

A rare and unusual new bittiine genus with two new species from the South Pacific (Cerithiidae, Gastropoda)

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Abstract

A new genus, *Limatium* **gen. n.**, and two new species, *L. pagodula* **sp. n.** and *L. aureum* **sp. n.** are described, found on outer slopes of barrier reefs and fringing reefs in the South Pacific. They are rare for cerithiids, which typically occur in large populations. The two new species are represented by 108 specimens sampled over a period of 30 years, only 16 of which were collected alive. Three subadults from the Philippines and Vanuatu likely represent a third species. In addition to their rarity, *Limatium* species are atypical for cerithiids in their smooth, polished, honey to golden brown shells with distinctive white fascioles extending suture to suture. The radula presents a unique morphology that does not readily suggest an affinity to any of the cerithiid subfamilies. Two live-collected specimens, one of each species and designated as holotypes, were preserved in 95% ethanol and sequenced. Bayesian analysis of partial COI and 16S rDNA sequences demonstrates a placement in the Bittiinae, further extending our morphological concept of the subfamily.

Keywords

Bittiinae, new genus, new species, marine, DNA

Introduction

The Cerithiidae is one of 19 families of Cerithioidea currently accepted, and with 219 species considered valid, it is one of the most diverse (Bouchet et al. 2017, MolluscaBase 2018). Members are distributed worldwide from tropical to temperate biotopes, most frequently in shallow waters, with a few species that extend into bathyal depths. As far as is known, most species are microherbivorous grazers and usually occur in large populations (e.g., Houbrick 1992). The family is subdivided into three Recent subfamilies: Cerithiinae, Argyropezinae, and Bittiinae (Bouchet et al. 2017), with the Cerithiinae and Bittiinae containing the majority of the species. As discussed in Strong and Bouchet (2013, and references therein), there is presently no known diagnostic feature of shell morphology or internal anatomy that allows unambiguous placement in Cerithiinae versus Bittiinae. The only possible exception may be internal features of the midgut, but this requires further study to confirm (Strong and Bouchet 2013). The notion that bittiines may be distinguished by small adult size is a frequent misperception.

Unusual polished, golden shells, less than one centimeter in adult length, of an unfamiliar species first became known to us in material collected by the RAPA 2002 expedition to the Austral Islands. Since then, material comprising at least two species has been sorted from residues collected during campaigns led by the MNHN, with particularly rich sources of specimens from the MONTROUZIER expedition to New Caledonia in 1993, and the LIFOU 2000 expedition to the Loyalty Islands. The earliest specimens located thus far were collected during the MUSORSTOM 3 cruise to the Philippines in 1985, from the early years of the Tropical Deep Sea Benthos program (Bouchet et al. 2008). Despite readily identifiable as belonging to the Cerithiidae, their subfamily placement was unclear. Early collections were represented mainly by empty shells, with only a handful of live-collected specimens that had been subsequently dried. This hampered the use of anatomical dissections to explore their systematic placement; the unique radula did not suggest an affinity to any of the cerithiid subfamilies. The ability to assess their affinities more robustly was possible only with the collection of the first live-collected specimen preserved in ethanol during the Moorea Biocode Project in 2008. In 2013 a specimen of a second species was preserved for molecular analysis during the TUHAA PAE 2013 cruise to the Austral Islands. Based on this material, we here describe a new genus, *Limatium* n. gen., with two new species, *L. pagodula* sp. n. and *L. aureum* sp. n.

Methods

The only two live-collected, fluid-preserved specimens were those used for sequencing and are the designated holotypes. The head-foot of each was removed through the aperture after drilling a small hole through the abapertural side of the penultimate whorl of the shell. The radulae of the holotypes were extracted and mounted for examination

via scanning electron microscopy. However, the radula of *Limatium pagodula* sp. n. was teratological with thin, flimsy, poorly formed teeth along its length; no other live-collected material exists for this species and the operculum is unknown. In addition to the holotype of *Limatium aureum* sp. n., a second specimen live collected in Rapa and subsequently dried was used to extract an operculum and a radula for comparative purposes.

The three radulae and single operculum were tissue digested overnight in 100 μ l of ATL lysis buffer (Qiagen, Inc.) containing ~50 μ g of Proteinase-K, sonicated and rinsed in de-ionized water. Cleaned radulae were mounted directly on glass coverslips; the operculum was attached to the cover slip using a carbon adhesive tab. The cover slips were then attached to aluminum stubs with carbon adhesive tabs, coated with 25–30 nm gold/palladium (60/40), and photographed using an Apreo scanning electron microscope (FEI Company) at the NMNH. Specimens of subadults and juveniles were selected for examination of protoconchs. These shells were mounted on aluminum stubs with Elmer's glue© and photographed uncoated in charge reduction mode using a Hitachi TM3000 scanning electron microscope (Hitachi High Technologies America, Inc.) also at the NMNH. Shells were photographed using a Canon EOS 50D camera with a Canon MP-E 65 mm f/2.8 1–5 \times macro lens and Canon MT-24EX macro twin light flash (Canon USA, Inc.).

The partial COI sequence for the holotype of *Limatium pagodula* sp. n., was produced under the Moorea Biocode Project (see Geller et al. 2013). For the other newly generated sequences, genomic DNA was extracted from roughly one cubic millimeter of 95% ethanol-preserved foot tissue using an automated phenol:chloroform extraction on the Autogenprep965 (Autogen, Holliston, MA) using the mouse tail tissue protocol with a final elution volume of 50 μ l. A 658 base pair (bp) fragment of the cytochrome *c* oxidase I (COI) gene was amplified using degenerate Folmer primers (dgLCO/dgHCO) (Meyer et al. 2005) with M13 tails, and using JGLCO (Geller et al. 2013) in combination with C1-N-2191R (*aka* “Nancy”) (Simon et al. 1994). A ~510 bp fragment of the 16S rRNA gene was amplified using the universal primers 16SAR/BR (Palumbi et al. 1991). PCR reactions were performed with 1 μ l of undiluted DNA template in 20 μ l volumes. Reaction volumes for COI contained 10 μ l of Promega Go-Taq® Hotstart Master Mix (1 unit Promega Go-Taq®, 400 μ M dNTPs, 4 mM MgCl₂), 0.3 μ l 10 μ M of each primer, 0.25 μ g/ μ l of BSA, and 1.25% DMSO. Amplification consisted of an initial denaturation step at 95 °C for 7 min, followed by 45 cycles of denaturation at 95 °C for 45 s, annealing at 42 °C for 45 s, extension at 72 °C for 1 min and a final extension at 72 °C for 5 min. Reaction volumes for 16S, also in 20 μ l volumes, contained 1 μ l of undiluted template DNA, 1 unit Biolase DNA Polymerase (Bioline), 2 μ l 10X reaction buffer, 500 μ M dNTPs, 2 mM MgCl₂, 0.25 μ g/ μ l of BSA, and 0.3 μ l 10 μ M of each primer. Amplification consisted of an initial denaturation step at 95 °C for 5 min, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 48 °C for 30 s, extension at 72 °C for 45 s and a final extension at 72 °C for 3 min. PCR products were purified prior to sequencing using the Exo-SAP-IT protocol (Amersham Biosciences, Piscataway, NY). Sequencing reactions were performed with 1 μ l of purified PCR product, 1.75 μ l BigDye buffer, and 0.5 μ l BigDye (ABI, Foster

City, CA), and run in the thermal cycler for 30 cycles of 30 s at 95 °C, 30 s at 50 °C, 4 min at 60 °C, and then held at 10 °C. Sequencing reactions were purified using Millipore Sephadex plates (MAHVN-4550, Millipore, Billerica, MA) per manufacturer's instructions and analyzed on an ABI 3730XL DNA Analyzer Capillary Array.

Chromatograms were trimmed, assembled, and edited as necessary in Geneious 11.0.2. Sequences were aligned separately for each gene with ClustalX (Thompson et al. 1997) using default parameters as implemented in Geneious. COI was translated into amino acids to check for stop codons and frameshift mutations. All newly generated sequences have been deposited in GenBank (Table 1).

The best fit partitions and models for phylogenetic analyses were determined with PartitionFinder 1.1.1 (Lanfear et al. 2012) which favored the following scheme: COI: SYM+I+G, F81+I, HKY+G, for the first, second and third codon position, respectively; and GTR+I+G for 16S. A subset of the cerithiid dataset of Strong and Bouchet (2013) was used, augmented with newly generated COI and 16S sequences for *Ittibittium houbrieki* (Ponder, 1993) and *Bittium reticulatum* (da Costa, 1778) (see Table 1). In addition to *Limatium*, the Bittiinae was represented by five of the 12 Recent genera currently accepted, four by their type species or their subjective synonyms (see Table 1). Bayesian analysis of the concatenated dataset for 29 cerithiids and one outgroup (Litiopidae) was inferred with MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) on the CIPRES Science Gateway, using the schemes and models indicated by PartitionFinder. Bayesian analyses, consisting of two independent replicates with four heated chains each (0.02), and three swaps per swapping cycle, were run for 50,000,000 Markov chain Monte Carlo (MCMC) generations with a sampling frequency of one tree every 1000 generations. The first 25% were discarded as burn-in. Tracer 1.6 (Rambaut et al. 2014) was used to assess MCMC convergence and to ensure that all ESS values exceeded 200. A majority rule consensus tree was constructed with the sumt command. Nodal support was assessed with posterior probability of each node.

