is light brownish and

translucent (becoming whitish when worn). The aperture is semi-ovate, with expanded and whitish lip and thin or thickened with whitish parietal callus. The columella is straight and dilated, with a rimate umbilicus.

Based on the original description, *A. chauldoensis* can be distinguished from *A. siamensis obesula* in having an elongate cylindrical shell and higher number of whorls, while the latter species has an ovate conic shell and a smaller number of whorls.

Discussion and conclusions

Cambodia has received the least attention from malacologists for inventorying the land snail fauna, compared to other adjacent countries within the Indo-Chinese region, e.g. Thailand (Hemmen and Hemmen 2001, BEDO 2017), Laos (Inkhavilay et al. 2019) and Vietnam (Schileyko 2011). The number of species recorded in this list is relatively low, compared to that of 231 species in Laos (Inkhavilay et al. 2019), 974 species in Thailand (BEDO 2017) and 477 species (only ‘pulmonates’) in Vietnam (Schileyko 2011). It is clear that this current list represents only a small fraction of the total land snail diversity in Cambodia. Our survey did not retrieve other land snail groups which are diverse and abundant in both Thailand and Vietnam, e.g. families Alycaeidae, Clausiliidae, and Plectopylidae. It is possible that the geography of the area without high mountains and other structured habitat types result in comparatively fewer species. In comparison, most of the species Vermeulen et al. (2019a, b) reported from Southern Cambodia are small (width less than 5 mm), with the largest species being *Sesara polita* that does not exceed 12 mm in width. However, most land snails collected in our study are large (more than 10 mm) and cover most taxonomic groups, with the exception of the families Assimineidae and Diplommatinidae, both of which have been reported by Vermeulen et al. (2019a, b). The difference in taxonomic composition between Vermeulen’s and our collection probably reflect different sampling methods. More thorough investigations combining several sampling methods may uncover more land snail diversity in this area.

Acknowledgements

We thank the members of Animal Systematics Research Unit of Chulalongkorn University and Animal Systematics and Molecular Ecology Laboratory of Mahidol University for their kind help during field trips in Cambodia. Special thanks go to Inland Fisheries Research and Development Institute (IFReDI), Fisheries Administration for the preparation of permission documents and data collection in Cambodia. The authors are also indebted to J. Ablett, F. Naggs and H. Taylor (NHM, London), P. Bouchet, V. Héros, D. Brabant and M. Caballer (project E-RECOLNAT: ANR-11-INBS-0004, MNHN, Paris) allowing the authors to examine the material housed in the type collections, the type material database and photographs. This project was mainly funded through grants received from the TRF Strategic Basic Research DBG

6080011 (2017–2019), Thailand Research Fund (TRF-DPG628001) and Center of Excellence on Biodiversity BDC-PG2-160012, and the Lee Kong Chian Natural History Museum. We also express our gratitude for the comments from F. Naggs and B. Páll-Gergely that have greatly improved the manuscript.

References

- Ancey C-F (1888) Nouvelles contributions malacologiques. VIII. Mollusques nouveaux de l'extrême-Orient. *Bulletins de la Société Malacologique de France* 5: 345–357.
- Ancey C-F (1907) Observations sur les Mollusques Gastéropodes sénestres de l'époque actuelle. *Bulletin Scientifique de la France et de la Belgique* 40[1906]: 187–206.
- Ascher JS, Heang P, Kheam S, Ly K, Lorn S, Chui SX, de Greef S, Chartier G, Phauk S (2016) A report on the bees (Hymenoptera: Apoidea: Anthophila) of Cambodia. *Cambodian Journal of Natural History* 2016: 23–39.
- AVMA (2013) AVMA guidelines for the euthanasia of animals. <https://www.avma.org/KB/Policies/Documents/euthanasia.pdf> [Accessed on 23 January 2017]
- Bain RH, Hurley MM (2011) A biogeographic synthesis of the amphibians and reptiles of Indochina. *Bulletin of the American Museum of Natural History* 2011: 1–138. <https://doi.org/10.1206/360.1>
- Bavay A, Dautzenberg P (1899) Description de coquilles nouvelles de l'Indo-Chine. *Journal de Conchyliologie* 42: 28–55, 275–296.
- BEDO (2017) Land Snails: Checklist of Molluscan Biodiversity in Thailand. BEDO, Bangkok, 300 pp. [in Thai]
- Bentham Jutting WSS van (1962) Coquilles terrestres nouvelles de quelques collines calcaires du Cambodge et du Sud Vietnam. *Journal de Conchyliologie* 102: 3–15.
- Bequaert JC (1950) Studies in the Achatinidae, a group of African land snails. *Bulletin of the Museum of Comparative Zoology, Harvard* 105: 1–216.
- Bowdich TE (1822) *Elements of Conchology: Including the Fossil Genera and the Animals*. J. Smith, and sold by Treuttel and Würtz, London, 75 pp. <https://doi.org/10.5962/bhl.title.12480>
- Breure ASH, Audibert C, Ablett JD (2018) Pierre Marie Arthur Morelet (1809–1892) and his contributions to malacology. *Nederlandse Malacologische Vereniging, Leiden*, 544 pp.
- Brumpt V, Audebaud G, Klein JM, Jolly M, Mazaud R, Goube P (1968) Incidence D'*Angiostrongylus cantonensis* (Chen) au Cambodge. *Bulletin de la Société de Pathologie exotique* 61: 444–462.
- Cowie RH, Hayes KA, Kim JR, Bustamente KM, Yeung NW (2018) *Parmarion martensi* Simroth, 1893 (Gastropoda: Ariophantidae), an intermediate host of *Angiostrongylus cantonensis* (rat lungworm), on Maui. *Bishop Museum Occasional Papers* 123: 7–10.
- Crosse H (1879) Mollusques nouveaux de Perak (Indo-Chine). *Journal de Conchyliologie* 27: 198–208.
- Crosse H, Fischer P (1863) Note sur la faune malacologique de Cochinchine, comprenant la description des espèces nouvelles ou peu connues. *Journal de Conchyliologie* 11: 343–379.

- Crosse H, Fischer P (1876) Mollusques Fluviatiles, recueillis au Cambodge, par la Mission scientifique française de 1873. *Journal de Conchyliologie* 24: 313–342.
- Crump M, Scott N (1994) Visual encounter surveys. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS (Eds) *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, 84–92.
- Dautzenberg P, Fischer H (1906) Liste des mollusques récoltés par M.H. Mansuy en Indo-Chine et au Yunnan et description d'espèces nouvelles. *Journal de Conchyliologie* 54: 343–471.
- Davis KE, Yu K, Rulli MC, Pichdara L, D'Odorico P (2015) Accelerated deforestation driven by large-scale land acquisitions in Cambodia. *Nature Geoscience* 8: 772–775. <https://doi.org/10.1038/ngeo2540>
- Do DS, Do VN (2019) Family Cyclophoridae in Vietnam (Gastropoda: Cyclophoroidea): the genus *Cyclophorus* Montfort, 1810. *Ruthenica* 29: 1–53.
- Do DS, Bui TC, Do VN (2020) The land snail genus *Opisthoporus* Benson in L. Pfeiffer, 1851 (Gastropoda: Caenogastropoda: Cyclophoridae) from Vietnam, with description of a new species. *Raffles Bulletin of Zoology* 68: 103–111.
- Duncan FM (1937) On the dates of publication of the Society's 'Proceedings' 1859–1926, with an appendix containing the dates of publication 1830–1858, compiled by F.H. Waterhouse; also of the 'Transactions' 1833–1869 by Henry Peavot, originally published in P.Z.S. 1893, 1913. *Proceedings of the Zoological Society of London, Series A* 107: 71–84. <https://doi.org/10.1111/j.1469-7998.1937.tb08500.x>
- Egorov RV (2009) *Treasure of Russian Shells; Supplement 3, A review of the genera of the recent terrestrial pectinibranch molluscs (synopsis mainly based on published data); Part II, Littoriniformes: Hainesiidae, Aciculidae, Cyclophoridae, Craspedopomatidae*. Colus-Doverie, R. Egorov, Moscow, 57 pp.
- Fischer-Piette E (1937) Dates de publication du "Journal de Conchyliologie" de 1861–1900. *Journal de Conchyliologie* 35: 88–92.
- Fischer H, Dautzenberg P (1904) Catalogue des mollusques terrestres et fluviatiles de l'Indo-Chine orientale cites jusqu'à ce jour. In: Mission Pavie, *Etudes diverses* 3: 390–450.
- Fischer PH (1973a) Les mollusques testaces du Cambodge. Premier partie: Introduction et Gastéropodes Prosobranches. *Journal de Conchyliologie* 90: 40–64.
- Fischer PH (1973b) Les mollusques testaces du Cambodge. Seconde partie: Gastéropodes Pulmonés, bivalves et bibliographie. *Journal de Conchyliologie* 90: 89–113.
- Fischer PH (1973c) Liste des mollusques testacés du Cambodge. *Cahiers du Pacifique* 17: 71–93.
- Fontanilla IKC, Sta. Maria IMP, Garcia JRM, Ghatte H, Naggs F, Wade CM (2014) Restricted genetic variation in populations of *Achatina (Lissachatina) fulica* outside of East Africa and the Indian Ocean Islands points to the Indian Ocean Islands as the earliest known common source. *PLoS ONE* 9: e105151. <https://doi.org/10.1371/journal.pone.0105151>
- Foon JK, Clements GR, Liew T-S (2017) Diversity and biogeography of land snails (Mollusca, Gastropoda) in the limestone hills of Perak, Peninsular Malaysia. *ZooKeys* 682: 1–94. <https://doi.org/10.3897/zookeys.682.12999>
- Freitag H, Doeurk B, Chhorn S, Khin C, Sin S, Ehlers S, Voges J, Garces J, Phauk S (2018) Aquatic Polyphaga (Insecta: Coleoptera) from Kampong Speu Province, Cambodia. *Cambodian Journal of Natural History* 2018: 90–100.

- Geissler P, Hartmann T, Ihlow F, Neang T, Seng R, Wagner P, Böhme W (2019) Herpetofauna of the Phnom Kulen National Park, northern Cambodia – An annotated checklist. *Cambodian Journal of Natural History* 2019: 40–63.
- Geissler P, Hartmann T, Ihlow F, Rödder D, Poyarkov Jr NA, Nguyen TQ, Ziegler T, Böhme W (2015) The Lower Mekong: an insurmountable barrier to amphibians in southern Indochina? *Biological Journal of the Linnean Society* 114: 905–914. <https://doi.org/10.1111/bij.12444>
- Godwin-Austen HH (1907) Land and Freshwater Mollusca of India, Including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula, Ceylon, and other Islands of the Indian Ocean. In: Taylor and Francis, Volume 2 (1898–1907): 47–238, pls. 70–117, London.
- Godwin-Austen HH, Nevill G (1879) Description of shells from Perak and the Nicobar Islands. *Proceeding of the Zoological Society of London* 1879: 734–740. <https://doi.org/10.1111/j.1096-3642.1879.tb02710.x>
- Grismer LL, Neang T, Chav T, Grismer JL (2008) Checklist of the amphibians and reptiles of the Cardamom region of southwestern Cambodia. *Cambodian Journal of Natural History* 2008: 12–28.
- Gupta A (2005) Chapter 3. Landforms of Southeast Asia. In: Gupta A (Ed.) *The Physical Geography of Southeast Asia*. Oxford University Press, Oxford, UK, 38–64.
- Hartmann T, Hüllen S, Geissler P, Handschuh M, Seng R, Miessen FW, Herder F (2013) Records of freshwater fish species from Phnom Kulen National Park, northwestern Cambodia. *Cambodian Journal of Natural History* 2013: 10–15.
- Hemmen J, Hemmen C (2001) Aktualisierte Liste der terrestrischen Gastropoden Thailands. *Schriften zur Malakozoologie* 18: 35–70.
- Hosoishi S, Park S-H, Ogata K (2015) A contribution to the knowledge of ant genera of Cambodia (Hymenoptera: Formicidae). *Cambodian Journal of Natural History* 2015: 144–147.
- Hosoishi S, Park S-H, Yamane S, Ogata K (2012) Species composition of ant prey of the pitcher plant *Nepenthes bokorensis* Mey (Nepenthaceae) in Phnom Bokor National Park, Cambodia. *Cambodian Journal of Natural History* 2012: 3–7.
- Hughes AC (2017) Understanding the drivers of Southeast Asian biodiversity loss. *Ecosphere* 8: e01624. <https://doi.org/10.1002/ecs2.1624>
- Hun S, Samorn V, Ith S, Chan B (2019) Rediscovery of the critically endangered giant land snail *Bertia cambojiensis* (Reeve, 1860) in Cambodia. *Cambodian Journal of Natural History* 2019: 128–130.
- Hutton T (1834) On the land-shells of India. *Journal of the Asiatic Society of Bengal* 3: 81–93.
- ICZN (1999) *International Code of Zoological Nomenclature*, Fourth Edition. International Trust for Zoological Nomenclature, London, 306 pp.
- Inkhavilay K, Siriboon T, Sutcharit C, Rowson B, Panha S (2016) The first revision of the carnivorous land snail family Streptaxidae in Laos, with description of three new species (Pulmonata, Stylommatophora, Streptaxidae). *ZooKeys* 589: 23–53. <https://doi.org/10.3897/zookeys.589.7933>
- Inkhavilay K, Sutcharit C, Bantaowong U, Chanabun R, Siriut W, Srisonchai R, Pholyotha A, Jirapatrasilp P, Panha S (2019) Annotated checklist of the terrestrial molluscs from Laos (Mollusca, Gastropoda). *ZooKeys* 834: 1–166. <https://doi.org/10.3897/zookeys.834.28800>

- Inkhavilay K, Sutcharit C, Panha S (2017) Taxonomic review of the tree snail genus *Amphidromus* Albers, 1850 (Pulmonata: Camaenidae) in Laos, with the description of two new species. *European Journal of Taxonomy* 330: 1–40. <https://doi.org/10.5852/ejt.2017.330>
- Jocque M, Wiesner J, Stock W (2019) Tiger beetle (Coleoptera: Cicindelidae) records from Kratie Province, Cambodia, with three new country records and an updated checklist for Cambodia. *Cambodian Journal of Natural History* 2019: 2–6.
- Khalik MZ, Hendriks KP, Vermeulen JJ, Schilthuizen M (2019) Conchological and molecular analysis of the “non-scaly” Bornean *Georissa* with descriptions of three new species (Gastropoda, Neritimorpha, Hydrocenidae). *ZooKeys* 840: 35–86. <https://doi.org/10.3897/zookeys.840.33326>
- Kobelt W (1908) Die gedeckelten Lungenschnecken (Cyclostomacea). In *Abbildungen nach der Natur mit Beschreibungen. Dritte Abteilung. Cyclophoridae I. Systematisches Conchylien-Cabinet von Martini und Chemnitz* 1 (19) [(3)]: 401–711, plates 51–103. [pp. 609–711, pls 80–103(1908)]. [Published in parts, dates follow Welter-Schultes (1999)] <https://doi.org/10.5962/bhl.title.119590>
- Kobelt W (1911) Die Gedeckelten Lungenschnecken (Cyclostomacea). In *Abbildungen nach der Natur mit Beschreibungen. Dritte Abteilung. Cyclophoridae II. Systematisches Conchylien-Cabinet von Martini und Chemnitz* 1 (19) [(3)]: 713–1048, pls 104–156. [pp. 713–816, pls 104–121 (1911)]. [Published in parts, dates follow Welter-Schultes (1999)]
- Kosterin OE (2012) A rapid survey of Odonata on Bokor Plateau, Preah Monivong National Park, Cambodia. *Cambodian Journal of Natural History* 2012: 75–86.
- Kosterin OE, Chartier G (2014) Two more Odonata species recorded for Cambodia. *Cambodian Journal of Natural History* 2014: 8–11.
- Kosterin OE, Chartier G, Holden J, Mey FS (2012) New records of Odonata from Cambodia, based mostly on photographs. *Cambodian Journal of Natural History* 2012: 150–163.
- Künstler J (1882) Sur cinq protozoaires parasites nouveaux. *Comptes Rendus des Séances de l'Académie des Sciences, Paris* 95: 347–349.
- Kuznetsov AG, Kuzminykh AA (1999) *Cambodiparmarion doroshenkoi* gen. et sp. nov. (Pulmonata, Helicarionidae) from Cambodia. *Ruthenica* 9: 113–116.
- Likhitrakarn N, Golovatch SI, Panha S (2015) A checklist of the millipedes (Diplopoda) of Cambodia. *Zootaxa* 3973: 175–184. <https://doi.org/10.11646/zootaxa.3973.1.7>
- Maassen WJM (2001) A preliminary checklist of the non-marine molluscs of West-Malaysia, A handlist. *De Kreukel, Supplement*: 1–155.
- Mabille J (1887a) *Molluscorum Tonkinorum diagnoses*. Meulan (Seine-Oise), 18 pp.
- Mabille J (1887b) Sur quelques mollusques du Tonkin. *Bulletins de la Société Malacologique de France* 4: 73–164.
- Martens EC von (1864) Hr. W. Peters theilte diagnosen neuer Heliceen aus dem ostasiatischen Archipel Von Hrn. Dr. Ed. von Martens mit. *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin* 1864: 523–529.
- Martens EC von (1867) *Die Preussische Expedition nach Ost-Asien*. Verlag der Königlichen Geheimen Ober-Hofbuchdruckerei, 477 pp.
- MolluscaBase (2020) MolluscaBase. <http://www.molluscabase.org> [Accessed on 3 May 2020]
- Morelet A (1865) Addition à la faune malacologique de l'Indo-Chine. *Journal de conchyliologie* 13: 225–228.

- Morelet A (1875) Séries conchyliologiques comprenant l'énumération de mollusques terrestres et fluviatiles recueillies pendant le cours de différents voyages, ainsi que la description de plusieurs espèces nouvelles 4. Savy, Paris, 377 pp.
- Morlet L (1883) Description d'espèces nouvelles de coquilles recueillies par M. Pavie au Cambodge. *Journal de Conchyliologie* 31: 104–110.
- Morlet L (1885) Description d'espèces nouvelles de Coquilles, recueillies par M. Pavie au Cambodge, 2nd article. *Journal de Conchyliologie* 32[1884]: 386–403. [Published in parts, dates follow Fischer-Piette (1937)]
- Morlet L (1886) Diagnose molluscorum novorum Cambodgiae. *Journal de Conchyliologie* 34: 74–75.
- Morlet L (1889) Catalogue des Coquilles recueillies par M. Pavie dans le Cambodge et le Royaume de Siam et description d'Espèces Nouvelles. *Journal de Conchyliologie* 37: 121–200.
- Morlet L (1890) Contribution à la Faune malacologique du Cambodge et du Siam. *Journal de Conchyliologie* 38: 119–122.
- Mouhot H (1864a) Travels in the central parts of Indochina (Siam), Cambodia, and Laos, during the Years 1858, 1859, and 1860. Volume 1. John Murray, Albemarle Street, London, 303 pp.
- Mouhot H (1864b) Travels in the central parts of Indochina (Siam), Cambodia, and Laos, during the Years 1858, 1859, and 1860. Volume 2. John Murray, Albemarle Street, London, 301 pp.
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hot-spots for conservation priorities. *Nature* 403: 853–858. <https://doi.org/10.1038/35002501>
- Nahok B, Tumpeesuwan S, Tumpeesuwan C (2020) *Anceyoconcha*, a replacement name for the preoccupied tree snail genus *Giardia* Ancey, 1907 (Pulmonata: Helicoidea: Camaenidae). *Raffles Bulletin of Zoology* 68: 80–90.
- Nantarat N, Sutcharit C, Tongkerd P, Ablett J, Naggs F, Panha S (2014a) An annotated catalogue of type specimens of the land snail genus *Cyclophorus* Monfort, 1810 (Caenogastropoda, Cyclophoridae) in the Natural History Museum, London. *ZooKeys* 411: 1–56. <https://doi.org/10.3897/zookeys.411.7258>
- Nantarat N, Tongkerd P, Sutcharit C, Wade CM, Naggs F, Panha S (2014b) Phylogenetic relationships of the operculate land snail genus *Cyclophorus* Montfort, 1810 in Thailand. *Molecular Phylogenetics and Evolution* 70: 99–111. <https://doi.org/10.1016/j.ympev.2013.09.013>
- Nantarat N, Sutcharit C, Tongkerd P, Wade CM, Naggs F, Panha S (2019) Phylogenetics and species delimitations of the operculated land snail *Cyclophorus volvulus* (Gastropoda: Cyclophoridae) reveal cryptic diversity and new species in Thailand. *Scientific Reports* 9: 7041. <https://doi.org/10.1038/s41598-019-43382-5>
- Naruse T, Yeo DCJ, Osawa M (2014) Notes on a collection of stomatopod and decapod crustaceans from Cambodia. *Cambodian Journal of Natural History* 2014: 24–36.
- Neang T, Grismer LL, Hun S, Phan C (2015) New herpetofauna records and range extensions for *Daboia siamensis* (Smith, 1917) and *Gekko petricolus* Taylor, 1962 from Cambodia. *Cambodian Journal of Natural History* 2015: 172–182.
- Panha S (1987) The breeding data of Thai edible land snail *Hemiplecta distincta* (Pfeiffer) (Pulmonata: Ariophantidae). *Venus* 46: 25–34.

- Pavie A (1904) Mission Pavie Indo-Chine, 1879–1895, Études Diverses, Recherches sur l'Histoire Naturelle de l'Indo-Chine Orientale. Paris, 549 pp.
- Pfeiffer L (1850) Beschreibungen neuer Landschnecken. Zeitschrift für Malacozoologie 7: 65–80.
- Pfeiffer L (1854) Descriptions of sixty-six new land shells from the collection of H. Cuming, Esq. Proceedings of the Zoological Society of London 20[1852]: 56–70. [Published in parts, dates follow Duncan (1937)]
- Pfeiffer L (1856) Descriptions of twenty-five new species of land shells, from the collection of H. Cuming, Esq. Proceedings of the Zoological Society of London 24: 32–36.
- Pfeiffer L (1861) Description of new land shells in the collection of Mr. H. Cuming, Esq. Proceedings of the Zoological Society of London 29: 190–196.
- Pfeiffer L (1862) Diagnoses de neuf espèces nouvelles provenant de Siam. Journal de Conchyliologie 10: 39–46.
- Pholyotha A, Sutcharit C, Panha S (2018) The land snail genus *Macrochlamys* Gray, 1847 from Thailand, with descriptions of five new species (Pulmonata: Ariophantidae). Raffles Bulletin of Zoology 66: 763–781.
- Pilsbry HA (1891) Manual of Conchology, Structural and Systematic, with Illustrations of the Species, Series 2 volume 6. The Academy of Natural Sciences of Philadelphia, PA, 324. [1890–1891] [pls 1–69. [p. 193–324 (1891)]]], 324 pp. <https://doi.org/10.1136/bmj.1.1571.324-a>
- Prasankok P, Panha S (2011) Genetic structure of the common terrestrial pulmonate snail, *Cryptozona siamensis* (Pfeiffer, 1856), in Thailand. Biochemical Systematics and Ecology 39: 449–457. <https://doi.org/10.1016/j.bse.2011.06.011>
- Richardson L (1983) Bradybaenidae: Catalogue of Species. Tryonia 9: 1–253.
- Richardson L (1985) Camaenidae: Catalogue of Species. Tryonia 12: 1–479.
- Robinson DG, Hovestadt A, Fields A, Breure ASH (2009) The land Mollusca of Dominica (Lesser Antilles), with notes on some enigmatic or rare species. Zoologische Mededelingen 83: 615–650.
- Rochebrune A-T de (1881a) Documents sur la faune malacologique de la Cochinchine et du Cambodge. Bulletin de la Société Philomathique de Paris 7: 35–74. <https://www.biodiversitylibrary.org/page/31660821>
- Rochebrune A-T de (1881b) Supplément aux documents sur la faune malacologique de la Cochinchine et du Cambodge. Bulletin de la Société Philomathique de Paris 7: 99–118.
- Shileyko AA (2003) Treatise on recent terrestrial pulmonate mollusks. 11. Trigonochlamyidae, Papillodermidae, Vitrinidae, Limacidae, Bielziidae, Agriolimacidae, Boettgerillidae, Camaenidae. Ruthenica Supplement 2: 1467–1626.
- Shileyko AA (2011) Check-list of land pulmonate molluscs of Vietnam (Gastropoda: Stylomatophora). Ruthenica 21: 1–68.
- Simroth H (1893) Ueber einige Parmarion-Arten. In: M. Weber (Ed.) Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien 3: 100–111.
- So N, Utsugi K, Shibukawa K, Thach P, Chhuoy S, Kim S, Chin D, Nen P, Chheng P (2019) Fishes of the Cambodian Freshwater Bodies. Inland Fisheries Research and Development Institute, Fisheries Administration, Phnom Penh, 197 pp.

- Sodhi NS, Posa MRC, Lee TM, Bickford D, Koh LP, Brook BW (2010) The state and conservation of Southeast Asian biodiversity. *Biodiversity and Conservation* 19: 317–328. <https://doi.org/10.1007/s10531-009-9607-5>
- Sor R, Segers H, Meas S (2015) Rotifers as bio-indicators of freshwater quality: a case study from the upper Cambodian Mekong River Basin. *Cambodian Journal of Natural History* 2015: 148–152.
- Stuart BL, Emmett DA (2006) A collection of amphibians and reptiles from the Elephant and Cardamom Mountains, southwestern Cambodia. *Fieldiana Zoology (New Series)* 109: 1–27. [https://doi.org/10.3158/0015-0754\(2006\)109\[1:ACOAAR\]2.0.CO;2](https://doi.org/10.3158/0015-0754(2006)109[1:ACOAAR]2.0.CO;2)
- Sutcharit C, Asami T, Panha S (2007) Evolution of whole-body enantiomorphy in the tree snail genus *Amphidromus*. *Journal of Evolutionary Biology* 20: 661–672. <https://doi.org/10.1111/j.1420-9101.2006.01246.x>
- Sutcharit C, Backeljau T, Panha S (2019a) Re-description of the type species of the genera *Ganesella* Blanford, 1863 and *Globotrochus* Haas, 1935; with description of a new *Ganesella* species from Thailand (Eupulmonata, Camaenidae). *ZooKeys* 870: 51–76. <https://doi.org/10.3897/zookeys.870.36970>
- Sutcharit C, Naggs F, Ablett J, Sang PV, Hao LV, Panha S (2019b) Notes on the sinistral helicoid snail *Bertia cambojiensis* (Reeve, 1860) from Vietnam (Eupulmonata, Dyakiidae). *ZooKeys* 885: 1–14. <https://doi.org/10.3897/zookeys.885.38980>
- Sutcharit C, Panha S (2006) Taxonomic review of the tree snail *Amphidromus* Albers, 1850 (Pulmonata: Camaenidae) in Thailand and adjacent areas: subgenus *Amphidromus*. *Journal of Molluscan Studies* 72: 1–30. <https://doi.org/10.1093/mollus/eyi044>
- Tan SK, Chan SY, Nguang LHS, Low MEY (2016) Making its way down the Peninsula: Discovery of the non-native *Cryptozonia siamensis* (L. Pfeiffer, 1856) in Singapore, with a note on its status in Peninsular Malaysia (Helicarionoidea: Ariophantidae). *Occasional Molluscan Papers* 5: 1–9.
- Thach NN (2017) New shells of Southeast Asia with 2 new genera and 85 new species. 48Hr-Books Company, Ohio, USA, 128 pp.
- Thach NN (2018) New shells of South Asia seashells-freshwater & land snails, 3 new genera, 132 new species & subspecies. 48HrBooks Company, Ohio, USA, 173 pp.
- Thiele J (1931) *Handbuch der systematischen Weichtierkunde*. Jena. Bd. I, Teil 2: 377–778.
- Tordoff AW, Baltzer MC, Fellowes JR, Pilgrim JD, Langhammer PF (2012) Key biodiversity areas in the Indo-Burma hotspot: Process, progress and future directions. *Journal of Threatened Taxa* 4: 2779–2787. <https://doi.org/10.11609/JotT.o3000.2779-87>
- Tsujino R, Kajisa T, Yumoto T (2019) Causes and history of forest loss in Cambodia. *International Forestry Review* 21: 372–384. <https://doi.org/10.1505/146554819827293178>
- Vaught KC (1989) A classification of the living Mollusca. In: Abbott RT, Boss KJ (Eds) *American Malacologists*, Melbourne, 189 pp.
- Vermeulen JJ, Luu HT, Keum T, Anker K (2019a) Land snail fauna of the Mekong Delta Limestone Hills (Cambodia, Vietnam): *Notharinia* Vermeulen, Phung et Truong, 2007, and a note on *Plectostoma* A. Adams, 1865 (Mollusca: Gastropoda: Caenogastropoda: Diplommatinidae). *Folia Malacologica* 27: 167–177. <https://doi.org/10.12657/fol-mal.027.015>

- Vermeulen JJ, Luu HT, Keum T, Anker K (2019b) New species of land snails (Mollusca: Gastropoda: Caenogastropoda and Pulmonata) of the Mekong Delta Limestone Hills (Cambodia, Vietnam). *Folia Malacologica* 27: 7–41. <https://doi.org/10.12657/folmal.027.001>
- Vermeulen JJ, Phung CL, Truong QT (2007) New species of terrestrial molluscs (Caenogastropoda, Pupinidae & Pulmonata: Vertiginidae) of the Hon Chong – Ha Tien limestone hills, Southern Vietnam. *Basteria* 71: 81–92.
- Welter-Schultes FW (1999) Systematisches Conchylien-Cabinet von Martini und Chemnitz (1837–1920), bibliography of the volumes in Göttingen. *Archives of Natural History* 26: 157–203. <https://doi.org/10.3366/anh.1999.26.2.157>
- Wikramanayake E, Dinerstein E, Loucks C, Olson D, Morrison J, Lamoreux J, McKnight M, Hedao P (2001) Terrestrial Ecoregions of the Indo-Pacific: A Conservation Assessment. Island Press, Washington, USA, 824 pp.
- Wood H, Gallichan J (2008) The new molluscan names of César-Marie-Felix Ancey including illustrated type material from the National Museum of Wales. *Studies in Biodiversity and Systematics of Terrestrial Organism from the National Museum of Wales. Biotir Report 3*. The Dorset Press, Dorchester, 162 pp.
- WWF (2019a) Southeastern Asia: Southern Cambodia stretching into Thailand and Vietnam. <https://www.worldwildlife.org/ecoregions/im0106> [Accessed on 26 November 2019]
- WWF (2019b) Southeastern Asia: Vietnam into Laos and Cambodia. <https://www.worldwildlife.org/ecoregions/im0152> [Accessed on 26 November 2019]
- Zettel H, Phauk S, Kheam S, Freitag H (2017) Checklist of the aquatic Hemiptera (Heteroptera: Gerromorpha and Nepomorpha) of Cambodia, with descriptions of new species of *Microvelia* Westwood, 1834 and *Ranatra* Fabricius, 1790. *Aquatic Insects* 38: 21–48. <https://doi.org/10.1080/01650424.2017.1332372>
- Zilch A (1960) Gastropoda, Euthyneura. In: Schindewolf OH (Ed.) *Handbuch der Paläozoologie*. Gebrüder Borntraeger, Berlin, 401–834.

Five new species of Aspidiotini (Hemiptera, Diaspididae, Aspidiotinae) from Argentina, with a key to Argentine species

Scott A. Schneider¹, Lucia E. Claps², Jiufeng Wei³, Roxanna D. Normark⁴,
Benjamin B. Normark^{4,5}

1 USDA, Agricultural Research Service, Henry A. Wallace Beltsville Agricultural Research Center, Systematic Entomology Laboratory, Building 005 - Room 004, 10300 Baltimore Avenue, Beltsville, MD 20705, USA

2 Universidad Nacional de Tucumán. Facultad de Ciencias Naturales e Instituto Miguel Lillo, Instituto Superior de Entomología “Dr. Abraham Willink”, Batalla de Ayacucho 491, T4000 San Miguel de Tucumán, Tucumán, Argentina **3** College of Agriculture, Shanxi Agricultural University, Taigu, Shanxi, 030801, China

4 Department of Biology, University of Massachusetts, 221 Morrill Science Center III 611 North Pleasant Street, Amherst, MA 01003, USA **5** Graduate Program in Organismic and Evolutionary Biology, University of Massachusetts, 204C French Hall, 230 Stockbridge Road Amherst, MA 01003, USA

Corresponding author: Scott A. Schneider (scott.schneider3@usda.gov)

Academic editor: Roger Blackman | Received 22 May 2020 | Accepted 5 June 2020 | Published 13 July 2020

<http://zoobank.org/1B7C483E-56E1-418D-A816-142EFEE8D925>

Citation: Schneider SA, Claps LE, Wei J, Normark RD, Normark BB (2020) Five new species of Aspidiotini (Hemiptera, Diaspididae, Aspidiotinae) from Argentina, with a key to Argentine species. ZooKeys 948: 47–73. <https://doi.org/10.3897/zookeys.948.54618>

Abstract

Five new species of armored scale insect from Argentina are described and illustrated based upon morphological and molecular evidence from adult females: *Chortinaspis jujuyensis* **sp. nov.**, *Clavaspis patagonensis* **sp. nov.**, *Hemiberlesia ozolita* **sp. nov.**, *Melanaspis lilloi* **sp. nov.**, and *Melanaspis targionoides* **sp. nov.** The genera *Chortinaspis* and *Melanaspis* are recorded for the first time from this country. An identification key to all recorded species from tribe Aspidiotini occurring in Argentina is provided.

Keywords

armored scale insects, *Chortinaspis*, *Clavaspis*, Coccoidea, Coccoomorpha, *Hemiberlesia*, *Melanaspis*, taxonomy

Introduction

Armored scale insects are ubiquitous, highly invasive herbivores that often become pests on trees, shrubs, and ornamentals (Miller and Davidson 1990; 2005; Normark et al. 2019). They comprise the largest family of scale insects (Hemiptera, Coccothraupidae, Diaspididae) with over 2600 species in 422 genera (García Morales et al. 2016). About one-quarter of armored scales belong to the tribe Aspidiotini Westwood, a particularly pestiferous group containing numerous cosmopolitan species (Miller and Davidson 1990; Schneider et al. 2019). At present the tribe comprises over 720 species in 88 genera; however, recent phylogenetic evidence has revealed rampant artificiality among these genera (Schneider et al. 2018), and their classification is in need of extensive revision.

This article describes five new species of Aspidiotini from Argentina. Generic designations are made following morphology and the best available evidence from molecular studies (Schneider et al. 2018; Normark et al. 2019), keeping in mind the ultimate goal to identify genera of Aspidiotini that delimit natural groups of species. This article also provides an identification key to the species of Aspidiotini recorded from Argentina (García Morales et al. 2016, last accessed 21.V.2020). This work adds to our knowledge of armored scale diversity in this region, for which a foundation has largely been established by Claps, Wolff, and colleagues (Claps and Terán 2001; Claps et al. 2001a; b; Claps and Wolff 2003; 2014; Granara de Willink and Claps 2003; and additional works).

Sixteen genera from tribe Aspidiotini are now recorded in Argentina (García Morales et al. 2016), including: *Acutaspis* Ferris, 1941; *Aonidiella* Berlese & Leonardi, 1896; *Aspidiotus* Bouché, 1833; *Chortinaspis* Ferris, 1938 (new record); *Chrysomphalus* Ashmead, 1880; *Clavaspis* MacGillivray, 1921; *Comstockaspis* MacGillivray, 1921; *Crenulaspidotus* MacGillivray, 1921; *Diaspidiotus* Berlese & Leonardi, 1896; *Hemiberlesia* Cockerell, 1897; *Lindingaspis* MacGillivray, 1921; *Melanaspis* Cockerell, 1897 (new record); *Mycetaspis* Cockerell, 1897; *Oceanaspidotus* Takagi, 1984; *Pseudisch-naspis* Hempel, 1900; and *Targionia* Signoret, 1869.

Materials and methods

Specimens were preserved in 100% ethanol and stored at -20 °C before being slide-mounted. Specimens were slide-mounted according to the joint DNA-morphology preparation protocol described in Normark et al. (2019), except that some specimens were prepared according to an earlier set of protocols. In the earlier protocols some specimens were ground to powder for DNA preparation and others from the same series were transferred directly to 10% KOH for mounting on microscope slides.

Morphological terminology conforms to descriptions and illustrations provided by Schneider et al. (2019). Measurements were made on a Zeiss Axio Imager.M2 (Carl Zeiss Microscopy, LLC, White Plains, NY, USA) microscope with the aid of an AxioCam and AxioVision software. Illustrations were made with the aid of a camera lucida. Slide-mounted specimens were examined by the authors under phase contrast and Differential Interference Contrast microscopy.

Depositories are abbreviated as follows: IFML, Instituto Fundación Miguel Lillo, Tucumán, Argentina; USNM, United States National Museum, scale insect collection at Agricultural Research Service, Beltsville, Maryland, USA; UMEC, University of Massachusetts Entomology Collection, Amherst, Massachusetts, USA.

Taxonomy

***Chortinaspis jujuyensis* Schneider, Claps, Wei, Normark & Normark, sp. nov.**

<http://zoobank.org/33040435-CC00-4B65-A5F8-687A02E4BCA8>

Figs 1, 2

Material examined. Holotype: ARGENTINA • 1 adult female; Jujuy, Humahuaca, Ruta 9, entrada a Iruya; 22.997S, 65.369W; 12.II.2002; L. E. Claps, P. Zamudio, L. Díaz-Briz, and P. Cabrera leg.; IFML, L. E. Claps catalog #12-02, # 1089 (D0265G). **Paratypes:** ARGENTINA • 2 adult females; same slide and data as holotype; IFML (D0265G) • 1 adult female; same data as holotype; IFML (D0265H) • 1 adult female; same data as holotype; IFML (D0265J) • 1 adult female; same data as holotype; IFML (D0265K) • 3 adult females; same data as holotype; UMEC (D0265I) • 1 adult female; same data as holotype; USNM (D0265L) • 1 adult female; same data as holotype; USNM (D0265M).