Results

Systematics

Family CERITHIIDAE J. Fleming, 1822

Subfamily BITTIINAE Cossmann, 1906

Limatium gen. n.

<http://zoobank.org/9FD47996-C44C-4D00-82A6-57FC9C619215>

Type species. *Limatium pagodula* sp. n.

Diagnosis. Shells of small size, 6 to 7 mm in adult length on average, with smooth, polished surface, golden honey to dark brown in color. Rachidian with hexagonal to septagonal basal plate, squarish to rectangular, with elevated central portion with

Table 1. Museum registration and GenBank accession numbers for specimens included in the phylogenetic analysis. Representatives of type species (or their subjective synonyms) of genera currently accepted as valid, indicated by ‘*’. Sequences previously published in the analysis of Strong and Bouchet (2013) in regular font, newly sequenced specimens in bold.

Species	Voucher	COI	16S	Locality
Litiopidae				
<i>Litiopa melanostoma</i> Rang, 1829 *	USNM 1199716	KC699870	KC699903	Marathon Key, Coco Plum Beach, Florida, USA, 24°43.45'N, 81°00.04'W.
Cerithiidae				
Bittiinae				
<i>Bittium varium</i> (Pfeiffer, 1840)	USNM 1199719	KC699852	KC699912	Sebastian Inlet, Florida, USA, 27°51.63'N, 80°26.95'W, 1 m.
<i>Bittium glareosum</i> Gould, 1861	MNHN IM- 2009-29804	KC699853	KC699905	INHACA 2011, Stn. MS14, Baixo Danae, 25°54.5'S, 33°2.8'E, 23–26 m.
<i>Bittium impendens</i> (Hedley, 1899)	USNM 1199720	KC699854	KC699911	Shark's Cove, Oahu, Hawaii, USA, 21°38.99'N, 158°3.8'W, 1 m.
<i>Bittium latreillei</i> (Payraudeau, 1826)	USNM 1199724	KC699855	KC699914	Espigon de Rocas, Benalmádena-Costa, Benalmádena, Spain 36°35.3'N, 04°31.7'W, 1–5 m.
<i>Bittium reticulatum</i> (da Costa, 1778) *	USNM 1462732	MH253703	MH253699	Espigon de Rocas, Benalmádena-Costa, Benalmádena, Spain 36°35.3'N, 04°31.7'W, 1–5 m..
<i>Bittium simplex</i> (Jeffreys, 1867)	USNM 1199729	KC699856	KC699913	Strait of Gibraltar, Isla de Tarifa, Spain, 36°00.3'N, 05°36.53'W, intertidal.
<i>Cacozeliana</i> <i>granarium</i> (Kienert, 1842) *	USNM 1200194	KC699857	KC699904	Long Reef, Sydney, New South Wales, Australia, 33°44.6'S, 151°19.1'E, intertidal.
<i>Ittibittium</i> <i>houbrieki</i> (Ponder, 1993)	MNHN IM- 2013-42433	MH253702	MH253698	Cape Naturaliste, Eagle Bay, Western Australia
<i>Ittibittium parvum</i> (Gould, 1861) *	USNM 1199730	KC699869	KC699902	Shark's Cove, Oahu, Hawaii, USA, 21°39.16'N, 158°3.75'W, intertidal.
<i>Limatium aureum</i> sp. n. (holotype)	MNHN IM- 2013-42460	MH253701	MH253697	TUHAA PAE 2013. Austral Islands, Maria. Pente externe récif barrière. 24 m. 21°47.8'S, 154°43'W.
<i>Limatium pagodula</i> sp. n. (holotype) *	UF 427943	MH253700		Moorea Biocode Project. French Polynesia, Society Islands, Moorea. Haapiti, just NW of Matauvau Pass outer reef slope, brushed from under rubble. 20–22 m. -17.568°, -149.884°.
<i>Pictorium kopperbergi</i> (Schepman, 1907) *	MNHN IM- 2009-26984	KC699871	KC699907	PANGLAO Marine Biodiversity Survey 2004, Stn. B10, Panglao I., Momo Beach, 9°36.5'N, 123°45.6'E, 3–14 m.
<i>Pictorium versicolor</i> Strong & Bouchet, 2013	MNHN IM- 2009-26994	KC699874	KC699910	SANTO Marine Biodiversity Survey 2006, Stn. EP36, E Aoré I., Aimbuei Bay, 15°33.1'S–15°33.3'S, 167°12.4/12.7'E, 20–60 m.
<i>Pictorium violaceum</i> Strong & Bouchet, 2013	MNHN IM- 2009-26986	KC699875	KC699909	SANTO Marine Biodiversity Survey 2006, Stn. EP36, E Aoré I., Aimbuei Bay, 15°33.1'S–15°33.3'S, 167°12.4/12.7'E, 20–60 m.
Cerithiinae				
<i>Cerithium</i> <i>atomarginatum</i> Dautzenberg & Bouge, 1933	USNM 1200200	KC699858	KC699899	Shark's Cove, Oahu, Hawaii, USA, 21°39.16'N, 158°3.75'W, intertidal.
<i>Cerithium balteatum</i> Philippi, 1848	MNHN IM- 2009-29697	KC699859	KC699889	SANTO Marine Biodiversity Survey 2006, Stn. DB53, Palikulo Bay, 15°28.8'S, 167°15.2'E, 5 m.
<i>Cerithium caeruleum</i> GB Sowerby II, 1855	MNHN IM- 2009-27010	KC699860	KC699894	Atimo Vatae Madagascar “Deep South” Survey 2010, Stn. TM2, Cap Ranavalona, 25°4.3'S, 46°57.7'E, 0–1 m.
<i>Cerithium egeum</i> Gould, 1849	USNM 1200201	KC699861	KC699900	Shark's Cove, Oahu, Hawaii, USA, 21°39.16'N, 158°3.75'W, intertidal.
<i>Cerithium lifuense</i> Melvill & Standen, 1895	MNHN IM- 2009-29698	KC699862	KC699890	SANTO Marine Biodiversity Survey 2006, Stn. DB53, Palikulo Bay, 15°28.8'S, 167°15.2'E, 5 m.

Species	Voucher	COI	16S	Locality
<i>Cerithium munitum</i> GB Sowerby II, 1855	MNHN IM- 2009-29699	KC699863	KC699891	SANTO Marine Biodiversity Survey 2006, Stn. DS4, Segond Channel, Coolidge wreck, 15°31.4'S, 167°14.1'E, 25 m.
<i>Cerithium nodulosum</i> Bruguère, 1792 *	MNHN IM- 2009-29700	KC699864	KC699893	SANTO Marine Biodiversity Survey 2006, Stn. VM45, N Malo I., Andwélé rivulet, 15°37.7'S, 167°08.6'E, intertidal.
<i>Cerithium rostratum</i> A Adams, 1855	USNM 1200202	KC699865	KC699901	Shark's Cove, Oahu, Hawaii, USA, 21°39.16'N, 158°3.75'W, intertidal.
<i>Cerithium salebrosus</i> GB Sowerby II, 1855	MNHN IM- 2009-29701	KC699866	KC699892	SANTO Marine Biodiversity Survey 2006, Stn. DR64, Palikulo Bay, 15°27.6'S, 167°14.3'E, 6–35 m.
<i>Clypeomorus bifasciata</i> (GB Sowerby II, 1855) *	MNHN IM- 2009-29702	KC699867	KC699888	SANTO Marine Biodiversity Survey 2006, Stn. ZM15, NW Malo, 15°38.1'S, 167°05.9'E, intertidal.
<i>Clypeomorus petrosa</i> (Wood, 1828)	MNHN IM- 2009-29703	KC699868	KC699887	SANTO Marine Biodiversity Survey 2006, Stn. LM23, Segond Channel, vicinity of Maritime College, 15°31.5'S, 167°09.6'E, intertidal.
<i>Pseudovertagus aluco</i> (Linnaeus, 1758) *	MNHN IM- 2009-29704	KC699883	KC699895	SANTO Marine Biodiversity Survey 2006, Stn. VM16, Bruat Channel, N coast of Malo I., 15°37.7'S, 167°11.0'E, intertidal.
<i>Rhinoclavis aspera</i> (Linnaeus, 1758)	MNHN IM- 2009-29705	KC699884	KC699896	SANTO Marine Biodiversity Survey 2006, Stn. FR29, Palikulo Bay, 15°27.9'S, 167°14.6'E, 5–35 m.
<i>Rhinoclavis fasciata</i> (Bruguère, 1792)	MNHN IM- 2009-29706	KC699885	KC699897	SANTO Marine Biodiversity Survey 2006, Stn. VM32, W Aésé I., 15°26.6'S, 167°15.2'E, intertidal.
<i>Rhinoclavis vertagus</i> (Linnaeus, 1767) *	MNHN IM- 2009-29707	KC699886	KC699898	SANTO Marine Biodiversity Survey 2006, Stn. VM40, Surunda Bay, 15°27.7'S, 167°13.2'E, intertidal.

rounded, U-shaped lower margin; cutting edge with three, sharply pointed cusps. Operculum paucispiral with large, subcentral nucleus.