Description ($N = 11$). Adult female presumed to secrete scale cover, not pupillaral. Appearance in life not recorded. Slide-mounted adult female 730–1110 (holotype 860, median 860) μm long, 590–800 (holotype 680, median 680) μm wide; broadest near mesothorax and metathorax. Body outline nearly oval. Derm membranous except for pygidium. Antennae simple, each with one thick, flagellate seta; distance between antennae 120–150 (median 130) μm . Without disc pores near anterior or posterior spiracles. **Lobes:** Pygidium with 2 pairs of well-developed sclerotized lobes extending from pygidial margin. Median lobes (L1) prominent and broad, roughly rectangular in shape with ragged edges; each lobe with basal scleroses nearly equal in length to L1, broad basally and tapering anteriorly; L1 separated by interlobular space about 1/4 width of L1; second lobes (L2) about 1/2 width of L1, smoothly rounded apically, without notches, L3 and L4 absent. **Paraphyses:** Absent. **Plates:** 1 pair of simple plates between L1, with shallow bifurcations, not deeply fringed, slightly longer than L1; 2 plates present in first space between L1 and L2, the plate immediately anterior to L1 simple and roughly triangular, the other roughly rectangular and apically fringed, both longer than L1; 2 plates anterior to L2, variously fringed, ranging from simple to fimbriate; plates absent beyond setae marking position of L3. **Ducts:** Dorsal pygidial macroducts of 1-barred type, long and slender, duct filaments about 6–8 times as long as width of orifices; 1 macroduct between L1 (rarely absent), extending beyond posterior margin of anal opening, 40–51 (median 45) μm in length; 5–9 clustered macroducts arising from first space between L1 and L2, 14–27 on abdominal segment VI, in elongate cluster arising from second space and widening anteriorly; 18–38 ducts on abdominal segment V, in irregular, elongate cluster arising from third space

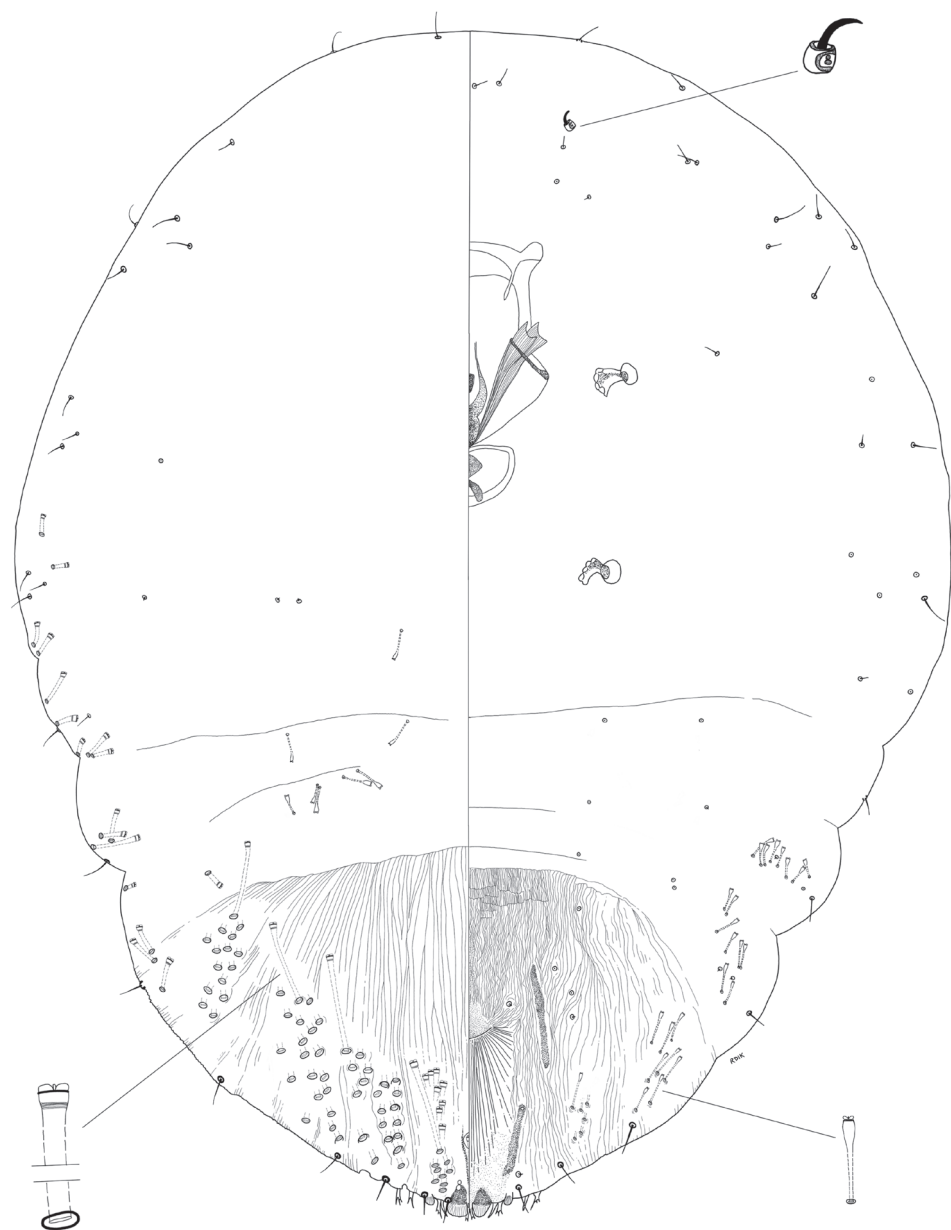


Figure 1. *Chortinaspis jujuyensis* sp. nov. Adult female, full body view, illustrated from the holotype (D0265G).

and widening anteriorly; 38–66 (median 48.5) macroducts on each side of pygidium in total. Submarginal cluster of 4–17 (median 11) macroducts present on abdominal segment IV; few marginal macroducts present on each of abdominal segments I–III and metathorax. Dorsal submedial groups of microducts present on each of abdominal

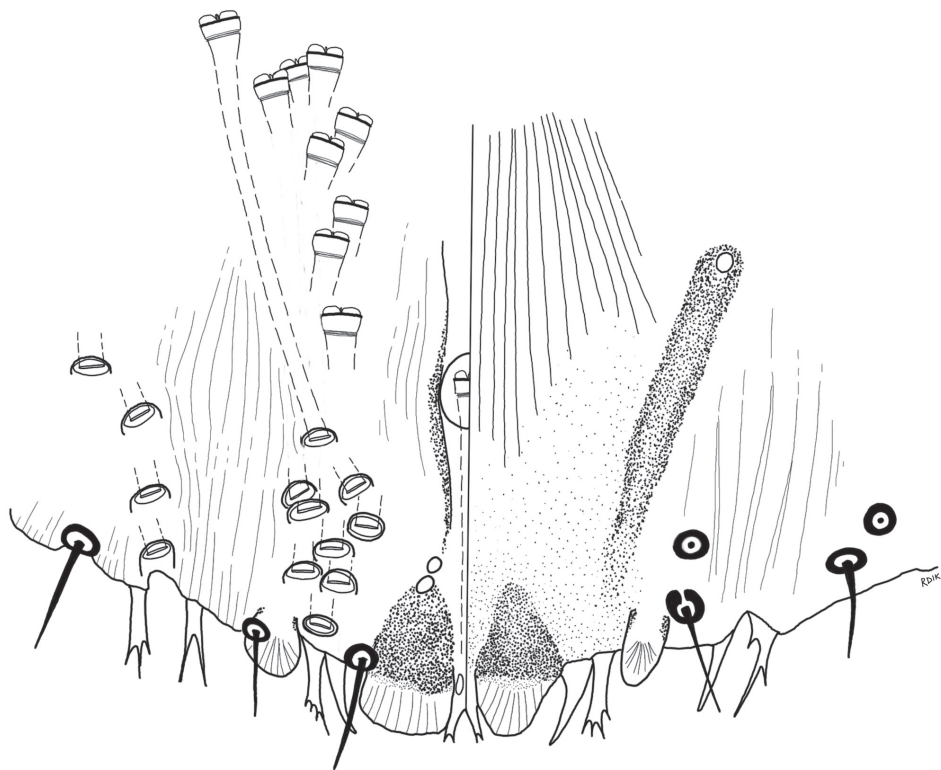


Figure 2. *Chortinaspis jujuyensis* sp. nov. Adult female, expanded view of pygidium, illustrated from the holotype (D0265G).

segments I–III. Small clusters of ventral submarginal microducts present on abdominal segments II–VI. **Anal opening:** Small and slightly oval, 11–17 (median 14) μm in diameter, positioned 2.2–3.3 (median 2.3) anal lengths from base of L1, located in posterior third of pygidium. **Perivulvar pores:** Absent.

DNA sequences. Several DNA sequences of *Chortinaspis jujuyensis* sp. nov. have been published, including fragments of 4 loci. None are from the holotype or paratypes, but all are from specimens collected in the same collecting event with the same data. Specimen D0265A was ground to powder during DNA preparation. Specimens D0265E and D0265F are mounted on microscope slides but are in poor condition; they are identifiable as *C. jujuyensis* sp. nov. but were not suitable for reliable measurements and therefore were not designated as paratypes. The sequenced loci and corresponding GenBank accession numbers are: the large ribosomal subunit (28S; D0265A, DQ145314.2; D0265E, MH933984.1), elongation factor 1-alpha (EF-1 α ; D0265A, DQ145426.1; D0265E, MH915708.1; D0265F, MH915709.1), carbamoylphosphate synthetase (CAD; D0265E, MH915983.1; D0265F, MH915984.1), and cytochrome oxidase I and II (COI-II; D0265, GQ424990.1; D0265E, MH916219.1 & MH916391.1; D0265F, MH916220.1 & MH916392.1). The small ribosomal sub-

nit (16S) sequences of the primary bacterial endosymbiont, *Uzinura diaspidicola*, of *C. jujuyensis* sp. nov. has also been published: GQ424853.1.

Informal synonyms. Specimens of *C. jujuyensis* sp. nov. have appeared in several published phylogenetic trees, and have been referred to variously as “Diaspidiotus sp undesc #2” (Morse and Normark 2006; Rugman-Jones et al. 2010), “Diaspidiotus sp. undesc.” (Gruwell et al. 2009), “Diaspidiotus sp” (Andersen et al. 2010), and “Chortinaspis ud0265” (Schneider et al. 2018; Normark et al. 2019).

Remarks. *Chortinaspis jujuyensis* sp. nov. shares similarities with *C. graminella* (Cockerell) and *C. frankliniana* Ferris. The median lobes of *C. jujuyensis* sp. nov. are apically truncate or nearly rectangular in shape like those of *C. graminella* and have rough apical edges like those of *C. frankliniana*. But *C. jujuyensis* sp. nov. can be distinguished from both species by its narrow, smooth second lobes, in contrast to the broadly truncate and notched second lobes seen in the other two species. It differs from *C. chortina* (Ferris) in that it lacks any plates anterior to the position of the third lobes.

Host plant. Not recorded.

Etymology. The specific epithet is an adjective formed from the name Jujuy, the province in which it was found + the suffix *-ensis*, meaning of or from a place.

Distribution. Argentina (Jujuy).

***Clavaspis patagonensis* Schneider, Claps, Wei, Normark & Normark, sp. nov.**

<http://zoobank.org/B7FD9835-4FAE-4CE0-8B8A-1E11DB6A4705>

Figs 3, 4

Material examined. Holotype: ARGENTINA • 1 adult female; Neuquén, PN Lanin, Pucará; 40.15S, 71.63W; 28.XI.2001; L. Claps and L. Díaz Briz leg.; IFML, L. E. Claps catalog # 16-01, #1090 (D0274E). **Paratypes:** ARGENTINA • 1 adult female; same slide as holotype; IFML (D0274E) • 1 adult female; same data as holotype; UMEC (D0274B) • 1 adult female; same data as holotype; USNM (D0274A).

Description ($N = 4$). Adult female presumed to secrete scale cover, not pupillarial. Appearance in life not recorded. Slide-mounted adult female 850–1240 (holotype 1240) μm long, 780–1000 (holotype 1000) μm wide; broadest near mesothorax. Body outline turbinate. Derm membranous throughout at maturity except for light pygidial sclerotization. Antennae simple, each with one spine-like seta. Distance between antennae 150–185 μm . Without disc pores associated with anterior or posterior spiracles. **Lobes:** Only L1 well developed and sclerotized, slightly wider than long, inner margins parallel or slightly converging, with 0–1 medial notch and 1–2 lateral notches; median lobes separated by space 1/5 their width; L2 and L3 absent in typical form, one specimen with single poorly formed L2 present in type series. **Paraphyses:** With 1 pair of paraphysis-like pyriform sclerotizations between L1; interlobular spaces between L1 and L2 and between L2 and L3 each with 2 clavate paraphyses, inner paraphysis slightly larger than outer paraphysis of each pair; paraphyses arising from lateral angle of L1 only slightly swollen at anterior end and directed away from meson. **Plates:** Difficult to

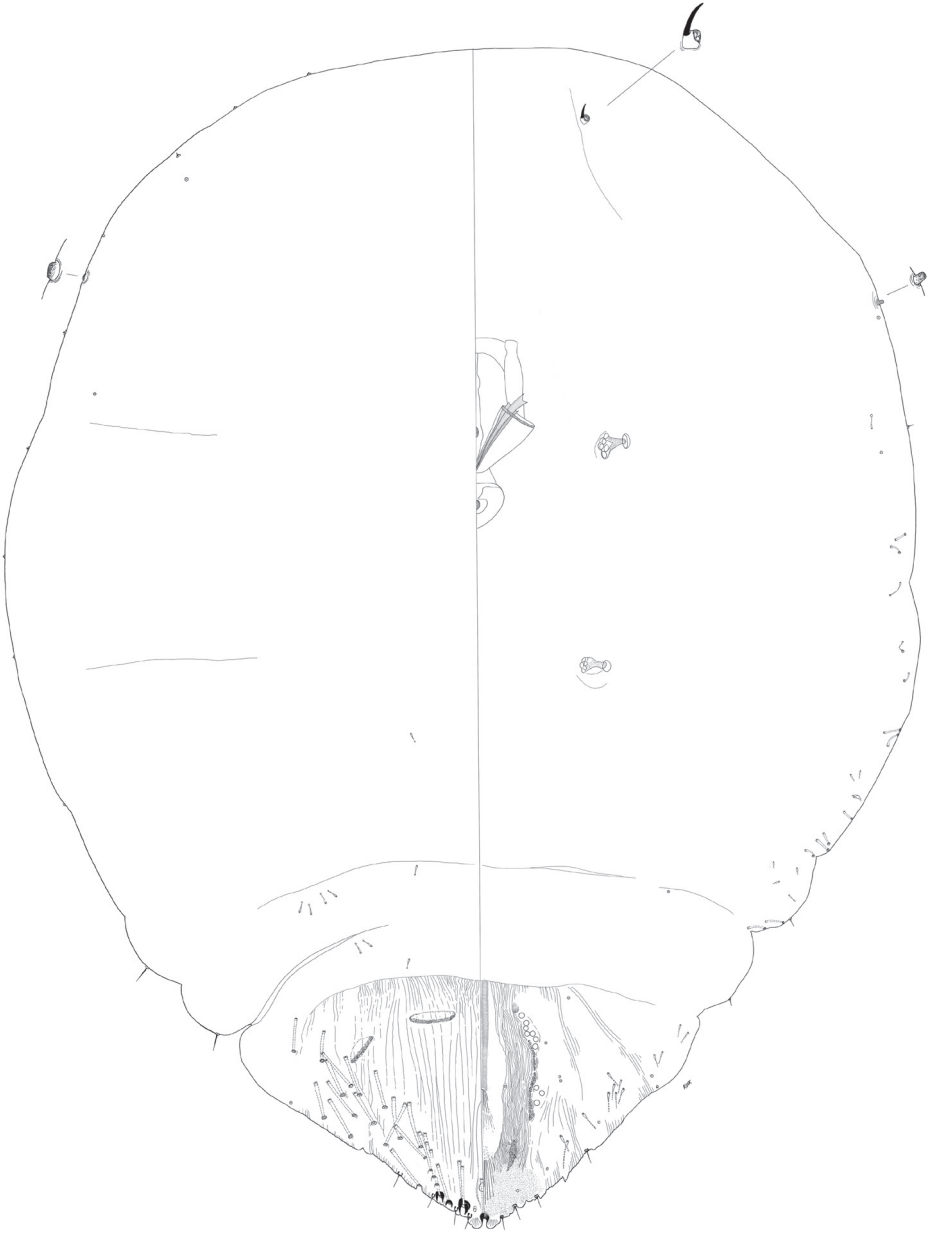


Figure 3. *Clavaspis patagonensis* sp. nov. Adult female, full body view, illustrated from the holotype (D0274E).

observe; apparently 1 or 2 present between L1 and L2, 2 present between L2 and L3, 0–3 beyond L3, all roughly rectangular with minor fringing at apex, about as long as L1.

Ducts: Dorsal pygidial macroducts of 1-barred type; one macroduct present between median lobes with duct exceeding beyond posterior margin of anal opening; with 2–3

macroducts arising from first interlobular space; roughly single-file row of 7–8 macroducts arising from second interlobular space; 8–13 in marginal and submarginal areas of abdominal segment V, arising from third interlobular space. Few pre-pygidial macroducts on marginal line from mesothorax to abdominal segment III, 1–3 per segment on each side, shorter than pygidial macroducts; 1–2 submarginal macroducts present on each side of abdominal segment IV; small sets of 1–4 short submedial macroducts present on each side of abdominal segments I–IV. Ventral marginal or submarginal microducts present in small groups on each segment from prothorax to abdominal segment VI. **Anal opening:** Positioned in posterior third of pygidium, 12–14 μm in diameter, positioned about 2 anal lengths from base of L1. **Perivulvar pores:** Divided into 4 or sometimes 5 groups, 2–7 in each anterolateral, 3–4 in each posterolateral group, and 0–2 in anterior group; 12–21 pores in total.

DNA sequences. DNA sequences of *Clavaspis patagonensis* sp. nov. have been published, all from one of the paratypes (D0274B): 28S, GenBank accession number KY218988.1; EF-1 α , MH915713.1 and KY221285.1; COIII, MH916221.1 and KY220694.1; 16S of primary endosymbiont (*Uzinura diaspidicola*), KY220094.1.

Informal synonyms. A specimen from the type series (D0274B) has appeared in published molecular-phylogenetic analyses, designated as “*Clavaspis undescr*” (Schneider et al. 2018) and “*Clavaspis ud0274*” (Normark et al. 2019).

Remarks. The traditional morphology-based assignment for this species would be in the genus *Diaspidiotus*, but recent molecular-phylogenetic studies have shown that *Diaspidiotus* is radically non-monophyletic and that the true affinities of this species lie with the genus *Clavaspis* (Schneider et al. 2018). The morphological character traditionally used to distinguish between these genera is the shape of paraphyses arising from the lateral angles of median lobes. In typical *Clavaspis* species, these paraphyses are swollen at the anterior end and directed toward the midline of the body or they have a detached knob giving them a mushroom-like appearance (Ferris 1938). In *C. patagonensis* sp. nov., the paraphyses are slightly swollen at the anterior end but they are pointing away from the midline, similar in appearance to those found in species of *Diaspidiotus* and other near relatives, like *Hemiberlesia*.

Adult females of *C. patagonensis* sp. nov. are nearly identical in appearance to *C. covilleae* (Ferris), but the species are separated on the phylogeny by several other members of *Clavaspis*. The two can be distinguished based on the shape of paraphyses arising from the lateral angles of median lobes and the distribution of macroducts. *Clavaspis patagonensis* sp. nov. has fairly narrow paraphyses and possesses one or two dorsal submarginal macroducts on abdominal segment IV. *Clavaspis covilleae* has broadly swollen paraphyses, typical of *Clavaspis*, and lacks any submarginal macroducts on abdominal segment IV. The new species could also be easily confused with *Diaspidiotus osborni* (Newell & Cockerell). In this case, *C. patagonensis* sp. nov. can be distinguished by possessing submarginal macroducts on IV, having more than one marginal macroduct on at least one pre-pygidial segment, lacking dorsal submarginal microducts on pre-pygidial segments, and having a prosoma that remains membranous in mature adult females. In contrast, *D. osborni* lacks submarginal macroducts on IV, typically has one marginal

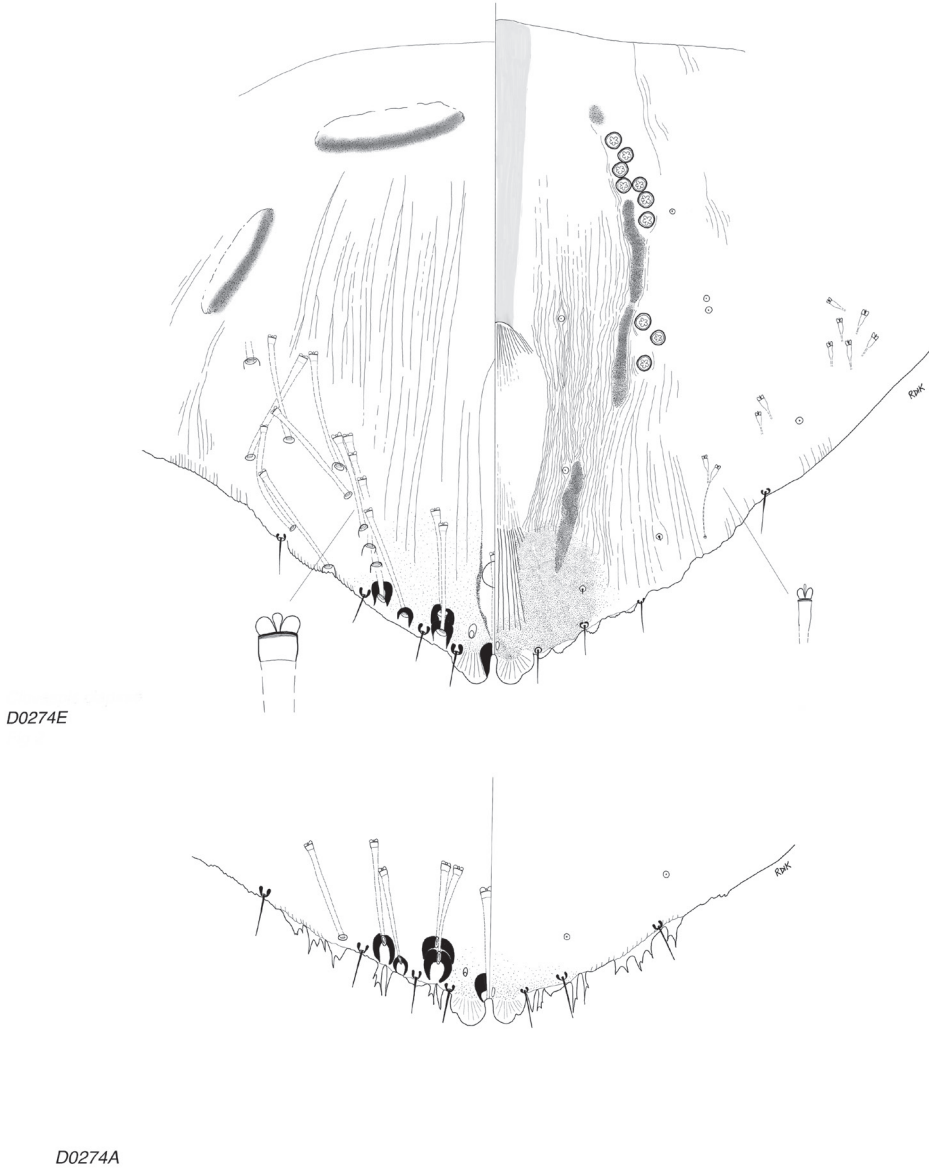


Figure 4. *Clavaspis patagonensis* sp. nov. Adult female, expanded view of pygidium, illustrated from the holotype (D0274E) and a paratype (D0274A), reflecting variation in the degree of visibility of the plates.

macroduct per pre-pygidial segment, has small groups of dorsal submarginal microducts on pre-pygidial segments, and the prosoma becomes sclerotized in mature adult females.

Host plant. *Embothrium coccineum* J. R. Forst. & G. Forst. (Proteaceae)

Etymology. The specific epithet is an adjective formed from the name Patagonia, the region in which it was found + the suffix *-ensis*, meaning of or from a place.

Distribution. Argentina (Neuquén).

***Hemiberlesia ozolita* Schneider, Claps, Wei, Normark & Normark, sp. nov.**

<http://zoobank.org/680825CA-8604-4D3C-9717-39B1AD53A423>

Figs 5, 6

Material examined. Holotype: ARGENTINA • 1 adult female; Jujuy, Humahuaca, camino a Aparzo; 23.20S, 65.10W; 14.II.2002; L. E. Claps, P. Zamudio, L. Díaz-Briz, P. Cabrera leg.; IFML, L. E. Claps catalog #22-02, #1091 (D0288D). **Paratypes:** ARGENTINA • 1 adult female; same slide and same data as holotype; IFML (D0288D) • 1 adult female; same data as holotype; USNM (D0288C) • 1 adult female; same data as holotype; USNM (D0288G) • 1 adult female; same data as holotype; UMEC (D0288F) • 1 adult female; same data as holotype; UMEC (D0288H) • 1 adult female; same data as holotype; UMEC (D0288I) • 1 adult female; same data as holotype; UMEC (D0288J).

Description ($N = 8$). Adult female presumed to secrete scale cover, not pupillarial. Appearance in life not recorded. Slide-mounted adult female 770–1050 (median 910, holotype 990) μm long, 660–810 (median 780, holotype 810) μm wide; broadest at mesothorax. Body outline nearly circular; derm of prosoma becoming slightly sclerotized at full maturity (body length $> 1\text{mm}$), otherwise derm membranous except for pygidium. Antennae simple, each with one spine-like seta; distance between antennae 120–180 (median 140) μm . Without disc pores near anterior or posterior spiracles. **Lobes:** Only L1 well developed, apically truncate, with one deep lateral notch; L2 and L3 represented by small unsclerotized points. **Paraphyses:** Interlobular spaces between L1 and L2 and between L2 and L3 each with 2 clavate paraphyses; first pair similar in length to L1 and second pair nearly 1/2 that length. **Plates:** All plates rather simple, roughly triangular in shape with minimal fringing, and shorter in length than L1. One, minute, simple pair between L1; 2 present between L1 and L2, each with 1–2 short lateral fringes; 3 present between L2 and L3, simple or with one lateral fringe; plates absent anterior of seta marking position of L3. **Ducts:** Dorsal pygidial macroducts of uniform size; 1 marginal macroduct present between median lobes, 30–37 (median 34) μm in length, surpassing posterior margin of anal opening; 3–5 (median 3.5) macroducts arising from space between L1 and L2 (abdominal segment VII), 10–16 (median 14) on abdominal segment VI, 13–24 (median 17) on abdominal segment V, with a total of 31–42 (median 34) dorsal macroducts on each side of pygidium. Clusters of pre-pygidial macroducts present on dorsal submargins, 11–17 (median 13) on each side of abdominal segment IV, 10–16 (median 12) on segment III, 8–11 (median 10) on segment II, fewer present up to mesothorax. Ventral microducts few; present on head and thorax in submarginal and submedial rows; present in submargins of abdominal segments I–VI. **Anal opening:** Oval, maximum diameter (length) 14–23 (median 20) μm , situated 20–31 (median 25) μm , approximately 3 anal lengths, anterior to base of L1. **Perivulvar pores:** Absent.

DNA sequences. DNA sequences of several loci of *Hemiberlesia ozolita* sp. nov. have been published from one paratype (D0288C) and one other individual from the type series that was ground to powder during the preparation of DNA (D0288A): 28S,

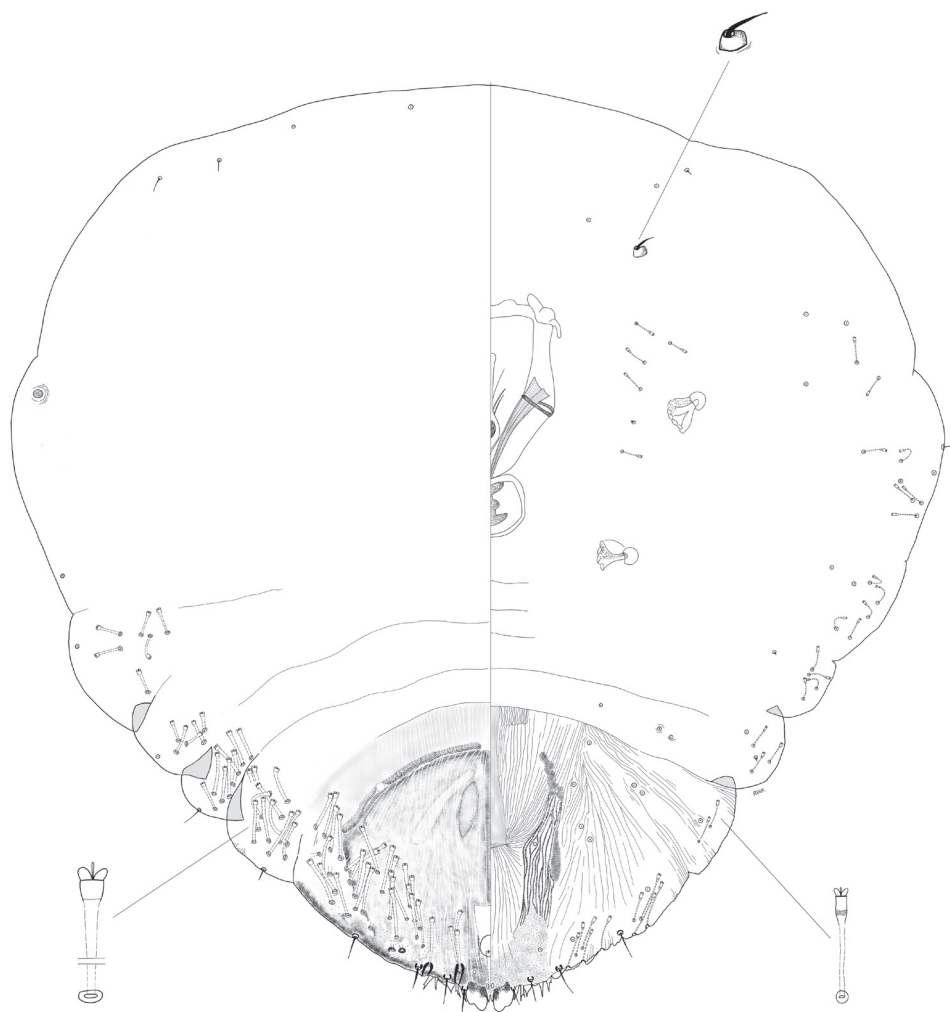


Figure 5. *Hemiberlesia ozolita* sp. nov. Adult female, full body view, illustrated from a paratype (D0288C).

GenBank accession numbers MH933989.1 (D0288C) and KY218997.1 (D0288A); EF-1 α , MH915719.1 (D0288C) and KY221290.1 (D0288A); COI-II, MH916225.1 and MH916397.1 (D0288C), GQ425001.1 (D0288A); 16S of primary endosymbiont (*Uzinura diaspidicola*), KY220099.1.

Informal synonyms. Specimens from the type series and their endosymbionts have appeared in several published phylogenetic trees, and have been referred to variously as “*Diaspidiotus* sp undesc #1” (Morse and Normark 2006; Rugman-Jones et al. 2010), “*Diaspidiotus* sp nov 1” (Andersen et al. 2010), and “*Hemiberlesia* ud0288” (Schneider et al. 2018; Normark et al. 2019).

Remarks. *Hemiberlesia ozolita* sp. nov. is most similar to *H. nothofagi* Williams, but *H. ozolita* sp. nov. is distinctive in having plates in the first space shorter than L1,

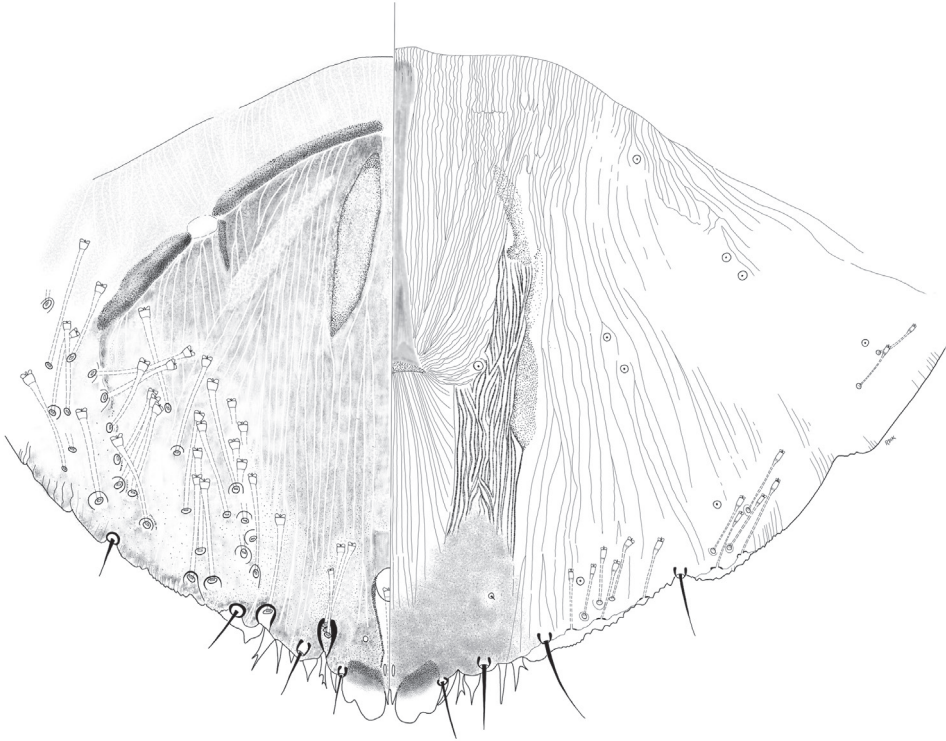


Figure 6. *Hemiberlesia ozolita* sp. nov. Adult female, expanded view of pygidium, illustrated from a paratype (D0288C).

3 plates beyond L2, anal opening relatively small ($< 25 \mu\text{m}$ in diameter), 31–42 macroducts on each side of the pygidium, and groups of ventral submarginal microducts running from the pygidium to the thorax. In contrast, *H. nothofagi* has plates in the first space exceeding L1 in length, 6–7 plates beyond L2, a large anal opening ($30 \mu\text{m}$ in diameter), about 26 pygidial macroducts per side, and few microducts present on the venter, not arranged in submarginal groups on thoracic and pre-pygidial segments. The new species is also similar to *H. rapax* except it has a much smaller anal opening and the pre-pygidial macroducts are longer, about as long as the pygidial macroducts.

Hemiberlesia ozolita sp. nov. constitutes the sister-lineage of a clade that includes all other sampled *Hemiberlesia* species and *Palinaspis sordidata*, according to the phylogenetic estimate of Schneider et al. (2018). The relatively small anal opening in this species is a trait shared in common with several other species formerly placed in *Abgrallaspis* that have since been transferred to *Hemiberlesia* (Normark et al. 2014), a decision supported by molecular evidence.

Host plant. Not recorded.

Etymology. The specific epithet is an adjective formed from the Greek terms *ozotos*, meaning branching, and *litos*, meaning simple, and is used to describe the distinctly simple pygidial plates of this species.

Distribution. Argentina (Jujuy).

***Melanaspis lilloi* Schneider, Claps, Wei, Normark & Normark, sp. nov.**

<http://zoobank.org/1559ADD4-4074-4033-B94B-4B1E4441A974>

Figs 7, 8

Material examined. *Holotype*: ARGENTINA • 1 adult female; Jujuy, 30 km N Humahuaca; 22.97S, 65.39W; 12.II.2002; L. E. Claps, P. Zamudio, L. Diaz-Briz, & P. Cabrera leg.; IFML, L. E. Claps catalog #5-02, #1092 (D0275L). *Paratypes*: ARGENTINA • 3 adult females; same data as holotype; USNM (D0275H) • 1 adult female; same data as holotype; USNM (D0275G) • 1 adult female; same data as holotype; USNM (D0275K) • 4 adult females; same data as holotype; UMEC (D0275I) • 1 adult female; same data as holotype; UMEC (D0275M) • 4 adult females; same data as holotype; IFML (D0275J) • 1 adult female; Jujuy, Humahuaca, entrada a Iruya; 22.997S, 65.356W; 12.II.2002; L. E. Claps, P. Zamudio, L. Diaz-Briz, & P. Cabrera leg.; IFML, L. E. Claps catalog #15-02 (D0297C).

Description ($N = 16$). Adult female presumed to secrete scale cover, not pupilarial. Appearance in life not recorded. Slide-mounted adult female 930–1610 (median 1350, holotype 1610) μm long, 820–1350 (median 1160, holotype 1330) μm wide; broadest near mesothorax. Body outline turbinate. Derm membranous throughout at maturity except for pygidium, which has characteristic dorsal sclerotized areas; sclerotization of these areas unusually heavy, such that paraphyses and basal scleroses of lobes difficult to discern clearly on some specimens. Antennae, simple, each with 1 long seta, distance between antennae 200–330 μm (median 260). Without disc pores near spiracles. **Lobes**: With 4 pairs of well-developed pygidial lobes, L1–L3 apically rounded and L4 truncate or pointed, notches absent from lobes; L1 slightly wider than long, median lobes separated by narrow space 0.15 times width of L1, with basal sclerosis about 1/2 width of L1 arising from mesal edge; L2 and L3 similar in size and shape, shorter and broader than L1; L4 somewhat variable in shape, truncate or with sloping edges. **Paraphyses**: Short and clavate, scarcely longer than L1; absent between L1, paraphysis formula 2-2-3 or 2-2-4; 1 interlobular paraphysis near outer corner of L1, 1 attached to inner corner of L2, 1 in interlobular space between L2 and L3, 1 attached to inner and outer corners of L3, 1 narrow paraphysis attached to inner corner of L4 and 2–3 narrow paraphyses in interlobular space between L3 and L4, these often fused into a single complex mass and difficult to count; several paraphysis-like sclerotizations surrounding macroduct orifices present beyond L4. **Plates**: Apparently absent. **Ducts**: Dorsal pygidial macroducts of 1-barred type, nearly uniform in size, with minute orifices and long slender ducts, most arranged in distinct furrows between sclerotized areas arising from interlobular spaces; 1 submarginal macroduct orifice immediately anterior to each L1, with ducts extending beyond posterior margin of anal opening; 10–21 (median 16) duct orifices in furrow of first space, originating between L1 and L2 and extending in elongate cluster anteriorly 60–85% of distance to anus, each duct about 120–130 μm in length; 18–40 (median 29) in furrow of second space, originating between L2 and L3 and extending anteriorly to a point laterad or anterolaterad of anus; 3–9 (median 6) on sclerotized area arising from L3; 2–24 (median 15) in furrow of third space, originating between L3 and L4 and extending anteriorly to a point anterolaterad of anus;

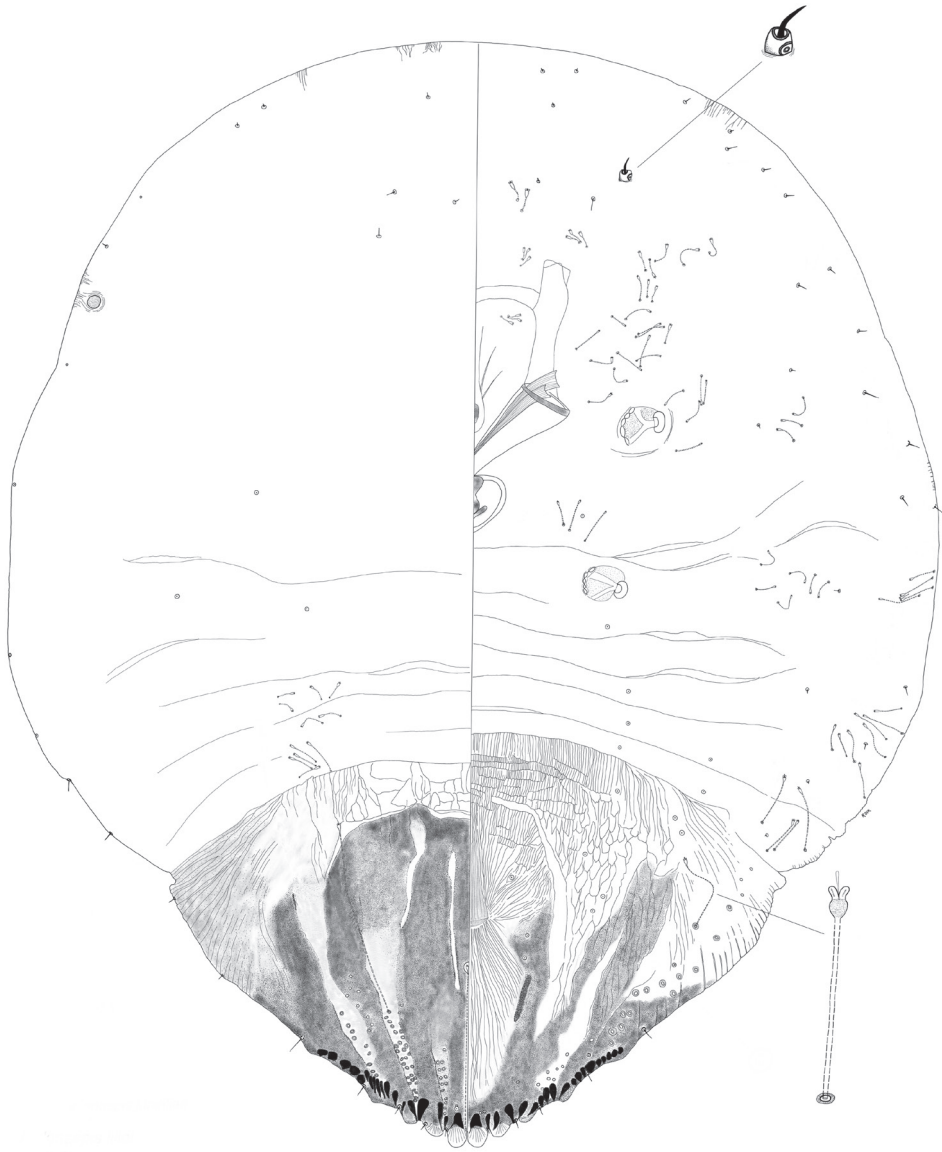


Figure 7. *Melanaspis lilloi* sp. nov. Adult female, full body view, illustrated from the holotype (D0275L).

duct orifices in furrows of second and third spaces membranous, especially towards anterolateral corner of furrow, or surrounded by partial or complete sclerotized ring, especially near posterior end and along medial margin of furrow; submedial clusters of dorsal macroducts present on each pre-pygidial abdominal segment, shorter and narrower than pygidial ducts. Ventral pygidial microducts similar to dorsal macroducts in size and shape and similarly arranged in rows on segments V–VII, 21–44 (median 33) on each side; ventral duct orifices on segment V each surrounded by conspicuous

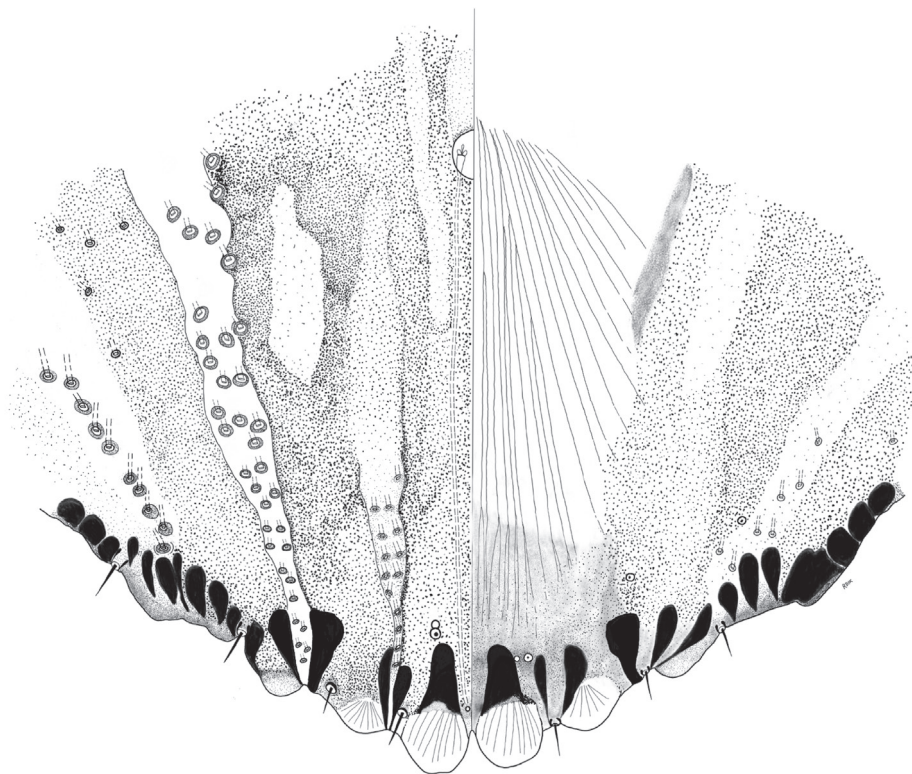


Figure 8. *Melanaspis lilloi* sp. nov. Adult female, expanded view of pygidium, illustrated from the holotype (D0275L).

sclerotized ring, degree of sclerotization decreasing towards anterolateral corner of segment; microducts also distributed along head, thorax, and pre-pygidial margins, as well as rows extending from marginal area toward each spiracle. **Anal opening:** Oval, 20–28 (median 24) μm long, positioned 3.5–6.3 (median 4.6) anal lengths (85–124, median 107 μm) from base of L1, near midpoint of pygidium. **Perivulvar pores:** Absent.