Etymology From the Latin adjective *limatus*, *-a*, *-um*, meaning polished, and the ending *-ium* of many cerithiid genera. Gender neuter.

Ecology. All known specimens of *Limatium* come from the outer slope of barrier reefs or, in islands without a coral reef lagoon, from the slope of the fringing reefs in the South Pacific (Fig. 1). Not a single specimen has been collected within a coral reef lagoon. The few live-taken specimens come from a confirmed bathymetric range of 10–100 m, with empty shells, potentially carried downslope, occasionally dredged from deeper water.

Remarks. *Limatium* differs from all other bittiine genera in the smooth, shiny, polished surface of the shell and its rich, golden honey to dark brown color. The two species known thus far are further distinguished by the distinctive white fascioles extending suture to suture and which may be a diagnostic feature of the genus, but further comparative material is required. No other bittiine is known to possess a rachidian basal plate that is hexagonal to septagonal in shape, with an elevated central portion; the cutting edge uniquely bears only three, sharply pointed, dagger-like cusps. The paucispiral operculum is also unique among bittiines as understood thus far.

Limatium pagodula sp. n.

<http://zoobank.org/127FB8BA-1F31-4D61-A73B-5D05E8AC659B>

Fig. 2

Type material. Holotype UF 427943 (Biocode No. MBIO19550, Specimen No. BMOO-03501,) (Fig. 2A, H); paratypes as listed below.

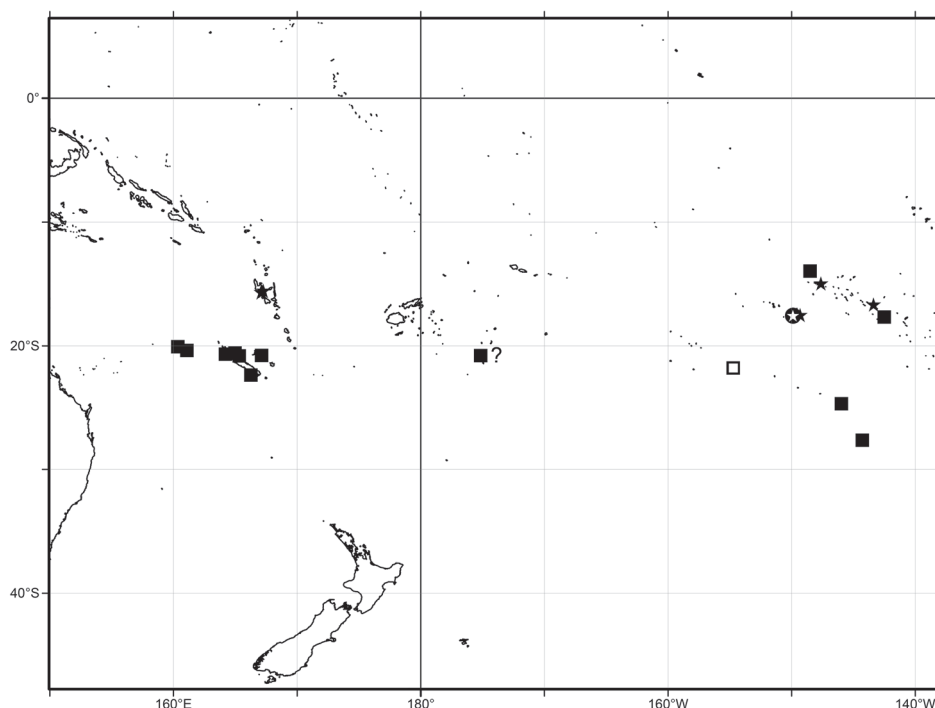


Figure 1. Distribution map of *Limatium pagodula* sp. n. (★) and *Limatium aureum* sp. n. (■) in the South Pacific. Symbols with white fill indicate the type localities of the two species, in the Society (*L. pagodula*) and the Austral islands (*L. aureum*). The provisional record “■?” is for the unusually tall and narrow specimen from Tonga that was tentatively allocated to *L. aureum*.

Type locality. French Polynesia, Society Islands, Moorea. Haapiti, just NW of Matauvau Pass outer reef slope, brushed from under rubble, 17°34.1'S, 149°53.0'W, 20–22 m (Moorea Biocode; collector's event ID MIB_087; *leg.* Chris Meyer & Christian McKeon; 20 October 2008).

Other material examined. FRENCH POLYNESIA. SOCIETY IS: Tahiti, grotte du chenal d'Arue, ca. 17°31'S, 149°31.3'W, 12 m, 1 empty shell (dd), USNM 1462729 ex coll. Letourneux (Fig. 2E); Tahiti, faille d'Arue, 33 m, 1 dd, USNM 1462730 ex coll. Letourneux. **TUAMOTU IS:** Makemo, secteur de Pohue, 16°40.1'S, 143°22.5'W, 63 m, 1 dd, paratype USNM 1462731 ex coll. Letourneux (Fig. 2B); Makemo, passe Arikitamiro, ca. 16°37.1'S, 143°33.9'W, 45–54 m, 9 dd in coll. Letourneux (Fig. 2D, F; 6 not seen); Rangiroa, passe de Tiputa, ca. 14°58.0'S, 147°37.5'W, 100 m, 2 dd in coll. Letourneux (not seen). **VANUATU. SANTO I.:** SANTO 2006: stn. ZB9, W. Malo I., 15°40.6'S, 167°05.1'E, 5–7 m, 1 dd, MNHN uncatalogued. – Stn. DS104, W. of Tutuba I., Vunatavoa Bay, 15°34.1'S, 167°16'E, 10–80 m, 1 dd, paratype MNHN IM-2014-6933 (Fig. 2C).

Etymology. From the Latin *pagoda*, with reference to the strongly angular whorls reminiscent of the upward curving roofs of Asian temples; *pagodula* is a diminutive, used as a noun in apposition.

Diagnosis. Shell [holotype, unless otherwise noted]. Shell narrow, slender, with high, conical spire, body whorl occupying ~45% of shell height, consisting of 9+ [first three whorls very encrusted] moderately convex but angular teleoconch whorls, suture impressed (Fig. 2A). Protoconch [very worn on holotype; description based on specimens illustrated in Fig. 2E–G] multispiral, of 2.5 whorls, with a sculpture of two strong, pustulose spiral keels at periphery, and a third, much lighter cord on the base, essentially covered by next whorl; strong, prosocline, axial riblets on sutural ramp, fading out abapically towards spiral keel; and irregular, elongated granules that cover the abapical part of the whorl and extend in between the two peripheral keels; protoconch/teleoconch transition sharp, with a lamellar terminal varix and a deeply indented sinusigera notch (Fig. 2E–G). Sculpture of teleoconch consisting of broad, poorly defined axial ribs forming a strong angular projection at adapical two-thirds of the whorl, crossed over by three (on body whorl 4) narrow, sharply defined spiral cords on exposed part of adult whorls, and a 4th, strongly raised, basal cord that is mostly covered by next whorl. Shell base slightly concave, with 7 unevenly spaced spiral cords. Siphonal canal very short, broadly open, constricted. Aperture circular-ovate, ~30% of shell height (in paratype, flaring and subquadrate, forming an angle where basal cord meets the outer lip). Anal canal indistinct. Columella concave with thinly callused columellar lip. Outer lip of aperture forming a terminal varix, subvertical on periphery, regularly convex on base. Shell surface smooth and shiny, as if waxed, color overall deep brown with broad, opaque white fascioles extending from suture to suture at irregular intervals, spiral cords on spire and base white, cord encircling the base brown with white blotches at regular intervals; columellar side of canal and columellar callosity white, parietal callosity transparent. Tip of teleoconch (first 1.5 whorl) white, protoconch dark brown. Dimensions: 6.50 × 2.65 mm. Average 5.98 ± 0.48 mm (n = 3).

External anatomy. Head-foot dark golden brown in color; cephalic tentacles with irregular white blotches and golden tips. Foot sole golden, with thin, transverse white lines, discontinuous across prominent longitudinal groove at midline; condition of pedal glands unknown. Epipodial skirt also with thin, transverse white to golden lines, present from propodium to large, projecting opercular lobe. Epipodial tentacles lacking.

Radula. The radula of the sequenced specimen was teratological, and we do not provide a detailed description or illustration. The gross features that were visible conform to those in *L. aureum* sp. n. (see below): a rachidian with broad hexagonal basal plate and elevated central portion with rounded base, cutting edge with three pointed cusps, lateral teeth with short lateral extensions roughly 1.5 times length of cutting edge, face of lateral teeth with buttress terminating in prominent, rounded knob midway down face of lateral teeth, outer edges of outer marginal teeth acusate.

Distribution and ecology. Society Islands and Tuamotus (French Polynesia); Vanuatu. Known only from the material examined. Only one specimen was collected alive, from the outer reef slope, brushed from under rubble, 20–22 m.

Remarks. The sequenced specimen from Moorea is designated as holotype, although its outer lip is not fully mature. In the fully adult paratype from Santo (Fig. 2C), the axial white fascioles are fewer, but are aligned from one whorl to the next, and there is a strong varix one-half whorl before the aperture.

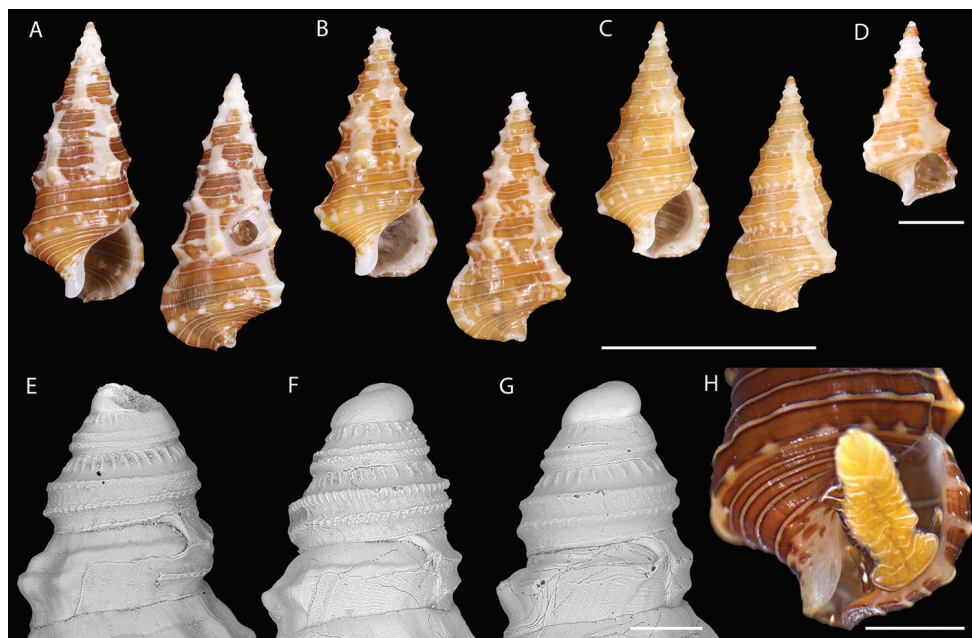


Figure 2. Shell and external morphology of *Limatium pagodula* sp. n. **A** Holotype, UF 427943. French Polynesia, Society Islands, Moorea **B** Paratype, USNM 1462731. Tuamotu Islands, Makemo, Pohue (ex. coll. Letourneux) **C** Paratype, MNHN IM-2014-6933. Vanuatu, Santo, W. of Tutuba I., SANTO 2006 stn. DS104 **D** Subadult. Tuamotu Islands, Makemo, Arikitamiro (coll. Letourneux) **E** Protoconch, USNM 1462729. Tahiti, grotte du chenal d'Arue (ex. coll. Letourneux) **F** Protoconch. Tuamotu Islands, Makemo, Arikitamiro (coll. Letourneux) (same as in 2D) **G** Protoconch, Tuamotu Islands, Makemo, Arikitamiro (coll. Letourneux) **H** Living animal, holotype UF 427943. French Polynesia, Society Islands, Moorea. Scale bars: 5 mm (**A–C**); 1 mm (**D, H**); 100 μ m (**E–G**).

***Limatium aureum* sp. n.**

<http://zoobank.org/6EF8F349-E899-4E59-A93D-1CECB0CA47C0>

Fig. 3A–H, K, L, N

Type material. Holotype MNHN IM-2013-42460 (Fig. 3A); paratypes as listed below.

Type locality. Austral Islands, Maria I., outer slope of barrier reef, 21°47.8'S, 154°43'W, 24 m [TUHAA PAE 2013 cruise, stn. AMA02, field number PB16_BC855; *leg.* A. Fedosov; 5 April 2013].

Other material examined (all in MNHN uncatalogued, except where noted): **FRENCH POLYNESIA.** AUSTRAL IS: RAPA Island expedition 2002: Stn. 6, off Baie de Ahurei, 27°36.8'S, 144°16.7'W, 42 m, 1 dd. – Stn. 8, SE of Tauna islet, 27°36.5'S, 144°17.7'W, 52–57 m, 7 dd (MNHN IM-2014-6928, Fig. 3L). – Stn. 28, Pointe Taekateke, 27°38.4'S, 144°20.6'W, 30 m, 1 dd. – Stn. 36, Pointe Kauira, 27°33.5'S, 144°20.8'W, 27 m, 1 live collected (lv), 2 dd (MNHN IM-2014-6920, IM-2014-6929, Fig. 3B, N). – Stn. 44, NW of Tauna islet, 27°36.3'S, 144°18.2'W, 30 m, 2 dd (MNHN IM-2014-6923, Fig. 3E). – BENTHAUS stn. DW1934, Banc Président Thiers, 24°40.6'S, 145°57.4'W, 560–1150 m, 1 dd. **TUAMOTU IS:** Makemo, secteur Pohue,

16°40.1'S, 143°22.5'W, 63 m, 1 dd, paratype USNM 1462727 ex coll. Letourneux; Makemo, passe Arikitamiro, ca. 16°37.1'S, 143°33.9'W, 45 m, 47 m and 54 m, 3 dd, in coll. Letourneux; Rangiroa, Passe de Tiputa, ca. 14°58.0'S, 147°37.5'W, 81 m and 100 m, 2 dd, USNM 1462728 ex coll. Letourneux. **NEW CALEDONIA.** Coral Sea. Lansdowne-Fairway Reefs. CORAIL 2 stn. DW26, 20°22'S, 161°05'E, 62 m, 1 lv (MNHN IM-2014-6921, Fig. 3C). – EBISCO stn. DW2622, 20°04'S, 160°21'E, 291–323 m, 1 dd. Mainland New Caledonia. LAGON Stn. 830, off Poindimié, 20°49'S, 165°19'E, 105–110 m, 4 dd. MONTROUZIER Stn. 1269, Récif Doiman off Touho, outer slope, 20°35.1'S, 165°08.1'E, 15–20 m, 4 dd. – Stn. 1331, Grand Récif de Koumac, outer slope, 20°40'–20°40.6'S, 164°11.2'–164°12.1'E, 55–57 m, 4 dd. – Stn. 1352, Grand Récif Aboré off Nouméa, outer slope, 22°22.2'S, 166°16.0/166°16.1'E, 27–35 m, 5 lv, 4 dd (MNHN IM-2014-6924, IM-2014-6927, Fig. 3F, K); – Stn. 1354, Grand Récif Aboré, outer slope, 22°22.3'S, 166°15.9'E, 27–37 m, 2 lv, 2 dd. BATHUS 1 stn. DW692, 20°35'S, 164°59'E, 140–150 m, 2 dd. **LOYALTY ISLANDS:** LIFOU 2000 Expedition, Baie du Santal: stn. 1418, 20°46.9'S, 167°07.9'E, 1–5 m, 1 dd (MNHN IM-2014-6926, Fig. 3H). – Stn. 1423, 20°54'S, 167°07.3'E, 12 m, 2 dd (MNHN IM-2014-6925, Fig. 3G). – Stn. 1429, 20°47.5'S, 167°07.1'E, 8–18 m, 2 dd. – Stn. 1432, 20°53.5'S, 167°02.7'E, 12–32 m, 2 dd. – Stn. 1434, 20°52.5'S, 167°08.1'E, 5–20 m, 2 dd. – Stn. 1441, 20°46.4'S, 167°02'E, 20 m, 2 dd. – Stn. 1442, 20°46.4'S, 167°02'E, 47 m, 1 dd. – Stn. 1443, 20°53.8'S, 167°07.3'E, 48–52 m, 3 dd. – Stn. 1445, 20°50.8'S, 167°09.7'E, 10–12 m, 1 dd. – Stn. 1448, 20°45.8'S, 167°01.6'E, 20 m, 4 dd. – Stn. 1449, 20°45.8'S, 167°01.6'E, 17 m, 1 dd. – Stn. 1450, 20°45.8'S, 167°01.6'E, 27–31 m, 1 dd. – Stn. 1451, 20°47.3'S, 167°06.8'E, 10–21 m, 3 dd. – Stn. 1453, 20°54.6'S, 167°02.1'E, 21–30 m, 1 dd. – Stn. 1454, 20°56.6'S, 167°02'E, 15–18 m, 2 dd. – Stn. 1455, 20°56.8'S, 167°02.7'E, 15–20 m, 1 lv, 1 dd. – Stn. 1456, 20°49.3'S, 167°10.4'E, 25–30 m, 1 lv, 1 dd. – Stn. 1457, 20°46.8'S, 167°02.8'E, 5–10 m, 2 lv, 1 dd. – Stn. 1461, 20°54'S, 167°02'E, 100–120 m, 1 lv, 1 dd. – Stn. 1469, 20°54.2'S, 167°00.4'E, 70–130 m, 2 dd.

Etymology. Latin adjective *aureus*, *-a*, *-um*, meaning golden, with reference to the background color of the shell.