DNA sequences. Several DNA sequences of *Melanaspis lilloi* sp. nov. have been published, including fragments of 4 loci from a paratype (D0275G): 28S, GenBank accession number KY218989.1; EF-1 α , MH915714.1 and KY221286.1; CAD, MH915988.1; and COI-II, KY22069.1 and MH916394.1. DNA sequences have also been published for other members of the type series that were ground to powder during DNA preparation; these include sequences of 28S (D0275D, DQ145363.2; D0297A, DQ145362.2 and KY219142.1), EF-1 α (D0275D, DQ145475.1; D0297A, DQ145474.1 and KY221295.1), and COI-II (D0275, GQ445417.1; D0297A, GQ425005.1). DNA sequences of the primary bacterial endosymbiont, *Uzinura diaspidicola*, of *M. lilloi* sp. nov. have also been published for ground-up individuals of the type series, including fragments of 16S rDNA (D0275, DQ133558.1 and DQ868836.1; D0297A, GQ424858.1) and 23S rDNA (D0275, DQ873248.1).

Informal synonyms. Specimens from the type series have appeared in several published phylogenetic trees, and have been referred to variously as “*Melanaspis* sp. nov.” (Gruwell et al. 2005) “*Melanaspis* sp. undesc #2” and “*Melanaspis* sp. undesc #3” (Gruwell et al. 2007; Morse and Normark 2006; Rugman-Jones et al. 2010), “*Melanaspis* sp. undesc.” (Gruwell et al. 2009), “*Melanaspis* sp. nov. 1” and “*Melanaspis* sp. nov. 2” (Andersen et al. 2010), and “*Melanaspis* ud0276” (Schneider et al. 2018; Normark et al. 2019).

Remarks. This species is very similar to *M. targionoides* sp. nov. The diagnosis and affinities of *M. lilloi* sp. nov. are discussed below under the remarks for *M. targionoides* sp. nov.

Host plant. Not recorded.

Etymology. The specific epithet is a noun in the genitive case, meaning “of Lillo”. It honors the Instituto Miguel Lillo, academic home of Lucia Claps and the other scientists who first collected the species described in this manuscript.

Distribution. Argentina (Jujuy).

***Melanaspis targionoides* Schneider, Claps, Wei, Normark & Normark, sp. nov.**

<http://zoobank.org/2416C2B7-1A4F-40E7-BEE3-18536816FF23>

Figs 9, 10

Material examined. Holotype: ARGENTINA • 1 adult female; Jujuy, entre Maimará & Tilcara; 23.586S, 65.408W; 13.II.2002; L. E. Claps, P. Zamudio, L. Diaz-Briz, & P. Cabrera leg.; IFML, L. E. Claps catalog #20-02, #1092 (D0272C). **Paratypes:** ARGENTINA • 1 adult female; same data as holotype; UMEC (D0272E) • 1 adult female; same data as holotype; UMEC (D0272F) • 4 adult females; Jujuy, Humahuaca, camino a Aparzo; 23.20S, 65.10W; 13.II.2002; L. E. Claps, P. Zamudio, L. Diaz-Briz, & P. Cabrera leg.; USNM, L. E. Claps catalog #23-02 (D0264D) • 1 adult female; same data as previous; USNM (D0264C) • 1 adult female; same data as previous; USNM (D0264E) • 1 adult female; same data as previous; USNM (D0264F) • 1 adult female; same data as previous; USNM (D0264G) • 3 adult females; Jujuy, 30 km N Humahuaca; 22.97S, 65.39W; 12.II.2002; L. E. Claps, P. Zamudio, L. Diaz-Briz, & P. Cabrera leg.; UMEC, L. E. Claps catalog #6-02 (D0276F) • 1 adult female; same data as previous; UMEC (D0276E) • 4 adult females; Jujuy, Humahuaca, entrada a Juella; 23.525S, 65.396W; 14.II.2002; L. E. Claps, P. Zamudio, L. Diaz-Briz, & P. Cabrera leg.; IFML, L. E. Claps catalog #26-02 (D0291D) • 1 adult female; same data as previous; IFML (D0291C).

Description ($N = 20$). Adult female presumed to secrete scale cover, not pupilarial. Appearance in life not recorded. Slide-mounted adult female 860–1720 (median 1130, holotype 1020) μm long, 730–1440 (median 960, holotype 860) μm wide; broadest near mesothorax. Body outline turbinate. Prosoma becoming sclerotized at full maturity (length > 1400 μm); derm otherwise membranous except for pygidium, which has characteristic dorsal sclerotized areas; sclerotization of these areas unusually

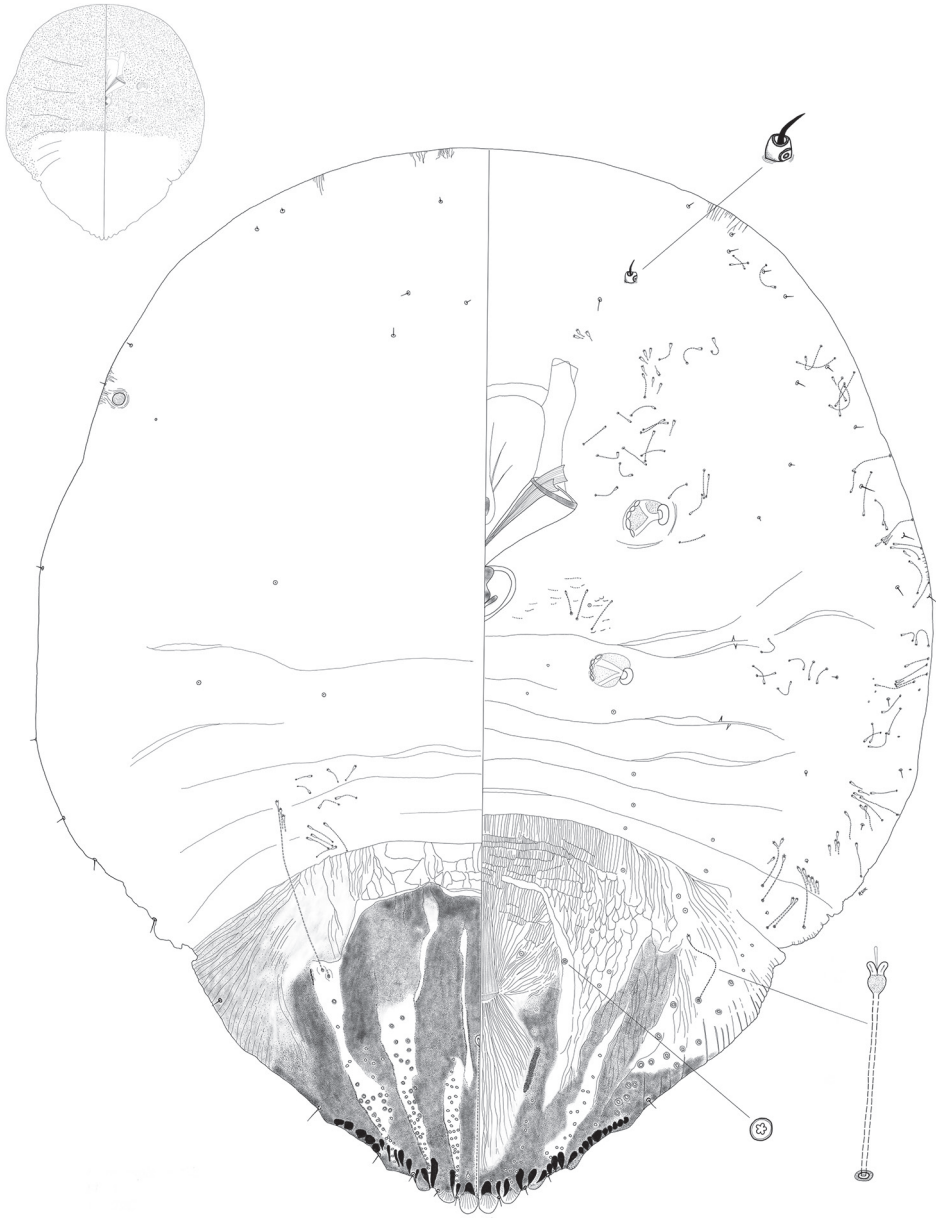


Figure 9. *Melanaspis targionoides* sp. nov. Teneral adult female, full body view, illustrated from the holotype (D0272C). Inset at upper left shows sclerotization pattern of a fully mature female, illustrated from a paratype (D0264E).

heavy, such that paraphyses and basal scleroses of lobes difficult to discern clearly on some specimens. Antennae simple, each with 1 long seta, distance between antennae 130–410 (median 230) μm . Without disc pores near spiracles. **Lobes:** With 4 pairs of

well-developed pygidial lobes, L1–L3 apically rounded and L4 truncate or pointed, notches absent from lobes; L1 slightly wider than long, median lobes separated by narrow space 0.15 times width of L1, with basal sclerosis about 1/2 width of L1 arising from mesal edge; L2 and L3 similar in size and shape, shorter and broader than L1; L4 somewhat variable in shape, truncate or with sloping edges. **Paraphyses:** Short and clavate, scarcely longer than L1; absent between L1, paraphysis formula 2-2-3 or 2-2-4; 1 interlobular paraphysis near outer corner of L1, 1 attached to inner corner of L2, 1 in interlobular space between L2 and L3, 1 attached to inner and outer corners of L3, 1 narrow paraphysis attached to inner corner of L4 and 2–3 narrow paraphyses in interlobular space between L3 and L4, these often fused into a single complex mass and difficult to count; several paraphysis-like sclerotizations surrounding macroduct orifices present beyond L4. **Plates:** Apparently absent. **Ducts:** Dorsal pygidial macroducts of 1-barred type, nearly uniform in size, with minute orifices and long slender ducts, most arranged in distinct furrows between sclerotized areas arising from interlobular spaces; 1 submarginal macroduct orifice immediately anterior to each L1, with ducts extending beyond posterior margin of anal opening; 17–36 (median 29) duct orifices in furrow of first space, originating between L1 and L2 and extending in elongate cluster anteriorly 90% of distance to anus or farther, anterior end of cluster usually directly laterad of anus, each duct about 120–130 μm in length; 18–53 (median 35) in furrow of second space, originating between L2 and L3 and extending anteriorly to a point laterad or anterolaterad of anus; 7–14 (median 9) on sclerotized area arising from L3; 15–30 (median 19) in furrow of third space, originating between L3 and L4 and extending anteriorly to a point anterolaterad of anus; duct orifices in furrows of second and third spaces each surrounded by sclerotized ring; submedial clusters of dorsal macroducts present on each pre-pygidial abdominal segment, shorter and narrower than pygidial ducts. Ventral pygidial microducts similar to dorsal macroducts in size and shape and similarly arranged in rows on segments V–VII, 23–51 (median 35) on each side; ventral duct orifices on segment V each surrounded by conspicuous sclerotized ring, degree of sclerotization decreasing towards anterolateral corner of segment; microducts also distributed along head, thorax, and pre-pygidial margins, as well as rows extending from marginal area toward each spiracle. **Anal opening:** Oval, 14–31 (median 20) μm long, positioned 4–9 (median 6) anal lengths (102–144 μm , median 129 μm) from base of L1, near midpoint of pygidium. **Perivulvar pores:** Absent or present; 0–11 (median 0, holotype 1) pores in total, distributed as one loose cluster on only one side of the body (5 of 7 individuals with pores present) or as one loose cluster on each side of the body.

DNA sequences. Several DNA sequences of *Melanaspis targionoides* sp. nov. have been published, including fragments of 3 loci from the holotype (D0272C): large ribosomal subunit (28S, GenBank accession number KY218986.1), elongation factor 1-alpha (EF-1 α , MH915711.1), and carbamoylphosphate synthetase (CAD, MH915986.1). DNA sequences have also been published for the paratypes D0276E (28S, KY218990.1; EF-1 α , MH915715.1; CAD, MH915989.1) and D0264C (28S, KY218983.1). Several other members of the type series were ground to powder dur-



Figure 10. *Melanaspis targionoides* sp. nov. Adult female, expanded view of pygidium, illustrated from the holotype (D0272C).

ing DNA preparation; morphological vouchers were not preserved, but DNA sequences were published. These include sequences of 28S (D0264A, DQ145361.2; D0264C, KY218983.1; D0291A, KY219004.1 and DQ145395.2), EF-1 α (D0264A, DQ145473.1), and cytochrome oxidase I and II (COI-II, D0276G, MH919222.2). An additional sequence of COI-II purporting to be from a member of the type series of this species, D0264A, was available on GenBank from 2010–2020 under accession number GQ424989.1. This was actually a sequence of a different species, *Aonidomytilus espinosai* Porter, GQ424988.1, erroneously assigned due to contamination or mislabeling; it has been retracted from GenBank. DNA sequences of the primary bacterial endosymbiont, *Uzinura diaspidicola*, of *M. targionoides* sp. nov. have also been published, including a fragment of the small ribosomal subunit (16S) of a paratype (D0264C, KY220091.1) and 2 ground-up specimens of the type series (D0264A, GQ424852.1; D0291A, DQ868844.1), and a fragment of the large ribosomal subunit (23S of D0291B, DQ873256.1).

Informal synonyms. Specimens from the type series and their endosymbionts have appeared in several published phylogenetic trees, and have been referred to variously as

“*Melanaspis* sp. nov.” (Gruwell et al. 2005), “*Melanaspis* sp undesc #1” and “*Melanaspis* sp undesc #4” (Gruwell et al. 2007; Morse and Normark 2006; Rugman-Jones et al. 2010), “*Melanaspis* sp. undesc.” (Gruwell et al. 2009), “*Melanaspis* sp nov 1” (Andersen et al. 2010), and “*Melanaspis* ud0276” (Schneider et al. 2018; Normark et al. 2019).

Remarks. This species is very similar to the previous one, *Melanaspis lilloi* sp. nov. The two were considered to belong to a single undescribed species, (“*Melanaspis* ud0276”) by Schneider et al. (2018) and Normark et al. (2019). The diversity of informal designations assigned to members of the two species prior to 2018 were record-keeping artifacts and did not reflect any diversity of evidence-based hypotheses. Careful study of the type series during the preparation of this manuscript revealed slight but consistent morphological differences between what are here regarded as separate species. The two species are also distinguishable by DNA, and appear as separate clusters in published phylogenies (Morse and Normark 2006; Normark et al. 2019). The pattern is seen most clearly in figure S2 of Normark et al. (2019), and is seen in each of the loci sampled from both species in that study: 2.2% divergence at 28S (compared to 0.14% within *M. lilloi* sp. nov.), 2.2–2.3% divergence at EF-1 α (compared to 0.12–0.35% within each species), and 1.45% divergence at the primary endosymbiont’s 16S locus (compared to 0.18–0.19% within each species). Although the species are morphologically very similar, *M. targionoides* sp. nov. has more numerous and more sclerotized dorsal ducts, along with sclerotization of the prosoma at full maturity. Specifically, the two species may be distinguished by the following characters. In *M. targionoides* sp. nov., the elongate cluster of dorsal ducts in the furrow of the first space (arising between L1 and L2) extends anteriorly at least 90% of the distance to the anus, its anterior end usually being directly lateral to the anus; in *M. lilloi* sp. nov., this cluster of dorsal ducts extends only 60–85% of the distance to the anus, its anterior end always lying posterolateral to the anus. In *M. targionoides* sp. nov. the furrow of the third space (arising between L3 and L4) has a single or double line of conspicuous subcircular sclerotized duct orifices extending from near the posterior margin to the anterior third of the pygidium; in *M. lilloi* sp. nov., the furrow of the third space has sclerotized duct openings only in the posterior third of the pygidium, with sometimes a few present further anteriorly along the medial edge of the furrow (lateral edge of the sclerotized area arising from L3) – these are often only partially sclerotized and anteroposteriorly compressed, thus appearing as partial ellipses rather than complete circles. *Melanaspis targionoides* sp. nov. has the prosoma sclerotized at full maturity (body length greater than 1.4 mm); *M. lilloi* sp. nov. has the prosoma membranous at full maturity. *Melanaspis targionoides* sp. nov. sometimes has perivulvar pores; *M. lilloi* sp. nov. lacks perivulvar pores.

Melanaspis targionoides sp. nov. and *M. lilloi* sp. nov. are referable to *Melanaspis* based upon the characteristic sclerotization pattern of the dorsal pygidium, and their placement in *Melanaspis* is supported by molecular evidence (Morse and Normark 2006; Andersen et al. 2010; Rugman-Jones et al. 2010; Schneider et al. 2018; Normark et al. 2019;). However, they possess a combination of traits often seen in species of *Targionia*, including the absence of plates, presence of numerous small, slender

macroducts arranged in distinct furrows, and simple, rounded pygidial lobes lacking notches. Plates are typically present in species of *Melanaspis* but can be highly reduced and difficult to view. The simple lobes and short paraphyses found in *M. targionoides* sp. nov. and *M. lilloi* sp. nov. are similar in appearance to those of *M. enceliae* (Ferris), but the number and distribution of macroducts is quite distinct from any other species observed for this genus.

Host plant. Not recorded.

Etymology. The specific epithet is an adjective describing the resemblance this species bears to others placed in *Targionia* by adding the suffix *-oides* to indicate likeness in form.

Distribution. Argentina (Jujuy).

Key to species of Aspidiotini in Argentina based on adult females

- 1 Paraphyses or paraphysis-like sclerotizations absent.....2
- Paraphyses or paraphysis-like sclerotizations present4
- 2 With two pairs of well-developed pygidial lobes, L3 entirely absent; perivulvar pores absent; margin of prosoma sclerotized
..... *Chortinaspis jujuyensis* sp. nov.
- With three pairs of well-developed pygidial lobes, L3 at least represented by narrow processes; perivulvar pores present; margin of prosoma membranous.....3
- 3 Anal opening about same size in diameter as length of L1, or longer; dorsal setae associated with outer corners of L2 and L3 slender, not thickened basally *Aspidiotus nerii* (Bouché)
- Anal opening noticeably shorter in diameter than length of L1; dorsal setae associated with outer corners of L2 and L3 thickened, swollen basally
..... *Oceanaspidiotus spinosus* (Comstock)
- 4 Paraphyses or paraphysis-like sclerotizations present anterior to position of L3.....5
- Paraphyses or paraphysis-like sclerotizations absent anterior to position of L3.....19
- 5 Dorsum of pygidium with several sclerotized areas divided by furrows, one of which isolates L2 from remaining sclerotized areas; anterior submarginal region of dorsal pygidium appears reticulated or striped with variously branching furrows; longest paraphyses attached to lobes, never arising from interlobular spaces (*Crenulaspidiotus*)6
- Pygidium not as described above, L2 not isolated on a distinct sclerotized area; dorsal submargins of pygidium without reticulated or branched furrows, region patterned by fine parallel cuticular lines running perpendicular to body margin; longest paraphyses often arising from interlobular spaces9
- 6 Interlobular paraphysis formula in first, second, and third spaces 1-1-1
..... *Crenulaspidiotus maurellae* (Laing)
- Interlobular paraphysis formula in first, second, and third spaces, 1-2-27

- 7 Ventral microducts present in area anterior to interlobular space between L3 and L4; dorsal submargin adjacent to L4 reticulate *Crenulaspidotus cyrtus* Miller & Davidson
- Ventral microducts present in area anterior to interlobular space between L3 and L4; dorsal submargin adjacent to L4 striped 8
- 8 Segments I and II with conspicuous pre-pygidial lobes *Crenulaspidotus greeneri* Miller & Davidson
- Segments I and II without conspicuous pre-pygidial lobes *Crenulaspidotus labillei* (Lizer & Trelles)
- 9 Body elongate, length approximately 2X maximum width *Pseudischnaspis bowreyi* (Cockerell)
- Body round or turbinate, length less than 2X maximum width 10
- 10 Pygidium elongate and apically acute, with wide base and straight or concave sides tapering to point; angle formed by lateral pygidial margins being less than 90 degrees (*Acutaspis*) 11
- Pygidium short and apically broad, margins usually convex; pygidial angle usually greater than 90 degrees 14
- 11 Cephalic margin of body with median notch; with slight indication of prothoracic tubercles; paraphysis arising from outer angle of L2 longer than any others arising between L2 and L3; paraphysis arising from outer angle of L3 among longest representatives *Acutaspis reniformis* (Cockerell)
- Cephalic margin of body without median notch; without any indication of prothoracic tubercles; paraphysis arising from outer angle of L2 shorter than at least one other paraphysis arising between L2 and L3; paraphysis arising from outer angle of L3 noticeably shorter than longest representatives 12
- 12 Derm sclerotized around body margins, leaving central portion membranous; adult female body can reach over 2 mm in length *Acutaspis scutiformis* (Cockerell)
- Derm membranous throughout except for pygidium; adult female body typically less than 2 mm in length 13
- 13 Perivulvar pores arranged in 4 small but distinct groups; longest paraphysis arising from interlobular space *Acutaspis paulista* (Hempel)
- Perivulvar pores in lateral groups alone, forming an irregular longitudinal series of pores; longest paraphysis arising from lateral angle of lobe *Acutaspis aliena* (Newstead)
- 14 Plates well developed and fimbriate; dorsal macroduct orifices vary in size *Lindingaspis rossi* (Maskell)
- Plates simple, minimally fringed, or absent; dorsal macroduct orifices of uniform size 15
- 15 Plates present; cephalic margin with sclerotized protuberance (*Mycetaspis*) 16
- Plates absent; cephalic margin without sclerotized protuberance 17

- 16 Median lobes each with broad basal sclerosis as wide as L1 at proximal base .
..... *Mycetaspis personata* (Comstock)
- Median lobes each with narrow basal sclerosis arising only from medial angle
of lobe *Mycetaspis apicata* (Newstead)
- 17 Dorsum of pygidium with heavily sclerotized areas separated by lightly scler-
otized pore furrows..... **18**
- Dorsum of pygidium without heavily sclerotized areas between pore furrows
..... *Targionia fabianae* Leonardi (in part)
- 18 Furrow of third space with continuous single or double row of conspicuous
sclerotized duct openings extending from submargin to anterior third of py-
gidium; furrow of first space usually with more than 20 duct orifices, extend-
ing from submargin at least 90% of distance to anus; prosoma sclerotized
at full maturity (when body length > 1.4 mm); with or without perivulvar
pores..... *Melanaspis targionoides* sp. nov.
- Furrow of third space without continuous row of sclerotized duct openings
extending from margin to anterior, sclerotized duct openings occurring only
in posterior third of furrow and sporadically along the medial margin; furrow
of first space usually with fewer than 20 duct orifices, extending from sub-
margin only 60–85% of distance to anus; prosoma remaining membranous;
without perivulvar pores *Melanaspis lilloi* sp. nov.
- 19 Pygidium with 3 definite pairs of sclerotized lobes, each similar in shape and
size..... **20**
- Pygidium with at most 2 definite pairs of sclerotized lobes of similar shape, if
present L3 represented by small sclerotized point..... **24**
- 20 Paraphyses often obscure and shorter than L1; prosoma of mature adult fe-
male heavily sclerotized; body reniform in shape (*Aonidiella*) **21**
- Paraphyses obvious and longer than L1; prosoma of mature adult female
membranous; body turbinate in shape (*Chrysomphalus*) **23**
- 21 With 24–38 dorsal macroducts on each side of pygidium; without apophyses
or scleroses anterolaterad of vulva *Aonidiella taxus* Leonardi
- With 20–26 dorsal macroducts on each side of pygidium; with apophyses or
scleroses anterolaterad of vulva..... **22**
- 22 Normally each apophysis anterolaterad of vulva with 2 associated scleroses;
paraphysis formula of 3-3-1 or 3-2-2 *Aonidiella aurantii* (Maskell)
- Normally each apophysis anterolaterad of vulva without adjacent scleroses;
rarely with faint scleroses; paraphysis formula of 2-2-0, 2-3-0, 3-3-0, 3-3-1 or
3-2-2 *Aonidiella citrina* (Coquillett)
- 23 Dorsal macroducts in second and third furrows few, arranged in single rows;
pre-pygidial abdominal segment II lacking a dorsal cluster of 4 or more
ducts..... *Chrysomphalus dictyospermi* (Morgan)
- Dorsal macroducts in second and third furrows more numerous, arranged in
double or triple rows; pre-pygidial abdominal segment II with a cluster of 4
or more dorsal ducts *Chrysomphalus pinnulifer* (Maskell)

24	Pygidial plates absent.....	<i>Targionia fabianae</i> Leonardi (in part)
–	Pygidial plates present.....	25
25	Distinctive plates between positions of L3 and L4, with 1 or 2 lateral tines around a central duct projecting from the body margin	<i>Comstockaspis perniciosus</i> (Comstock)
–	Plates between positions of L3 and L4 absent, simple or fringed, without a protruding central microduct.....	26
26	Distance between posterior margin of anus and apex of L1 within about 2X longest anal diameter	27
–	Distance between posterior margin of anus and apex of L1 about or exceeding 3X longest anal diameter.....	33
27	Perivulvar pores absent.....	28
–	Perivulvar pores present	31
28	L1 and L2 each with 1 lateral notch.....	<i>Hemiberlesia diffinis</i> (Newstead)
–	L1 with 1 medial and 1 lateral notch, L2 without notches	29
29	L2 with rounded apex, similar in shape to L1	<i>Hemiberlesia corporifusca</i> (Chiesa Molinari)
–	L2 pointed, distinctly different in shape.....	30
30	L2 represented by unsclerotized point; L3 entirely absent, represented at most by rounded projection; anal opening fairly large but located at least 1X anal diameter from apex of L1	<i>Hemiberlesia nothofagi</i> Williams
–	L2 and L3 both represented by small sclerotized points; anal opening very large and located less than 1X anal diameter from apex of L1	<i>Hemiberlesia rapax</i> (Comstock)
31	L2 and L3 represented at most by small unsclerotized points; plates beyond L3 simple, minimally fringed.....	<i>Hemiberlesia lataniae</i> (Signoret)
–	L2 with medial and lateral notches, L3 pointed and sclerotized; plates beyond L3 well developed and fringed	32
32	L2 unsclerotized, often blending in with surrounding plates; all plates highly fringed and exceeding L1 in length	<i>Hemiberlesia palmae</i> (Cockerell)
–	L2 sclerotized, easily distinguishable from plates; some plates minimally fringed and approximately same length as L1	<i>Hemiberlesia cyanophylli</i> (Signoret)
33	L3 well developed; anal opening about equal in size to 1 median lobe	34
–	L3 represented at most by slight projection or unsclerotized point; anal opening clearly smaller than 1 median lobe	35
34	L1 with basal sclerosis; anal opening longer than wide; paraphyses between L1 and L2 represented by doubled pairs, forming small furrow with 4–6 macroducts	<i>Hemiberlesia latastei</i> (Cockerell)
–	L1 without basal sclerosis; anal opening wider than long; paraphyses between L1 and L2 represented by single pair, with 2 macroducts arising from interlobular space.....	<i>Hemiberlesia mendax</i> McKenzie

35	Perivulvar pores absent.....	36
–	Perivulvar pores present	38
36	Paraphyses arising from outer angle of L1 without swollen knob at anterior end, about equal in length to L1	<i>Hemiberlesia ozolita</i> sp. nov.
–	Paraphyses arising from outer angle of L1 with swollen knob at anterior end, noticeably longer than length of L1	37
37	Paraphysis arising from outer angle of L1 mushroom-shaped in appearance; plates fringed and at least as long as L1	<i>Clavaspis herculeana</i> (Cockerell & Hadden)
–	Paraphysis arising from outer angle of L1 swollen at anterior end but not mushroom-shaped; plates all simple and shorter in length than L1	<i>Clavaspis subsimilis</i> (Cockerell)
38	L2 well developed or represented by sclerotized projection of pygidial margin	39
–	L2 represented at most by unsclerotized point	40
39	Posterior apex of L2 in line with or posterior to apex of L1; plates well developed, as long as L1.....	<i>Diaspidiotus ancylus</i> (Putnam) (leaf form)
–	Posterior apex of L2 anterior to apex of L1; plates poorly developed, shorter in length than L1	<i>Diaspidiotus ostreaeformis</i> (Curtis)
40	Minimally fringed plates present between L1–L2 and L2–L3, absent or present anterior to position of L3, broad-based with 2 or 3 fringes when present; with 1 or 2 submarginal macroducts on dorsum of IV	<i>Clavaspis patagonensis</i> sp. nov.
–	Well fringed plates present between L1–L2 and L2–L3, only simple plates present anterior to position of L3; without submarginal macroducts on dorsum of IV	41
41	L1 without medial notch, with 1 lateral notch; with 2 simple plates between median lobes; 30 or more perivulvar pores present.....	<i>Diaspidiotus ancylus</i> (Putnam) (bark form)
–	L1 with 1 medial and 1 lateral notch; without plates between median lobes; fewer than 30 perivulvar pores present	<i>Diaspidiotus uvae</i> (Comstock)

Additional online resources aiding in the identification of Aspidiotini are provided by Schneider et al. (2019) and Dooley (2006).

Acknowledgements

We thank all those who helped LEC collect specimens: P. Zamudio, L. Díaz-Briz, L. Guardia Claps, and P. Cabrera. Specimens were collected under permits to LEC from the government of Jujuy province (File #0646-076 Resolution #264) and the National Parks Administration (APN) (Resolution # 0039079). Specimens were prepared by

N. Vajda, B. Peters, R. Carlton, M. Fizdale, M. Nichols, A. Krewinski, and E. Stangle. JW's participation was supported by the China Scholarship Council. This research was supported in part by the National Science Foundation (DEB-0447880, DEB-1258001). It was also supported in part by the U. S. Department of Agriculture's National Institute of Food and Agriculture, and by the University of Massachusetts Amherst Biology Department and Center for Agriculture, Food, and the Environment, under project number MAS00535. It was also supported in part by the U.S. Department of Agriculture's Agricultural Research Service. The authors have declared that no competing interests exist. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture. The contents are solely the responsibility of the authors and do not necessarily represent the official views of the USDA or NIFA. USDA is an equal opportunity provider and employer.

References

- Andersen JC, Wu J, Gruwell ME, Gwiazdowski R, Santana SE, Feliciano NM, Morse GE, Normark BB (2010) A phylogenetic analysis of armored scale insects (Hemiptera: Diaspididae), based upon nuclear, mitochondrial, and endosymbiont gene sequences. *Molecular Phylogenetics and Evolution* 57: 992–1003. <https://doi.org/10.1016/j.ympev.2010.05.002>
- Claps LE, Terán AL (2001) Diaspididae (Hemiptera: Coccoidea) asociadas a cítricos en la provincia de Tucumán (República Argentina). *Neotropical Entomology* 30: 391–402. <https://doi.org/10.1590/S1519-566X2001000300009>
- Claps LE, Wolff VRS (2003) Cochinillas Diaspididae (Hemiptera: Coccoidea) frecuentes en plantas de importancia económica de la Argentina y Brasil. *Publicación Especial de la Sociedad Entomológica Argentina* 3: 58 pp.
- Claps LE, Wolff VRS (2014) Diaspididae. In: Roig-Juñent S, Claps LE, Morrone JJ (Eds) *Biodiversidad de Artrópodos Argentinos volumen 3 INSUE - UNT*, San Miguel de Tucumán, Argentina, 293–302.
- Claps LE, Wolff VRS, González RH (2001a) Catálogo de las Diaspididae (Hemiptera: Coccoidea) exóticas de la Argentina, Brasil y Chile. *Revista de la Sociedad Entomologica Argentina* 60: 9–34.
- Claps LE, Wolff VRS, González RH (2001b) Catálogo de las especies de Diaspididae (Hemiptera: Coccoidea) nativas de Argentina, Brasil y Chile. *Insecta Mundi* 13: 239–256.
- Dooley JW (2006) Key to the genera of the Aspidiotini. [https://keys.lucidcentral.org/keys/v3/Dones_Lourdes/other%20files/aspidiotini%20\(diaspididae\)%20genera.pdf](https://keys.lucidcentral.org/keys/v3/Dones_Lourdes/other%20files/aspidiotini%20(diaspididae)%20genera.pdf) [accessed 5.vi.2020]
- Ferris GF (1938) *Atlas of the Scale Insects of North America*. Oxford University Press, London, 277 pp.
- García Morales M, Denno BD, Miller DR, Miller GL, Ben-Dov Y, Hardy NB (2016) ScaleNet: A Literature-based model of scale insect biology and systematics. *Database* 2016: bav118. <https://doi.org/10.1093/database/bav118>

- Granara de Willink MC, Claps LE (2003) Cochinillas (Hemiptera: Coccoidea) presentes en plantas ornamentales de la Argentina. *Neotropical Entomology* 32: 475–488. <https://doi.org/10.1590/S1519-566X2003000400013>
- Gruwell ME, Morse GE, Normark BB (2007) Phylogenetic congruence of armored scale insects (Hemiptera: Diaspididae) and their primary endosymbionts from the phylum Bacteroidetes. *Molecular Phylogenetics and Evolution* 44: 267–280. <https://doi.org/10.1016/j.ympev.2007.01.014>
- Gruwell ME, von Dohlen CD, Patch K, Normark BB (2005) Preliminary PCR survey of bacteria associated with scale insects (Hemiptera: Coccoidea). In: Erkökçü LB, Kaydan MB (Eds) *Proceedings of the Tenth International Symposium on Scale Insect Studies*. Scientific and Technical Research Council of Turkey, Ankara, Adana, Turkey, 101–116 pp.
- Gruwell ME, Wu J, Normark BB (2009) Diversity and phylogeny of *Cardinium* (Bacteroidetes) in armored scale insects (Hemiptera: Diaspididae). *Annals of the Entomological Society of America* 102: 1050–1061. <https://doi.org/10.1603/008.102.0613>
- Miller DR, Davidson JA (1990) A list of the armored scale insect pests. In: Rosen D (Ed.) *Armoured scale insects: their biology, natural enemies and control*. Elsevier, Amsterdam, 299–306.
- Miller DR, Davidson JA (2005) *Armored scale insect pests of trees and shrubs* (Hemiptera: Diaspididae). Cornell University Press, Ithaca, NY, 442 pp.
- Morse GE, Normark BB (2006) A molecular phylogenetic study of armoured scale insects (Hemiptera: Diaspididae). *Systematic Entomology* 31: 338–349. <https://doi.org/10.1111/j.1365-3113.2005.00316.x>
- Normark BB, Morse GE, Krawinski A, Okusu A (2014) Armored scale insects (Hemiptera: Diaspididae) of San Lorenzo National Park, Panama, with descriptions of two new species. *Annals of the Entomological Society of America* 107: 37–49. <https://doi.org/10.1603/AN13110>
- Normark BB, Okusu A, Morse GE, Peterson DA, Itioka T, Schneider SA (2019) Phylogeny and classification of armored scale insects (Hemiptera: Coccoidea: Diaspididae). *Zootaxa* 4616: 001–098. <https://doi.org/10.11646/zootaxa.4616.1.1>
- Rugman-Jones PF, Andersen JC, Morse GE, Normark BB, Stouthamer R (2010) Molecular phylogenetic placement of the recently described armored scale insect *Abgrallaspis aguacatae* and several congeners (Hemiptera: Diaspididae). *Annals of the Entomological Society of America* 103: 30–38. <https://doi.org/10.1093/aesa/103.1.30>
- Schneider SA, Fizdale M, Normark BB (2019) An online interactive identification key to common pest species of Aspidiotini (Hemiptera, Coccoidea, Diaspididae), version 1.0. *ZooKeys* 867: 87–96. <https://doi.org/10.3897/zookeys.867.34937>
- Schneider SA, Okusu A, Normark BB (2018) Molecular phylogenetics of Aspidiotini armored scale insects (Hemiptera: Diaspididae) reveals rampant paraphyly, curious species radiations, and multiple origins of association with *Melissotarsus* ants (Hymenoptera: Formicidae). *Molecular Phylogenetics and Evolution* 129: 291–303. <https://doi.org/10.1016/j.ympev.2018.09.003>

***Odontomachus davidsoni* sp. nov. (Hymenoptera, Formicidae), a new conspicuous trap-jaw ant from Ecuador**

Philipp O. Hoenle¹, John E. Lattke², David A. Donoso^{3,4}, Christoph von Beeren¹, Michael Heethoff¹, Sebastian Schmelzle¹, Adriana Argoti⁵, Luis Camacho⁶, Bernhard Ströbel⁷, Nico Blüthgen¹

1 Ecological Networks, Department of Biology, Technical University of Darmstadt, Darmstadt, Germany **2** Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil **3** Departamento de Biología, Escuela Politécnica Nacional, Quito, Ecuador **4** Centro de Investigación de la Biodiversidad y Cambio Climático, Universidad Tecnológica Indoamérica, Quito EC170103, Ecuador **5** Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador **6** Department of Zoology, University of British Columbia, Vancouver, Canada **7** University of Applied Sciences, Darmstadt, Germany

Corresponding author: Philipp Hoenle (philipp.hoenle92@gmail.com); John Lattke (piquihuye@gmail.com)

Academic editor: Brian Lee Fisher | Received 22 November 2019 | Accepted 27 March 2020 | Published 13 July 2020

<http://zoobank.org/A4DA6A84-D9A9-452D-BB07-300D6F5A2F02>

Citation: Hoenle PO, Lattke JE, Donoso DA, von Beeren C, Heethoff M, Schmelzle S, Argoti A, Camacho L, Ströbel B, Blüthgen N (2020) *Odontomachus davidsoni* sp. nov. (Hymenoptera, Formicidae), a new conspicuous trap-jaw ant from Ecuador. ZooKeys 948: 75–105. <https://doi.org/10.3897/zookeys.948.48701>

Abstract

One of the largest species in its genus, *Odontomachus davidsoni* Hoenle, Lattke & Donoso, **sp. nov.** is described from workers and queens collected at lowland forests in the Chocó-Darién bioregion in coastal Ecuador. The workers are characterized by their uniform red coloration, their large size (16–18 mm body length), and their frontal head striation that reaches the occipital margin. DNA barcodes (COI) and high resolution 2D images of the type material are provided, as well as an updated key for the Neotropical species of *Odontomachus*. In addition, a three-dimensional digital model of the worker holotype and a paratype queen scanned with DISC3D based on photogrammetry is presented, for the first time in a species description. Findings of large and conspicuous new species are uncommon around the world and suggest that these Ecuadorian rainforests may conceal many more natural treasures that deserve conservation.

Resumen

Describimos una especie nueva, entre las más grandes conocidas del género *Odontomachus*. La nueva especie, *Odontomachus davidsoni* Hoenle, Lattke & Donoso, sp. nov., es descrita a partir de obreras y reinas

recolectadas en bosques de tierras bajas en la bioregión Chocó-Darién de la costa del Ecuador. Las obreras se caracterizan por su coloración rojiza uniforme, su grande tamaño (largo del cuerpo 16–18 mm), y la estriación del frente cefálico que alcanza el margen occipital. Proveemos códigos de barras de DNA (COI) e imágenes 2D de alta resolución para el material tipo y así como una guía de identificación actualizada para las especies neotropicales del género *Odontomachus*. Por primera vez en una descripción de especies, se proveen imágenes 3D de un escáner fotogramétrico DISC3D. Los hallazgos de especies grandes y conspicuas son poco comunes alrededor del mundo y sugieren que estos bosques lluviosos ecuatorianos pueden contener muchos más tesoros naturales que merecen ser conservados.

Keywords

3D scan, DNA barcoding, DISC3D, integrative taxonomy, Northwest Ecuador, Ponerinae, tropical forest

Introduction

Members of the genus *Odontomachus* Latreille, 1804 are among the most conspicuous and recognizable ants of the subfamily Ponerinae. All members of the genus exhibit trap jaws, a character shared with the sister genus *Anochetus* Mayr, 1861 (Schmidt and Shattuck 2014) and several other unrelated genera (Larabee and Suarez 2014). Trap jaws are long, slender mandibles that are mainly used for predation and secondarily in some taxa to catapult the ant into the air as a predator escape response (Larabee and Suarez 2015). Trap jaws function via a special clamping mechanism with the mandibles opening at a 180-degree angle and snap shut at high speeds upon physical contact with mechanosensory hairs (Gronenberg et al. 1993; Gronenberg 1995). *Odontomachus* typically comprises medium- to large-sized ants with a pantropical distribution including subtropical regions. The genus currently contains a total of 72 species (Bolton 2018), with the highest diversity found in the Neotropics and South-East Asia (Larabee et al 2016; Guenard et al 2017; Matos-Maraví et al. 2018).

Ecuador, with at least 18 *Odontomachus* species (Salazar et al. 2015), is among the countries showing the highest species diversity recorded for this genus. In general, Ecuadorian biodiversity is comparatively high, because the country comprises three vastly distinct bioregions: the Amazon basin in East Ecuador, the Chocó-Darién bioregion in the North-West, and the Tumbesian drylands in the South of the country which are divided by the Andes, one of the highest mountain chains in the world (Salazar and Donoso 2013; Salazar et al. 2015). While ants of the Ecuadorian Amazon have received some attention (e.g., Donoso et al. 2009; Wilkie et al. 2010), ant research is severely lacking in the highly threatened areas of the Chocó-Darién (Donoso and Ramón 2009; Donoso 2017) and in the southern drylands (Dominguez et al. 2016; Lattke et al. 2016). Notably, the Chocó-Darién is home for several large and rare *Odontomachus* species, including *O. mormo* Brown, 1976, and *O. cornutus* Stitz, 1933, both of which are only known from few collections (Rodriguez 2008). Since Brown's (1976) global revision of the genus, the taxonomy of the New World species has remained relatively stable, with one additional species described in the United States (Deyrup & Cover 2004) and none for the Neotropics except for *O. scalptus* Brown, 1978, from Tena, in the Ecuadorian Amazon.