Diagnosis. Shell [holotype, unless otherwise noted]. Shell short, squat, with regular, conical spire, body whorl occupying ~46% of shell height, consisting of 9+ [tip of teleoconch and protoconch missing] rather flat teleoconch whorls, suture impressed (Fig. 3A). Protoconch [description based on specimens illustrated in Fig. 3K, L] multispiral, of 2.5 whorls, with a complex sculpture of two strongly pustulose, thick and heavy spiral keels at periphery, and a third, much lighter cord on the base, partly covered by next whorl; strong, prosocline, axial riblets on sutural ramp, fading out abapically towards spiral keel; and irregular, short, elongated or rounded granules that cover the abapical part of the whorl and may extend in between the two peripheral keels; protoconch/teleoconch transition sharp, with a lamellar terminal varix and a deeply indented sinusigera notch (Fig. 3K, L). On early teleoconch whorls sculpture consisting of closely-set axial ribs intersected by three spiral cords together forming beaded intersections, abapicalmost cord stronger, forming an angular projection at intersection with ribs; axial and spiral sculpture becoming weaker on exposed parts of subadult and adult

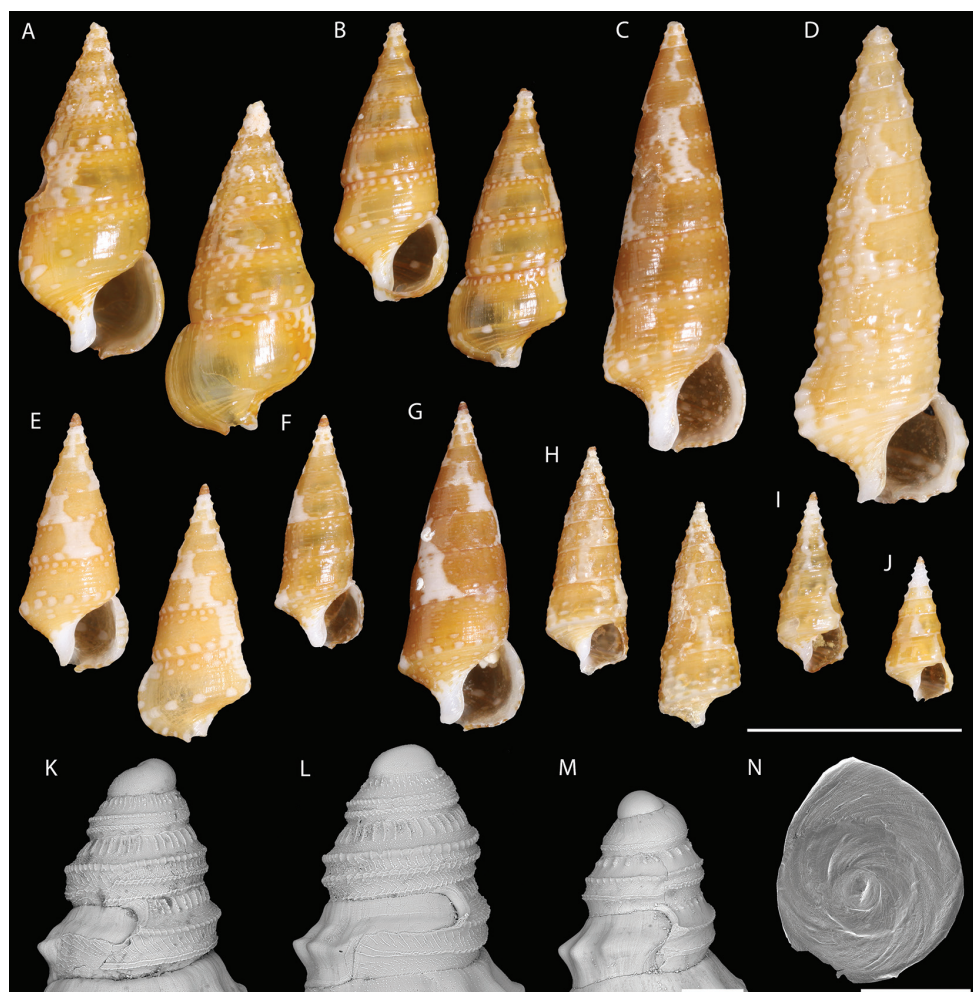


Figure 3. Shell and operculum morphology of *Limatium aureum* sp. n. (**A–H, K, L, N**) and *Limatium* sp. (**I, J, M**). *Limatium aureum* sp. n.: **A** Holotype, MNHN IM-2013-42460. Austral Islands, Maria **B** Austral Islands, Pointe Kauira, RAPA 2002 stn. 36 (MNHN IM-2014-6920) **C** New Caledonia, CO-RAIL 2 stn. DW26 (MNHN IM-2014-6921) **D** Tonga, between Eua and Tongatapu, BORDAU 2, stn. DW1512 (MNHN IM-2014-6922) **E** Austral Islands, NW of Tauna Islet, RAPA 2002 stn. 44 (MNHN IM-2014-6923) **F** New Caledonia, Grand Récif Aboré off Nouméa, MONTROUZIER stn. 1352 (MNHN IM-2014-6924). **G** Loyalty Islands, LIFOU 2000 stn. 1423 (MNHN IM-2014-6925) **H** Loyalty Islands, LIFOU 2000 stn. 1418 (MNHN IM-2014-6926) **K** Protoconch, New Caledonia, Grand Récif Aboré off Nouméa, MONTROUZIER stn. 1352 (MNHN IM-2014-6927) **L** Protoconch, Austral Islands, SE of Tauna Islet, RAPA 2002 stn. 8 (MNHN IM-2014-6928) **N** Operculum, Austral Islands, Pointe Kauira, RAPA 2002 stn. 36 (MNHN IM-2014-6829) (same as in 3B). *Limatium* sp.: **I** Philippines, W of Mindoro, MUSORSTOM 3 stn. DR117 (MNHN IM-2014-6830) **J** Vanuatu, Santo, W of Tutuba, SANTO 2006 stn. DS103 (MNHN IM-2014-6831) **M** Protoconch, Vanuatu, Santo, West of Tutuba I., SANTO 2006 stn. DS103 (MNHN IM-2014-6832) (same as in 3J). Scale bars: 5 mm (**A–J**); 100 µm (**K–M**); 500 µm (**N**).

whorls, until an almost smooth last whorl; last whorl with weakly defined basal cord encircling convex base bearing six well defined, raised cords. Siphonal canal very short, broadly open, not constricted. Aperture circular-ovate, ~32% of shell height. Anal canal indistinct. Columella concave with very thinly callused columellar lip. Outer lip of aperture slightly thickened, but not forming a terminal varix, subvertical on periphery, regularly convex on base. Shell surface smooth and shiny, as if waxed, color overall rich honey to golden brown with broad, opaque, irregular white fascioles extending from suture to suture at irregular intervals; adapical and basal cords with alternating white and honey blotches at regular intervals; columellar side of anal and columellar callosity white, parietal callosity transparent. Tip of teleoconch (first whorl) white, protoconch dark brown. Dimensions: 7.97×3.40 mm. Average 6.83 ± 1.47 mm ($n = 12$).

Operculum. Subcircular, paucispiral, comprising three whorls. Nucleus large, sub-central, ~72% of operculum length.

Radula. Rachidian (Fig. 4A–C, E, F) with roughly hexagonal to septagonal basal plate, squarish to rectangular, broader than tall, with elevated central portion with rounded, U-shaped lower margin. Cutting edge bearing one strong central and two lateral long, dagger-like pointed cusps; central cusp up to twice as long as lateral cusps. Lateral teeth (Fig. 4A, B, C, E–F) with short lateral extensions, roughly 1.5 times length of cutting edge. Cutting edge with large central, pointed cusp and single, large pointed inner cusp and two to four tapering outer denticles. Thickened buttress extending down face of marginal tooth slightly outside central cusp, terminating in prominent, bluntly rounded peg roughly halfway down face (Fig. 4F). Marginal teeth (Fig. 4A, C–D, E) similar in shape and denticulation. Inner marginal teeth with large pointed central cusp, two to three tapering inner pointed cusps and one to two outer pointed denticles. Outer marginal teeth with large, pointed, central cusp, two to three tapering inner pointed cusps and a smooth, acusate outer edge.

Distribution and ecology. Austral Islands and Tuamotus (French Polynesia); Loyalty Islands, mainland New Caledonia, and Coral Sea. Known only from the material examined. Collected alive in 10–100 m, empty shells to 560–1150 m were undoubtedly carried downslope.

Remarks. The holotype is “untypical” in the sense that it is an unusually broad specimen that, however, seems to be connected by morphologically intermediate specimens to forms that are more slender and with a strong cord delimiting the basal disc. All these specimens share a color pattern of alternating white and honey blotches on the subsutural and basal cords, in addition to ill-defined axial white fascioles, on an overall rich, golden honey background. Another type of variation comes from the extension/persistence of the spiral cords on subadult/adult whorls – with specimens almost completely smooth on the periphery of the last whorl and others with strong spiral cords persisting onto the last whorl.

An empty shell collected from Tonga (BORDAU 2 stn. DW1512, between Eua and Tongatapu, $21^{\circ}19'S$, $175^{\circ}01'W$, 183–184 m) (MNHN IM-2014-6922, Fig. 3D) is unusually tall and narrow, with spiral and axial sculpture persisting onto the last whorl; its color pattern, however, is very similar to that of *L. aureum* and we tentatively consider it to belong to that species.