We describe a surprisingly large new species, i.e., *O. davidsoni* sp. nov., from the Ecuadorian Chocó-Darién region that rivals in size *O. mormo*, previously considered the largest species of New World *Odontomachus*. We use morphological and genetic analyses to distinguish it from other *Odontomachus* species and use, for the first time in insect taxonomy, textured 3D-models to present a digital version of the holotype, a queen and several other specimens.

Materials and methods

Sampling and geographic origin

Specimens of *O. davidsoni* were collected and observed in field trips to the Reserva Río Canandé in Ecuador (Esmeraldas Province) from February 2018 to April 2019. We searched for specimens by walking through the forest and examining the vegetation and recently fallen trees. Alate queens were collected with light traps directly located at the Ec lodge of the Reserve. We collected exclusively by hand, and specimens were preserved in vials containing 96% ethanol. Photographs of living specimens were taken with a Nikon D5300 camera body (Nikon Corp., Tokio, JP) and a Laowa 60mm f2.8 2× macro lens (Venus Optics, Hefei, China). The Ministerio de Ambiente de Ecuador issued the permits for collection (MAE-DNB-CM-2017-0068) and exportation (41-2018-EXP-CM-FAU-DNB/MA and 144-2019-EXP-CM-FAU-DNB/MA).

Photogrammetry

The worker holotype, two worker paratypes, and one paratype queen were mounted with water-soluble insect glue on the tip of an insect needle and imaged using the Darmstadt Insect Scanner (DISC3D, Ströbel et al. 2018). Specimens were imaged with extended depth of field (EDOF) using calibrated stacks of 19 images with 4 megapixels (Ströbel et al. 2018). EDOF images were taken from 398 viewing angles (in total 7562 images were recorded) and used for photogrammetric reconstruction and texturing in PhotoScan Professional 1.4.5. (Agisoft LLC, St. Petersburg, Russia) with the highest quality settings and visibility consistent mesh generation. Polygons corresponding to the insect pin were removed from the resulting mesh and the mesh was slightly smoothed (with a factor of 0.5). In addition, the holotype and queen models were textured using the “average” option resulting in 5000 × 5000 pixel texture maps. Textures were sharpened and cleaned in Adobe Photoshop CS6 13.0 (Adobe Inc., San Jose, CA, USA). We furthermore provide videos with added light effects created with Blender (Blender Foundation; Amsterdam, NL; Suppl. materials 1, 2).

Additional stacking pictures were taken with a Canon EOS 7D with a MPE 65mm lens (Canon, Tokyo, Japan) and a Keyence VHX-5000 (Keyence Deutschland BmH, Neu-Isenburg, Germany) with a Z20 lens. Stacking pictures were assembled with Helicon Focus Version 7 (Helicon Soft Ltd., Kharkiv, Ukraine) software, and further edited with Adobe Photoshop CS6 13.0 (Adobe Inc., San Jose, CA, USA).

Morphological data

Morphological measurements of three workers (the holotype and two paratypes) and one alate queen were performed using 3D-models embedded in PDF files obtained with DISC3D. The measurements obtained through such models are more precise and reproducible than traditional ocular micrometer measurements, partly since parallax errors are avoided (see Ströbel et al. 2018). Measurements were taken with Adobe Acrobat Reader DC (version 11.0.23; Adobe Inc., San Jose, CA, USA) following the definitions described in MacGown et al. (2014) and Brown (1976), with the exception of head and petiole height measurements (see definitions below). As Brown (1976) already recognized, heads of *Anochetus* and *Odontomachus* can have a relatively trapezoid or more rectangular shape in frontal view, which is a reliable indicator to help differentiate between species. To discern between these shapes, we included the head ocular width (HoW – synonymous with HW in other studies, e.g., MacGown et al. 2014) and head vertexal width (HvW, see below). We measured two paratype workers with a binocular with measuring eyepiece only (see Suppl. material 3). The morphological values given in the species description however solely derive from measurements of the 3D scan of workers ($N = 3$) and queen ($N = 1$) for reasons of consistency. All measurements are given in millimeters. Additional to the measurements we give a detailed morphological description of *Odontomachus davidsoni* sp. nov. The morphological terminology, including those of surface sculpturing, is based on definitions found in Wilson (1955), Harris (1979) and Keller (2011).

Measurement definitions

All measurements are given in millimeter.

CI	Cephalic index. $HW/HL \times 100$.
EL	Eye length. Maximum length of eye as measured normally in oblique view of the head to show full surface of eye.
FL	Femur length. Maximum length of hind femur.
HL	Head length. Maximum length of head in full-face view, excluding mandibles, measured from anteriormost point of clypeal margin to midpoint of a line across the posterior margin.
HoW	Head ocular width. Maximum width of head at ocular prominence in full-face view, measured in the same plane as HL.
HvW	Head vertexal width. Width of head at vertex in full-face view, measured in the same plane as HL. An imaginary line is drawn parallel to the cephalic posterior margin and perpendicular lines are extended anterad to where the posterolateral cephalic curve meets the lateral cephalic margin.
MI	Mandible index. $ML/HL \times 100$
ML	Mandible length. The straight-line length of mandible at full closure, measured in the same plane as HL, from mandibular apex to anterior clypeal margin.

MsL	Mesosoma length. Maximum length of mesosoma, measured in lateral view, a diagonal line from the cervical shield to the posterolateral propodeal edge.
PrW	Pronotum width. Maximum width of pronotum in dorsal view.
PtH	Petiole height. Direct linear distance from the apex of petiolar needle to ventral subpetiolar process measured in the same plane as PtL
PtL	Petiole length. Maximum length of petiole in lateral view.
PtW	Petiole width. Maximum width of petiole in dorsal view.
SI	Scape index. $SL/HW \times 100$.
SL	Scape length. Maximum chord length of antennal scape in dorsal view excluding basal constriction.

Museum abbreviations

The collection abbreviation is taken from Evenhuis (2020). The specimens used in this study are deposited at the following institutions:

DZUP	Department of Zoology, Universidade Federal do Paraná, Curitiba, Brazil
MCZ	Havard Museum of Comparative Zoology, Cambrigde, Massachusetts, USA
MEPN	Museo de Colecciones Biológicas Gustavo Orcés, Escuela Politécnica Nacional, Quito, Ecuador
RBINS	Royal Belgium Institute of Natural Sciences, Brussels, Belgium
QCAZ	Zoology Museum at the Pontifical Catholic University of Ecuador, Quito, Ecuador

Molecular analyses

We sequenced the classical mitochondrial barcode region for animals, a 658-base pair (bp) region of the *cytochrome oxidase subunit I* gene (COI), for two *O. davidsoni* sp. nov. specimens and six specimens of six additional *Odontomachus* species (*O. erythrocephalus* Emery, 1840, *O. mormo*, *O. chelifér* (Latreille, 1802), *O. meinerti* Forel, 1805, *O. cf. mayi* Mann, 1912, *O. hastatus* (Fabricius, 1804); see Suppl. material 4 for collection data). Specimens were identified by PH. We used whole specimens for non-destructive DNA extraction using the Qiagen 96 DNeasy Blood & Tissue Kit (Quiagen, Venlo, Netherlands) following the standard protocol with one exception: we shortened the protein lysis step to 2h–3h to avoid any damaging of the specimens, which keeps specimens intact and in good condition so as to serve as morphological vouchers (e.g., von Beeren et al. 2016). We amplified COI using the primer combination LCO1490 / HCO2198 (Folmer et al. 1994). PCRs were set up as described previously by von Beeren et al. (2016). Purification and sequencing of PCR products in forward and reverse direction were outsourced to Macrogen Europe B.V. (Amsterdam, Netherlands). The laboratory information management system Geneious Prime 2019.1.3 was used to process and analyse sequences (<https://www.geneious.com>).

To evaluate whether COI can be used as reliable species discriminator for *O. davidsoni* sp. nov. we further included available data of published COI sequences of Neo-

tropical *Odontomachus* species. For this, we analyzed *Odontomachus* COI sequences from the New World. We downloaded 264 published COI sequences by using the following search terms in the Barcode of Life database system (www.boldsystems.org; search criteria: *Odontomachus*; “United States”; USA; Mexico; Cuba; Haiti; “Dominican Republic”; “Puerto Rico”; “British Virgin Islands”; Montserrat; “Antigua and Barbuda”; Dominica; “St Lucia”; Barbados; Grenada; “Trinidad and Tobago”; Guatemala; Honduras; Belize; “El Salvador”; Nicaragua; “Costa Rica”; Panama; Colombia; Venezuela; Ecuador; Guyana; Suriname; “French Guiana”; Brazil; Peru; Bolivia; Paraguay; Chile; Argentina; Uruguay”; accessed on 15 May 2019).

Published and newly acquired data from this study were then analyzed together. We first performed several quality checks. Sequences lacking species identifications, sequences containing ambiguous bases, and sequences smaller than 400bp were sorted out. We then used the MUSCLE algorithm (Edgar 2004) to align COI sequences and, on this basis, sorted out additional sequences which showed gaps and/or additional bases in the sequence alignment. No apparent stop codons were detected in the analyzed *Odontomachus* dataset. Finally, we extracted unique sequences (or COI haplotypes) from the dataset resulting in 94 distinct COI sequences of 16 *Odontomachus* species. For eight of those specimens lateral habitus images were uploaded to BOLD. BOLD process IDs of sequences are given in Suppl. material 5.

We used a Neighbor-Joining (NJ) tree as simple clustering approach of DNA barcode data to depict genetic differences and to examine the reliability of COI as possible molecular identifier of *O. davidsoni* sp. nov. Note that it was not our goal to evaluate whether COI can serve as a reliable identification character in the entire genus. We thus did not define species boundaries in other *Odontomachus* species based on intraspecific p-distance thresholds and barcoding gaps as it is often done so in other barcoding studies. Except for our own identifications (see above) we used and relied on species identifications that were deposited together with COI sequences in GenBank. The NJ tree was analyzed in MEGA 10.0.5 (Kumar et al. 2018) based on p-distances with pairwise deletion of missing data. P-distances simply give the proportion of bases that differ in pairwise sequence comparisons. Metadata of the NJ tree are given in Suppl. material 6 as Newick formatted file.

Results

Key to Neotropical *Odontomachus* species

This key is a modification of the keys of Rodriguez (2008) and Brown (1976), both of which contain many additional helpful figures as well as detailed morphological descriptions. Please note that this key does not include the species native to the USA such as the Florida endemic *O. relictus* Deyrup & Cover, 2004, for which we recommend using the key of MacGown et al. (2014).

From the Rodriguez (2008) key only the herewith described *O. davidsoni* sp. nov. is added as new. However, the classification of *Odontomachus brunneus* has been cleared up. Originally, it was thought to be distributed in South and Central America, but it is now clear that it is restricted to the Southern USA, and previous material that has been identified as such probably belongs to *O. ruginodis* Smith, 1937 (MacGown et al. 2014).

For easy identification, we recommend to point mount workers of *Odontomachus* by bending the tip of the point and gluing it to the pleura so as to leave the space between the hind coxae exposed. This is because the metasternal process is an important identification characteristic and it might be obscured otherwise.

English key

- 1 Petiole pedunculate to subpedunculate, in lateral view the anterodorsal margin of the gaster forms a single convexity that ascends posterad at approximately 45° (Fig. 1A)..... 2
- Petiole sessile, not subpendunculate, in lateral view the anterodorsal margin of the first gaster segment forming a much steeper slope (>45°) with a more or less distinct vertical anterior face (Fig. 1B) 4
- 2 Dorsal surface of the head with deep striation that reaches to the nuchal collar; color uniform ferruginous to dark red..... ***O. davidsoni* sp. nov.**
- Posterior third to half of dorsal surface of head smooth and shining; color variable 3
- 3 Without metasternal process; mesonotum almost hairless; larger body size (HL > 4 mm). Ground living..... ***O. mormo***
- With metasternal process; dorsal surface of mesonotum covered in small erect setae; smaller body size (HL < 3.8 mm). Arboreal ***O. hastatus***
- 4 Dorsal surface of head distinctly striate to or nearly to the nuchal carina 5
- Posterior third to half of dorsal surface of head smooth and shining, or nearly so 22
- 5 Disc (dorsal surface) of first gastric segment predominantly smooth, punctulate, alutaceous, or reticulate; striation absent, or if present, mixed with other sculpture and distinct only on the posterior half of the disc..... 6
- Disc of first gastric segment distinctly and evenly striate over its entire surface, at least as seen from dorsal view 17
- 6 Mesonotum longitudinally striate ***O. yucatecus* Brown, 1976**
- Mesonotum prevalingly transversely striate 8
- 7 Head more or less bright red (frontal area often infuscate), contrasting with blackish-brown body and yellow legs; size medium..... ***O. erythrocephalus***
- Color combination otherwise; if head is distinctly red, then trunk is red also, or legs are dark..... 8
- 8 Sternum immediately in front of and between metathoracic coxae produced as a slender, acute pair of teeth or spines; disc of first gastric segment densely

- and finely shagreened and pubescent, usually opaque; body brown, legs yellow to brown ***O. haematodus* (Linnaeus, 1758)**
- Sternum in front of metathoracic coxae with a low transverse ridge, sometimes notched in the middle or bilobed, but not produced as acute, paired teeth **9**
- 9 Petiole predominantly smooth and shiny, with the anterior border erected or slightly convex, and the apex produced into a large spine with posterior orientation; head, mesosoma and petiole with a clear red coloration and the gaster dark brown ***O. insularis* Guérin-Ménéville, 1844**
- Petiole differently shapes, color combination varies **10**
- 10 Anterior face of petiolar node as seen from the side rising steeply from anterior margin, then passing through an obtuse angle into a long section concave in outline to the root of the apical spine; labial palpi 4-merous ***O. bradleyi* Brown, 1976**
- Petiole differently shaped **11**
- 11 Metasternal process like an arc with or without middle division; petiole smooth or a little striate, with both the anterior and posterior margin convex; the petiolar spine forms gradually, without clear distinction from petiole ***O. cf. brunneus* Patton, 1894** (possibly *Odontomachus ruginodis*; *O. brunneus* is apparently restricted to southeastern US. The status of the Central and South American populations comparable with *O. brunneus* need to be established.)
- Metasternal process absent, bilobed or triangular; petiole differently shapes or if both sides convex, with a clear differentiation of the spine from the rest of the petiole **12**
- 12 Metasternal process absent **13**
- Metasternal process bilobed or triangular **14**
- 13 Black coloration; Node of petiole with a pair of prominent posterolateral tumosities at about mid-height and without striation; apex as seen from side abruptly narrowed to an axially erect, acute tooth ***O. biumbonatus* Brown, 1976**
- Node of petiole without paired posterolateral tumosities; Posterior face of petiole less concave, with short petiolar spine (0.1 mm).... ***O. clarus* Roger, 1861**
- 14 Anterior margin of petiole at least weakly convex **15**
- Anterior margin of petiole basal of the node concave or straight **16**
- 15 Metasternal process completely bilobed; color generally dark ***O. bauri* Emery, 1892**
- Metasternal process formed by an obtuse wide lobe followed by a transverse flange which is produced into a triangular process; usually light color ***O. biolleyi* Forel, 1809**
- 16 Petiole strongly transversely striate, with a clearly differentiated spine; small species (TL 8.6–9.35 mm) ***O. ruginodis* Smith, 1937**
- Petiole without or only weak striation and with spine not clearly differentiated from the petiole; large species (TL 12 mm) ***O. laticeps* Roger, 1861**

- 17 First gaster segment with only one type of sculpture, which is either punctulate or striate **18**
- First gaster segment with a combination of punctulate and reticulate sculpture **21**
- 18 First gaster segment punctulate on its entire surface.... *O. opaciventris* Forel, 1899
- First gaster segment striate on most of its surface, at least in dorsal view ... **19**
- 19 Transverse striation patterns on the gaster; large and slender *O. chelifera* (Latreille, 1802)
- Longitudinal striation on the dorsal gaster surface **20**
- 20 Mesonotum strongly convex, but broadly sulcate and longitudinally striate on at least the anterior half near midline *O. caelatus* Brown, 1976
- Mesonotum gently but evenly convex, transversely striate *O. laticeps*
- 21 Mesonotum with longitudinal striation *O. scalptus* Brown, 1978
- Mesonotum with transverse striation *O. meinerti* Forel, 1805
- 22 Ocular prominences each produced anterolaterally into a stout, acute, oblique, toothlike process *O. cornutus* Stitz, 1933
- Ocular prominences bluntly rounded, as usual **24**
- 23 Antennal scapes very short, not reaching posterior border of head in full-face view; very small species with broad head *O. spissus* Kempf, 1962
- Antennal scapes surpassing posterior border of head viewed full-face **24**
- 24 Apex of mandible with only 2 large teeth (intercalary tooth lacking)..... *O. allolabis* Kempf, 1974
- Apex of mandible with 3 teeth **25**
- 25 Mesepisternum with a prominent, narrowly rounded anteroventral lobe projecting conspicuously on each side when trunk is viewed from above..... *O. mayi* Mann, 1912
- Mesepisternum with at most a low, inconspicuous convexity on its anteroventral margin **26**
- 26 Petiole clearly differentiated spine; larger species (HL > 2.8 mm) *O. affinis* Guérin-Ménéville, 1844
- Both faces of petiole converge into a thick spine that is flattened laterally; smaller species (HL < 2.8 mm) *O. panamensis* Forel, 1899

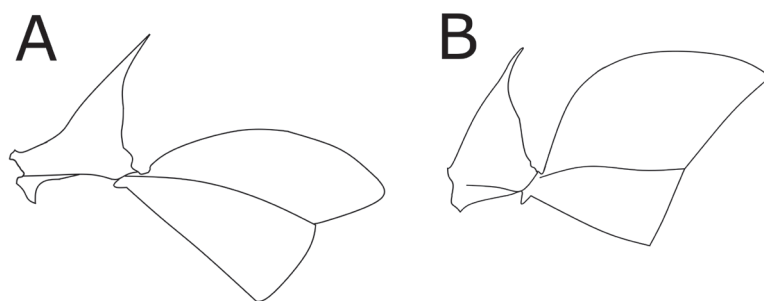


Figure 1. Lateral view of petiole and first gaster segment of *O. hastatus* (left) and *O. bauri* (right).

Spanish key

- 1 Pecíolo en vista lateral pedunculado a semi-pedunculado, el perfil anterodorsal del primer segmento del gáster forma una convexidad continua con una pendiente de aproximadamente 45° (Fig. 1A) **2**
- Pecíolo sésil, no semi-pedunculado, el perfil anterior del primer segmento del gáster relativamente vertical y bien diferenciado del perfil dorsal, con una pendiente mayor de 45° (Fig. 1B) **4**
- 2 Superficie dorsal de la cabeza con estrías que llegan hasta la carena nugal, color ferruginoso..... ***O. davidsoni* sp. nov.**
- Superficie dorsal de la cabeza con estrías que tan sólo ocupan de la mitad a dos tercios de la región anterior de la cabeza, color es variable **3**
- 3 Espacio entre las coxas posteriores liso, sin proceso ni estrías; mesonotum casi sin pelos; gran tamaño (LC > 4 mm). Hormiga del suelo ***O. mormo***
- Espacio entre las coxas posteriores con un proceso bilobulado y siempre estriado; mesonotum con muchos pelos; más pequeña (LC < 3.8 mm). Hormiga arbórea ***O. hastatus***
- 4 Superficie dorsal de la cabeza con estrías que llegan hasta la carena nugal o muy cerca de ésta **5**
- Superficie dorsal de la cabeza con estrías que tan sólo ocupan de la mitad a dos tercios de la región anterior de la cabeza..... **22**
- 5 Primer segmento del gaster predominantemente liso y brillante, opaco o suavemente reticulado..... **6**
- Primer segmento del gaster con escultura que puede ser de un sólo tipo o una mezcla de varios (estriado, punteado, estriado- punteado)..... **17**
- 6 Mesonoto estriado longitudinalmente..... ***O. yucatecus***
- Mesonoto estriado transversalmente..... **7**
- 7 Cabeza de color rojo claro que contrasta con cuerpo marrón oscuro a negro y extremidades amarillas ***O. erythrocephalus***
- Diferente combinación de color; si la cabeza es rojo claro, entonces el mesosoma debe ser también rojo o las extremidades de un color oscuro; o la cara anterior del pecíolo es recta o cóncava..... **8**
- 8 Metaesterno, exactamente entre las coxas posteriores posee un par de espinas o dientes agudos; primer segmento del gaster reticulado, usualmente opaco; cuerpo marrón, extremidades de color amarillo a marrón ***O. haematodus***
- Metasterno sin o con proceso, el cual puede ser bilobulado, dividido en la mitad o redondeado..... **9**
- 9 Pecíolo predominantemente suave y brillante, con borde anterior recto o ligeramente convexo, el ápice de éste se estrecha formando una espina larga, delgada que está dirigida posteriormente; cabeza, mesosoma y pecíolo de color rojo claro y gaster marrón oscuro ***O. insularis***
- Pecíolo de diferente forma; combinación de color variada **10**

- 10 Cara anterior del nodo peciolar se levanta casi verticalmente desde el margen anterior, luego pasa por un ángulo obtuso a una sección larga y cóncava que forma una espina apical..... ***O. bradleyi***
- Peciolo con forma diferente **11**
- 11 Proceso metasternal como un arco con o sin división en el medio; peciolo suavemente o poco estríado, la cara anterior es convexa, al igual que la posterior; la espina del peciolo se va formando gradualmente, lo cual hace que no sea claramente diferenciada de éste..... ***O. cf. brunneus*** (Posiblemente se trata de *O. ruginodis*. *O. brunneus* aparentemente esta restringida al sureste de los EEUU. El estatus de las poblaciones centro y suramericanas que son comparables con *O. brunneus* aún esta por definirse.)
- Proceso metasternal ausente, bilobulado o triangular; peciolo con diferente forma o si ambos lados son convexos hay una espina claramente diferenciada del resto del peciolo **12**
- 12 Proceso metasternal ausente **13**
- Proceso metasternal bilobulado o triangular **14**
- 13 Color negro; nodo del peciolo con un par de prominencias posterolaterales y sin estrías; ápice en vista lateral se estrecha hasta formar un diente agudo axialmente erguido..... ***O. biumbonatus***
- Color claro; nodo del peciolo sin prominencias o si las posee tiene estrías; cara posterior del peciolo al menos débilmente cóncava, la espina peciolar es corta (0.1mm) ***O. clarus***
- 14 Cara anterior del peciolo al menos débilmente convexa **15**
- Parte anterior basal del nodo peciolar cóncava o recta **16**
- 15 Proceso metasternal completamente bilobado; color oscuro generalmente....
..... ***O. bauri***
- Proceso metasternal formado por un lóbulo ancho obtuso, seguido de un reborde transversal que se observa como un proceso de forma triangular; color claro generalmente..... ***O. biolleyi***
- 16 Peciolo fuertemente estríado transver- salmente, presenta una espina claramente diferenciada, especies pequeñas (8.6- 9.35mm) ***O. ruginodis***
- Peciolo sin estrías o suavemente estríado, la espina no está claramente diferenciada del peciolo, especies grandes (TL 12 mm) ***O. laticeps***
- 17 Primer segmento del gaster con un sólo tipo de escultura, que puede ser punteada o estriada **18**
- Primer segmento del gaster con una combinación de escultura punteada y reticulada **21**
- 18 Primer segmento del gaster punteado a lo largo de toda su superficie
O. opaciventris
- Primer segmento del gaster estríado a lo largo de toda su superficie, al menos en vista dorsal **19**
- 19 Estrías transversales curvas en el gaster; especies grandes y delgadas ***O. chelifera***
- Estrías longitudinales en el dorso del gaster..... **20**

- 20 Mesonoto fuertemente convexo, pero fuertemente surcado y estriado longitudinalmente al menos en la mitad del área de la parte..... *O. caelatus*
- Mesonoto suave pero uniformemente convexo, estriado transversalmente..... *O. laticeps*
- 21 Mesonoto estriado longitudinalmente..... *O. scalptus*
- Mesonoto estriado transversalmente..... *O. meinerti*
- 22 Prominencias oculares con un proceso agudo, oblicuo a manera de diente ... *O. cornutus*
- Prominencias oculares redondeadas..... 23
- 23 Escapos antenales muy cortos que no alcanzan el borde posterior de la cabeza *O. spissus*
- Escapos antenales sobrepasan el borde posterior de la cabeza..... 24
- 24 Dos dientes grandes en el ápice de la mandíbula *O. allolabis*
- Tres dientes en el ápice de las mandíbulas 25
- 25 Mesepisterno con un lóbulo anteroventral redondeado y prominente que se proyecta a los lados del mesosoma en vista dorsal..... *O. mayi*
- Mesopleura con una convexidad inconspicua en su margen anteroventral... 26
- 26 Pecíolo convexo en ambas caras, con una espina delgada claramente diferenciada; más grande (LC>2.8 mm)..... *O. affinis*
- Pecíolo con ambas caras convexas, las cuales convergen en una espina gruesa y aplanada lateralmente; más pequeña (LC<2.8 mm)..... *O. panamensis*

***Odontomachus davidsoni* Hoenle, Lattke & Donoso, sp. nov.**

<http://zoobank.org/6FF7413B-42DA-4386-87D4-09C8FB06F70D>

Figures 2, 3

Type material examined. Complete list of localities in Suppl. material 9. Unique museum specimen identifiers are given in brackets after each specimen identification code.

Type locality. Ecuador • Esmeraldas, Reserva Río Canandé; 0.5281N, 79.2070W; ca. 330 m; 21 February 2019; P. Hoenle & G. Villagomez leg.; collection code PE39; single worker near large fig tree in mature forest.

Holotype specimen. Ecuador • 1 worker; Esmeraldas, Reserva Río Canandé; 0.5281N, 79.2070W; ca. 330 m; 21 February 2019; P. Hoenle & G. Villagomez leg.; collection code PE39; single worker near large fig tree in mature forest; specimen code PE39_01; [MEPN5074].

Paratype workers. Ecuador • 3 workers; Esmeraldas, Reserva Río Canandé; 0.5252N, 79.2079W; ca. 320 m; 04 February 2019; P. Hoenle & A. Argoti leg.; collection code PE23; hand sampling on Cecropia tree, same location as Odonto_Phil; specimen codes PE23_01, PE23_02, PE_23_03; [MCZ-ENT00731935].

Ecuador • 2 workers; Esmeraldas, Reserva Río Canandé; 00.5263N, 79.2117W; ca. 310 m; 06 February 2019; P. Hoenle leg.; collection code PE25; workers on recently large, fallen tree; specimen codes PE25_01, PE25_02; [RBINS IG 34167].

Ecuador • 4 workers; Esmeraldas, Reserva Río Canandé; 0.5238N, 79.2130W; ca. 330 m; 11 February 2019; P. Hoenle leg.; collection code PE36; nest in fallen branch in secondary forest (former cacao plantation); specimen codes PE36_01 [RBINS IG 34167]; PE36_02, PE36_03, PE36_04; [MEPN_5075].

Ecuador • 4 workers; Esmeraldas, Reserva Río Canandé; 0.5252N, 79.2079W; ca. 320 m; 29 May 2018; P. Hoenle & A. Argoti leg.; collection code Odonto_Phil; hand sampling on Cecropia tree. Same colony as PE23; One point-mounted worker; specimen code: Odon_Phil_02 [DZUP 548819], (BOLD ID: ODECU002-19) and one point-mounted worker with the same locality data but collected on 20 May 2018, specimen code Odon_Phil_01 [DZUP 548820]; (BOLD ID: ODECU001-19); Two workers mounted with permanent glue on top of needle specimen codes Odon_Phil_3, Odon_Phil_4; [PH private collection]

Paratype queens. Ecuador • 2 queens; Esmeraldas, Reserva Río Canandé; 0.5263N, 79.2129W; ca. 340 m; 25 January 2019; P. Hoenle leg.; collection code PE24; 2 alate queens, ex. light trap at the Río Canandé station, 8 pm.; specimen codes PE24_01 [MCZ-ENT00731935], PE24_02 [MEPN_5076].

Ecuador • 1 queen; Esmeraldas, Reserva Río Canandé; 0.5263N, 79.2129W; ca. 340 m; 13 April 2019; P. Hoenle leg.; collection code PE87, 1 alate queen, ex. light trap at the Río Canandé station, 9 pm.; specimen code PE87_01; [RBINS IG 34167].

Ecuador • 1 queen; Esmeraldas, Reserva Río Canandé; 0.5263N, 79.2129W; ca. 340 m; 09 May 2018; P. Hoenle & A. Argoti leg.; collection code Odon_Phil_queen; ex. light trap at Canandé Lodge; specimen code Odon_Phil_queen_01; [PH private collection].

Ecuador • 1 queen; Esmeraldas, Kumanii Lodge near Cotocachi-Cayapas Reserve; 0.7539N, -78.9208W; ca. 40 m; 14 April 2006; L. Camacho leg.; ex. light tap; [QCA-ZI 15167].

Specimens used for 3D scan: 1 holotype worker (PE39_01), 1 paratype worker (PE23_01), 1 paratype worker (PE36_01), 1 paratype queen (PE24_01)

Specimens used for DNA barcoding: Paratype workers DZUP 548819 (BOLD ID: ODECU002-19) & DZUP 548820 (BOLD ID: ODECU001-19)

Diagnosis of workers. Measurements ($N = 3$): HL 3.91–4.09, HoW 2.67–2.76, HvW 1.65–1.74, ML 2.62–2.70, SL 4.22–4.43, EL 0.62–0.71, MsL 6.00–6.20, PrW 1.49–1.57, PtW 0.59–0.64, PtL 1.53–1.57, PtH 2.20–2.23, FL 5.28–5.37, CI 67.48–68.53, SI 158.05–160.74, MI 65.28–69.05.

Long (TL > 17 mm), but slender, ferruginous to yellow brown body with striae on cephalic dorsum from antennal insertions to vertex, mandible with over 15 pre-apical teeth and denticles, pronotal dorsum with concentric to transverse striae. Petiole strongly pedunculate with posteriorly inclined apical spine, gaster smooth and shining.

Description of the holotype worker. Head elongate in dorsal view, anterior and posterior margins approximately of same width, posterior cephalic margin mostly transverse; head widest across eyes, at anterior one-third of head length; lateral cephalic margin posterior to eye sinuous. Median furrow deep, extends anterad to antennal fossa where it fades; occipital ridge distinctly delineated by antennal fossa, extending posteromedially, joining broad ridge that runs parallel to median furrow. Extraocular

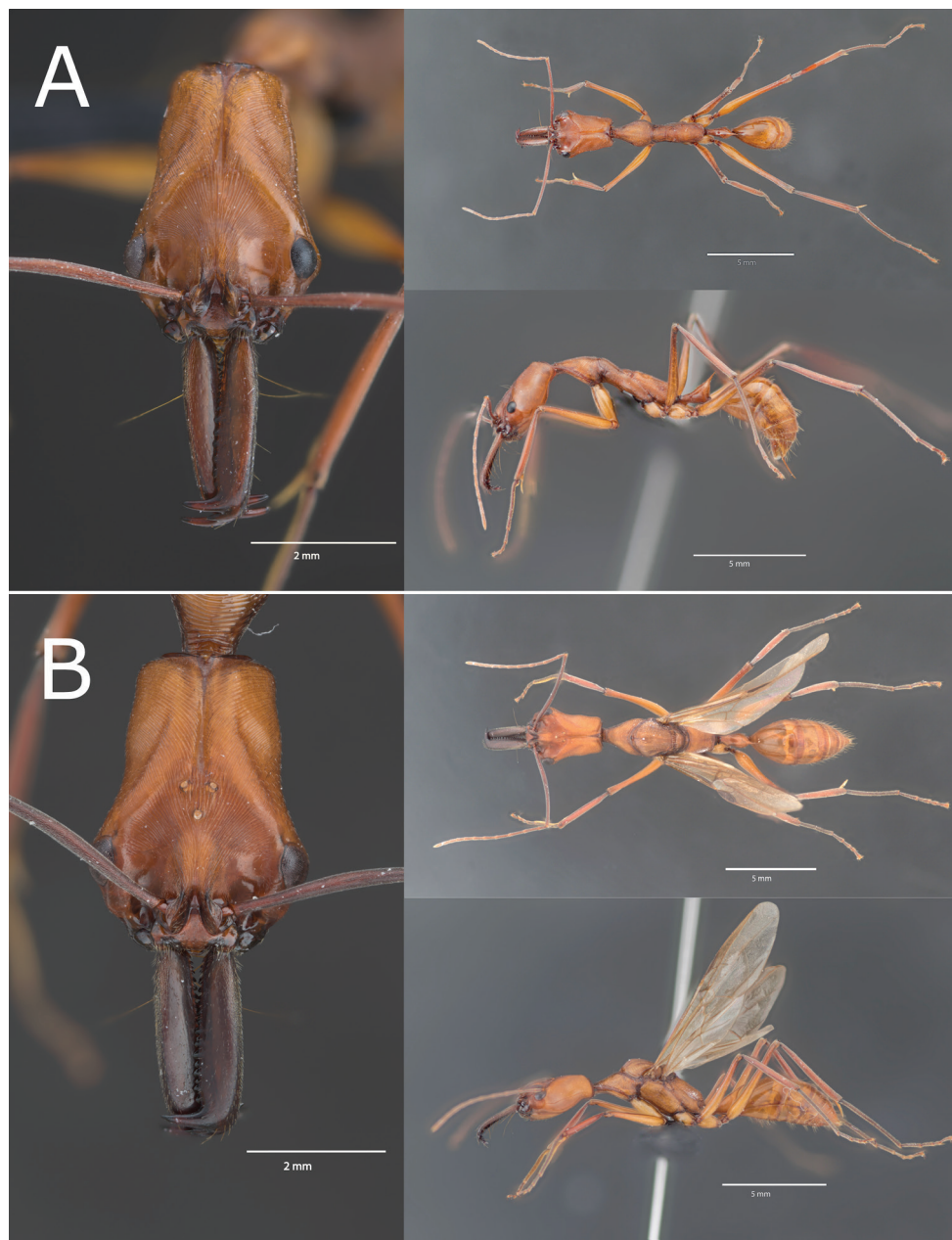


Figure 2. *Odontomachus davidsoni* sp. nov. stacking pictures **A** Worker paratype (specimen PE23_01) **B** Queen paratype (specimen PE24_01). Additional pictures in Suppl. material 7. Scale bars: 2 mm (left); 5 mm (right).

furrow broad and shallow, temporal prominence broad and weakly elevated. Cephalic surface with well-defined striae that diverge posterad from between frontal carina, reaching vertex, striae fade away on most of lateral cephalic surface with some striae reaching posteroventral cephalic surface. Ocular ridge smooth closest to eye and striate

towards cephalic median region. Cephalic dorsal surface anterad of eye and between eye and antennal sclerite mostly smooth. Scape slender and slightly arched, SL longer than HL, scape widest just anterad of mid length, finely punctulate; funicular segment elongated and slender, segment I half as long as segment II.

Median clypeus mostly smooth and shining, posteriorly projecting as flattened triangular surface between frontal carina; carina defines narrow elevated region that descends posteriorly and extends to antennal fossa; frontal carina narrow, width not greater than scape width; carina steeply elevated over posteromedian clypeal surface. Ventral cephalic surface mostly smooth and shining. Labium drop-shaped, anteroventral surface very convex, PF 4,4. Buccal cavity with lateral hypostomal tooth. Mandibular masticatory margin with basal row of six denticles and eleven blunt triangular, relatively short teeth apicad of denticles. One or more teeth closest to apex may be broken. Mandibular apex tridentate, ventral tooth with basal tooth. Mandibular dorsal surface mostly smooth, with sparse piligerous punctulae, but dorsolaterally with abundant punctulae, ventral surface smooth and shining.

Pronotal dorsum with concentric striation that become progressively transverse and elongate medially towards posterior margin, in lateral view striae appear anteriorly transverse, medially curving and U-shaped, posteriorly oblique to almost vertical. Posterolateral pronotal margin with short convex lobe. Mesosoma relatively slender and elongate, in lateral view pronotal dorsal margin straight to weakly convex, forming a posteriorly ascending slope, mesonotum anterior margin slightly higher than posterior pronotal margin, mesonotal dorsal margin mostly straight to weakly convex, descending to metanotal groove. Dorsal mesosomal margin between metanotal sulcus and metanotal spiracle forms brief convexity, propodeal anterodorsal margin brief and convex, dorsal margin mostly straight, three times longer than declivity, declivity forms blunt obtuse angle with dorsal margin. Propleuron mostly smooth and shining with narrow transverse band of sparse weak rugulae anteriorly and posteriorly.

Mesonotum with transverse striae that extend uninterrupted laterally to anepisternum and ventrally to mesosternum, katepisternum mostly smooth and shining except for sparse striae anteriorly and posteroventrally. Bulla of metathoracic spiracle semispherical, weakly sculpted, opening shaped as transverse slit. Propodeum and metanotum transversely striate. Mesometapleural suture distinct, propodeal-metapleural suture weakly impressed. No carina or visible suture between mesopleuron and mesosternum, mesosoma in hypothetical cross-section at mid-length forms relatively uniform ovoid. Mesosternum with median longitudinal region raised as low and broad convex ridge; metasternal process bidentate, teeth short and blunt. Propodeal spiracle slit-shaped, transverse to oblique, not elevated.

Petiole in lateral view slightly pedunculate, node shaped as posteriorly sloping cone with acute apical needle, anterior node margin weakly convex, posterior margin vertical, straight to weakly convex; anteroventral process prominent, triangular; node smooth and shining. Abdominal tergite 3 in lateral view with anterodorsal margin forming single convexity to posterior margin, ascending posterad at approximately 45°; ventral margin of tergite 3 briefly concave at prora, then broadly convex and

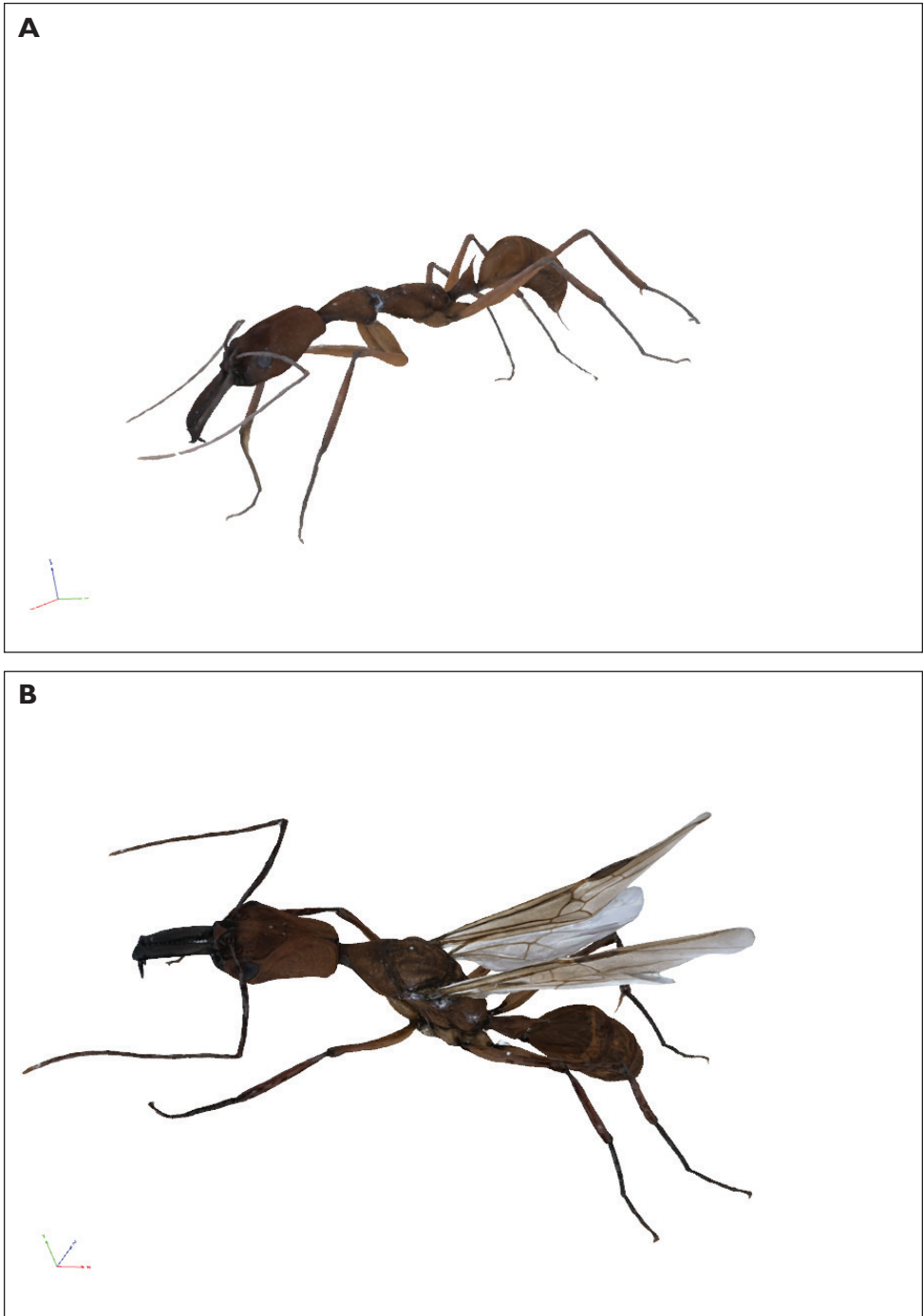


Figure 3. 3D models of *Odontomachus davidsoni* sp. nov. **A** 3D scan of *Odontomachus* holotype (PE39_01). **B** 3D scan of queen (PE24_01). Additional 3D models of two more paratypes in Suppl. material 8.

mostly at the same level as prora. Constriction between abdominal segments 3, 4 weak to negligible; gaster smooth and shining.