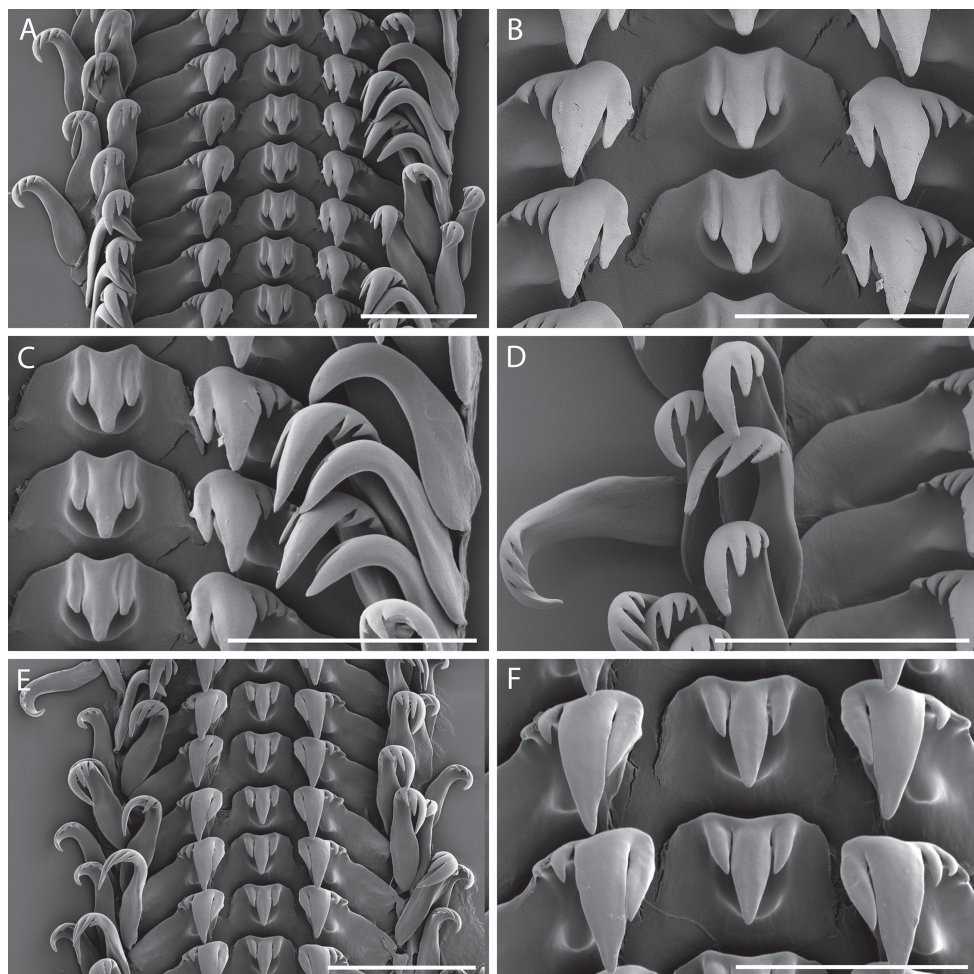


Figure 4. Radula morphology of *Limatium aureum* sp. n. **A–D** Holotype, MNHN IM-2013-42460, Austral Islands, Maria **E, F** Austral Islands, Pointe Kauira, RAPA 2002 stn. 36 **A** Radular ribbon **B** Detail of rachidian and lateral teeth **C** Detail of half row, showing outer edges of lateral and marginal teeth **D** Detail of marginal teeth, showing inner edges **E** Radular ribbon of second specimen, showing variation in length of cusps **F** Detail of rachidian and lateral teeth, showing variation in width of rachidian and in length of cusps. Scale bar: 50 μ m (**A, C, D, E**); 40 μ m (**B**); 30 μ m (**F**).

Limatium sp.

Fig. 3I, J, M

Material examined. **PHILIPPINES:** MUSORSTOM 3 Stn. DR117, W of Mindoro, 12°31'N, 120°39'E, 92–97 m, 1 lv (MNHN IM-2014-6930, Fig. 3I). **VANUATU:** SANTO 2006 stn. DS103, W of Tutuba I., Vunatavoa Bay, 15°34.1'S, 167°16'E, 10–80 m, 2 dd (MNHN IM-2014-6931, IM-2014-6932, Fig. 3J, M).

Remarks. Three specimens (Fig. 3I, J, M) show an overall resemblance to *L. aureum*, but differ in a manner that we think they are not conspecific. The three specimens

from the Philippines and Vanuatu are subadults; their color pattern does not have the articulated white and golden honey spiral cords. The specimens from Vanuatu have a single cord on the base versus five in the specimen from the Philippines, and these two specimens may not even be conspecific. The protoconch of a Vanuatu specimen (Fig. 3M) is distinctly smaller than in *L. aureum*, consisting of only two whorls, with fewer and shorter axial riblets on the ramp, and simpler, less ornamented spiral keels. No specimen of this or any other *Limatium* has been obtained in the Philippines despite extensive sampling by lumun-lumun for the commercial shell trade (G. Poppe and S. Tagaro, pers. comm.).

Phylogenetic analysis

Bayesian analysis of the concatenated COI and 16S dataset recovered the monophyly of the Cerithiinae and Bittiinae, although the latter is not statistically supported. *Limatium* is monophyletic (PP = 1) and is robustly supported (PP = 0.99) within the Bittiinae as the sister group to *Cacozeliana* Strand, 1928. *Ittibittium* and *Pictorium* are also monophyletic both with robust support (PP = 1). The clade including the type species of *Bittium* Gray, 1847 [*B. reticulatum*, *B. latreillei* (Payraudeau, 1826), *B. simplex* (Jeffreys, 1867)] also received high support (PP = 1).

Discussion

Houbrick's (1993) generic review of the Bittiinae published 25 years ago remains the authoritative resource for comparative anatomy and systematics of bittiines. At that time, Houbrick (1993) recognized nine genera in the *Bittium*-group: *Bittium*, *Argyropeza*, *Bittiolium*, *Cacozeliana*, *Ittibittium*, *Lirobittium*, *Neostylidium* [then as *Stylidium*], *Varicopeza*, and *Zebittium*; *Cassiella* was identified as a possible member but its placement uncertain given the paucity of anatomical data. In 2006, Bandel established a separate subfamily for *Argyropeza*. Since then, the Bittiinae has been expanded (MolluscaBase 2018) to include the Recent genera *Cerithidium* (provisionally excluded by Houbrick 1993), and *Pictorium*.

Despite the absence of a diagnostic feature that allows unambiguous placement in the subfamily (Strong and Bouchet 2013), the common perception of bittiines is that they are small in adult size, turreted, with a predominating beaded or spiral sculpture, and cream, gray, tan to dull brown in color. This concept of bittiine teleoconch morphology was expanded by the description of the genus *Pictorium*, based on a small type species formerly placed in *Cerithium*, with a pupoid, brilliantly colored reddish-purple shell (Strong and Bouchet 2013). *Limatium* species differ from all other bittiines in their smooth, glossy, polished shells with a rich honey to golden brown background color. This unique shell morphology is unknown in the Cerithiidae and further expands the conchological concept of the subfamily. The distinctive white fascioles also

may be a diagnostic feature of the genus, but further comparative material is required to be certain, particularly of the suspected additional species from Vanuatu and the Philippines. Clearly, more material, and more sequencable material, is needed to understand intraspecific variation within *Limatium*.

In addition to shell morphology, *Limatium* differs from known bittiines in several unique features of the radula. Most possess a rachidian with an attached basal portion and a freely projecting face. The face of the tooth has a central to basal constriction that can be quite strongly developed in some species. Thickenings at the lower, outer corners of the tooth extend onto the radular membrane beyond the sides of the tooth. The upper projecting margin of the tooth often forms a prominent crest from below which the teeth project. The cutting edge spans the entire anterior edge of the tooth, or the majority of it, and bears a single, strong central cusp and two to three denticles on each side (e.g., Houbrick 1980b, 1993, Gofas 1987, Ponder 1993, Hasegawa 1998). The rachidian of *Limatium* has a basal plate that is hexagonal to septagonal in shape, with a central elevated portion that has a U-shaped, rounded lower edge roughly midway down the face of the tooth. The cutting edge is restricted to this elevated portion, and bears only three dagger-like cusps. This configuration is unknown among the Bittiinae, and even more broadly among the Cerithiidae. In terms of operculum morphology, most bittiines are characterized by a multispiral operculum (Houbrick 1980b, 1993, Gofas 1987, Hasegawa 1998); *Bittium* and *Cassiella* differ in possessing an ovate, paucispiral operculum with a small nucleus (Houbrick 1993, Ponder 1993). In contrast, *Limatium* possesses a subcircular, paucispiral operculum of only ~3 whorls and a large nucleus. Argyropezinae conform to the bittiine configuration of rachidian morphology and possess a circular, multispiral operculum (Houbrick 1980a).