Coxae mostly smooth with abundant minute piligerous punctulae, punctulae denser on tibiae. Protibial apex with single seta, spur with basal translucent lamella. Probasitarsus with row of short, stiff hairs and parallel row of short setae opposite spur. Meso and metatibial apex each with two spurs, one pectinate, one simple; each also with 3 setae, each seta widely separated from each other. Body pilosity generally short and scattered with little pubescence; dorsal surface with few standing hairs: one on head where antennal fossa and nuchal carina almost meet, few on gastral sterna. Head and mandibular dorsum with sparse appressed pubescence, hairs straight on mandible and arched on head. Mandibular ventral surface next to masticatory margin with row of five flagellate long hairs plus two long trigger hairs at base. Scape with dense appressed pubescence, no standing hairs. Mesosoma with sparse appressed to subdecumbent small hairs, node with longer hairs; gaster mostly with sparse short, appressed to decumbent hairs with suberect hairs towards posterior end of gaster. Mandible and other buccal appendages, antenna, tibiae, and tarsi ferruginous brown to brown. Body mostly ferruginous to brownish yellow, head dark anterad and gaster darker posterad; trochanters and apex of femora tend to be darker.

Queen. Measurements ($N = 1$): HL 4.30, HoW 3.8, HvW 1.99, ML 2.87, SL 4.46, EL 0.75, MsL 6.78, PrW 2.22, PtW 0.79, PtL 1.68, PtH 2.40, FL 5.46, CI 71.63, SI 144.81, MI 66.74.

Mesosoma developed for wings, head with three ocelli. Queen with larger dimensions than worker: HoW > 3.3; MsL > 6.5; PrW > 1.9 mm., otherwise similar.

Male. Unknown.

Etymology. The species epithet is a patronym in genitive case honoring Stuart Carleton Davidson, the founder of Clyde's Restaurant Group, Washington, DC. Stuart had a lifelong interest in our environment, and would have loved this amazing ant.

Comparison to similar species. *Odontomachus davidsoni* most closely resembles *O. hastatus* by sharing a relatively large size, a red to brown color, a head which has in dorsal view a great difference between ocular and vertexal width, a relatively slender habitus, a bilobed metasternal process (Fig. 4A), and a pedunculate petiole with a posterior inclining node topped by a long dorsal needle. Together with *O. mormo* both species also share an evenly convex anterior margin of abdominal tergite III that in lateral view ascends posterad at an approximate 45° angle (Fig. 4B).

Compared to *O. hastatus*, *O. davidsoni* is clearly larger: The HL range of *O. hastatus* is 2.81–3.67 mm (Brown, 1976) versus 3.91–4.09 mm. Further, it has coarse striae throughout the dorsal cephalic surface, whereas the striae on *O. hastatus* are fine and limited to the area between the frontal carina and the antennal fossa, not extending to the occipital ridge. The pronotum in *O. hastatus* frequently presents smooth and shining areas on the pronotal disc or its sides, where it is always striate in *O. davidsoni*.

While the body size of *O. davidsoni* is similar to *O. mormo* (HL 4.14–4.36 (Brown 1976)), both species can be clearly distinguished by the striation pattern on the head: The striation in *O. mormo* does not reach the occipital ridge and there is instead a large

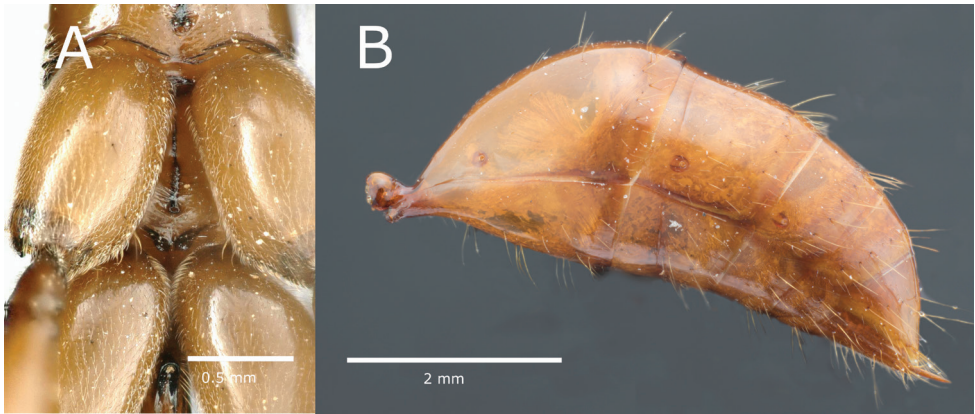


Figure 4. *Odontomachus davidsoni* ventral picture of metasternal process (specimen: Odon_Phil_3) and lateral image of gaster (specimen Odon_Phil_4).

and shiny area on the cephalic dorsum, while in *O. davidsoni* the entire cephalic dorsum is covered in coarse striae. Further, *O. mormo* does not possess a metasternal process, while *O. davidsoni* has a rounded bilobed metasternal process. *O. mormo* is almost hairless on the entire dorsal body surface including the petiole, whereas *O. davidsoni* body possesses a few appressed to decumbent hairs on the mesonotum, and many long erect hairs on the petiole. Overall, *O. mormo* has a more brownish coloration (very similar to *O. chelififer*), in contrast to the red coloration in *O. davidsoni*.

When using the key to Neotropical *Odontomachus* species by Rodriguez (2008) this species will be taken easily to couplet 13, whereupon it will not fit any of the two alternatives: *O. ruginodis* nor *O. laticeps*. It is clearly larger than *O. ruginodis*, which also differs in its dark brown color, sessile petiole, and a very short stubby petiolar needle. *O. laticeps* is smaller, dark brown, with a sessile and relatively erect petiole bearing a shorter dorsal needle. Using the identification key in Brown (1976: 111), or the key in Antwiki (2015), this species is easily taken to couplet 14 where it becomes stuck as it fits neither alternative, *O. bauri* nor *O. laticeps*. Both of these ants are much smaller, dark brown, have a sessile, erect petiolar node with a relatively shorter dorsal needle, and the anterior dorsal margin of abdominal tergite III in lateral view is mostly vertical.

Molecular analyses. We successfully amplified DNA barcodes of two *Odontomachus davidsoni* workers, a 569 bp fragment and a 668 bp fragment (GenBank accession numbers MN454765 and MN454766, respectively). The two specimens came from the same nest and had identical sequences. *Odontomachus davidsoni* barcodes were clearly distinguishable from COI sequences of other *Odontomachus* species (Fig. 5) as indicated by the minimum interspecific p-distance of 0.09 in pairwise comparisons (range of p-distances in 94 pairwise comparisons: 0.09–0.14; Fig. 5). A search in the BOLD identification database for the closest sequence match yielded similar results of 90.76% and 90.67% sequence similarity to *O. chelififer* (private, not pub-

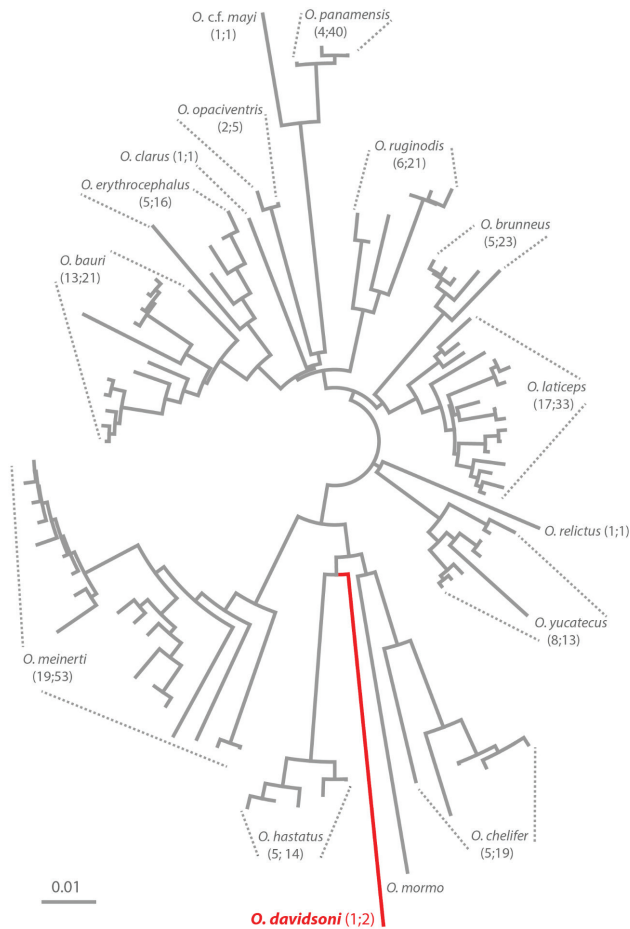


Figure 5. Neighbor-Joining (NJ) tree of *Odontomachus* COI sequences. The NJ tree is based on p-distances (scale bar). First digit in parentheses gives the number of identified COI haplotypes of a given species and the second one the total number of available COI sequences for this species. GenBank accession numbers are given in Suppl. material 5 and Newick tree file are given in Suppl. material 6.

lished yet) and *O. hastatus* (GenBank accession number: KU504889), respectively (accession date 28 May 2019).

Biology and distribution. Workers of *O. davidsoni* were only found in the Río Canandé Reserve and its neighboring reserve Tesoro Escondido (Fig. 6). Alate queens were collected with light traps in April 2006 (Kumanii Lodge, Cotocachi-Cayapas Reserve, leg. Camacho), April and June 2018, as well as in February, March and April 2019 (Canandé Lodge, Río Canandé Reserve, leg. Hoenle). In 2018 and 2019 we frequently visited a tree in a selectively logged area of the Canandé Reserve where a few workers of the species were spotted. Foraging workers were observed predominantly during nighttime between 8 pm and 11 pm. On at least five occasions during daytime (i.e., between 9 am and 5 pm) the plot was visited, but only once foraging



Figure 6. *Odontomachus davidsoni* collection sites. Blue dots show collection sites in Esmeraldas Province (Ecuador) within the reserves Río Canandé, Tesoro Escondido and Cotacachi-Cayapas.



Figure 7. *Odontomachus davidsoni* worker sitting on a leaf in its natural habitat.

workers were observed. Although their exact nest position was not detected, workers were predominantly foraging on a liana attached to a *Cecropia* tree. The tree had a diameter of 63 cm at breast height and an estimated height of 20 m. Workers could be observed walking straight up on it until they were out of sight in a height of approx.

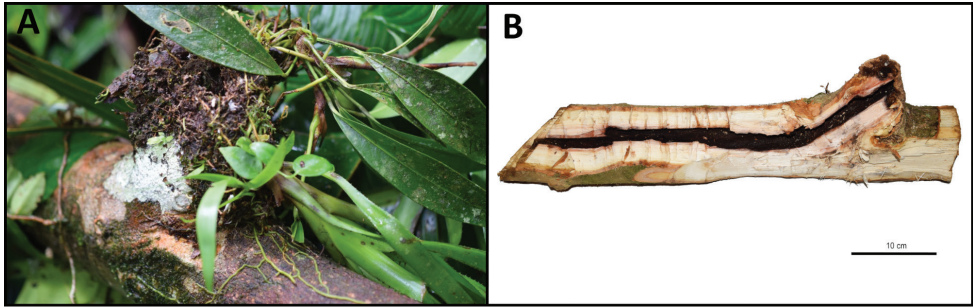


Figure 8. Nest of *Odontomachus davidsoni* **A** Nest found under natural conditions with bromeliad covering the nest entrance **B** Nest architecture visible after opening a fallen tree branch with a machete. Scale bar: 100 mm.



Figure 9. Colony of *O. davidsoni*. This colony was kept in the field laboratory after taking it out from the twig nest (Fig. 8). The sole dealate queen is marked with a red arrow.

10 m. Workers were never seen foraging on the ground, and we thus assume that they primarily forage in the canopy. Workers were observed to sit still on the surface of leaves with their mandibles open, probably waiting to ambush prey (Fig. 7).

On the 11th of February 2019 we collected what looked like a complete nest in a fallen branch (Fig. 8; GPS data: 0.5238N, 79.2130W). The nest contained one dealate queen and 18 workers, as well as brood in all development stages (Fig. 9). We assume that this colony was not fully grown because it contained no alates (despite other colo-

nies having alates at this time). The single nest entry was located under a bromeliad (Fig. 8A). We opened all parts of the nest with a machete, revealing a 40cm long tubular chamber within the center of the branch (Fig. 8B). It does not look like the ants themselves carved it, hence it was probably a pre-existing cavity.

We kept the colony for three months (11 February–15 April 2019) for further observations. The colony accepted various smaller insects as food, including flies, crickets, and termites. However, insects larger than 2 cm (e.g., large cicadas, moths, large crickets) were usually not accepted. Furthermore, the colony had *ad libitum* access to sugar water which was frequently visited. In accordance with field observations, the colony showed most activity during nighttime. No recruitment to offered food resources was observed. Due to the possibly threatened status of this ant species, the colony was released at the end of our observation time on a tree bromeliad nearby the Canandé lodge.

Discussion

We here formally described the species *Odontomachus davidsoni*. It is morphologically and genetically different from any other of the New World *Odontomachus* species. It rivals in size *O. mormo*, the largest known *Odontomachus* in the Americas, but the dark brown color, more sessile and robust petiole, mostly smooth cephalic dorsum, and lack of a metasternal process in *O. mormo* will easily permit the distinction between the two species. Unfortunately, there are few measurements available for gauging the dimensions of *O. mormo* (Brown 1976: 118; Rodriguez 2008: 156) but it seems safe to affirm that together with *O. chelifer* these species share the position as the largest known *Odontomachus* in the Americas.

Sequence similarities of COI barcodes suggested that *O. davidsoni* might be most closely related to *O. hastatus*, *O. mormo*, and *O. chelifer*. However, more informative phylogenetics/-genomics analyses are necessary to draw robust conclusions. This is because a single mitochondrial locus does not allow us to reliably infer phylogenetic relationships and because our species coverage is incomplete (ten Neotropical *Odontomachus* species do not possess published barcodes). Morphological characters suggest that *Odontomachus davidsoni* is most closely related to *Odontomachus hastatus*, which shares the arboreal and nocturnal foraging lifestyle (Camargo and Oliveira 2011; Rodrigues and Oliveira 2014). The species are easily separated by the lack of striation at the occipital margin in *O. hastatus* and the uniform red coloration of *O. davidsoni*. Both species seem to live in sympatry: our closest record of *O. hastatus* is in a linear distance of approximately 727 m to *O. davidsoni* (390 m vs. 300 m elevation, respectively). Other *Odontomachus* species found in the vicinity are *O. mormo*, *O. chelifer*, *O. bauri*, *O. erythrocephalus*, and *O. meinerti* (PH, pers. obs.), which highlights the high local species richness in the reserve.

Our species description is accompanied by 3D scans of three workers and a queen (Fig. 3, Suppl. material 8). This offers morphological details of the new species to the reader and the ability to take exact trait measurements. 3D imaging techniques, and in particular micro-computed X-ray tomography (μ CT), are becoming more frequently used in taxonomy and functional morphology, including studies on ants (Faulwetter et

al. 2013; Akkari et al. 2015; Garcia et al. 2017; Sarnat et al. 2017; Staab et al. 2018). Garcia et al. (2017) provided a comprehensive overview of the benefits and caveats of μ CT scans for such purposes. The 3D scans used in our study were produced via photogrammetry. This technique has some advantages as well as disadvantages over μ CT scans, e.g., it is comparatively inexpensive and requires little manual work, but it provides no internal structure and has a comparatively low spatial resolution (Ströbel et al. 2018). The resulting surface model can thus lack taxonomically important structural features such as the head striation in the case of *O. davidsoni*. On the other hand, the resulting 3D surface models are texturized, thus also providing information on specimen color, which is lacking in μ CT scans. A further disadvantage of DISC3D scans is that structures that are obscured in the physical specimen, e.g., through leg positioning or characters laying underneath the glue, are not recovered in a resulting 3D model. Overall, we argue that the 3D scans are a good addition to the traditional morphological description and stacking images by providing valuable 3D models that everyone can easily access and use for reliable trait measurements. Additionally, the 398 EDOF images, that the 3D models are based on, allow for an even more detailed inspection of the specimens in comparison to the texture on the 3D model.

The new species was discovered in the Chocó-Darién bioregion in Ecuador, probably one of the most biodiverse regions on earth, and at the same time one of the most threatened ones (Dinerstein et al. 1995; Olson and Dinerstein 1998; Myers et al. 2000). Research in this region is scarce, with many undescribed endemic species still awaiting scientific discovery and description (Donoso et al. 2009). The fact that a large and conspicuous ant like the herein described trap-jaw ant *O. davidsoni* remained unknown to science until now suggests that a hidden diversity remains to be discovered in this region. Similar to other biodiversity hotspots, increasing deforestation and conversion of forests to agriculture threatens the biodiversity of the Chocó-Darién bioregion, bearing the risk that many endemic and even yet undescribed species become extinct before being detected. With the description of a new, conspicuous trap-jaw ant, probably endemic to the region, we hope to provide additional reasons to protect this threatened biodiversity hotspot.

Conclusion

Odontomachus davidsoni is a noteworthy discovery in a vastly understudied and highly threatened area, the Chocó-Darién region of Ecuador. We sincerely hope that conservation efforts will continue and expand to protect this unique and important biodiversity hotspot.

Acknowledgements

We thank the Fundación Jocotoco and the associated Tesoro Escondido for logistic support and their permission to do research on their forest properties and in particular Martin Schaefer for initiating this collaboration. We like to thank especially the

local support from the park staff in the Canandé and Tesoro Escondido reserve, that made the field collection easier and made two great field stays possible: Bryan Amayo, Alcides Zombrano, Roberto de la Cruz, Jorge Zambrano, Amado de la Cruz, Yadria Giler, Patricio Encarnación, and Vanessa Moreira.

The species name was auctioned for a good cause at the anniversary of the Rainforest Trust, and we like to thank them and the highest bidder for this opportunity to aid in the conservation efforts and research in the Chocó area.

We would like to thank Brian L. Fisher as well as three reviewers for helpful comments on the manuscript. We acknowledge support by the German Research Foundation and the Open Access Publishing Fund of Technische Universität Darmstadt. PH was supported by a scholarship from the German National Academic Foundation. CvB received funding from the German Research Foundation (DFG: BE 5177/4-1 & BE 5177/4-2). SS was funded by the German Federal Ministry of Education and Research (BMBF), project NOVA (05K2016 / 05K16RDD).

References

- Akkari N, Enghoff H, Metscher BD (2015) A new dimension in documenting new species: high-detail imaging for Myriapod taxonomy and first 3D cybertype of a new millipede species (Diplopoda, Julida, Julidae). *PLoS ONE* 10(8): e9135243. <https://doi.org/10.1371/journal.pone.0135243>
- Antwiki (2015) Key to *Odontomachus* of the New World. Accessed 17 Sept 2018. http://www.antwiki.org/wiki/index.php?title=Key_to_Odontomachus_of_the_New_World&oldid=398024
- Bolton B (2018) An online catalog of the ants of the world. Accessed 20 Sept 2018. <http://antcat.org>
- Brown Jr WL (1976) Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section A. Introduction, subtribal characters. Genus *Odontomachus*. *Studia Entomologica* 19: 67–171.
- Camargo RX, Oliveira PS (2012) Natural history of the Neotropical arboreal ant, *Odontomachus hastatus*: nest sites, foraging schedule, and diet. *Journal of Insect Science* 12: 1–9. <https://doi.org/10.1673/031.012.4801>
- Deyrup M, Cover S. (2004) A new species of *Odontomachus* ant (Hymenoptera: Formicidae) from inland ridges of Florida, with a key to *Odontomachus* of the United States. *Florida Entomologist* 87: 136–144. [https://doi.org/10.1653/0015-4040\(2004\)087\[0136:ANSO OA\]2.0.CO;2](https://doi.org/10.1653/0015-4040(2004)087[0136:ANSO OA]2.0.CO;2)
- Dinerstein EA, Olsen DM, Graham DJ, Webster AL, Primm SA, Bookbinder MP, Ledec G (1995) Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean. The World Bank, Washington, DC, 129. <https://doi.org/10.1596/0-8213-3295-3>
- Dominguez DF, Bustamante M, Albuja RA, Castro A, Lattke JE, Donoso DA (2016) COI barcodes for ants (Hymenoptera: Formicidae) of drylands in the south of Ecuador. *Ecosistemas* 25(2): 76–78. <https://doi.org/10.7818/ECOS.2016.25-2.09>
- Donoso DA, Salazar F, Maza F, Cárdenas RE, Dangles O (2009) Diversity and distribution of type specimens deposited in the Invertebrate section of the Museum of Zoology QCAZ,

- Quito, Ecuador. *Annales de la Société Entomologique de France* (n.s.) 45(4): 437–454. <https://doi.org/10.1080/00379271.2009.10697628>
- Donoso DA, Ramón G (2009) Composition of a high diversity leaf litter ant community (Hymenoptera: Formicidae) from an Ecuadorian pre-montane rainforest. *Annales de la Société Entomologique de France* (n.s.) 45(4): 487–499. <https://doi.org/10.1080/00379271.2009.10697631>
- Donoso DA (2017) Tropical ant communities are in long-term equilibrium. *Ecological Indicators* 83: 515–523. <https://doi.org/10.1016/j.ecolind.2017.03.022>
- Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32(5): 1792–1797. <https://doi.org/10.1093/nar/gkh340>
- Evenhuis NL (2020) The insect and spider collections of the world website. Available at: <http://hbs.bishopmuseum.org/codens/> [Last accessed 20 Feb 2020].
- Faulwetter S, Vasileiadou A, Kouratoras M, Dailianis T, Arvanitidis C (2013) Micro-computed tomography: Introducing new dimensions to taxonomy. *ZooKeys* 263: 1–45. <https://doi.org/10.3897/zookeys.263.4261>
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3(5): 294–299.
- Garcia FH, Fischer G, Liu C, Audisio TL, Alpert GD, Fisher BL, Economo EP (2017) X-Ray microtomography for ant taxonomy: An exploration and case study with two new *Tera-taner* (Hymenoptera, Formicidae, Myrmicinae) species from Madagascar. *PLOS ONE* 12: e0172641. <https://doi.org/10.1371/journal.pone.0172641>
- Gronenberg W, Tautz J, Hölldobler B (1993) Fast trap jaws and giant neurons in the ant *Odontomachus*. *Science* 262: 561–563. <https://doi.org/10.1126/science.262.5133.561>
- Gronenberg W (1995) The fast mandible strike in the trap-jaw ant *Odontomachus*. *Journal of Comparative Physiology A* 176: 399–408. <https://doi.org/10.1007/BF00219065>
- Guenard B, Weiser M, Gomez K, Narula N, Economo EP (2017) The Global Ant Biodiversity Informatics (GABI) database: a synthesis of ant species geographic distributions. *Myrmecological News* 24: 83–89. https://doi.org/10.25849/myrmecol.news_024:083
- Harris RA (1979) A glossary of surfacing sculpturing. *Occasional papers in Entomology, State of California, Department of Food and Agriculture* 28: 1–31.
- Keller RA (2011) A phylogenetic analysis of ant morphology (Hymenoptera: Formicidae) with special reference to the poneromorph subfamilies. *Bulletin of the American Museum of Natural History* 355: 1–90. <https://doi.org/10.1206/355.1>
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35: 1547–1549. <https://doi.org/10.1093/molbev/msy096>
- Larabee FJ, Suarez A (2014) The evolution and functional morphology of trap-jaw ants (Hymenoptera: Formicidae). *Myrmecological News* 20: 25–36.
- Larabee FJ, Suarez A (2015) Mandible-Powered Escape Jumps in Trap-Jaw Ants Increase Survival Rates during Predator-Prey Encounters. *PLoS ONE* 10(5): e0124871. <https://doi.org/10.1371/journal.pone.0124871>
- Larabee FJ, Fisher BL, Schmidt CA, Matos-Maraví P, Janda M, Suarez AV (2016) Molecular phylogenetics and diversification of trap-jaw ants in the genera *Anochetus* and *Odontoma-*

- chus* (Hymenoptera: Formicidae). Molecular Phylogenetics and Evolution 103: 143–154. <https://doi.org/10.1016/j.ympev.2016.07.024>
- Latkje J, Vélez M, Aguirre M (2016) Survey of ants in dry forests of southwestern Ecuador (Hymenoptera: Formicidae). Sociobiology 63(3): 909–918. <https://doi.org/10.13102/sociobiology.v63i3.1044>
- MacGown JA, Boudinot B, Deyrup M, Sorger DM (2014) A review of the Nearctic *Odontomachus* (Hymenoptera: Formicidae: Ponerinae) with a treatment of the males. Zootaxa 3802: 515. <https://doi.org/10.11646/zootaxa.3802.4.6>
- Matos-Maraví P, Matzke NJ, Larabee FJ, Clouse RM, Wheeler WC, Sorger DM, Suarez AV, Janda M (2018) Taxon cycle predictions supported by model-based inference in Indo-Pacific trap-jaw ants (Hymenoptera: Formicidae: Odontomachus). Molecular Ecology 27(20): 4090–4107. <https://doi.org/10.1111/mec.14835>
- Myers N, Mittermeier RA, Mittermeier CG et al. (2000) Biodiversity hotspots for conservation priorities. Nature 403(6772): 853–858. <https://doi.org/10.1038/35002501>
- Olson DM, Dinerstein E (1998) The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. Conservation Biology 12(3): 502–15. <https://doi.org/10.1046/j.1523-1739.1998.012003502.x>
- Rodrigues PAP, Oliveira PS (2014) Visual navigation in the Neotropical ant *Odontomachus hastatus* (Formicidae, Ponerinae), a predominantly nocturnal, canopy-dwelling predator of the Atlantic rainforest. Behavioural Processes 109: 48–57. <https://doi.org/10.1016/j.beproc.2014.06.007>
- Rodriguez J (2008) Género *Odontomachus* Latreille. In: Jiménez E, Fernández F, Arias TM, Lozano-Zambrano FH (Eds) Sistemática, biogeografía y conservación de las hormigas cazadoras de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, 148–170.
- Salazar F, Donoso DA (2013) New ant (Hymenoptera: Formicidae) records for Ecuador deposited at the Carl Rettenmeyer ant collection in the QCAZ Museum. Boletín Técnico 11, Serie Zoológica 8–9: 151–177.
- Salazar F, Reyes-Bueno F, Sanmartín D, Donoso DA (2015) Mapping continental Ecuadorian ant species. Sociobiology 62(2): 132–162. <https://doi.org/10.13102/sociobiology.v62i2.132-162>
- Sarnat EM, Friedman NR, Fischer G, Lecroq-Bennet B, Eonomo EP (2017) Rise of the spiny ants: diversification, ecology and function of extreme traits in the hyperdiverse genus *Pheidole* (Hymenoptera: Formicidae). Biological of the Linnean Society 122: 514–538. <https://doi.org/10.1093/biolinnean/blx081>
- Schmidt CA, Shattuck SO (2014) The Higher Classification of the Ant Subfamily Ponerinae (Hymenoptera: Formicidae), with a Review of Ponerine Ecology and Behavior. Zootaxa 3817(1): 1–242. <https://doi.org/10.11646/zootaxa.3817.1.1>
- Staab M, Garcia FH, Liu C, Xu ZH, Eonomo EP (2018) Systematics of the ant genus *Proceratium* Roger (Hymenoptera, Formicidae, Proceratiinae) in China – with descriptions of three new species based on micro-CT enhanced next-generation-morphology. ZooKeys 770: 137–192. <https://doi.org/10.3897/zookeys.770.24908>
- Ströbel B, Schmelzle S, Blüthgen N, Heethoff M (2018) An automated device for the digitization and 3D modelling of insects, combining extended-depth-of-field and all-side multi-view imaging. ZooKeys 759: 1–27. <https://doi.org/10.3897/zookeys.759.24584>

- von Beeren C, Maruyama Y, Kronauer DJC (2016) Cryptic diversity, high host specificity and reproductive synchronization in army ant associated *Vatesus* beetles. *Molecular Ecology* 25: 990–1005. <https://doi.org/10.1111/mec.13500>
- Wilkie KTR, Mertl AL, Traniello JFA (2010) Species Diversity and Distribution Patterns of the Ants of Amazonian Ecuador. *PLOS ONE* 5: e13146. <https://doi.org/10.1371/annotation/832d6104-4f9f-42eb-88a5-b2b1fc4480ca>
- Wilson EO (1955) A monographic revision of the ant genus *Lasius*. *Bulletin of the Museum of Comparative Zoology* 113: 1–204.

Supplementary material I

Video of *Odontomachus davidsoni* holotype 3D model

Authors: Philipp O. Hoenle, John E. Lattke, David A. Donoso, Christoph von Beeren, Michael Heethoff, Sebastian Schmelzle, Adriana Argoti, Luis Camacho, Bernhard Ströbel, Nico Blüthgen

Data type: multimedia

Explanation note: Rendered video of the 3D scan of the holotype specimen.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.948.48701.suppl1>

Supplementary material 2

Video of *Odontomachus davidsoni* queen paratype 3D model

Authors: Philipp O. Hoenle, John E. Lattke, David A. Donoso, Christoph von Beeren, Michael Heethoff, Sebastian Schmelzle, Adriana Argoti, Luis Camacho, Bernhard Ströbel, Nico Blüthgen

Data type: multimedia

Explanation note: Rendered video of the 3D scan of the queen paratype.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.948.48701.suppl2>

Supplementary material 3

Table with measurements

Authors: Philipp O. Hoenle, John E. Lattke, David A. Donoso, Christoph von Beeren, Michael Heethoff, Sebastian Schmelzle, Adriana Argoti, Luis Camacho, Bernhard Ströbel, Nico Blüthgen

Data type: measurements

Explanation note: Table containing all available measurements of holo- and paratypes of *Odontomachus davidsoni*.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.948.48701.suppl3>

Supplementary material 4

DNA barcode information

Authors: Philipp O. Hoenle, John E. Lattke, David A. Donoso, Christoph von Beeren, Michael Heethoff, Sebastian Schmelzle, Adriana Argoti, Luis Camacho, Bernhard Ströbel, Nico Blüthgen

Data type: barcode information

Explanation note: Table containing a list of the barcoded individuals and their associated collection and repository data.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.948.48701.suppl4>

Supplementary material 5

Used BOLD barcodes

Authors: Philipp O. Hoenle, John E. Lattke, David A. Donoso, Christoph von Beeren, Michael Heethoff, Sebastian Schmelzle, Adriana Argoti, Luis Camacho, Bernhard Ströbel, Nico Blüthgen

Data type: BOLD accession numbers

Explanation note: List of BOLD barcode accession numbers used in this study.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.948.48701.suppl5>

Supplementary material 6

NJ tree

Authors: Philipp O. Hoenle, John E. Lattke, David A. Donoso, Christoph von Beeren, Michael Heethoff, Sebastian Schmelzle, Adriana Argoti, Luis Camacho, Bernhard Ströbel, Nico Blüthgen

Data type: newick tree file

Explanation note: Newick file of the COI comparisons.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.948.48701.suppl6>

Supplementary material 7

Additional detail images of *O. davidsoni*

Authors: Philipp O. Hoenle, John E. Lattke, David A. Donoso, Christoph von Beeren, Michael Heethoff, Sebastian Schmelzle, Adriana Argoti, Luis Camacho, Bernhard Ströbel, Nico Blüthgen

Data type: multimedia

Explanation note: Contains additional detail pictures of the new species.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.948.48701.suppl7>

Supplementary material 8

Additional 3D scans of two more paratype workers

Authors: Philipp O. Hoenle, John E. Lattke, David A. Donoso, Christoph von Beeren, Michael Heethoff, Sebastian Schmelzle, Adriana Argoti, Luis Camacho, Bernhard Ströbel, Nico Blüthgen

Data type: multimedia

Explanation note: This file contains two additional 3D scans of two more paratype workers.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.948.48701.suppl8>

Supplementary material 9

Table of localities

Authors: Philipp O. Hoenle, John E. Lattke, David A. Donoso, Christoph von Beeren, Michael Heethoff, Sebastian Schmelzle, Adriana Argoti, Luis Camacho, Bernhard Ströbel, Nico Blüthgen

Data type: occurrence

Explanation note: Table of known *Odontomachus davidsoni* localities.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.948.48701.suppl9>

Online social media tells a story of *Anaselina*, *Paraselina*, and *Selivinga* (Orthoptera, Tetrigidae), rare Australian pygmy grasshoppers

Josip Skejo^{1,2}, Matthew Connors³, Michael Hendriksen², Nick Lambert⁴, Griffin Chong⁵, Ian McMaster⁶, Nick Monaghan⁷, David Rentz^{3,8}, Reiner Richter⁹, Kathy Rose¹⁰, Damjan Franjević¹

1 University of Zagreb, Faculty of Science, Department of Biology, Evolution Lab, HR-10000 Zagreb, Croatia
2 Heinrich – Heine University, Institute for Molecular Evolution, D-40225, Düsseldorf, Germany **3** James Cook University, Douglas, Queensland, 4811, Australia **4** 8 Belbowrie Road, Toormina, New South Wales, 2452, Australia **5** citizen scientist (minor), Brisbane, Queensland, 4104, Australia **6** Mount Mellum, Queensland, 4550, Australia **7** Life Unseen, Melbourne, Victoria, Australia **8** 19 Butler Dr Kuranda, Queensland, 4881, Australia **9** PO Box 37, Monbulk, Victoria, 3793, Australia **10** 968 Wilsons Creek Road Mullumbimby, New South Wales, 2482, Australia

Corresponding author: Josip Skejo (skejo.josip@gmail.com); Damjan Franjević (damianf@zg.biol.pmf.hr)

Academic editor: Tony Robillard | Received 5 April 2020 | Accepted 25 May 2020 | Published 13 July 2020

<http://zoobank.org/80C4C9D2-C3ED-4209-BB6C-F6EAA7AF6E8E>

Citation: Skejo J, Connors M, Hendriksen M, Lambert N, Chong G, McMaster I, Monaghan N, Rentz D, Richter R, Rose K, Franjević D (2020) Online social media tells a story of *Anaselina*, *Paraselina*, and *Selivinga* (Orthoptera, Tetrigidae), rare Australian pygmy grasshoppers. ZooKeys 948: 107–119. <https://doi.org/10.3897/zookeys.948.52910>

Abstract

Knowledge on the pygmy grasshoppers of Australia is, despite the numerous endemics being described from this unique continent, still scarce. Of interest is the *Vingselina* genus group, including genera *Anaselina* Storozhenko, 2019, *Paraselina* Storozhenko, 2019, *Selivinga* Storozhenko, 2019 and *Vingselina* Sjöstedt, 1921. The systematic position of this group, currently assigned to Batrachideinae (Bufonidini), is probably not correct. In this study new records are presented of *Anaselina minor* (Sjöstedt, 1921), *Paraselina brunneri* (Bolívar, 1887), *P. trituberculata* (Sjöstedt, 1932), and *Selivinga tribulata* Storozhenko, 2019,

all except *A. minor* the first records of the species since their original descriptions. The first photographs of living specimens of *A. minor*, *P. brunneri*, *P. trituberculata* and *S. tribulata* are provided and their habitats described. All the records were compiled by citizen scientists who use online social media, such as iNaturalist. Lastly, *P. multifora* (Rehn, 1952) **syn. nov.** represents a junior synonym of *P. brunneri*.

Keywords

barkhopper, Batrachideinae, citizen science, Cladonotinae, Flickr, iNaturalist, New South Wales, Queensland, relics, Tetrigoidea

Introduction

A long history of existence in isolation has resulted in Australia being one of the strongholds of Earth's biodiversity. It is a place where more than 80% of fauna and flora are endemic (Egerton and Lochman 2009, Williams et al. 2011), such as monotremes (Monotremata), numerous marsupials (Marsupialia), emus (*Dromaius novaehollandiae*), lyrebirds (e.g., *Menura alberti*), or the Wollemi pine (*Wollemia nobilis*) (Waisbecker and Beck 2015; Jones et al. 1995). Especially interesting are eastern rainforests, which harbor great number of endemics and relics, and should be considered a world biodiversity hotspot (Williams et al. 2011). Those rainforests are inhabited by Australian barkhoppers and helmed groundhoppers, small pygmy grasshoppers (Orthoptera: Tetrigidae: genera *Anaselina*, *Paraselina*, *Selivinga*, *Vingselina*) found on bark, and among the rarest grasshoppers on the planet from the point of view of the numbers of records (Bolívar 1887; Sjöstedt 1921, 1932; Rehn 1952; Storozhenko 2019). The Australian barkhoppers and helmed groundhoppers are currently assigned to the subfamily Batrachideinae and the tribe Bufonidini, together with *Vilma* from the Solomon Islands, *Hyperboella* from New Caledonia, and *Bufonides* from New Guinea (Storozhenko 2019; Skejo et al. 2020). Previous authors included those genera in Cladonotinae (Rehn 1952) and where they really belong remains an open question. Altogether, six species are known, chronologically sorted by the time of discovery: 1) *Paraselina brunneri* (Bolívar, 1887), 2) *Vingselina crassa* Sjöstedt, 1921, 3) *Anaselina minor* (Sjöstedt, 1921), 4) *P. trituberculata* (Sjöstedt, 1932), 5) *P. multifora* (Rehn, 1952), 6) *Selivinga tribulata* Storozhenko, 2019 (Bolívar 1887; Sjöstedt 1921, 1932; Rehn 1952; Storozhenko 2019). Sjöstedt (1921) defined the genus *Vingselina*, while Storozhenko (2019) defined *Anaselina*, *Paraselina*, and *Selivinga*.

In this study, we present eleven new records of Australian tetrigids that exhibit characters between Batrachideinae and Cladonotinae (Rehn 1952; Storozhenko 2019). Namely, we present records of *Paraselina brunneri* from iNaturalist, *P. trituberculata* from Flickr, *A. minor* from the field, and *Selivinga tribulata* from Flickr, one blog, and the field (Figure 1). These are the first findings of those species since their original descriptions, except in the case of *A. minor*. Also, we propose synonymy of *Paraselina multifora* syn. nov. with *P. brunneri*. With this paper, we show that online social media platforms are a modern tool for studying unreachable biodiversity.

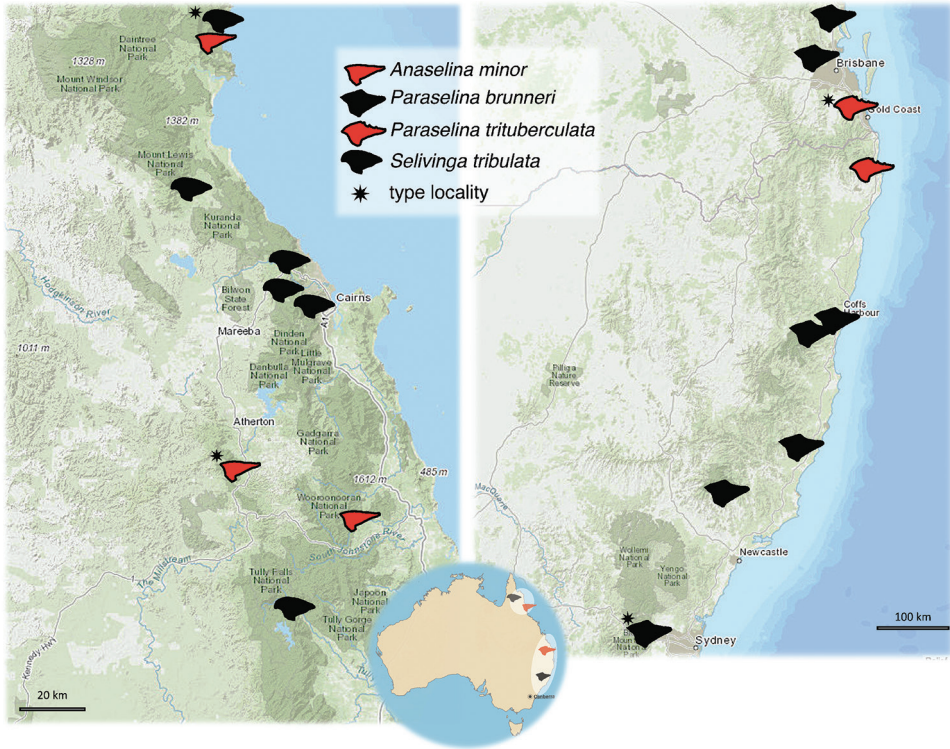


Figure 1. Updated distribution map of the Australian pygmy grasshoppers – *Anaselina minor*, *Paraselina brunneri*, *P. trituberculata*, and *Selivinga tribulata*. Each species is represented by its unique symbol, the silhouette of the species pronotum. The small map of Australia shows two regions inhabited by the barkhoppers.

Materials and methods

Taxonomy and nomenclature

Taxonomy follows Storozhenko's (2019) division of the subfamily Batrachideinae into Batrachideini, Bufonidini, and Cassitettigini. Australian Batrachideinae (genera *Anaselina* – 1 sp., *Paraselina* – 2 spp. after our study, *Selivinga* – 1 sp., and *Vingselina* – 1 sp.) belong to Bufonidini, together with *Bufonides* (New Guinea), *Hyperyoella* (New Caledonia), and *Vilma* (Solomon Islands) (Steinmann 1973; Storozhenko 2019; Skejo et al. 2020; Cigliano et al. 2020). Nomenclature is in accordance with the International Code of Zoological Nomenclature (ICZN 1999).

Morphological terminology

We follow the morphological terminology presented by Tumbrinck (2014a, 2014b, 2015) and Storozhenko (2019). All the important morphological characters used to distinguish members of the group are related to the pronotum: 1) the shape and height

of the median carina of the pronotum, 2) the shape of the frontomedial projection of the pronotum, and 3) the fashion of the pronotal ending.

Museum abbreviations

We have examined type specimens of all the Australian Batrachideinae: Bufonidini, and those specimens are the only published specimens of said species. The exception are a few non-type specimens of *Anaselina minor*, originating from Cape Tribulation, deposited in the Zoological Institute of the Russian Academy of Sciences (**ZIN**) and depicted by Storozhenko (2019). In the following museums, the type materials of the here-reported Australian Batrachideinae have been deposited:

- MCZ US** Museum of Comparative Zoology of Harvard University in Cambridge, Massachusetts, USA (types of *Vingselina multifora* Rehn, 1952);
- NHMW** Naturhistorisches Museum Wien, Wien, Austria (types of *Diotarus brunneri* Bolívar, 1887);
- NHRS** Naturhistoriska riksmuseet, Stockholm, Sweden (types of *Vingselina minor* Sjöstedt, 1921, and types of *Vingselina crassa* Sjöstedt);
- QM** Queensland Museum, Queensland, Brisbane, Australia (types of *Vingselina trituberculata* Sjöstedt, 1932);
- ZIN** Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (types of *Selivinga tribulata* Storozhenko, 2019).

Online social media

Eight new records were posted on online social media by citizen scientists and then identified by specialists: iNaturalist (Table 1: records 5, 6, 9, 10, 16, Table 2), Flickr (Table 1: records 12, 14, Table 2), and the NM's blog (Table 2: record 15). All photographs are reproduced here. Besides new records from online social media, MC observed *A. minor* in one and *S. tribulata* in two additional localities (Table 1: records 17, 18).

Results

New records of *Anaselina*, *Paraselina*, and *Selivinga*

In addition to the published specimens, which are mostly the type specimens' records deposited in museum collections (see Storozhenko 2019), we present eleven new records (Table 1.) of these rare Australian pygmy grasshoppers, *Anaselina minor*, *Selivinga tribulata*, *Paraselina brunneri*, and *P. trituberculata*. All the records, except the one of *A. minor*, are the first records since the species descriptions. All known species belonging to the aforementioned genera are flightless and endemic. New and old records are summarized in Table 1 and depicted in the map (Figure 1).

Table 1. All the known records of *Anaselina minor*, *Paraselina brunneri* (= *Paraselina multifora*), *Paraselina trituberculata*, and *Selivinga tribulata*, the Australian endemic Batrachideinae/Cladonotinae (*P. tritub.* – *Paraselina trituberculata*, NSW – New South Wales, QLD – Queensland, HT – holotype, LT – lectotype, PT – paratype, * – new records).

	Locality	Coordinates	Date	Specimen data	Reference	N
<i>A. minor</i>	QLD: Herberton	(17.38S, 145.42E)	early 1900s	1♀ HT, Mjöberg, NHRS	Sjöstedt 1921	1
	QLD: Cape Tribulation tropical rainforest	16.117S, 145.433E	10.–30.III.2000.	2 ♂♂ + 1♀, S. Storozhenko (ZIN)	Storozhenko 2019	2
	QLD: Wooroonooran	17.653S, 145.718E	05.X.2019.	1♂, M. Connors	This study*	3
<i>P. brunneri</i>	NSW: Sydney	(33.68S, 150.56E)	1860s	1♀ LT, Frauenfeld, NHMW	Bolívar 1887	4
	NSW: Lansdowne Forest: Starrs Creek	31.6997S, 152.5129E	07.IV.2019.	1♀, R. Richter	iNaturalist*	5
	NSW: Upper Orara	30.2801S, 152.9441E	29.I.2019.	1♀, N. Lambert	iNaturalist*	6
	NSW: Dorrigo: 900 m a.s.l. (Macleay Range)	(30.40S, 152.65E)	1930s	1♀ HT; 2♀♀ PTs, Darlington, MCZ US	Rehn 1952: <i>P. multifora</i>	7
	NSW: Salisbury	(32.19S, 151.56E)	12.II.1932.	1♀ PT, MCZ US		8
	QLD: Mount Mellum	26.8239S, 152.9199E	29.I.2019.	1 indiv., I. McMaster	iNaturalist*	9
	QLD: Mount Glorious	27.3161S, 152.7308E	02.I.2019.	1♂, G. Chong	QuestaGame, iNaturalist*	10
<i>P. tritub.</i>	QLD: Mount Tambourine	(27.88S, 153.18E)	28.X.1912.	1♀ HT, Brisbane	Sjöstedt 1932	11
	NSW: Wilsons Creek	28.5713S, 153.4265E	30.I.2013.	1♂, K. Rose	Flickr*	12
<i>S. tribulata</i>	QLD: Cape Tribulation	16.1166S, 145.4333E	10.–30.III.2000.	1♀ HT; 2♀♀, 1♂ PTs, author, ZIN	Storozhenko, 2019	13
	QLD: Kuranda	16.8050S, 145.6385E	10.XI.2010.	D. Rentz	Flickr*	14
	QLD: Julatten: Kingfisher Park	16.5940S, 145.3399E	15.X.2013.	N. Monaghan	LifeUnseen*	15
	QLD: Cardwell: Tully Gorge	17.7749S, 145.6504E	15.XI.2017.	M. Connors	iNaturalist*	16
	QLD: Speewah Conservation Park	16.88S, 145.64E	05.II.2019.	M. Connors	This study*	17
	QLD: Redlynch	16.889S, 145.686E	14.IV.2019.	M. Connors	This study*	18

Table 2. Australian Batrachideinae of the genera *Paraselina* and *Selivinga* in online social media. The number from the table accompanies the number of the record from Table 1.

Species	Observer	Link to the observation(s)	N
<i>Paraselina brunneri</i>	Reiner Richter	https://www.inaturalist.org/observations/22360480	5
	Nick Lambert	https://www.inaturalist.org/observations/19947697	6
	Ian McMaster	https://www.inaturalist.org/observations/35283526	7
	Griffin Chong	https://www.inaturalist.org/observations/19373510	10
<i>P. trituberculata</i>	Kathy Rose	https://www.flickr.com/photos/imbala/8466615980	11
<i>Selivinga tribulata</i>	David Rentz	https://www.flickr.com/photos/naturenoises/7570494412	14
	Nick Monaghan	https://www.lifeunseen.smugmug.com/insects/grasshoppers-crickets-katyids/grasshoppers-suborder-caelifer/tetrigidae-pygmy-grasshoppers	15
	Matthew Connors	https://www.inaturalist.org/observations/37612204	16

1. *Anaselina minor* (Sjöstedt, 1921), Tiny helmed groundhopper

The Tiny helmed groundhopper (Figure 2) was described under the name *Vingselina minor* one century ago (Sjöstedt 1921), based on a single female from Herberton, which lacks hind legs. Storozhenko (2019) re-described the species based on freshly collected individuals from Cape Tribulation. The species is readily distinguished from other Australian taxa by the set of the following characters: 1) flat pronotum, whose anterior margin only partly covers the fastigium; 2) short pronotum, leaving most of the abdomen uncovered; and 3) prominent fastigium (in lateral view).

The species has hitherto been known from two localities, the type locality (Sjöstedt 1921) and the Cape Tribulation (Storozhenko 2019). Here we also report a third locality, Wooroonooran, ca. 30 km NW of the type locality. The species inhabits rainforests, where it can be found in wet, but also in relatively dry leaf litter (Figure 2).

2. *Paraselina brunneri* (Bolívar, 1887), Angled Australian barkhopper

The Angled Australian barkhopper *Paraselina brunneri* (Figure 3) was hitherto only known to us from a single female holotype, collected in the surroundings of Sydney, and described more than 130 years ago by Bolívar (1887). The species has never been recorded since.

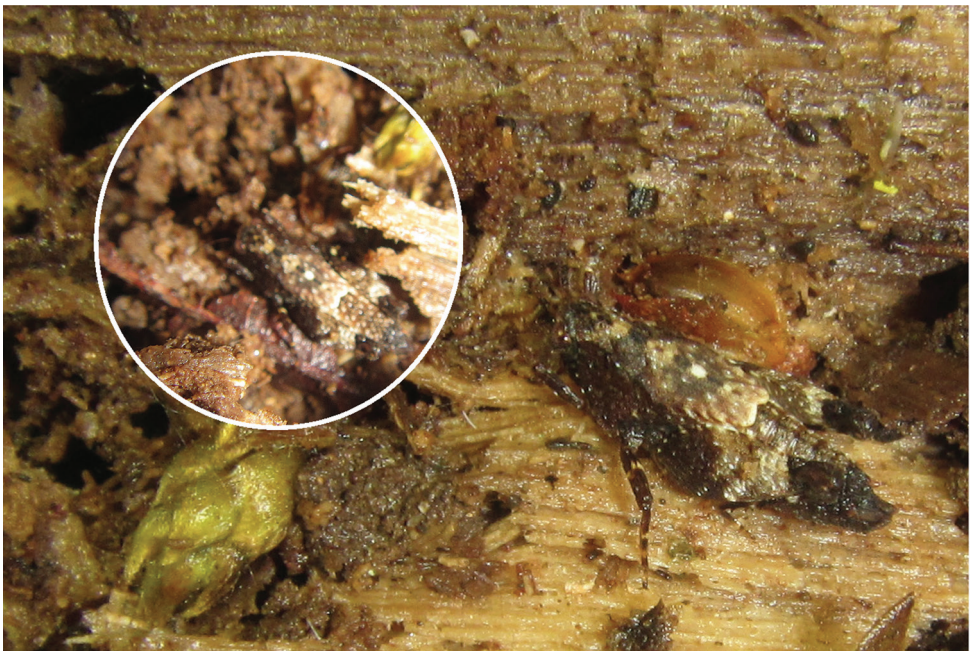


Figure 2. The Tiny helmed groundhopper, *Anaselina minor*, a male in the natural habitat in Wooroonooran (Matthew Connors). Note the uncovered part of the abdomen and bilobate apex of the flat pronotum.

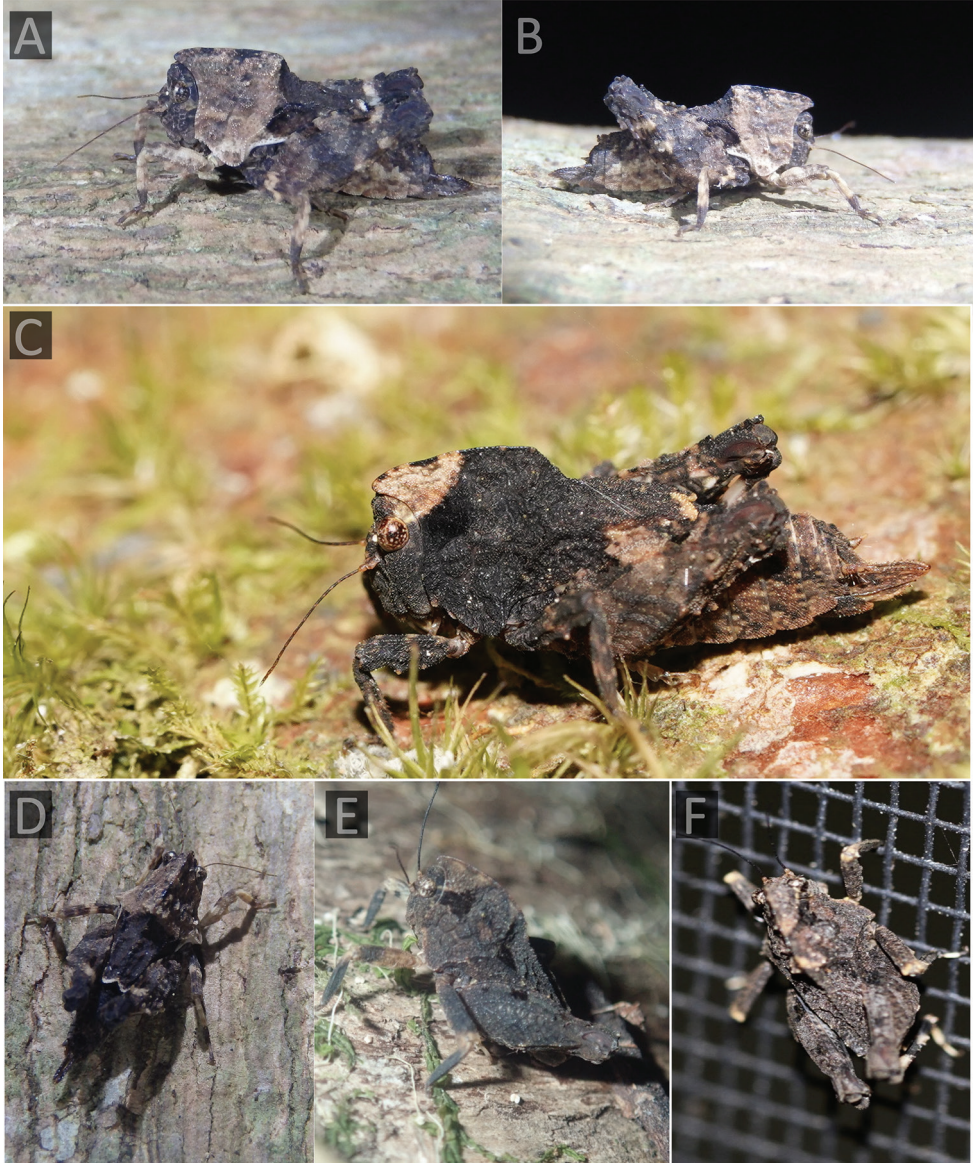


Figure 3. The Angled Australian barkhopper, *Paraselina brunneri* (= *P. multifora* syn. nov.). **A, B, D** a female from Upper Orara (Nick Lambert) **C** a female from Lansdowne forest (Reiner Richter) **E** a male from Mt. Glorious (Griffin Chong) **F** individual from Mt. Mellum (Ian McMaster).

Rehn (1952), when describing *P. multifora* (as *Vingselina multifora*) based on a female holotype and three female paratypes, from Dorrigo (Macleay Range) and Salisbury, did not see Bolívar's type, but only Sjöstedt's (1921) drawings with which he made the comparisons.

Now, after examination of the holotype of *P. brunneri* (see Cigliano et al. 2020), compared with types of *P. multifora* (see Rehn 1952) as well as with four new records (Table 1), the conclusion is clear that *P. multifora* represents a synonym of *P. brunneri*. The species inhabits rainforests of SE Queensland and NE New South Wales (Figure 1), where it dwells on bark. Griffin Chong noticed a specimen of this unusual grasshopper (Figure 3E) as an irregular bump on the bark of a tree he was walking past on the Morelia track (Mt Glorious).

Rehn (1952) described *P. multifora* but was unable to examine the holotype of *P. brunneri*. Our new records belong to the same species as Rehn's (1952) four type specimens, and the holotype of *P. brunneri*. This species is thus known from nine specimens originating from seven localities (Table 1) and its valid name is *Paraselina brunneri*. Hence *Vingselina multifora* Rehn, 1952 syn. nov. represents a junior subjective synonym of *Paraselina brunneri*.

There is considerable infraspecific variability in size, coloration, and angulation of the median carina of the pronotum. Differences separating *P. multifora* from *P. brunneri*, reported by Rehn (1952) and based on Sjöstedt's figure are not reliable. Those characters were 1) the prominence of the compound eyes (same in all specimens), 2) the angle of the median carina of the pronotum (reported to be more angular in *P. multifora*, but when looking at the types, the situation is opposite, with the type of *P. brunneri* being more angled), and 3) the size of hind femora (length of hind femora of *P. brunneri* holotype are 6.5 mm, while in *P. multifora* they measure 4.8–5.8 mm).

The types of the two taxa are very similar, but in addition we have new records, which provide evidence of this infraspecific variability, especially in the size and morphology of the median carina of the pronotum.

3. *Paraselina trituberculata* (Sjöstedt, 1932), Triple-bump Australian barkhopper

The Triple-bump Australian barkhopper *Paraselina trituberculata* (Figure 4) was described almost 90 years ago (Sjöstedt 1932) from a single female (holotype) from the rainforest of the Mount Tamborine, and has never been reported again.

Here, we not only report the species for the first time since the description, but also report a male specimen for the first time. The specimen was photographed by Kathy Rose and uploaded to Flickr, where it was accidentally discovered by Josip Skejo and with help of Josef Tumbrinck identified as *Paraselina trituberculata*. The male was found in the rainforest of Wilsons Creek sitting on bark that was full of mushrooms (Figure 4, Table 1). Wilsons Creek is ca. 70 km SE from the Mount Tamborine, the type locality of the species.

The species is known from two rainforest localities (Figure 1) situated on the border of Queensland and New South Wales, south of Brisbane. *P. trituberculata* is easily distinguished from Australian Batrachideinae and all the other pygmy grasshoppers in the world by the angled pronotum (high in the cephalic part, low in caudal part) that bears three smaller warts on the median carina (Figure 4).



Figure 4. The Triple-bump Australian barkhopper, *Paraselina trituberculata* (Sjöstedt, 1932), a male in his habitat in Wilsons Creek (Kathy Rose).

4. *Selivinga tribulata* Storozhenko, 2019, Tribulation helmed groundhopper

The Tribulation helmed groundhopper (Figure 5) was described under the name *Selivinga tribulata* in 2019 by Storozhenko. This is the first crested Australian species to be described and one of the most easily recognizable species from the continent. Not only is it easily identifiable by its prominent crest, but also by the low position of the antennal grooves.

The species inhabits the northern part of Queensland and is, for now, known from Cape Tribulation (the type locality), Kuranda (Figure 6), Tully Gorge, and Kingfisher Park (see Figure 1). *Selivinga tribulata* is a rainforest species. It can be found in relatively dry leaf litter as well as the normally moist leaf litter that one associates with rainforests, but also is attracted to light. In Kuranda (Queensland) adults have been observed every month of the year.

Even though the species has been described only recently, DR had already been aware of its existence since 2000, and there is indeed a notable population in the author's garden (see habitat in Figure 6). Specimens were observed in every month of the year. JS found photos of the species a few years ago in Flickr and fortunately, in 2019, the name for the species became available.

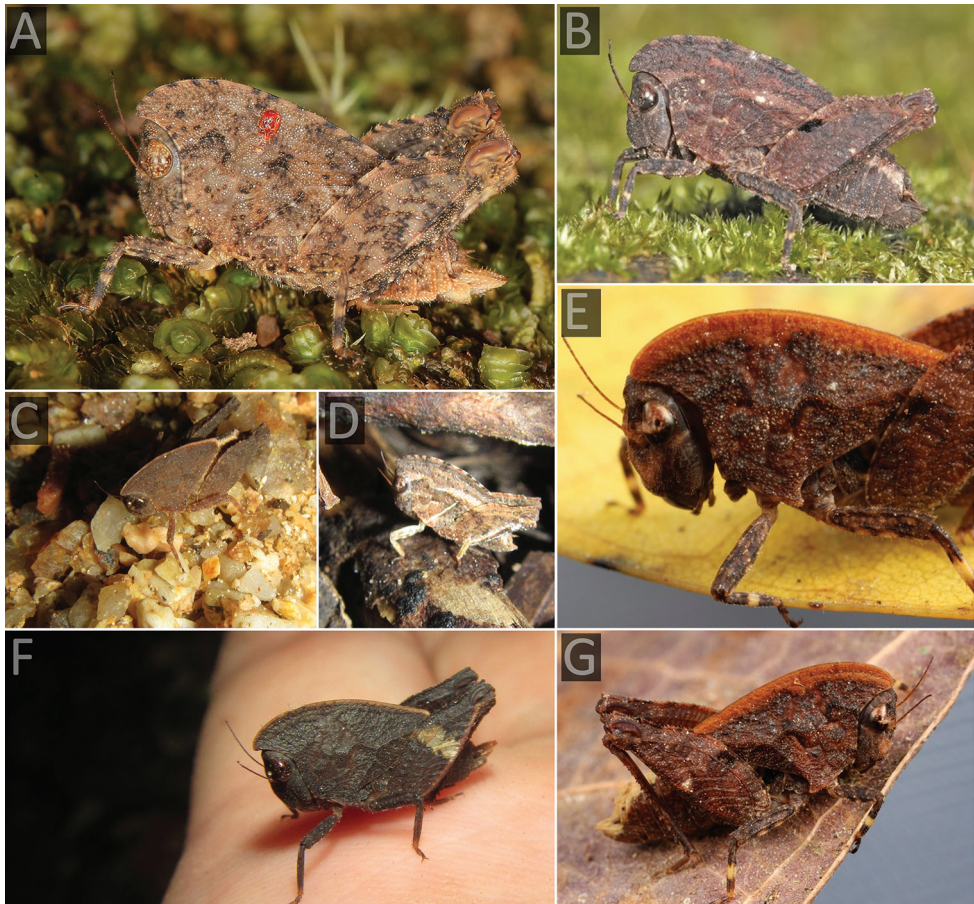


Figure 5. The Tribulation helmed groundhopper, *Selivinga tribulata*, Living specimens in natural habitat. **A** Female from Kuranda (David Rentz) **B** male from Kuranda (David Rentz), male from Tully Range (Matthew Connors) **D** nymph from Redlynch (Matthew Connors) **E, G** a male from Kingfisher park (Nick Monaghan) **F** female from Speewah (Matthew Connors).

Discussion

Even though throughout the study we call them Batrachideinae, and even though Australian barkhoppers and helmed groundhoppers were recently placed in the tribe Bufonidini, together with New Guinean *Bufonides*, it remains questionable as to where *Anaselina*, *Paraselina*, *Selivinga*, *Vingselina*, and *Vilma* really belong. Rehn (1952) placed those genera under Cladonotinae and noted that they should not be assigned to Batrachideinae, as they bear similarities with *Diotarus* and *Piezotettix*, which are true Cladonotinae. They were assigned to Batrachideinae, with no later discussion as to whether they should be (Storozhenko 2019). *Bufonides*, after which the Bufonidini obtained their name, has a rather different morphology: it has antennae with more



Figure 6. Habitat of the Tribulation helmed groundhopper, *Selivinga tribulata*. Rainforest in Kuranda, Queensland, rich in dry leaf litter (David Rentz).

than 20 segments (Hinton 1940), a typical Batrachideinae character, contrary to less than 18 in the Australian genera, so it is questionable that they belong to the same group as *Bufo*. It is clear that systematics based on morphological characters alone has limitations, and new studies based on molecular analysis are therefore needed. It is also clear that the current subfamilies that are recognized since 1887 (Bolívar 1887), are in need of revision, as many of these are clearly polyphyletic or paraphyletic taxa (e.g., Metrodorinae and Cladonotinae) (pers. comm. H. Devriese).

Poor taxonomic knowledge does not prevent us from assessing distributions of Australian barkhoppers, nor from separating species. Species of the genera *Anaselina*, *Paraselina*, and *Selivinga* inhabit humid forests of eastern Australia and are easily distinguishable from each other. In the past it was difficult to study material from different places rapidly. In this study, we show that mainly with records from online social media

platforms we can add knowledge to the biology and taxonomy of certain species. Today, it is much easier to study material from all over the world and communicate with experts and citizen scientists. Citizen science records contributed to the knowledge of morphology of *Paraselina brunneri* and *P. multifora*, which had not been recorded for many decades. From these photos, we have found that specimens vary in certain morphological traits and that micro-differences used to separate *P. brunneri* from *P. multifora* are not species-specific, so *P. multifora* should be considered a synonym of *P. brunneri*.

Anaselina minor is the smallest member of the *Vingselina* genus group, now known from three localities in the northern Queensland. *Selivinga tribulata* was described only last year from Cape Tribulation and here we report three new localities for this species, with a description and depiction of its habitat. We also present the very first record of *Paraselina trituberculata* since its description, and confirm that the species is only overlooked, not extinct. Social media platforms are already used by scientists, and studies which will make it available for people to record and learn about species in a more visual and simple manner, are strongly needed.

In conclusion, *A. minor*, *P. brunneri*, *P. trituberculata*, and *S. tribulata* are easily identifiable, but rare species. Most of the knowledge on their biology was hitherto based on old museum specimens. Here, with united forces of citizens, who post photos online, and experts, who use online social platforms in order to identify specimens, we present an annotated distribution map of the aforementioned species, as well as a taxonomic scrutiny on the system of their classification. Citizen science is not age-limited nor profession-limited. In 2020, anybody and everybody can contribute to biodiversity studies. Evidence is presented by the authors of this study, among which there are an 11-year-old boy and a retired English teacher.

Acknowledgements

We are thankful to Karmela Adžić and Maks Deranja for sending necessary literature, reading early versions of the manuscript, and for providing valuable comments, criticism, and corrections. JS thanks Sergey Yuryevich Storozhenko and Josef Tumbrinck for numerous fruitful discussions, especially on Batrachideinae taxonomy and biogeography. Griffin Chong is 11 years old and has co-authored this study with the consent of his mother, Dr Jacki Liddle, to whom we express our thanks; he photographed the specimen when he was nine years old. Thanks go to the reviewers H. Devriese and J. Tumbrinck, whose corrections and comments improved quality of the manuscript. The study was JS's idea. JS, MH, and DF wrote the manuscript, edited the figures, and prepared the map. DR, IM, KR, MC, NL, NM, and RR took the photographs and provided data on the habitat of *A. minor* (MC), *Paraselina brunneri* (IM, NL, RR, GC), *P. trituberculata* (KR), and *Selivinga tribulata* (DR, MC, NM). All the authors commented on and approved the final version of the manuscript. Open access was funded by the Heinrich – Heine Universität Düsseldorf: Open Access Publishing.

References

- Bolívar I (1887) Essai sur les Acridiens de la tribu des Tetrigidae. Annales de la Société Entomologique de Belgique 31: 175–313. [pl. 4, 5]
- Cigliano MM, Braun H, Eades DC, Otte D (2020) Orthoptera Species File. Version 5.0/5.0. <http://Orthoptera.SpeciesFile.org> [Accessed at March 16 2020]
- Egerton L, Lochman J (2009) Wildlife of Australia. Allen & Unwin, Jacana Books, Crows Nest, NSW, 448 pp.
- Hinton HE (1940) A revision of the genus *Bufo* Bolivar (Orthoptera: Tetrigidae). Proceedings of the Royal Entomological Society of London (B) 9: 30–38. <https://doi.org/10.1111/j.1365-3113.1940.tb00338.x>
- Jones WG, Hill KD, Allen JM (1995) *Wollemia nobilis*, a new living Australian genus and species in the Araucariaceae. Telopea 6(2–3): 173–176. <https://doi.org/10.7751/telopea19953014>
- Rehn JAG (1952) The grasshoppers and Locust (Acridoidea) of Australia. vol. I: Tetrigidae and Eumastacidae. Commonwealth Scientific and Industrial Research Organization, Australia, Melbourne, 326 pp.
- Sjöstedt Y (1921) Acridiidea Australica. Monographie der bisher von Australien bekannten Heuschrecken mit kurzen Fühlern. Kongliga Svenska Vetenskaps-Akademiens Handlingar 62(3): 1–318.
- Sjöstedt Y (1932) Acridiidea aus dem Queensland Museum zu Brisbane. Arkiv för Zoologi 23A(11): 1–21.
- Skejo J, Deranja M, Adžić K (2020) Pygmy Hunchback of New Caledonia: *Notredamia dora* gen. n. et sp. n. – a new Cladonotin (Caelifera: Tetrigidae) genus and species from Oceania. Entomological News 129(2): 170–185. <https://doi.org/10.3157/021.129.0206>
- Storozhenko SY (2019) New taxa of pygmy grasshoppers from Australia with notes on classification of the subfamily Batrachideinae (Orthoptera: Tetrigidae). Zoosystematica Rossica 28(1): 94–107. <https://doi.org/10.31610/zsr/2019.28.1.94>
- Tumbrinck J (2014a) Taxonomic revision of the Cladonotinae (Orthoptera: Tetrigidae) from the islands of South-East Asia and from Australia, with general remarks to the classification and morphology of the Tetrigidae and descriptions of new genera and species from New Guinea and New Caledonia. In: Telnov D (Ed.) Biodiversity, biogeography and nature conservation in Wallacea and New Guinea 2. The Latvian Entomological Society, Riga, 345–396.
- Tumbrinck J (2014b) *Wiemersiella* gen. nov.: eine neue Dornschröckengattung von Neuguinea (Orthoptera: Tetrigidae, Batrachideinae). Entomologie heute 26: 73–85.
- Tumbrinck J (2015) New species of *Palaioscaria* Günther, 1936 (Orthoptera: Tetrigidae, Batrachideinae) from New Guinea. Suara Serangga Papua 9(2): 29–46.
- Weisbecker V, Beck R (2015) Marsupial and monotreme evolution and biogeography. In: Klieve A, Hogan L, Johnston S, Murray P (Eds) Marsupials and monotremes: nature's enigmatic mammals. Nova Science Publishers, New York, NY, 1–25.
- Williams KJ, Ford A, Rosauer DF, De Silva N, Mittermeier R, Bruce C, Larsen FW, Margules C (2011) Forests of East Australia: the 35th biodiversity hotspot. In Zachos FE, Hebel JC (Eds) Biodiversity hotspots. Springer, Berlin, Heidelberg, 295–310. https://doi.org/10.1007/978-3-642-20992-5_16

Checklist of rodents and insectivores of the Crimean Peninsula

Nikolay N. Tovpinets¹, Igor L. Evstafiev¹, Valeriy V. Stakheev²,
Andrey A. Lisovsky³

1 *Centre of Hygiene and Epidemiology in the Republic of Crimea and city of Sevastopol, Russia* **2** *The Southern Scientific Centre of the Russian Academy of Sciences, Rostov-on-Don, Russia* **3** *Zoological Museum of Moscow State University, Moscow, Russia*

Corresponding author: Valeriy V. Stakheev (stvaleriy@yandex.ru)

Academic editor: R. López-Antoñanzas | Received 3 April 2020 | Accepted 10 June 2020 | Published 13 July 2020

<http://zoobank.org/08C44E76-286B-4DC1-83F2-FE7603C7397A>

Citation: Tovpinets NN, Evstafiev IL, Stakheev VV, Lisovsky AA (2020) Checklist of rodents and insectivores of the Crimean Peninsula. ZooKeys 948: 121–127. <https://doi.org/10.3897/zookeys.948.51275>

Abstract

A dataset comprising 6806 records is presented of 17 (of total 24) rodent and insectivore species from the Crimean Peninsula collected during a 35-year period. All records are stored in the Public Mammal Database (Mammals of Russia; <http://rusmam.ru/>). The density of occurrence points allows visual evaluation of species distribution, even on large-scale maps. Each record contains the species name, locality description, and geographic coordinates, coordinate accuracy, date and author of the record, data source, and the method of species identification.

Keywords

Crimean Peninsula, insectivores, rodents, spatial distribution

Introduction

Small mammals [in particular, Rodentia (rodents) and Eulipotyphla (insectivores)] represent one of the most substantial components of the majority of terrestrial ecosystems. Being among the most diverse and abundant mammalian orders, rodents and insectivores play a critical role in maintaining the ecosystem. They also serve as reservoirs

of many infectious diseases of humans, livestock, and wildlife being thus important from the perspective of public health (Evstafiev 2017). It is not surprising that studies of rodent and insectivore diversity and distribution have a long history.

Crimean fauna is heterogeneous and consists of two sharply different groups of species, steppe and mountain (Puzanov 1949). Steppe species penetrated Crimea from the northeast of Black Sea region recently. Mountain fauna is rather autochthonous. Crimean Mountains provided refuge for forest related species during the last glaciation cycle (Markova 2011).

The history of mammalogical studies in the Crimean Peninsula has earlier been described by Dulitskiy (2001a, 2001b), whereas the general characteristics of the mammalian fauna of the Peninsula can be found in Nikolskiy (1891), Puzanov (1927), and Vshivkov (1966). However, information on rodents and insectivores provided in these publications is purely descriptive. More detailed account of the distribution, ecology, and medical and agricultural importance of these animals in the Crimean Peninsula has been reported by Tovpinets and Evstafiev (Tovpinets and Evstafiev 2010; Tovpinets 2012; Evstafiev 2015, 2016, 2017). However, these publications did not present specific data on all known localities for a given species, while maps and observation lists have geographical uncertainty and lack time references.

Here, we publish a checklist of rodent and insectivore records across the Crimean Peninsula for the first time. This checklist was based on comprehensive surveys of small mammals carried out from 1983 until 2018.

Insectivores are represented in Crimea by six species belonging to two families (Dulitskiy 2001a).

Family Erinaceidae Fischer, 1814

1. Northern white-breasted hedgehog *Erinaceus roumanicus* Barrett-Hamilton, 1900

Family Soricidae Fischer, 1814

2. Eurasian pygmy shrew *Sorex minutus* Linnaeus, 1766
3. Caucasian pygmy shrew *Sorex volnuchini* Ognev, 1921
4. Mediterranean water shrew *Neomys anomalus* Cabrera, 1907
5. Bicolored white-toothed shrew *Crocidura leucodon* Hermann, 1780
6. Lesser white-toothed shrew *Crocidura suaveolens* Pallas, 1811

Rodents are represented by 18 species belonging to 5 families.

Family Sciuridae Fischer, 1817

1. Red squirrel *Sciurus vulgaris* Linnaeus, 1758
2. Pygmy ground squirrel *Spermophilus pygmaeus* Pallas, 1778

Family Sminthidae Brandt, 1855

3. Southern birch mouse *Sicista lorigera* Nordmann, 1839

Family Allactagidae Vinogradov, 1925

4. Great jerboa *Allactaga major* Kerr, 1792

Family Cricetidae Fischer, 1817

5. Gray dwarf hamster *Cricetulus migratorius* Pallas, 1773
6. Common hamster *Cricetus cricetus* Linnaeus, 1758
7. Muskrat *Ondatra zibethicus* Linnaeus, 1766
8. Northern mole vole *Ellobius talpinus* Pallas, 1770
9. Common vole *Microtus arvalis* Pallas, 1778
10. East European vole *Microtus rossiaemeridionalis* Ognev, 1924
11. Social vole *Microtus socialis* Pallas, 1773

Family Muridae Illiger, 1811

12. Pygmy wood mouse *Sylvaemus uralensis* Pallas, 1811
13. Steppe wood mouse *Sylvaemus witherbyi* Thomas, 1902
14. Yellow-necked wood mouse *Sylvaemus flavicollis* Melchior, 1834
15. House mouse *Mus musculus* Linnaeus, 1758
16. Mound-building mouse *Mus spicilegus* Petenyi, 1882
17. Norway rat *Rattus norvegicus* Berkenhout, 1769
18. Black rat *Rattus rattus* Linnaeus, 1758

Six species (*Erinaceus roumanicus*, *Sciurus vulgaris*, *Spermophilus pygmaeus*, *Allactaga major*, *Ondatra zibethicus*, and *Ellobius talpinus*) reported earlier for the Crimean Peninsula (Dulitskiy 2001a) have not been detected during our surveys because our methods are inadequate for these species. Two of them (*Sciurus vulgaris* and *Ondatra zibethicus*) have been recently introduced to the Crimean Peninsula (Dulitskiy 2001a).

In general, rodent and insectivore fauna of the Crimean Peninsula is depauperated. For instance, some species that are common in neighboring regions with similar environment such as Taman Peninsula and the northeast of Black Sea coast, are absent from Crimea. These include shrews of the superspecies *Sorex araneus* Linnaeus, 1758, the greater blind mole rat *Spalax microphthalmus* Gldenstdt, 1770, and Strand's birch mouse *Sicista strandi* Formosov, 1931 (Stakheev et al. 2017). Species, which are common in the Caucasus Mountains are also absent in mountainous Crimea (voles of the *Terricola* subgenus, and the dormice *Dryomys nitedula* Pallas, 1778 and *Glis glis* Linnaeus, 1766). However, the Caucasian pygmy shrew *Sorex volnuchini* has recently

been found in Crimea (Vega et al. 2020) but we have no information on this species in the current study.

From an ecological perspective, xerophilous species comprise the largest group, it includes nine species. Some xerophiles (*Spermophilus pygmaeus*, *Allactaga major*, *Cricetulus migratorius*, *Ellobius talpinus*, *Microtus socialis*, and *Mus spicilegus*) occur only in plains and submontane habitats, whereas other species (*Sylvaemus witherbyi* and *Crocidura leucodon*) invade mountains as well.

Dendrophile rodents and insectivores are represented by four species only (*S. vulgaris*, *Neomys anomalus*, *Sylvaemus flavicollis*, and *Sylvaemus uralensis*). Of them, the only true arboreal species *S. vulgaris* is not an aboriginal Crimean species but has been introduced to the peninsula.

A large group of species is associated with human settlements. Eleven species (*Crocidura suaveolens*, *Sylvaemus witherbyi*, *Sylvaemus uralensis*, *Sylvaemus flavicollis*, *Mus musculus*, *Rattus norvegicus*, *Rattus rattus*, *Microtus obscurus*, *Microtus socialis*, *Cricetus cricetus*, *Cricetulus migratorius*) have repeatedly been recorded in residential areas (Evs-tafiev 2016). However, only three species, the house mouse *Mus musculus*, Norway *Rattus norvegicus* and black rats *Rattus rattus*, are truly commensal. In addition, the common hamster *Cricetus cricetus* is often found in urban environment, e.g., from the outskirts to the central regions of the city of Simferopol (Surov et al. 2016).

Taxonomic coverage

The dataset contains 6806 records of rodent and insectivore species from the Crimean Peninsula (Table 1).

Table 1. Number of records of rodents and insectivores collected in the Crimean Peninsula.

№	Species	Number of records
1	<i>Sorex</i> cf. <i>minutus</i> (<i>S. minutus</i> or <i>S. volnuchini</i>)	42
2	<i>Neomys anomalus</i>	10
3	<i>Crocidura leucodon</i>	108
4	<i>Crocidura suaveolens</i>	649
5	<i>Sicista lorigera</i>	38
6	<i>Cricetulus migratorius</i>	337
7	<i>Cricetus cricetus</i>	9
8	<i>Microtus socialis</i>	787
9	<i>Microtus arvalis</i>	7
10	<i>Microtus rossiameridionalis</i>	3
11	<i>Microtus</i> cf. <i>arvalis</i> (<i>M. arvalis</i> and <i>M. rossiameridionalis</i>)	571
12	<i>Sylvaemus uralensis</i>	579
13	<i>Sylvaemus witherbyi</i>	2021
14	<i>Sylvaemus flavicollis</i>	308
15	<i>Mus musculus</i>	1082
16	<i>Mus spicilegus</i>	247
17	<i>Rattus norvegicus</i>	7
18	<i>Rattus rattus</i>	1

Taxonomic ranks

Kingdom: Animalia

Phylum: Chordata

Class: Mammalia

Order: Eulipotyphla, Rodentia

Family: Erinaceidae, Soricidae, Sminthidae, Cricetidae, Muridae

Genus: *Sorex*, *Neomys*, *Crocidura*, *Sicista*, *Cricetulus*, *Cricetus*, *Microtus*, *Sylvaemus*, *Mus*, *Rattus*

Species: *Sorex* cf. *minutus*, *Neomys anomalus*, *Crocidura leucodon*, *Crocidura suaveolens*, *Sicista lorigera*, *Cricetulus migratorius*, *Cricetus cricetus*, *Microtus socialis*, *Microtus arvalis*, *Microtus rossiameridionalis*, *Sylvaemus uralensis*, *Sylvaemus witherbyi*, *Sylvaemus flavicollis*, *Mus musculus*, *Mus spicilegus*, *Rattus norvegicus*, *Rattus rattus*

Spatial coverage

The data set covers the entire Crimean Peninsula. Coordinate box: 44°23'N to 46°13'N Latitude; 32°28'E to 36°38'E Longitude.

Temporal coverage

The data were collected from 1983 to 2018.

Method

The major part of the data set was obtained during epizootiological survey of the Crimean Peninsula. Mammals were captured using small spring snap-traps (120 × 55 mm) deposited for one night in a line of 50–100 traps with a distance of 5 m between them and baited with bread and sunflower oil. The voucher specimens are stored in the personal collection N. Tovpinets, Simpheropol (zootonik@gmail.com). Data on *Cricetus cricetus*, *Rattus norvegicus*, and *Rattus rattus* were obtained via direct observations and/or detection of the traces of their activities (tracks, burrows, etc.).

Dataset description

Each record contains species name after Lisovsky et al. (2019), geographic coordinates, description of locality and habitat, coordinate accuracy (in meters), date and author of the record, data source (museum specimen, photo availability etc.), type of

information used for species identification (morphology, cytogenetics, genetics, etc.), and relative abundance per 100 traps/nights.

The dataset is compiled in the public database ‘Mammals of Russia’ (<http://rusmam.ru/>; Lissovsky et al. 2018), where all records are validated by experts.

Character encoding: UTF-8;

Language: Russian/English;

License: Creative Commons Attribution 4.0 International = CC BY 4.0;

Digital identifiers: http://rusmam.ru/sample/records?id=2_b9486

Acknowledgments

We thank B. Krasnov and N. Nedialkov for their valuable comments and corrections of the manuscript.

This study was supported by the Russian Science Foundation; Grant number 18-14-00093.