The phylogenetic analysis supported *Limatium* and *Cacozeliana* as sister taxa, although more comprehensive taxon sampling is required to assess the affinities of bittiine genera. The analysis confirmed that *Bittium*, as presently conceived is polyphyletic (Strong and Bouchet 2013). Inclusion of the type species, *Bittium reticulatum*, for the first time allows us to tie the genus-group name to a clade including *B. latreillei* and *B. simplex*. As in the analysis of Strong and Bouchet (2013), *Bittium impendens*, only cautiously retained in *Bittium* by Houbrick (1993), is robustly supported as the sister group to *Pictorium*; *Bittium glareosum* is the sister to them but its placement is not supported. Additional sampling is required to resolve the affinities of Indo-Pacific species currently placed in *Bittium*, with *Bittium* s.s. possibly retained only for species from the Atlantic.

Limatium is exceptionally rare, represented in museum and personal collections by a scant 108 specimens known to us as enumerated herein, only 16 of them collected alive. As described in Strong and Bouchet (2013), *Pictorium* also had been rare in museum collections and had never been collected alive prior to the 1980's. Like *Limatium*, the latter genus is also small and found in steep, hard-bottom habitats that are too deep for diving and too steep for dredging. The use of lumun-lumun and tangle nets in the commercial shell trade in the Philippines, and the adoption of new collecting techniques as brushing baskets and suction sampling in biodiversity surveys (Albano et al. 2011), have

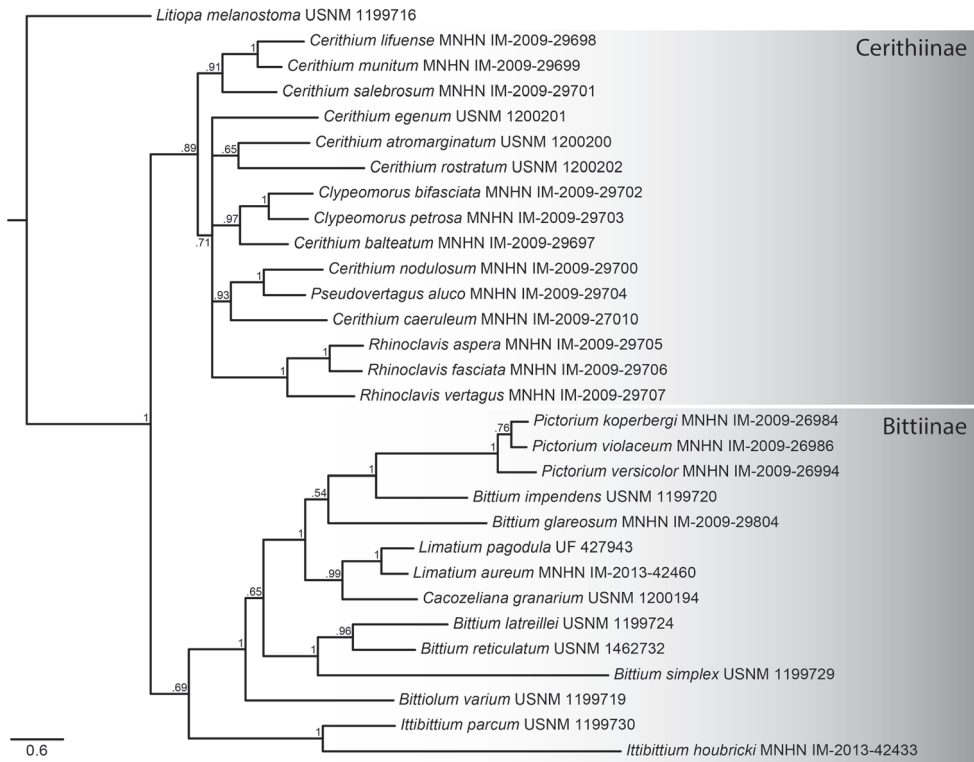


Figure 5. Phylogeny of Cerithiidae based on Bayesian analysis of partial COI and 16S sequences. Catalogue numbers for vouchers indicated after species name. Posterior probabilities greater than .50 are shown at the nodes. See Table 1 for details.

revolutionized access to these challenging habitats. While the number of specimens of *Pictorium* rose dramatically particularly since 2004, the number of *Limatium* specimens also has increased but not so dramatically, and live collected specimens remain elusive. The unique radular morphology of *Limatium* suggests a life habit different from that of most other bittiines, which may explain why they remain so tantalizingly rare.

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Revision of genus *Pericalus* from China, with descriptions of four new species (Carabidae, Lebiini, Pericalina)

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Abstract

Nine taxa of the genus *Pericalus* Macleay from China are revised, with four new species described: *Pericalus gibbosus* **sp. n.** (type locality: Putao, Myanmar; one paratype from Mêdog, Xizang), *Pericalus elegans* **sp. n.** (type locality: Mêdog, Xizang), *Pericalus acutidens* **sp. n.** (type locality: Longchuan, Yunnan), and *Pericalus obscuratus* **sp. n.** (type locality: Fanjingshan, Guizhou). Four taxa are newly recorded from China: *Pericalus ornatus ornatus* Schmidt-Göbel (Yunnan, Hainan), *P. obtusipennis* Fedorenko (Yunnan), *P. amplus* Andrewes (Yunnan), and *P. dux* Andrewes (Yunnan). *Pericalus formosanus* Dupuis is newly ranked as a subspecies of *P. ornatus* Schmidt-Göbel. An improved key to world species of the subgenus *Pericalus* is provided, along with distribution maps and images of habitus and male and female genitalia for all Chinese species.

Keywords

Carabidae, China, *Pericalus*, new species, key

Introduction

The genus *Pericalus* belongs to the subtribe Pericalina (Carabidae: Lebiini), distributed in the tropical regions of Oriental-Australasian Realm: the easternmost reaches New Ireland (*P. novaeirlandiae*), and the westernmost reaches south India (*P. fascinator*). *Pericalus* is close to the following four Oriental genera: *Lioptera* Chaudoir, *Coptodera* Dejean, *Trichocoptodera*

Louwerens and Gidda Andrewes. These five genera belong to the *Pericalus* genus-group (Shpeley and Ball 2000) in having the following three character states: mentum without a median tooth, palpifer with one long seta, and the terminal labial palpomere fusiform.

Two distinct subgenera in *Pericalus* are recognized, distinguished by their different pronotal characters. The subgenus *Coeloprotopus*, including 20 described species, was well documented with a recent complete review (Baehr 1994), and two additional species described later (Baehr 2000a, 2003). In contrast, study on the subgenus *Pericalus* was relatively weak, only with incomplete keys published (Dupuis 1913, Andrewes 1937, Jedlička 1963, Baehr 2000b) until 2017. When preparing an early draft of the present paper, a study focusing on Vietnamese *Pericalus* species with a key for all known species in the subgenus was published (Fedorenko 2017). However, species determination in this subgenus is still not clearly solved; for example, some species lack clear definition and diagnoses, and *P. formosanus sensu* Fedorenko, 2017 actually belongs to a new species also distributed in China.

The previous study of *Pericalus* from China was very inadequate. Only one species, *P. formosanus*, was recorded in Taiwan, and the fauna in the Chinese continent is almost unreported (Kabak 2003). Our examined material shows that the *Pericalus* beetles are common and diverse in tropical regions of China (south Yunnan, Hainan, south Xizang). During recent expeditions to Guizhou, Guangxi, south Xizang, and north Myanmar, three very rare and narrowly distributed new species were collected. After detailed morphological study, all specimens from China were identified, with four new records for the country. Moreover, one common species from southwest Yunnan, south Xizang, and north Myanmar previously determined as *P. ornatus* is attributed to a new species, *P. acutidens* sp. n. *Pericalus ornatus formosanus* is newly ranked as a subspecies based on the almost identical male genitalia and slightly external differences with the nominal typical subspecies. Thus the fauna of *Pericalus* in China has eight species and one subspecies in total, all belonging to the subgenus *Pericalus*.

The present paper aims to review all nine taxa of the genus *Pericalus* from China, with the descriptions of the four new species, and to provide an improved key to accommodate all known taxa of *Pericalus* (s. str.) but two dubious and little known species, which are discussed.

Materials and methods

This work is based on the examination of 218 specimens from China and some other Southeast Asian counties. A total of 19 taxa of the subgenus *Pericalus* were treated, with 15 of them examined. Examined material for species outside of Chinese fauna were cited as well. Most specimens are from the collection of IZAS. Collections cited in the present paper are indicated by the following abbreviations:

- CCCC Collection of Changchin Chen, Tianjin, China
CRS Collection of Riccardo Sciaaky, Milano, Italy

IRSN	Institut Royal des Sciences Naturelles, Brussels, Belgium
IZAS	Institute of Zoology, Chinese Academy of Science, Beijing, China
NHML	The Natural History Museum, London, United Kingdom
NMPC	Národní Muzeum Přírodovědecké Muzeum, Prague, Czech Republic
NNML	Naturalis Nationaal Natuurhistorisch Museum, Leiden, Netherland
OUM	Oxford University Museum of Natural History, Oxford, UK
SNU	Shanghai Normal University, Shanghai, China
ZMMU	Zoological Museum of the Moscow State University, Moscow, Russia
ZSM	Zoologische Staatssammlungen, München, Germany

Body length was measured from the apical margin of the labrum to the elytral apex; head width (**HW**) was the greatest width including eyes; pronotum length (**PL**) was measured along its median line; and pronotum width (**PW**) was the greatest width of the pronotum; elytra length (**EL**) was measured from elytral base to apex; elytra width (**EW**) was the combined width of each elytron at its widest points; **D2** was the distance of the second elytral discal setigerous pore to elytra base. All measurements were based on examined materials only. Details of methods for dissection, and terminology follow our previous work (Shi et al. 2013). Distribution maps were created in Adobe Photoshop software based on examined materials and confirmed records from literature. Unconfirmed records from literature are marked by empty circles in the maps.