References

- Dulitskiy AI (2001a) Mammals of Crimea. Crimean educational-pedagogical state publishing house, Simferopol, 224 pp.
- Dulitskiy AI (2001b) Biodiversity of Crimea. Mammals: history, status, protection, perspectives. Sonat, Simferopol, 208 pp.
- Evstafiev IL (2015) The results of a thirty-year study of small mammals of Crimea. Part 1. Introduction, fauna composition, distribution. Proceedings of the Theriological School 13: 20–34. <https://doi.org/10.15407/ptt2015.13.020>
- Evstafiev IL (2016) The results of a thirty-year study of small mammals of Crimea. Part 2. Species ecology. Proceedings of the Theriological School 14: 103–120. <https://doi.org/10.15407/ptt2016.14.103>
- Evstafiev IL (2017) The results of a thirty-year study of small mammals of Crimea. Part 3. Fauna of parasites and epizootology. Proceedings of the Theriological School 15: 111–135. <https://doi.org/10.15407/ptt2017.15.111>
- Lissovsky AA, Sheftel BI, Saveljev AP, Ermakov OA, Kozlov YA, Smirnov DG, Stakheev VV, Glazov DM (2019) Mammals of Russia: species list and applied issues. Archives of Zoological Museum of Moscow State University. 56: 1–191.
- Lissovsky AA, Sheftel BI, Stakheev VV, Ermakov OA, Smirnov DG, Glazov DM, Strelnikov DP, Ekonomov AV, Titov SV, Obolenskaya EV, Kozlov YA, Saveljev AP (2018) Creating an integrated information system for the analysis of mammalian fauna in the Russian Federation and the preliminary results of this information system. Russian Journal of Theriology 17(2): 85–90. <https://doi.org/10.15298/rusjtheriol.17.2.04>

- Markova AK (2011) Small mammals from Palaeolithic sites of the Crimea. *Quaternary International* 231: 22–27. <https://doi.org/10.1016/j.quaint.2010.07.016>
- Nikolskiy AM (1891) *Vertebrates of Crimea*. Printing House of the Imperial Academy of Sciences, St. Petersburg, 484 pp.
- Puzanov II (1929) *Fauna of Crimea*. Krymizdat, Simferopol, 34 pp.
- Puzanov II (1949) Peculiarity of the Crimean fauna and its origin. *Proceedings of Gorkiy State University* 14: 5–32.
- Stakheev VV, Bogdanov AS, Kornienko SA, Makarikov AA, Fomina ES (2017) Small mammals of the Taman Peninsula. *Polythematic online scientific journal of Kuban State Agrarian University* 131(07): 700–708. <https://doi.org/10.21515/1990-4665-131-059>
- Surov AV, Poplavskaya NS, Bogomolov PL, Kropotkina MV, Katzman EA, Feoktistova NY, Tovpinetz NN (2016) Synurbization of the common hamster (*Cricetus cricetus* L., 1758). *Russian Journal of Biological Invasions* 7(1): 69–76. <https://doi.org/10.1134/S2075111716010094>
- Tovpinets NN (2012) Statistical structure of the population of small mammals of Crimea. In: Zagorodnyuk Igor (Eds) *Dynamics of biodiversity. Collection of scientific reports*. Publishing house of Luhansk Taras Shevchenko national University, Lugansk, 150–153.
- Tovpinets NN, Evstafiev IL (2010) Distribution and population dynamics of Micromammalia in Crimea. *Proceedings of the Theological School* 10: 95–106. <https://doi.org/10.15407/ptt2010.10.095>
- Vega R, McDevitt AD, Stojak J, Mishta A, Wójcik JM, Kryštufek B, Searle JB (2020) Phylogeographical structure of the pygmy shrew: revisiting the roles of southern and northern refugia in Europe. *Biological Journal of the Linnean Society* 129(4): 901–917. <https://doi.org/10.1093/biolinnean/blz209>
- Vshivkov FN (1966) *Mammals*. Krym, Simferopol, 88 pp.

Supplementary material I

Cadastre of Rodents and Insectivores of the Crimean Peninsula

Authors: Nikolay N. Tovpinets, Igor L. Evstafiev, Valeriy V. Stakheev, Andrey A. Lisovsky

Data type: morphological, genetic

Explanation note: The dataset contains 6806 records of 17 (out of 23) rodent and insectivore species from the Crimean Peninsula, collected during a 35-year period mainly during epizootological surveys of the peninsula.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.948.51275.suppl1>

Strandings of cetaceans on the Espírito Santo coast, southeast Brazil, 1975–2015

Luis Felipe S. P. Mayorga¹, Ralph E. T. Vanstreels¹, Renata C. C. Bhering¹,
Natália Mamede², Luiz M. B. Costa³, Flavia C. F. Pinheiro⁴, Luciano W. D. Reis⁵,
Alessandro Trazzi⁶, Wilson Luiz Chevitarese Meirelles⁶,
Alan Marques Ribeiro⁷, Salvatore Siciliano^{8,9}

1 Instituto de Pesquisa e Reabilitação de Animais Marinhos, Avenida Mário Gurgel S/N, Cariacica, Espírito Santo, Brazil **2** Instituto Aqualie, Avenida Doutor Paulo Japiassú Coelho 714, Juiz de Fora, Minas Gerais, Brazil **3** Alcom Indústria e Comércio, Rodovia BR-101 km 409, Itapemirim, Espírito Santo, Brazil **4** Associação Ambiental Voz da Natureza, Rua Coronel Schwab Filho S/N, Vitória, Espírito Santo, Brazil **5** Instituto Mamíferos Aquáticos, Rua dos Radioamadores 357, Salvador, Bahia, Brazil **6** CTA–Serviços em Meio Ambiente, Avenida Saturnino Rangel Mauro 283, Vitória, Espírito Santo, Brazil **7** A&R Consultoria e Treinamento, Rua Porfírio Furtado 125, Santa Leopoldina, Espírito Santo, Brazil **8** Laboratório de Biodiversidade, Instituto Oswaldo Cruz/Fiocruz, Pavilhão Mourisco, sala 217, Av. Brasil, 4365, Manguinhos, Rio de Janeiro, RJ, 21040-900, Brazil **9** Grupo de Estudos de Mamíferos Marinhos da Região dos Lagos, Rua São José 1260, Araruama, Rio de Janeiro, Brazil

Corresponding author: Luis Felipe S. P. Mayorga (luisfelipe@ipram-es.org.br)

Academic editor: Nilton Cáceres | Received 29 January 2020 | Accepted 21 April 2020 | Published 13 July 2020

<http://zoobank.org/B51B8773-0778-40C9-BD9F-090F85DE4D85>

Citation: Mayorga LFSP, Vanstreels RET, Bhering RCC, Mamede N, Costa LMB, Pinheiro FCF, Reis LWD, Trazzi A, Meirelles WLCM, Ribeiro AM, Siciliano S (2020) Strandings of cetaceans on the Espírito Santo coast, southeast Brazil, 1975–2015. ZooKeys 948: 129–152. <https://doi.org/10.3897/zookeys.948.50468>

Abstract

Espírito Santo state is located on the eastern margin of Brazil, in a transitional tropical-subtropical area (18°S–21°S) dominated by oligotrophic waters. With the exception of humpback whales (*Megaptera novaeangliae*), the cetacean community of Espírito Santo has been understudied. In addition to the chronic impacts from fisheries, marine pollution, urban development, and coastal habitat degradation, in November 2015 the cetacean communities of Espírito Santo were challenged by the greatest environmental disaster in Brazil's history. The Mariana dam disaster caused 60 million cubic meters of mining waste to be washed into the Doce River, which ultimately flowed to the coastal waters of Espírito Santo, with a high concentration of heavy metals. This study reviews and updates information on cetacean strandings in

the state of Espírito Santo (excluding humpback whales) prior to this disaster. From 1975 to September 2015, there were 461 recorded cetacean strandings, representing 20 species. An average 1.18 strandings per 100 km per month were recorded since a state-wide daily beach survey program was implemented in October 2010, contrasting with the 0.14 strandings per 100 km per month in previous years. Six species comprised the majority (94.7%) of stranding events: Guiana dolphin (*Sotalia guianensis*), Franciscana (*Pontoporia blainvillei*), rough-toothed dolphin (*Steno bredanensis*), bottlenose dolphin (*Tursiops truncatus*), sperm whale (*Physeter macrocephalus*), and melon-headed whale (*Peponocephala electra*). Oceanic cetaceans stranded most frequently on the southern portion of Espírito Santo, where the continental platform is narrower, whereas the strandings of coastal cetaceans such as Guiana dolphins and Franciscanas were concentrated near estuaries, especially the Doce River. This is particularly concerning in face of the Mariana dam disaster, which drastically altered the estuarine and coastal environment associated with the Doce River.

Keywords

Atlantic Ocean, coast, estuary, Doce River, Odontoceti, Mysticeti, South America

Introduction

Records of cetacean strandings provide reliable data on the occurrence of species and are good indicators of species richness, relative abundance and spatial distribution (Maldini et al. 2005, Pyenson 2010, 2011), and can be used to inform the management of marine resources (Leeney et al. 2008, Peltier et al. 2014). In coastal areas, cetaceans may be impacted by artisanal fisheries (de Freitas Netto and Di Benedetto 2007, 2008, de Freitas Netto and Siciliano 2007), marine traffic (e.g., acoustic pollution, collisions) (Pinheiro et al. 2019) and changes in geomorphology waves due to urban occupation of coastal areas (Albino et al. 2001, Ribeiro and Siqueira 2012).

Espírito Santo state is located on the eastern margin of Brazil (Figure 1), in a transitional tropical-subtropical area (18°S–21°S). The marine environment of Espírito Santo hosts a substantial fish diversity (Floeter et al. 2007, Pinheiro et al. 2015a, b) and is an important winter breeding grounds of humpback whales (*Megaptera novaeangliae*) that migrate annually from the South Sandwich Archipelago (Siciliano 1995, Siciliano et al. 2012), constituting one of the main tourist attraction in the region. Furthermore, the region also has great conservation significance for small coastal cetaceans such as Franciscanas (*Pontoporia blainvillei*) and Guiana dolphins (*Sotalia guianensis*) (de Freitas Netto and Di Benedetto 2007, 2008, de Freitas Netto and Siciliano 2007).

In November 2015, the marine environment of Espírito Santo suffered drastic impacts from the greatest environmental disaster in Brazil's history, the Mariana dam disaster. After the rupture of an iron ore tailings dam, approximately 60 million cubic meters of mining waste were washed into the Doce River at the Mariana municipality, Minas Gerais state. The toxic brown mud released by this disaster flowed through the Doce River until reaching the sea at Linhares, Espírito Santo. The toxic effects of the heavy metal-contaminated mudflow became a major concern for the marine fauna along the Espírito Santo coast (Frainer et al. 2016, Marta-Almeida et al. 2016, Miranda and Marques 2016, Gomes et al. 2018). While studies are still under way in

order to evaluate the impacts of the Mariana dam disaster on the marine environment of Espírito Santo, this study provides a compilation of the data on cetaceans strandings in the 40 years preceding the disaster, providing a historical baseline for the region.

Materials and methods

Study area

The coastline of Espírito Santo state extends approximately 392 km from Riacho Doce stream (18.3475S, 39.6692W) to Itabapoana River (21.3067S, 40.9583W) (Figure 1A). The northern coast of Espírito Santo corresponds to the southern half of the Abrolhos Bank, a sediment-capped volcanic bank that encompasses the most important coralline reefs of the South Atlantic (Moura et al. 2013). Southeast from the Abrolhos Bank, the Vitória-Trindade ridge is a series of volcanic seamounts that extends east, culminating in Trindade Island and Martim Vaz Archipelago approximately 1,200 km from the mainland (Fainstein and Summerhayes 1982). The coastal waters of Espírito Santo are dominated by tropical oligotrophic waters of the Brazilian current coming from the north, but are also under the influence of the seasonal coastal upwelling from the south (Schmid et al. 1995). The region combines coral reef ecosystems in the north and rocky reefs ecosystems in the south (transitioning at approximately 19°S) (Floeter et al. 2001). The highest primary biological productivity occurs at a 50 km-wide strip along the continental coastline, but significant biological productivity also occurs on the Abrolhos Bank and adjacent areas (Figure 1C) (NASA Earth Observatory 2019). The tropical monsoon climate is characterized by intensive and prolonged rains in summer and dry weather in winter, with east and northeast winds predominating in the summer and south and southeast winds occurring intermittently during winter (Nimer 1989). There are a number of river mouths along the coast of Espírito Santo, the most significant being the Doce River with an average flow ranging from 190 m³/s (September) to 650 m³/s (January) (Pinto et al. 2015). Human population density is highest on the southern half of Espírito Santo state, with a particularly high density on the coast of Vitória and Vila Velha municipalities (Figure 1C) (Centro Internacional de Agricultura Tropical et al. 2005); in contrast, Martim Vaz Archipelago is uninhabited and Trindade Island (Figure 1B) has a small military meteorological station with less than 40 people year-round.

Data compilation

Data on strandings was derived from the published literature (including detailed data from articles previously published by the authors), publicly available reports, museum specimens and newspaper articles. Records of by-caught individuals that were brought ashore for necropsy were also included. Records of cetacean strandings were compiled from 01 January 1975 to 30 September 2015. The region is breeding grounds

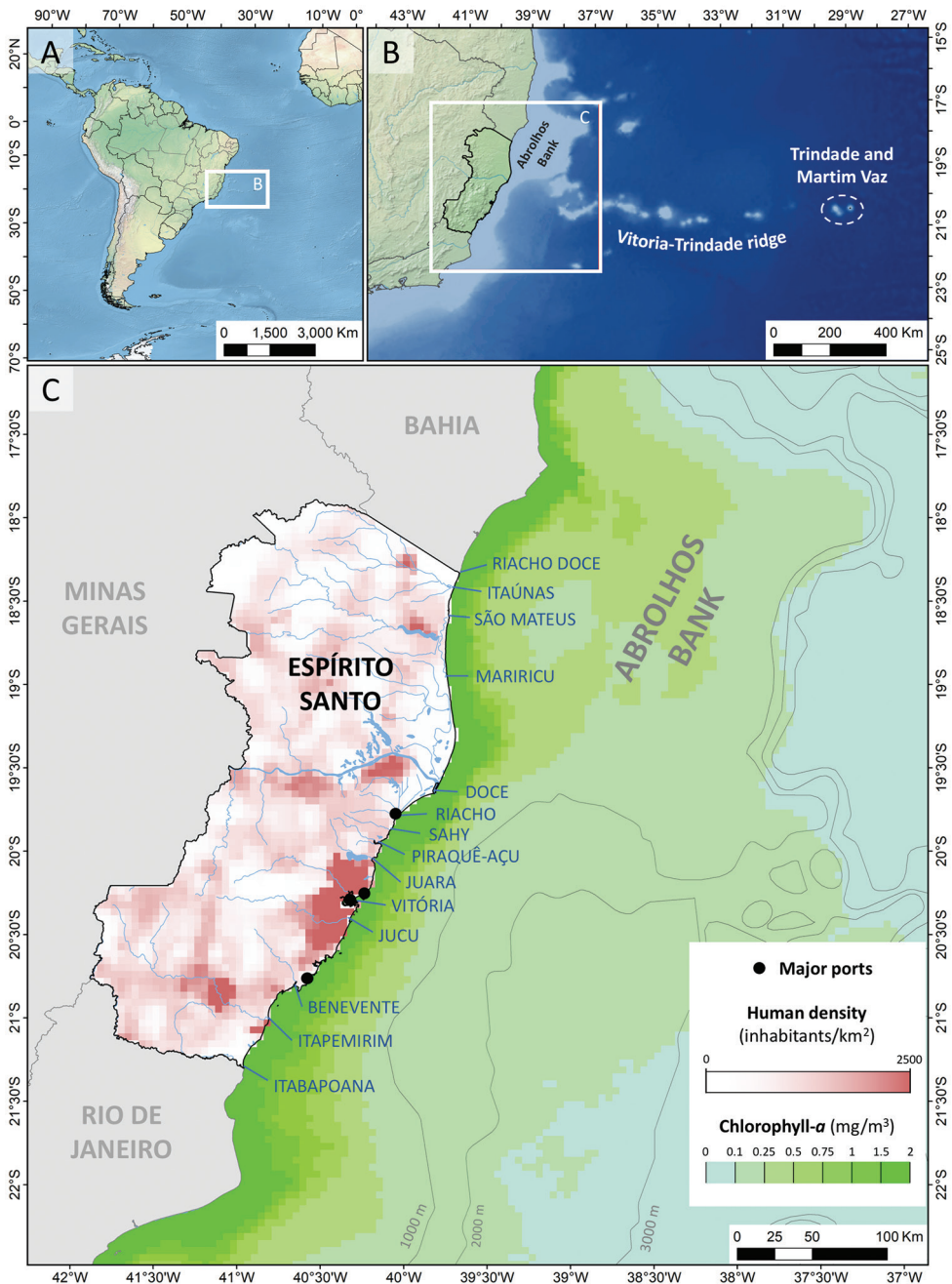


Figure 1. Physical, biological, and human characteristics of the coast of Espírito Santo state, southeast Brazil. Legend: **A, B** Location of Espírito Santo and Trindade and Martim Vaz Islands **C** human population density, major ports, isobaths, sea surface chlorophyll-*a* concentration, estuaries, and bays in the study area. Data sources: (Centro Internacional de Agricultura Tropical et al. 2005, Becker et al. 2009, NASA Earth Observatory 2019).

to *M. novaeangliae*, and this species has been the subject of long-term research efforts (Martins et al. 2013, Bezamat et al. 2015) and its strandings were not included in this report and will be analyzed separately.

It should be noted that beach monitoring effort was considerably irregular during the study period. Until 2010, with the exception of a brief period of systematic beach surveys in 1989 (Ramos et al. 1994, Siciliano 1995, Siciliano et al. 2002), the detection of strandings largely relied on the public reporting them to local NGOs and researchers. In October 2010, the Campos and Espírito Santo Basins Beach Monitoring Project (Projeto de Monitoramento de Praias das Bacias de Campos e Espírito Santo—PMP-BC/ES) was initiated as a requirement by federal environmental authorities for licensing of oil production in the region. Through PMP-BC/ES, the entire coastline of Espírito Santo was monitored by land on a daily basis, and any marine mammal strandings were recorded in a standardized manner.

For each stranding, the following data was compiled: species, date, sex (male, female, unknown sex), age group (calf, juvenile, adult, unknown age), and location. Geographic coordinates (decimal latitude and longitude, Datum WGS1984) were obtained for each stranding and were classified as: (a) “precise” when they were reported by the original source and indicated a location on the coastline of Espírito Santo, (b) “adjusted” when the coordinates provided by the original source were not sufficiently precise to indicate a location on the coastline, and had to be adjusted to represent the nearest location on the coastline, or (c) “approximate” when no coordinate was provided by the original source and an approximate location on the coastline was derived from a text description (e.g., name of the beach or city).

Spatial and statistical analyses

Geographic coordinates were plotted and used to create kernel density heat maps using ArcGIS 10 (ESRI, Redlands, CA, USA). Although the Trindade and Martim Vaz islands are part of Vitória municipality, they were considered separately. The species discovery curve was obtained by plotting the cumulative number of species recorded as the number of strandings increased chronologically. For each stranding, the lunar cycle day (LCD) was calculated, in days, by subtracting the date of the preceding New Moon (obtained from United States Naval Observatory 2019) from the date of stranding. The lunar phase of each stranding was then classified as: (a) “Waxing” when $4 \leq \text{LCD} \leq 10$, (b) “Full” when $11 \leq \text{LCD} \leq 17$, (c) “Waning” when $18 \leq \text{LCD} \leq 24$, and (d) “New” when $\text{LCD} \leq 3$ or $\text{LCD} \geq 25$. One-proportion tests were used to determine whether the proportion of males and females was different from an even distribution (excluding individuals of unknown sex) for the six most frequent species. Chi-Square tests were used to determine whether the number of strandings was heterogeneously distributed between the two most frequent species in relation to age groups, lunar phases and months. Significance level was 0.05 for all tests.

Table 1. Recorded cetacean strandings (excluding *Megaptera novaeangliae*) along the coast of Espírito Santo state, southeast Brazil, from January 1975 to September 2015. The number of stranded individuals is represented as “Male : Female : Unknown sex”.

Family	Species	Common name	Calf	Juvenile	Adult	Unknown age	Total
Balaenidae	<i>Eubalaena australis</i>	Southern right whale	–	–	–	0:0:1	0:0:1
Balaenopteridae	<i>Balaenoptera acutorostrata</i>	Common Minke whale	1:0:0	0:1:0	–	1:0:0	2:1:0
	<i>Balaenoptera borealis</i>	Sei whale	–	–	–	0:0:1	0:0:1
Delphinidae	<i>Globicephala macrorhynchus</i>	Short-finned pilot whale	–	1:0:0	–	–	1:0:0
	<i>Grampus griseus</i>	Risso's dolphin	1:0:0	–	1:0:0	–	2:0:0
	<i>Orcinus orca</i>	Orca	–	0:1:0	–	–	0:1:0
	<i>Peponocephala electra</i>	Melon-headed whale	0:1:0	0:0:1	2:1:0	0:0:1	2:2:2
	<i>Pseudorca crassidens</i>	False killer whale	–	–	–	0:1:0	0:1:0
	<i>Stalia guianensis</i>	Guiana dolphin	5:3:7	33:19:37	54:24:66	10:1:85	102:47:195
	<i>Stenella attenuata</i>	Pantropical spotted dolphin	1:0:0	1:0:0	–	0:0:1	2:0:1
	<i>Stenella frontalis</i>	Atlantic spotted dolphin	–	–	0:1:0	–	0:1:0
	<i>Stenella longirostris</i>	Spinner dolphin	–	0:1:0	0:1:0	0:0:1	0:2:1
	<i>Sterna bredanensis</i>	Rough-toothed dolphin	0:0:2	2:0:0	3:4:1	1:0:2	6:4:5
Kogiidae	<i>Tursiops truncatus</i>	Bottlenose dolphin	–	1:0:0	7:1:1	0:0:4	8:1:5
	<i>Kogia breviceps</i>	Pygmy sperm whale	–	–	–	0:0:1	0:0:1
	<i>Kogia sima</i>	Dwarf sperm whale	–	–	–	0:0:1	0:0:1
	<i>Phocoena spinipinnis</i>	Burmeister's porpoise	–	–	1:0:0	–	1:0:0
	<i>Physeter macrocephalus</i>	Sperm whale	1:0:0	0:1:0	1:0:0	1:0:7	3:1:7
Pontoporiidae	<i>Pontoporia blainvilliei</i>	Franciscana	2:2:4	1:0:2	0:2:13	0:1:20	3:5:39
Ziphiidae	<i>Ziphius cavirostris</i>	Cuvier's beaked whale	–	–	0:3:1	–	0:3:1
	Total		11:6:13	39:23:40	69:37:82	13:3:125	132:69:260

Results

A total of 461 strandings was recorded, representing 20 cetacean species (Table 1, Suppl. material 1). Odontoceti corresponded to 456 individuals (98.9%) and 17 species (85%), and Mysticeti corresponded to 5 individuals (1.1%) and 3 species (15%). Six species had more than five recorded strandings: Guiana dolphin (*Sotalia guianensis*, 344 individuals), Franciscana (*P. blainvillei*, 47), rough-toothed dolphin (*Steno bredanensis*, 15), common bottlenose dolphin (*Tursiops truncatus*, 14), sperm whale (*Physeter macrocephalus*, 11), and melon-headed whale (*Peponocephala electra*, 6). The remaining 14 species comprised 24 individuals. The spatial distribution of the mainland strandings is shown in Figures 2, 3. The species discovery curve is shown in Figure 4. The annual and latitudinal distribution of strandings is summarized in Figure 5; it should be noted that Figure 5B does not include two strandings of Cuvier's beaked whales (*Ziphius cavirostris*) recorded at Trindade Island. There were on average 0.14 recorded strandings per 100 km per month until September 2010 (before PMP-BC/ES) and 1.18 recorded strandings per 100 km per month since October 2010 (during PMP-BC/ES).

The sex ratio was biased towards males in *S. guianensis* ($Z = 4.516$, $p < 0.001$; 95% CI of the proportion of males = 60.4–75.9%) and *T. truncatus* ($Z = 2.334$, $p = 0.02$; 95% CI = 51.8–99.7%). For the remaining species, sex ratio was not significantly different from an even distribution (all $p > 0.30$). The age distribution was different between *S. guianensis* and *P. blainvillei* ($\chi^2 = 21.288$, $df = 2$, $p < 0.001$), with adults being the most frequent category in both species (respectively, 58% and 67%) but calves being more frequent in *S. guianensis* (31%) than in *P. blainvillei* (17%).

The monthly distribution of strandings of *S. guianensis* and *P. blainvillei* was significantly different ($\chi^2 = 26.596$, $df = 11$, $p = 0.005$) with *S. guianensis* strandings occurring year-round with peaks in March, August and November, whereas those of *P. blainvillei* were predominantly concentrated from January to March (Figure 6A). The strandings were similarly distributed in *S. guianensis* and *P. blainvillei* ($\chi^2 = 6.697$, $df = 3$, $p = 0.082$), with both species (along with *T. truncatus*) presenting a higher number of strandings during waning moon (Figure 6B).

Discussion

Twenty species were recorded in this study (21 spp. if humpback whales are included), representing nearly half of Brazil's known diversity of cetaceans (45 spp.) (Paglia et al. 2012). The cetacean fauna of Espírito Santo is largely composed by small and medium-sized tropical coastal and oceanic species, similarly to that of the Northeastern coast of Brazil (Meirelles et al. 2009, Batista et al. 2012), however with fewer Caribbean species and species related to upwelling fronts such as pantropical and Atlantic spotted dolphins (*Stenella attenuata* and *Stenella frontalis*, respectively) and Bryde's whales (*Balaenoptera brydei*) (Costa et al. 2017). In certain respects, the cetacean community of Espírito Santo arguably bears similarity to that other pantropical oligotrophic regions

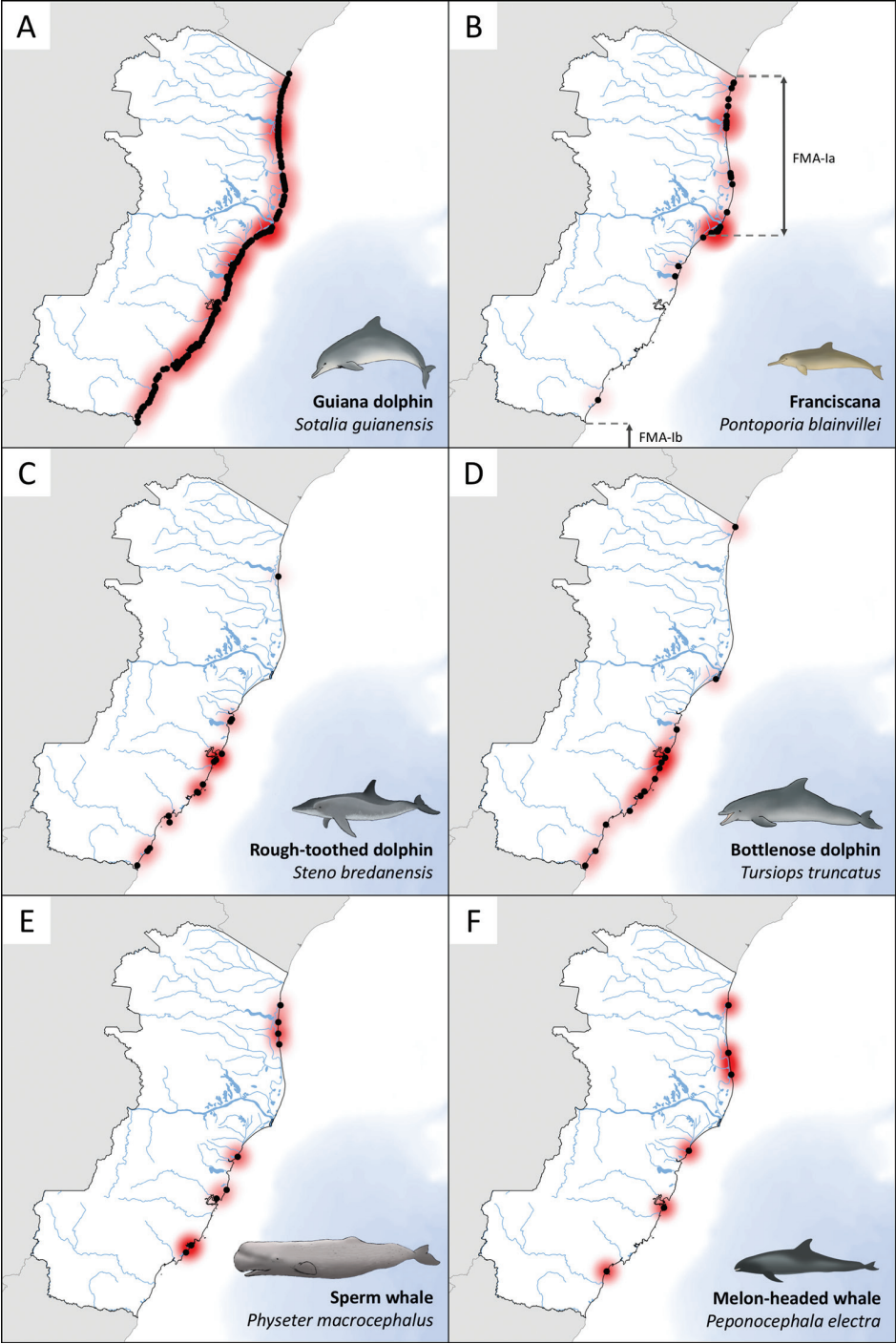


Figure 2. Geographic distribution of the six most frequently stranded cetacean species (excluding *Megaptera novaeangliae*) along the coast of Espírito Santo state, southeast Brazil, from January 1975 to September 2015. The limits of the Franciscana Management Areas (FMA) are shown in **B**.

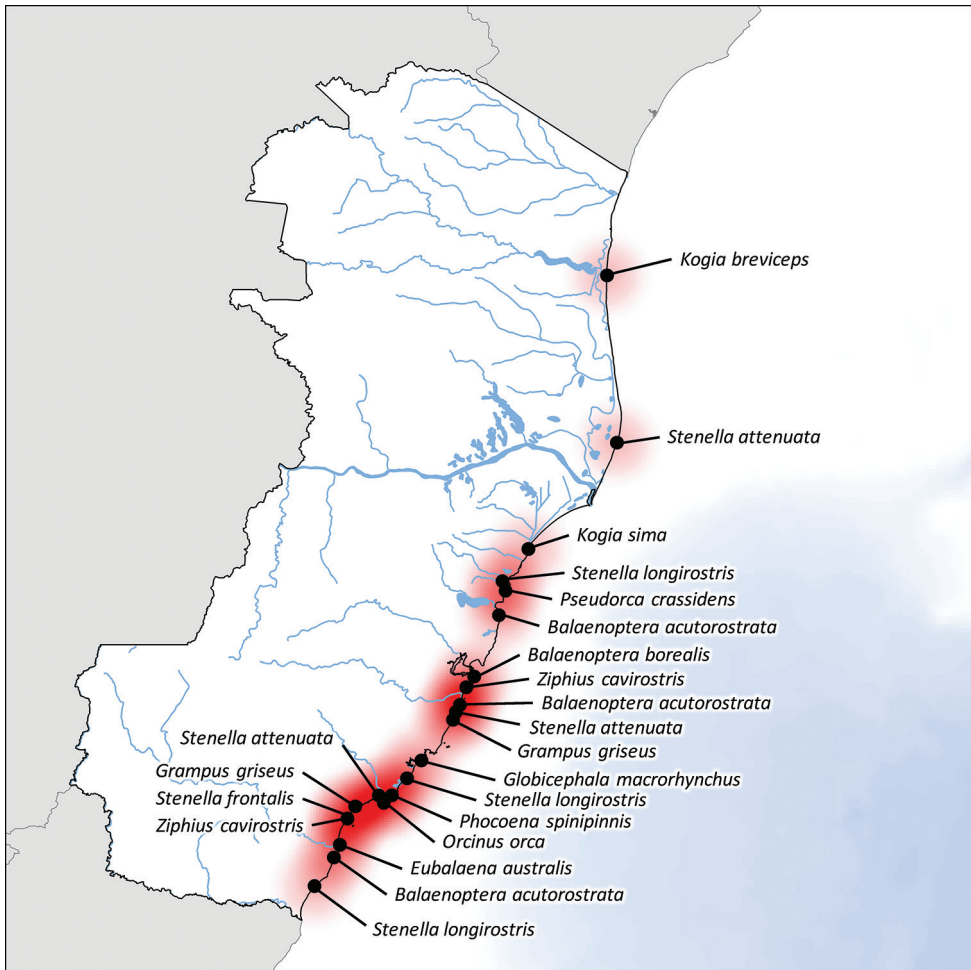


Figure 3. Geographic distribution of the least frequently stranded cetacean species along the coast of Espírito Santo state, southeast Brazil, from January 1975 to September 2015.

such as the Western Tropical Indian Ocean, the Eastern Tropical Pacific and the Gulf of Mexico (Ballance and Pitman 1998). The species discovery curve suggests that the discovery rate has slowed down but a plateau has not yet been reached, and logarithmic regression suggests an additional three species would have been recorded if the number of recorded strandings had been doubled. The vast majority (99%) of the individuals in this study were odontocetes, however this is a biased proportion because we did not include humpback whales in the dataset (their strandings will be analyzed separately).

The average number of recorded strandings increased by 750% after the start of a daily beach survey program (PMP-BC/ES), illustrating how the occurrence of strandings can be greatly underestimated in the absence of such survey efforts. During the period when daily beach surveys were conducted (October 2010 to September 2015),

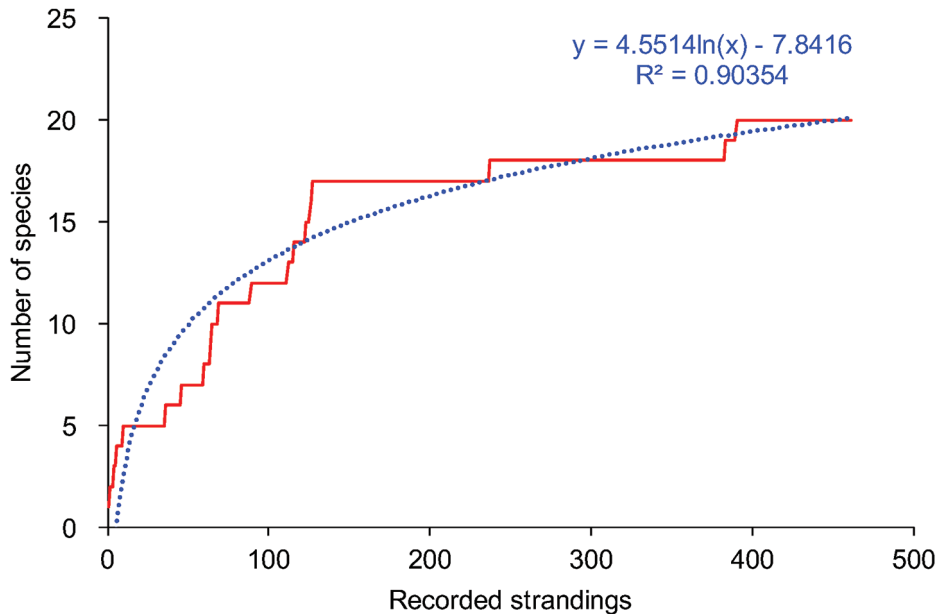


Figure 4. Species discovery curve for the number of cetacean species occurring in Espírito Santo waters based on stranding recordings.

there was a relatively low rate of 1.2 recorded strandings per 100 km per month. This is not an unexpected result, considering the oligotrophic tropical waters of the region (Schmid et al. 1995). In comparison, a similar beach survey program at the Paraná and Santa Catarina states, southern Brazil, has recorded an average of 6.6 strandings per 100 km per month (data from 01/01/2016–31/12/2018, excluding humpback whales; Projeto de Monitoramento de Praias 2019).

Six species were most frequent and represented nearly 95% of all strandings: *S. guianensis* (74.6%), *P. blainvillei* (10.2%), *S. bredanensis* (3.3%), *T. truncatus* (3.0%), *P. macrocephalus* (2.4%) and *P. electra* (1.3%). The fact that the two most frequently recorded species (*S. guianensis* and *P. blainvillei*) are coastal-dwelling suggests that the stranding probability might be influenced by the natural distribution of these species, and therefore stranding data might systematically underrepresent the abundance of pelagic species in the continental waters of Espírito Santo.

Interestingly, strandings were unevenly distributed with regards to the lunar phase. Previous studies have obtained contradictory results in this respect, showing that strandings may be more frequent during full or new moon in New Zealand and Canada (Cordes 1982, Lad and Brabyn 1993, Wright 2005) and during waxing moon in Great Britain (Wright 2005). In this study, strandings of Guiana dolphins, Franciscanas and Common bottlenose dolphins, were most frequent in waning moon, whereas no evident pattern was noted for the remaining species. While this ecological dynamic is not yet understood, potential factors that may drive uneven lunar distribu-

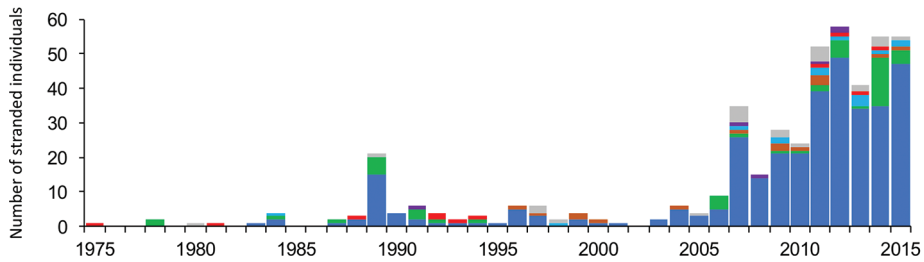
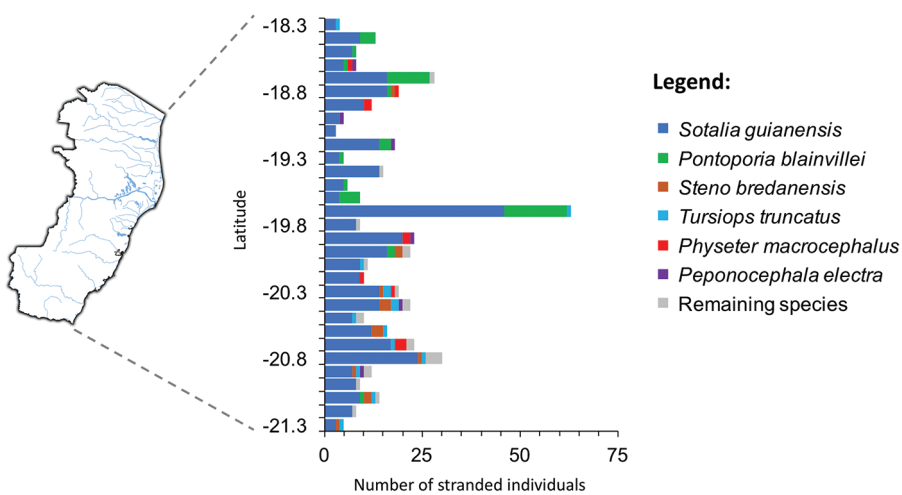
(A) Annual distribution**(B) Latitudinal distribution**

Figure 5. Annual and latitudinal distribution of recorded cetacean strandings (excluding *Megaptera novaeangliae*) along the coast of Espírito Santo state, southeast Brazil, from January 1975 to September 2015.

tion in cetacean strandings include changes in tidal magnitude (Cordes 1982, Lad and Brabyn 1993, Wright 2005), behavioral responses to geomagnetism (Kirschvink et al. 1986, Nishimura and Fukushima 2009) and planktonic growth and migration cycles (Hernandez-Leon et al. 2002, Last et al. 2016).

Guiana dolphin, *Sotalia guianensis* (van Bénédén, 1864)

Guiana dolphins were frequently recorded throughout the Espírito Santo coast, with hotspots of occurrence in estuaries. The Doce River estuary was a particularly significant hotspot for strandings of this species, in agreement with previous studies that suggested this is an important habitat for the Guiana dolphin (Pinheiro 2014).

Previous studies found that most Guiana dolphins stranded in Brazil are immature males (Lima et al. 2017), which is consistent with the sex ratio of 68% males recorded

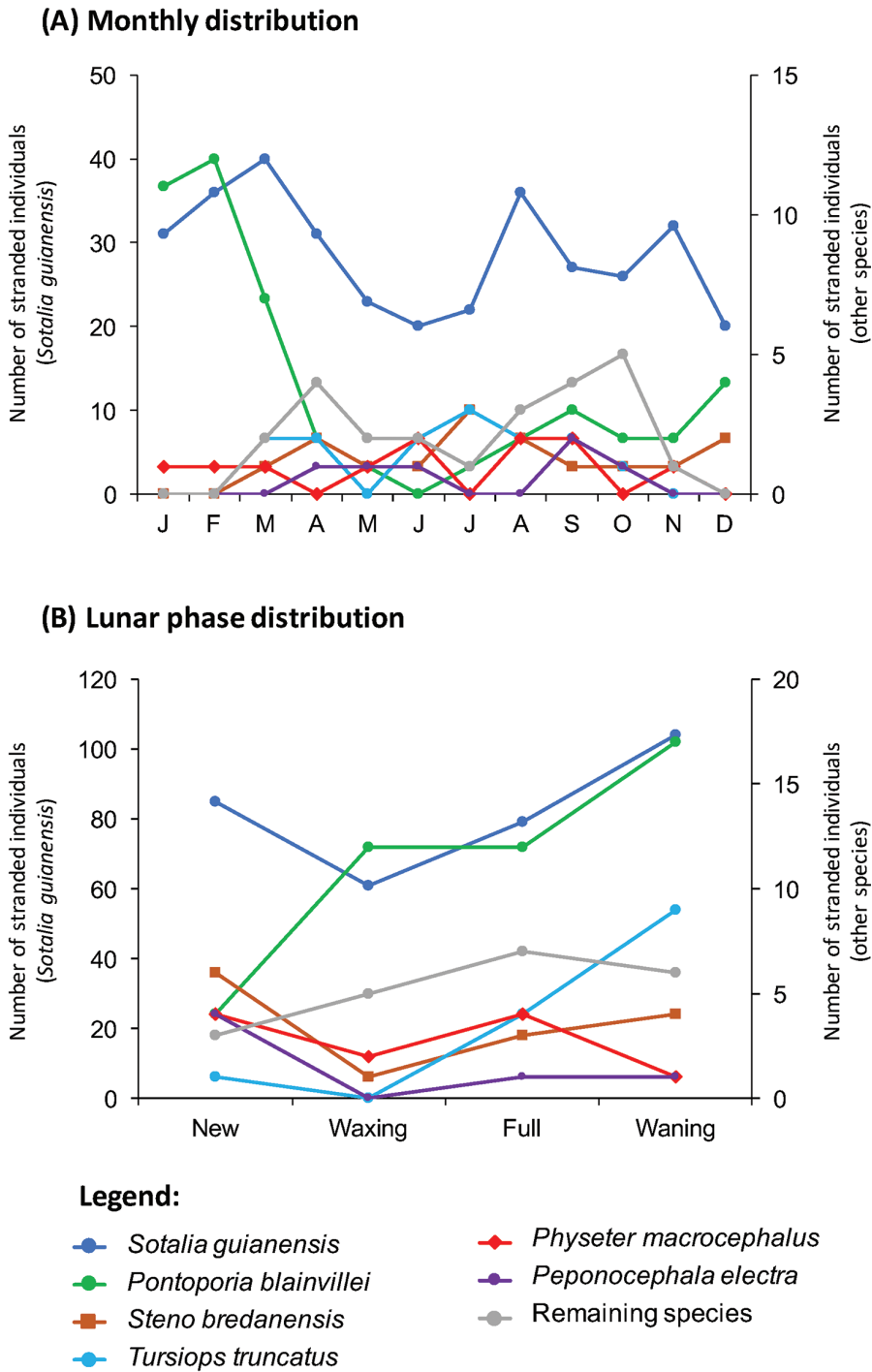


Figure 6. Monthly and lunar phase distribution of recorded cetacean strandings (excluding *Megaptera novaeangliae*) along the coast of Espírito Santo state, southeast Brazil, from January 1975 to September 2015.

in this study. The species is known to be frequently bycaught in gillnets in Espírito Santo (Barros et al. 1997, de Freitas Netto and Barbosa 2003, de Freitas Netto and Di Benedetto 2008), especially before reaching sexual maturity, with 80% of bycaught individuals corresponding to male individuals younger than 6 years (Rosas et al. 2003, Di Benedetto and Ramos 2004). The finding that stranded individuals were also predominantly young males (at least for the subset of 149 individuals for which sex was determined, bearing in mind that sex was not determined for 57% of Guiana dolphin strandings in this study) suggests that a substantial proportion of the strandings recorded in this study might correspond to individuals that were bycaught in gillnets and then washed ashore. The spatial hotspots and temporal distribution of Guiana dolphin strandings could therefore be partly related to an uneven distribution in gillnet fishing effort rather than being exclusively explained by the species' ecology (de Freitas Netto and Di Benedetto 2007, Prado et al. 2016). In this context, the large number of strandings at the Doce River estuary might be interpreted as the result of the overlap of the high density of Guiana dolphins with a particularly intense local gillnet fishing effort (Pinheiro 2014). Furthermore, bycatch could also help explaining the February-March peak in strandings, potentially reflecting increased fishing efforts in anticipation to the Easter holidays.

The Guiana dolphin is a regionally abundant species that is highly sensitive to environmental impacts such as fisheries bycatch (Rosas et al. 2003, Di Benedetto and Ramos 2004), human disturbance (Filla et al. 2009), chemical pollution (Lailson-Brito et al. 2010, Moura et al. 2014) and pathogen outbreaks (Gonzales-Viera et al. 2013, Groch et al. 2018). These characteristics, in addition to being classified as Near Threatened (Secchi et al. 2019), render the Guiana dolphin a prime candidate to serve as an ecosystem sentinel for the coastal waters of eastern and southeastern Brazil (Moura et al. 2014).

Franciscana, *Pontoporia blainvillei* Gervais & d'Orbigny, 1844

The population of Franciscanas is split into four Franciscana Management Areas (FMA) based on its ecogeography, morphology and genetics (Secchi et al. 2003, Cunha et al. 2014). The study area corresponds to FMA-Ia, which extends from the northern limit of the Espírito Santo state (18.3S) to the Doce River estuary (19.7S) (Figure 2B). The species' distribution has a hiatus of approximately 220 km from Doce River to the southern limit of Espírito Santo (21.3S), where FMA-Ib begins (Cunha et al. 2014, Danilewicz 2018). Our finding that there were only three recorded strandings within the hiatus in 40 years is in agreement with genetic studies that indicated limited gene flow between FMA-Ia and FMA-Ib (Cunha et al. 2014).

Most strandings occurred near the mouth of large rivers, especially of the Doce and São Mateus rivers, which is consistent with the species' reliance on turbid waters to feed (Siciliano et al. 2002). Doce River is recognized as a particularly important foraging area within FMA-Ia, thanks to its high productivity and turbidity (Siciliano et al. 2002). The strandings of Franciscana also showed marked seasonality, with 64% of the records occurring from January to March. This pattern matches the summer increases in rainfall and river flow (Pinto et al. 2015), which might encourage the species to

come closer to the shore to take advantage from the increased biological productivity. It is also worth noting that although the presence of lesions suggestive of bycatch was not systematically recorded, at least 14 individuals (32%) had clear indications of interaction with fisheries such as net marks, rostral fractures or attached ropes/nets.

The Franciscana is currently classified as Vulnerable (Secchi et al. 2019), and FMA-Ia is the smallest and least-studied population of Franciscanas, with a remarkably low genetic diversity and gene flow to/from other populations (Secchi et al. 2003, Cunha et al. 2014), and an estimated population of 653 individuals (Danilewicz 2018). With an average of 0.43 strandings per month in recent years (since daily beach surveys were implemented), it may be estimated that the annual number of recorded strandings corresponds to ca. 0.8% of the FMA-Ia population. This is likely an underestimation of the true mortality rate, as in other studies the number of stranded cetacean carcasses has been found to represent between 0% and 6.2% of the total mortality, depending on the species (Williams et al. 2011). If the 6.2% upper estimate is used, this would imply that the true mortality might be 16.1 times higher than the number of recorded strandings, i.e., an annual mortality of ca. 12.9% of the FMA-Ia population. It is therefore clear that the survival of the Franciscana population at Espírito Santo requires urgent efforts to mitigate the human impacts, especially at the estuaries on the northern coast of the state (Doce, São Mateus, Mariricu and Itaúnas rivers).

Rough-toothed dolphin, *Steno bredanensis* G. Cuvier in Lesson, 1828

With the exception of one record at São Mateus, the strandings of rough-toothed dolphins were limited to the southern portion of Espírito Santo, where the continental platform is narrower. This may be related to the dietary habits of this species, which feeds predominantly on mesopelagic fish (depth 200–1,000 m) (Berta 2015), and therefore likely prefers to forage in deeper waters than those of the Abrolhos Bank. The recorded strandings of rough-toothed dolphins also appear to concentrate near the larger cities of the southern coast (Vitória/Vila Velha and Guarapari/Anchieta), which might reflect a greater probability of opportunistic detection prior to the daily beach survey program. It is worth noting that one of these strandings involved an adult male that starved due to large quantities of plastic bags in its gastrointestinal tract (Bhering et al. 2010), illustrating the impacts that marine pollution can have on this species (Meirelles and Barros 2007). It is also interesting to note that several rough-toothed dolphin strandings occurred in pairs, with two individuals stranding in the same general area within a few months (e.g., records A370 and A371, A375 and A376, A378 and A379 in Suppl. material 1). It is unclear whether this is a coincidence or if instead it represents a group/familiar dynamic (e.g., mother-calf pairs), and further studies are warranted to evaluate this possibility.

Common bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821)

With the exception of two records (Conceição da Barra and Linhares municipalities), the strandings of common bottlenose dolphins were limited to the southern portion

of Espírito Santo. However, unlike the rough-toothed dolphin, common bottlenose dolphins have a flexible diet that includes prey from coastal waters (Wells and Scott 2009), and therefore it would be reasonable to expect this species would be common in the Abrolhos Bank. A possible explanation is that the species is concentrating at the Vitória eddy (Schmid et al. 1995). Because the Greater Vitória metropolitan area was the main hotspot for common bottlenose dolphin strandings, another potential explanation would be that these animals are attracted by the fisheries targeting small pelagic fishes that operate from that area and with which this species is known to interact (Zappes et al. 2011). It is worth noting that although the Itaipava fishing fleet is the largest in the state, it focuses primarily on longline fishing of dolphinfish and tuna (Bugoni et al. 2008), which would not be attractive for common bottlenose dolphins.

Sperm whale, *Physeter macrocephalus* Linnaeus, 1758

Sperm whale strandings were diffusely distributed along the Espírito Santo coast, without well-defined hotspots. At-sea observations suggest that sperm whales tend to concentrate along the central coast of Bahia, especially at the Camamu-Almada Basin, and occur at much lower densities in Espírito Santo (Batista et al. 2012). The number of strandings of this species in this study was relatively high compared to similar surveys conducted in other portions of the Brazilian coastline (Prado et al. 2016, Vianna et al. 2016, Costa et al. 2017), which suggests this species probably forages along the Vitória-Trindade ridge and occasionally approaches the Espírito Santo coast. It is worth noting that previous studies suggested that the species might be most abundant in Espírito Santo waters in winter and spring, from July to November (Batista et al. 2012), but this was not evident in the strandings recorded in this study.

Melon-headed whale, *Peponocephala electra* (Gray, 1846)

Melon-headed whales are relatively common on the coast of northeast Brazil, including Bahia, where a mass stranding event involving 240 individuals was recorded on 1987 (Lodi et al. 1990). Strandings were diffusely distributed along the Espírito Santo coast, without well-defined hotspots. The number of strandings of this species in this study was relatively high compared to similar surveys conducted in other portions of the Brazilian coastline (Prado et al. 2016, Vianna et al. 2016, Costa et al. 2017), which is consistent with at-sea surveys showing that melon-headed whales are occasionally seen along the coast of Espírito Santo (Wedekin et al. 2009, 2014). It is worth noting that there was one instance where a live individual stranded in the state, but it later died and its death was attributed to plastic ingestion (Costa et al. 2012), illustrating the impacts of plastic pollution can have on this species.

Other species

The remaining 14 species comprised 24 individuals, predominantly corresponding to small species with tropical oceanic distribution. Most of these records were at the

southern portion of Espírito Santo, which suggests that the narrower continental platform may have increased the probability of stranding.

The only baleen whales recorded in this study were common Minke whale (*Balaenoptera acutorostrata*), Sei whale (*Balaenoptera borealis*) and southern right whale (*Eubalaena australis*). These species are known to occasionally occur in the region during their winter migration in the Southwest Atlantic (Zerbini et al. 1997, Berta 2015). Based on their predicted distribution, the following mysticetes that would be expected to occur in the study area (besides humpback whales) but were not recorded in this study are: Antarctic Minke whales (*Balaenoptera bonaerensis*), Bryde's whales, and Blue whales (*Balaenoptera musculus*); the southern coast of Espírito Santo is also on the distribution limit for the Fin whale (*Balaenoptera physalus*) (Berta 2015, International Union for Conservation of Nature and Natural Resources 2019).

With the exception of the Burmeister's porpoise (*Phocoena spinipinnis*), the remaining records of odontocetes are within the known distribution of each species (Berta 2015, International Union for Conservation of Nature and Natural Resources 2019). Burmeister's porpoises are small odontocetes that inhabit the coastal waters of South America (Berta 2015). Although the species' distribution extends as far north as 5°46'S on the Pacific coast (northern Peru), its distribution on the Atlantic coast is generally considered to be restricted south of 27°55'S (Santa Catarina state, Brazil) (International Union for Conservation of Nature and Natural Resources 2019). This species is rare in southern Brazil, with only one record in Santa Catarina and six records in Rio Grande do Sul despite over 30 years of systematic beach surveys (Prado et al. 2016, Vianna et al. 2016). Therefore, the Burmeister's porpoise recorded in Espírito Santo, more than 1,120 km from the species' northern Atlantic distribution limit, clearly represents an extra-limital record. This could be related to a straggling individual or perhaps a carcass brought by fishing vessels. The later hypothesis is strengthened by the fact that the specimen stranded at Anchieta municipality, one of the ports of the Itaipava fishing fleet which is known to operate along the South Brazil Bight (continental waters from Rio Grande do Sul to São Paulo) (Bugoni et al. 2008).

Based on their distribution range, the following odontocetes would also have been expected to occur in the study area but were not recorded in this study: long-beaked common dolphin (*Delphinus capensis*), short-beaked common dolphin (*Delphinus delphis*), pygmy killer whale (*Feresa attenuata*), Fraser's dolphin (*Lagenodelphis hosei*), Blainville's beaked whale (*Mesoplodon densirostris*), Clymene dolphin (*Stenella clymene*), and striped dolphin (*Stenella coeruleoalba*) (Berta 2015, International Union for Conservation of Nature and Natural Resources 2019).

Implications for conservation

Our results suggest that the Doce River estuary may be a particularly significant area for cetaceans in Espírito Santo, especially Guiana dolphins and Franciscanas. For this reason, the impacts that the Mariana dam disaster may have had on these species, both of which were already threatened with extinction, are acutely concerning. The mudflow resulting from this incident had a high concentration of heavy metals (Frainer et al.

2016, Marta-Almeida et al. 2016, Miranda and Marques 2016, Gomes et al. 2018), and cetaceans are particularly at risk of intoxication due to biomagnification along the food chain (Fossi and Panti 2018). Furthermore, the extent of the mudflow led to substantial impacts to the marine environment which likely also affected prey availability for these species (Frainer et al. 2016, Miranda and Marques 2016). Environmental impact studies to evaluate the consequences of this disaster on the marine fauna of Espírito Santo are underway, and our results will serve as a baseline for comparison for post-2015 stranding data (e.g., number and species of strandings, seasonal distribution, etc.).

Four threatened species were recorded in this study: Guiana dolphin (Vulnerable), Franciscana (Vulnerable), sperm whale (Vulnerable), and Sei whale (Endangered) (International Union for Conservation of Nature and Natural Resources 2019). It is remarkable that three of these species (Guiana dolphin, Franciscana, and sperm whale) were amongst the most frequently recorded in this study. Considering their differences in habitat use and body size, it is clear that these factors alone could not explain their particularly high frequency. Instead, our data suggest that these species are either particularly abundant or experience high mortality in the study area. In particular, the Franciscana presents a critical conservation challenge, as its small population in northern Espírito Santo is known to be genetically distinct and geographically isolated (Secchi et al. 2003, Cunha et al. 2014, Danilewicz 2018), and our results suggest that this population already experienced high annual mortality prior to the Mariana dam disaster.

Although the seamounts along the Vitória-Trindade ridge likely provide attractive habitat for marine fauna (Floeter et al. 2007, Pinheiro et al. 2015a, b), including cetaceans (Wedekin et al. 2014), only two strandings were recorded at Trindade Island, both of Cuvier's beaked whales. Such a small number of recorded strandings is likely due to a combination of the relatively small size of the island (6.1×2.2 km), the small human population (< 40 inhabitants) and the lack of systematic beach surveys (which would be extremely difficult due to the steep terrain). The lack of recorded strandings therefore should not be interpreted as an indication that this region is not a significant habitat for cetaceans. The impacts that the mudflow from the Mariana dam disaster may have had on cetacean communities along the Vitória-Trindade ridge therefore also merits careful consideration.

Lastly, it is worth highlighting that strandings of sperm whales and melon-headed whales occurred with an unexpectedly high frequency in comparison to other similar surveys conducted in portions of the Brazilian coastline (Meirelles et al. 2009, Prado et al. 2016, Vianna et al. 2016, Costa et al. 2017), which suggests that these deep-oceanic species might aggregate off the southern coast of Espírito Santo. Additional studies employing aerial and boat transects, telemetry and acoustic surveys are therefore warranted to investigate this hypothesis and determine important areas for cetaceans in the region.

Acknowledgements

We are grateful to the numerous researchers, staff members, volunteers that have contributed to the beach survey and opportunistic stranding response over the years. We are thankful to the direct or indirect contributions of Instituto de Pesquisa e Reabili-

tação de Animais Marinhos (IPRAM), Instituto Estadual de Meio Ambiente e Recursos Hídricos (IEMA), Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA), Instituto Baleia Jubarte (IBJ), Organização Consciência Ambiental (ORCA), CTA Meio Ambiente, Scitech Environmental Science and Technology Ltda., Petrobras, Museu de Zoologia da Universidade de São Paulo (MZ-USP), Museu Nacional da Universidade Federal do Rio de Janeiro (MN-UFRJ), and Posto Oceanográfico Ilha da Trindade (POIT) da Marinha do Brasil. Projeto de Monitoramento de Praias das Bacia de Campos e Espírito Santo - PMP-BC/ES is one of the monitoring programs required by Brazil's federal environmental agency, IBAMA, for the environmental licensing process of oil production and transport by Petrobras. We thank the reviewer Luís M.D. Barcellos for the helpful comments.

References

- Albino J, Paiva D, Machado G (2001) Geomorfologia, tipologia, vulnerabilidade erosiva e ocupação urbana das praias do litoral do Espírito Santo, Brasil. *Geografares*: 63–69. <https://doi.org/10.7147/GEO2.1141>
- Ballance LT, Pitman RL (1998) Cetaceans of the western tropical Indian Ocean: Distribution, relative abundance, and comparisons with cetacean communities of two other tropical ecosystems. *Marine Mammal Science* 14: 429–459. <https://doi.org/10.1111/j.1748-7692.1998.tb00736.x>
- Barros N, Barbosa L, Gasparini J (1997) Distribuição e biologia de mamíferos marinhos no litoral do Espírito Santo, Brasil. *Resumos do XI Encontro de Zoologia do Nordeste*. Fortaleza, Brazil.
- Batista RLG, Schiavetti A, Santos UA dos, Reis M do SS dos (2012) Cetaceans registered on the coast of Ilhéus (Bahia), northeastern Brazil. *Biota Neotropica* 12: 31–38. <https://doi.org/10.1590/S1676-06032012000100003>
- Becker J, Sandwell D, Smith W, Braud J, Binder B, Depner J, Fabre D, Factor J, Ingalls S, Kim S (2009) Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. *Marine Geodesy* 32: 355–371. <https://doi.org/10.1080/01490410903297766>
- Berta A (2015) Whales, dolphins, & porpoises: a natural history and species guide. The University of Chicago Press, Chicago, 288 pp. <https://doi.org/10.7208/chicago/9780226183220.001.0001>
- Bezamat C, Wedekin LL, Simões-Lopes PC (2015) Potential ship strikes and density of humpback whales in the Abrolhos Bank breeding ground, Brazil. *Aquatic Conservation: Marine and Freshwater Ecosystems* 25: 712–725. <https://doi.org/10.1002/aqc.2523>
- Bhering R, Barbosa L, Mayorga L, Silveira L, Rangel M, Marchesi M (2010) Ingestão de lixo plástico por golfinho-de-dentes-rugosos (*Steno bredanensis*) encalhado no Espírito Santo, Brasil. In: *Resumos do V Simpósio Brasileiro sobre Animais Silvestres e Selvagens*. Viçosa, Brazil. http://www.globalgarbage.org/praias/downloads/V-SBASS-2010/Ingestao_de_lixo_plastico_por_golfinho-de-dentes-rugosos_encalhado_no_Espirito_Santo.pdf [April 30, 2020]

- Bugoni L, Neves TS, Leite Jr NO, Carvalho D, Sales G, Furness RW, Stein CE, Peppes FV, Giffoni BB, Monteiro DS (2008) Potential bycatch of seabirds and turtles in hook-and-line fisheries of the Itaipava Fleet, Brazil. *Fisheries Research* 90: 217–224. <https://doi.org/10.1016/j.fishres.2007.10.013>
- Centro Internacional de Agricultura Tropical, United Nations Environment Program, Center for International Earth Science Information Network, Columbia University, World Bank (2005) Latin American and Caribbean Population Database. Version 3. <http://gisweb.ciat.cgiar.org/population/dataset.htm> [October 2, 2019]
- Cordes D (1982) The causes of whale strandings. *New Zealand Veterinary Journal* 30: 21–24. <https://doi.org/10.1080/00480169.1982.34865>
- Costa AF, Siciliano S, Emin-Lima R, Martins BML, Sousa MEM, Giarrizzo T (2017) Stranding survey as a framework to investigate rare cetacean records of the north and north-eastern Brazilian coasts. *ZooKeys*: 111–134. <https://doi.org/10.3897/zookeys.688.12636>
- Costa P, Carvalho A, Barbosa L, Silveira L (2012) Ingestão de lixo plástico por *Peponocephala electra* (Gray 1846) encalhada viva no litoral do Espírito Santo–Brasil. *Resumos do Congresso Brasileiro de Oceanografia*. Rio de Janeiro, Brazil. <http://www.globalgarbage.org/praias/downloads/v-cbo-2012/1660.pdf> [April 30, 2020]
- Cunha HA, Medeiros BV, Barbosa LA, Cremer MJ, Marigo J, Lailson-Brito J, Azevedo AF, Solé-Cava AM (2014) Population structure of the endangered franciscana dolphin (*Pontoporia blainvillei*): reassessing management units. *PLoS One* 9: e85633. <https://doi.org/10.1371/journal.pone.0085633>
- Danilewicz D (2018) New distribution and abundance assessment of two isolated Franciscana populations in southeastern Brazil through aerial surveys: Implications to fishery management. In: *Resumos do XVII Reunião de Trabalho e XII Congresso da Sociedade e de Especialistas em Mamíferos Aquáticos*. Lima, Peru. http://solamac.org/solamac/portugues/conteudo_ler/279/eventos+anteriores/conferencias/ [April 30, 2020]
- Di Beneditto APM, Ramos RMA (2004) Biology of the marine tucuxi dolphin (*Sotalia fluviatilis*) in south-eastern Brazil. *Journal of the Marine Biological Association of the United Kingdom* 84: 1245–1250. <https://doi.org/10.1017/S0025315404010744h>
- Fainstein R, Summerhayes C (1982) Structure and origin of marginal banks off eastern Brazil. *Marine Geology* 46: 199–215. [https://doi.org/10.1016/0025-3227\(82\)90080-9](https://doi.org/10.1016/0025-3227(82)90080-9)
- Filla G de F, Monteiro F, EL de A (2009) Monitoring tourism schooners observing estuarine dolphins (*Sotalia guianensis*) in the estuarine complex of Cananéia, south-east Brazil. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19: 772–778. <https://doi.org/10.1002/aqc.1034>
- Floeter SR, Krohling W, Gasparini JL, Ferreira CE, Zalmon IR (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. *Environmental Biology of Fishes* 78: 147–160. <https://doi.org/10.1007/s10641-006-9084-6>
- Floeter SR, Guimarães RZ, Rocha LA, Ferreira CEL, Rangel CA, Gasparini JL (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecology and Biogeography* 10: 423–431. <https://doi.org/10.1046/j.1466-822X.2001.00245.x>

- Fossi MC, Panti C (2018) Marine Mammal Ecotoxicology: Impacts of Multiple Stressors on Population Health. Academic Press, London.
- Frainer G, Siciliano S, Tavares D (2016) Franciscana calls for help: the short and long-term effects of Mariana's disaster on small cetaceans of South-eastern Brazil. International Whaling Commission Papers SC/66b/SM/04. <https://www.researchgate.net/publication/328913117> [April 30, 2020]
- de Freitas Netto R, Barbosa LA (2003) Cetaceans and fishery interactions along the Espírito Santo State, Southeastern Brazil during 1994–2001. Latin American Journal of Aquatic Mammals 2: 57–60. <https://doi.org/10.5597/lajam00033>
- de Freitas Netto R, Siciliano S (2007) Contribuição ao conhecimento da distribuição da toninha *Pontoporia blainvillei* (Gervais & d'Orbigny, 1844) no estado do Espírito Santo, sudeste do Brasil. Boletim do Museu de Biologia Mello Leitão 21: 35–45. http://boletim.sambio.org.br/pdf/21_03.pdf [April 30, 2020]
- de Freitas Netto R, Di Benedetto APM (2007) Diversidade de artefatos da pesca artesanal marinha do Espírito Santo. Biotemas 20: 107–119. <https://periodicos.ufsc.br/index.php/biotemas/article/view/20736> [April 30, 2020]
- de Freitas Netto R, Di Benedetto APM (2008) Interactions between fisheries and cetaceans in Espírito Santo State coast, southeastern Brazil. Revista Brasileira de Zoociências 10: 55–63. <https://periodicos.ufjf.br/index.php/zoociencias/article/view/24086> [April 30, 2020]
- Gomes LC, Chippari-Gomes AR, Miranda TO, Pereira TM, Merçon J, Davel VC, Barbosa BV, Pereira ACH, Frossard A, Ramos JPL (2018) Genotoxicity effects on *Geophagus brasiliensis* fish exposed to Doce River water after the environmental disaster in the city of Mariana, MG, Brazil. Brazilian Journal of Biology 79: 659–664. <https://doi.org/10.1590/1519-6984.188086>
- Gonzales-Viera O, Marigo J, Ruoppolo V, Rosas F, Kanamura C, Takakura C, Fernández A, Catto-Dias J (2013) Toxoplasmosis in a Guiana dolphin (*Sotalia guianensis*) from Parana, Brazil. Veterinary Parasitology 191: 358–362. <https://doi.org/10.1016/j.vetpar.2012.09.012>
- Groch KR, Santos-Neto EB, Díaz-Delgado J, Ikeda JM, Carvalho RR, Oliveira RB, Guari EB, Bisi TL, Azevedo AF, Lailson-Brito J (2018) Guiana dolphin unusual mortality event and link to cetacean morbillivirus, Brazil. Emerging Infectious Diseases 24: 1349. <https://doi.org/10.3201/eid2407.180139>
- Hernandez-Leon S, Almeida C, Yebra L, Arístegui J (2002) Lunar cycle of zooplankton biomass in subtropical waters: biogeochemical implications. Journal of Plankton Research 24: 935–939. <https://doi.org/10.1093/plankt/24.9.935>
- International Union for Conservation of Nature and Natural Resources (2019) IUCN Red List of Threatened Species. Version 2019-3. <https://www.iucnredlist.org/> [November 3, 2019]
- Kirschvink J, Dizon A, Westphal J (1986) Evidence from strandings for geomagnetic sensitivity in cetaceans. Journal of Experimental Biology 120: 1–24. <https://jeb.biologists.org/content/120/1/1> [April 30, 2020]
- Lad F, Brabyn MW (1993) Synchronicity of whale strandings with phases of the moon. In: Gatsonis C, Hodges JS, Kass RE, Singpurwalla ND (Eds) Case Studies in Bayesian Statistics. Springer New York, New York, 362–376. https://doi.org/10.1007/978-1-4612-2714-4_12

- Lailson-Brito J, Dorneles P, Azevedo-Silva C, Azevedo A, Vidal L, Zanelatto R, Lozinski C, Azeredo A, Fragoso A, Cunha H (2010) High organochlorine accumulation in blubber of Guiana dolphin, *Sotalia guianensis*, from Brazilian coast and its use to establish geographical differences among populations. *Environmental Pollution* 158: 1800–1808. <https://doi.org/10.1016/j.envpol.2009.11.002>
- Last KS, Hobbs L, Berge J, Brierley AS, Cottier F (2016) Moonlight drives ocean-scale mass vertical migration of zooplankton during the Arctic winter. *Current Biology* 26: 244–251. <https://doi.org/10.1016/j.cub.2015.11.038>
- Leeney RH, Amies R, Broderick AC, Witt MJ, Loveridge J, Doyle J, Godley BJ (2008) Spatio-temporal analysis of cetacean strandings and bycatch in a UK fisheries hotspot. *Biodiversity and Conservation* 17: 2323. <https://doi.org/10.1007/s10531-008-9377-5>
- Lima J, Carvalho A, Azevedo C, Barbosa L, Silveira L (2017) Variation of age and total length in *Sotalia guianensis* (Van Bénédén, 1864) (Cetacea, Delphinidae), on the coast of Espírito Santo state, Brazil. *Brazilian Journal of Biology* 77: 437–443. <https://doi.org/10.1590/1519-6984.13215>
- Lodi L, Siciliano S, Capistrano L (1990) Mass stranding of *Peponocephala electra* (Cetacea, Globicephalinae) on Piracanga Beach, Bahia, northeastern Brazil. *Scientific Reports of Cetacean Research* 1: 79–84. <https://www.icrwhale.org/pdf/shin00179-84.pdf> [April 30, 2020]
- Maldini D, Mazzuca L, Atkinson S (2005) Odontocete stranding patterns in the main Hawaiian Islands (1937–2002): how do they compare with live animal surveys? *Pacific Science* 59: 55–68. <https://doi.org/10.1353/psc.2005.0009>
- Marta-Almeida M, Mendes R, Amorim F, Cirano M, Dias J (2016) Fundão Dam collapse: Oceanic dispersion of River Doce after the greatest Brazilian environmental accident. *Marine Pollution Bulletin* 112: 359–364. <https://doi.org/10.1016/j.marpolbul.2016.07.039>
- Martins CCA, Andriolo A, Engel MH, Kinan PG, Saito CH (2013) Identifying priority areas for humpback whale conservation at Eastern Brazilian Coast. *Ocean & Coastal Management* 75: 63–71. <https://doi.org/10.1016/j.ocecoaman.2013.02.006>
- Meirelles A, Barros H (2007) Plastic debris ingested by a rough-toothed dolphin, *Steno bredanensis*, stranded alive in northeastern Brazil. *Biotemas* 20: 127–131. <https://periodicos.ufsc.br/index.php/biotemas/article/view/20791> [April 30, 2020]
- Meirelles ACO, Monteiro-Neto C, Martins AM, Costa AF, Barros HM, Alves MDO (2009) Cetacean strandings on the coast of Ceará, north-eastern Brazil (1992–2005). *Journal of the Marine Biological Association of the United Kingdom* 89: 1083–1090. <https://doi.org/10.1017/S0025315409002215>
- Miranda LS, Marques AC (2016) Hidden impacts of the Samarco mining waste dam collapse to Brazilian marine fauna – an example from the staurozoans (Cnidaria). *Biota Neotropica* 16. <https://doi.org/10.1590/1676-0611-BN-2016-0169>
- Moura JF, Hauser-Davis RA, Lemos L, Emin-Lima R, Siciliano S (2014) Guiana dolphins (*Sotalia guianensis*) as marine ecosystem sentinels: ecotoxicology and emerging diseases. *Reviews of Environmental Contamination and Toxicology*. Springer, Switzerland, 1–29. https://doi.org/10.1007/978-3-319-01619-1_1
- Moura RL, Secchin NA, Amado-Filho GM, Francini-Filho RB, Freitas MO, Minte-Vera CV, Teixeira JB, Thompson FL, Dutra GF, Sumida PYG (2013) Spatial patterns of benthic

- megahabitats and conservation planning in the Abrolhos Bank. *Continental Shelf Research* 70: 109–117. <https://doi.org/10.1016/j.csr.2013.04.036>
- NASA Earth Observatory (2019) Chlorophyll concentration (1 month – AQUA/MODIS). https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MY1DMM_CHLORA [October 2, 2019]
- Nimer E (1989) *Climatologia do Brasil*. Instituto Brasileiro de Geografia e Estatística, Brasília, 422 pp.
- Nishimura T, Fukushima M (2009) Why animals respond to the full moon: Magnetic hypothesis. *Bioscience Hypotheses* 2: 399–401. <https://doi.org/10.1016/j.bihy.2009.06.006>
- Paglia A, Fonseca G, Rylands A, Herrmann G, Aguiar L, Chiarello A, Leite Y, Costa L, Siciliano S, Kierulff M, Mendes S, Tavares V, Mittermeier R, Patton J (2012) Annotated Checklist of Brazilian Mammals. *Occasional Papers in Conservation Biology* 6: 1–82. <https://www.researchgate.net/publication/288902447> [April 30, 2020]
- Peltier H, Jepson P, Dabin W, Deaville R, Daniel P, Van Canneyt O, Ridoux V (2014) The contribution of stranding data to monitoring and conservation strategies for cetaceans: Developing spatially explicit mortality indicators for common dolphins (*Delphinus delphis*) in the eastern North-Atlantic. *Ecological Indicators* 39: 203–214. <https://doi.org/10.1016/j.ecolind.2013.12.019>
- Pinheiro F (2014) Padrões de uso de habitat do boto-cinza (*Sotalia guianensis*) na região da foz do rio Doce, Sudeste do Brasil. Master Thesis. Universidade Federal do Espírito Santo, Vitória, Brazil. <http://repositorio.ufes.br/handle/10/1325> [April 30, 2020]
- Pinheiro FCF, Pinheiro HT, Teixeira JB, Martins AS, Cremer MJ (2019) Opportunistic development and environmental disaster threat Franciscana dolphins in the Southeast of Brazil. *Tropical Conservation Science* 12: 1–7. <https://doi.org/10.1177/1940082919847886>
- Pinheiro HT, Joyeux J-C, Madureira JMC, Martins A (2015a) Fish diversity of a southwestern Atlantic coastal island: aspects of distribution and conservation in a marine zoogeographical boundary. *Check List* 11: 1615. <https://doi.org/10.15560/11.2.1615>
- Pinheiro HT, Mazzei E, Moura RL, Amado-Filho GM, Carvalho-Filho A, Braga AC, Costa PA, Ferreira BP, Ferreira CEL, Floeter SR (2015b) Fish biodiversity of the Vitória-Trindade Seamount Chain, southwestern Atlantic: an updated database. *PLoS One* 10: e0118180. <https://doi.org/10.1371/journal.pone.0118180>
- Pinto W, Lima G, Zanetti J (2015) Comparative analysis of models for times to series modeling and forecasting of scheme of average monthly streamflow of the Doce River, Colatina, Espírito Santo, Brazil. *Ciência e Natura* 26: 1–11. <https://doi.org/10.5902/2179460X17143>
- Prado JH, Mattos PH, Silva KG, Secchi ER (2016) Long-term seasonal and interannual patterns of marine mammal strandings in subtropical western South Atlantic. *PLoS One* 11: e0146339. <https://doi.org/10.1371/journal.pone.0146339>
- Projeto de Monitoramento de Praias (2019) Sistema de Informação de Monitoramento da Biota Aquática. <https://segurogis.petrobras.com.br/simba/web/login> [October 2, 2019]
- Pyenson ND (2010) Carcasses on the coastline: measuring the ecological fidelity of the cetacean stranding record in the eastern North Pacific Ocean. *Paleobiology* 36: 453–480. <https://doi.org/10.1666/09018.1>

- Pyenson ND (2011) The high fidelity of the cetacean stranding record: insights into measuring diversity by integrating taphonomy and macroecology. *Proceedings of the Royal Society B: Biological Sciences* 278: 3608–3616. <https://doi.org/10.1098/rspb.2011.0441>
- Ramos R, Di Benedetto A, Fernandes L (1994) Relatório, Plano de Conservação e Manejo de Pequenos Cetáceos – Projeto Cetáceos. Fundação Brasileira para a Conservação da Natureza, Rio de Janeiro, Brazil. <https://www.icmbio.gov.br/portal/faunabrasileira/plano-de-acao-nacional-lista/839> [April 30, 2020]
- Ribeiro LCM, Siqueira M da PS (2012) Portos e cidades: expansão e modernização dos portos de Vitória (sec. XX-XXI). *Dimensões*: 385–412. <https://periodicos.ufes.br/dimensoes/article/view/4323> [April 30, 2020]
- Rosas FCW, Barreto AS, Monteiro-Filho EL de A (2003) Age and growth of the estuarine dolphin (*Sotalia guianensis*) (Cetacea, Delphinidae) on the Paraná coast, southern Brazil. *Fishery Bulletin* 101: 377–383. <http://aquaticcommons.org/15132/> [April 30, 2020]
- Schmid C, Schäfer H, Zenk W, Podestá G (1995) The Vitória eddy and its relation to the Brazil Current. *Journal of Physical Oceanography* 25: 2532–2546. [https://doi.org/10.1175/1520-0485\(1995\)025%3C2532:TVEAIR%3E2.0.CO;2](https://doi.org/10.1175/1520-0485(1995)025%3C2532:TVEAIR%3E2.0.CO;2)
- Secchi E, Santos M, Reeves R (2019) *Sotalia guianensis*. The IUCN Red List of Threatened Species. <https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T181359A144232542.en> [October 22, 2019]
- Secchi ER, Danilewicz D, Ott PH (2003) Applying the phylogeographic concept to identify Franciscana dolphin stocks: implications to meet management objectives. *Journal of Cetacean Research and Management* 5: 61–68. <https://archive.iwc.int/?r=250&k=e170e4fe54> [April 30, 2020]
- Siciliano S (1995) Preliminary report on the occurrence and photo-identification of humpback whales in Brazil. Report of the International Whaling Commission 45: 138–140. <http://www6.ensp.focruz.br/repositorio/resource/356241> [April 30, 2020]
- Siciliano S, Di Benedetto A, Ramos R (2002) A toninha *Pontoporia blainvillei* nos Estados do Rio de Janeiro e Espírito Santo, costa sudeste do Brasil: caracterização dos habitats e fatores de isolamento das populações. *Boletim do Museu Nacional* 476: 1–15. <https://www.researchgate.net/publication/285641490> [April 30, 2020]
- Siciliano S, Moura JF de, Filgueiras HR, Rodrigues PP, Leite Jr N de O (2012) Sightings of humpback whales on the Vitória-Trindade chain and around Trindade Island, Brazil. *Brazilian Journal of Oceanography* 60: 455–459. <https://doi.org/10.1590/S1679-87592012000300016>
- United States Naval Observatory (2019) Phases of the Moon. <http://aa.usno.navy.mil/data/docs/MoonPhase.php> [April 10, 2019]
- Vianna T dos S, Loch C, Castilho PV de, Gaidzinski MC, Cremer MJ, Simões-Lopes PC (2016) Review of thirty-two years of toothed whale strandings in Santa Catarina, southern Brazil (Cetacea: Odontoceti). *Zoologia (Curitiba)* 33. <https://doi.org/10.1590/S1984-4689zool-20160089>
- Wedekin L, Rossi-Santos M, Baracho C, Cypriano-Souza A, Simões-Lopes P (2014) Cetacean records along a coastal-offshore gradient in the Vitória-Trindade Chain, western South

- Atlantic Ocean. *Brazilian Journal of Biology* 74: 137–144. <https://doi.org/10.1590/1519-6984.21812>
- Wedekin L, Marcondes M, Baracho C, Rossi-Santos M, Neto E, Groch K, Neves M (2009) Comunidade de cetáceos da plataforma e talude continental do sul do banco dos Abrolhos, Espírito Santo, Brasil. In: Resumos do VI Encontro Nacional sobre Conservação e Pesquisa de Mamíferos Aquáticos e II Simpósio Nordestino de Mamíferos Aquáticos. Salvador, Brazil.
- Wells RS, Scott MD (2009) Common bottlenose dolphin: *Tursiops truncatus*. In: Perrin W, Würsig B, Thewissen J (Eds) *Encyclopedia of marine mammals*. Elsevier, Burlington, 249–255. <https://doi.org/10.1016/B978-0-12-373553-9.00062-6>
- Williams R, Gero S, Bejder L, Calambokidis J, Kraus SD, Lusseau D, Read AJ, Robbins J (2011) Underestimating the damage: interpreting cetacean carcass recoveries in the context of the Deepwater Horizon/BP incident. *Conservation Letters* 4: 228–233. <https://doi.org/10.1111/j.1755-263X.2011.00168.x>
- Wright AJ (2005) Lunar cycles and sperm whales (*Physeter macrocephalus*) strandings on the north Atlantic coastlines of the British Isles and eastern Canada. *Marine Mammal Science* 21: 145–149. <https://doi.org/10.1111/j.1748-7692.2005.tb01214.x>
- Zappes CA, Andriolo A, Simões-Lopes PC, Di Benedetto APM (2011) ‘Human-dolphin (*Tursiops truncatus* Montagu, 1821) cooperative fishery’ and its influence on cast net fishing activities in Barra de Imbé/Tramandaí, Southern Brazil. *Ocean & Coastal Management* 54: 427–432. <https://doi.org/10.1016/j.ocecoaman.2011.02.003>
- Zerbini AN, Secchi ER, Siciliano S, Simões-Lopes PC (1997) A review of the occurrence and distribution of whales of the genus *Balaenoptera* along the Brazilian coast. Report of the International Whaling Commission 47: 407–417. <https://www.researchgate.net/publication/256845647> [April 30, 2020]

Supplementary material I

Historical records of cetacean strandings along the coast of Espírito Santo state, southeast Brazil, 1975–2015

Authors: Luis Felipe S. P. Mayorga, Ralph E. T. Vanstreels, Renata C. C. Bhering, Natália Mamede, Luiz M. B. Costa, Flavia C. F. Pinheiro, Luciano W. D. Reis, Alessandro Trazzi, Wilson Luiz Chevitarese Meirelles, Alan Marques Ribeiro, Salvatore Siciliano
Data type: occurrences

Explanation note: List of the historical records of cetacean strandings along the coast of Espírito Santo state, southeast Brazil, including information on the date, location, coordinates, species, age group, sex, museum accession code, field observations and reference/source.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.948.50468.suppl1>