Taxonomy

Subgenus *Pericalus* (*s. str.*) Macleay, 1825

Macleay 1825: 15. Type species: *Pericalus cicindeloides* Macleay, 1825, by monotypy.

Diagnosis. The genus *Pericalus* is distinguished from other genera of Pericalina by the combination of the following characters: dorsal surface glabrous, except for the eighth and ninth elytral intervals which are generally sparsely and very finely setose; black or metallic in color, elytra either unicolorous or with two groups of yellowish patches; eyes strongly prominent; labrum elongate, apex deeply notched; clypeus with apical margin straight; terminal labial palpomere fusiform in both sexes; labial palpifer with one long seta; mentum without median tooth; paraglossa membranous, longer than ligula; third interval of elytra with two to four setigerous pores, the first one near base, the last one very close to apex; fourth tarsomere simple; claws smooth.

The subgenus *Pericalus* is different from the subgenus *Coeloprotopus* Chaudoir by its body size being usually larger; in having the lateral channel of the pronotum widely explanate, with the lateral bead indistinct; and the pronotum subequal to the width of head across eyes.

Distribution. The subgenus *Pericalus* containing 19 taxa has an Asia mainland-Sundaland distribution pattern. More than half of them (eleven taxa) are distributed

through the Asian continent tropical-subtropical areas, and the most diverse region is located in northern Myanmar, northeast India, southeast Xizang, and west Yunnan. The remaining eight taxa are distributed in the Sundaland region (Greater Sunda Islands and Malay Peninsula). There are no species endemic to the Philippines or islands in the Wallacea region, but one species is widely distributed in each region, *P. cicindeloides* in the Philippines, and *P. baehri* in Sulawesi.

Habitat. Many adults of the subgenus *Pericalus* were collected in daytime under barks of fallen logs in tropical or subtropical forests. Some others were collected during night, fast running on surfaces of dead logs, or occasionally attracted by lights. Species in this subgenus usually have a rather flat habitus, adapting for living under tree bark.

Taxonomic characters. The most important taxonomic characters in this subgenus are: (1) dorsal coloration, including elytral pattern; (2) number of setigerous pores on the third interval; (3) shape of elytral outer apical angles; and (4) shape of elytral sutural apical angles.

The supposed ground plan for the subgenus is supposed to include two groups of yellowish patches on the elytron (unicolorous in four species); body very flat (but convex in *P. gibbosus*); elytra with microsculpture consisting of distinct, very transverse meshes (but nearly isodiametric in *P. dux* and *P. elegans*); outer apical angles of elytra distinct, acuminate to rounded; elytral sutural angles sharp or blunt; third interval of the elytra with three setigerous pores (but four pores in four species, usually two in *P. o. formosanus*).

The shape of outer apical angles of elytra can be classified into the following four basal forms: **acuminate**, apex forming a very sharp angle, strongly projecting, less than 90 degrees (Fig. 21), present in seven species; **acute**, apex forming a sharp and distinct angle, not or weakly projecting, more than 90 degrees (Figs 22, 24), in two species; **obtuse**, apex forming an indistinct angle, more than 90 degrees (Figs 23, 25), in five species; **rounded**, apex fully rounded, not angulate (Figs 26–32), in seven species. There are some taxa, such as *P. o. formosanus*, with one form of outer apical angle in general (obtuse), but very rarely other forms can be present in a few individuals (rounded or acute).

Most taxa (15 of 19) of the subgenus have two, the anterior and posterior, groups of yellowish patches on elytra; variation includes four and two pattern forms respectively. For different species or individuals belonging to same pattern form, pale markings on certain intervals may be obsolete or their positions moved.

There are four basic forms for anterior patches: **round**, in six taxa. Usually a single large round or nearly round spot (Figs 1–3, 7–11) occupies some of the third to eighth intervals, two to five intervals in width. In some individuals of *P. ornatus* (Fig. 12), the spot is somewhat transverse and irregular, similar to the zigzag form, but generally less transverse and with less displacement of odd and even pale markings. **Zigzag**, in five species. A transverse serrated band occupies the third to seventh intervals (Figs 6, 13–15), with pale markings on odd intervals anteriorly placed and those of even intervals posteriorly placed. Sometimes pale markings on the third and/or seventh intervals are obsolete. In *P. baehri* pale markings on the third interval are placed much more anteriorly to those on the remainder of the odd intervals. **Separated**, in two species. The basic

pattern includes five small separated spots, only one interval in width for each, placed on the third to seventh intervals respectively. Sometimes spots on the sixth and seventh intervals are obsolete. Longitudinal positions for all spots are similar to those of the zigzag pattern. **Double**, a special pattern only for *P. cordicollis*. The double pattern form is composed of two adjacent large spots: the inner one is in the third and fourth intervals, posteriorly placed; the outer one is in the fifth to eighth intervals, anteriorly placed.

Two basic forms exist for posterior patches: **separated**, in eleven taxa. The basic pattern is composed of three separate spots (Figs 7–12): the first one is in the second and third intervals, posteriorly placed; the pale marking on the second interval is occasionally obsolete. The second one is in the fourth to sixth intervals, anteriorly placed; the pale marking on the fourth interval is occasionally obsolete; the pale marking on the sixth interval is adjacent to that on the fifth (*P. cordicollis*, and some *P. ornatus* and *P. acutidens*, Figs 7, 11, 12), placed much anteriorly to that on the fifth and forming a small separate spot (*P. amplus*, *P. obtusipennis*, *P. obscuratus*, Figs 6, 13–15), or obsolete (the remaining four species and most *P. ornatus* and *P. acutidens*, Figs 8–10). The third one is in the seventh and eighth intervals, posteriorly placed, sometimes a little before the first spot; the pale marking on the eighth interval is usually obsolete, but present in *P. cordicollis*, and some individuals of some other species. **Single**, in three species. The basic pattern is a single large round spot in some of the second to seventh intervals, two to four intervals in width (Figs 1–3). In a few individuals of *P. longicollis*, the pale marking on the third interval is present and placed posteriorly to the main spot, but is obsolete in most individuals.

Key to the world species of the subgenus *Pericalus*

- 1 Third elytra interval with four setigerous pores.....2
- Third elytra interval with two or three setigerous pores4
- 2 Elytra dark with two groups of yellowish patches, the anterior one zigzag, the posterior one separate; elytral outer apical angles rounded; India, Myanmar, Vietnam, China (Yunnan)*P. amplus* Andrewes
- Elytra unicolorous, black or metallic, without yellowish patch; elytral outer apical angles acute, or obtuse3
- 3 Dorsal surface with strong metallic luster, bluish, greenish or violaceous; Borneo, Sumatra, Java, Malay Peninsula, the Philippines.....*P. cicindeloides* Macleay
- Dorsal surface black, with very faint purplish luster; India*P. fascinator* Andrewes
- 4 Elytral sutural angles spiniform; the middle setigerous pore placed posterior to the midpoint of elytra ($D2/EL > 0.52$)5
- Elytral sutural angles blunt; the middle setigerous pore placed anterior to the midpoint of elytra ($D2/EL < 0.46$) or rarely lacking9
- 5 Elytra cupreous green, without patch; elytral outer apical angles rounded (Fig. 31); China (Médog, Zayü).....*P. elegans* sp. n.
- Elytra dark with yellowish patch; elytral outer apical angles acuminate (as in Fig. 21); Malaysia, Indonesia6

- 6 Elytral anterior patch round or zigzag, forming single continues patch7
- Elytral anterior patch separate, divided into three to five small spots.....8
- 7 Elytra metallic blue or green; posterior patch single; Sumatra, Borneo, Malay Peninsula *P. longicollis* Chaudoir
- Elytra metallic blue-violaceous; posterior patch separate, composed of three to five small spots; Sumatra, Java, Borneo, Sulawesi *P. baehri* Fedorenko
- 8 Elytra metallic blue-violaceous; Malay peninsula *P. violaceus* Andrewes
- Elytra black, at most with faint metallic luster; Sumatra, Java, Bali *P. guttatus* Chevrolat
- 9 Elytral outer apical angles acuminate, acute or obtuse (Figs 21–25)10
- Elytral outer apical angles rounded (Figs 26–32).....14
- 10 Elytral anterior patch composed of two large spots, sometimes partly conjoint; Borneo *P. cordicollis* Andrewes
- Elytral anterior patch round or zigzag form, forming single continues patch...11
- 11 Elytral lateral border strongly incised near anterior third and then expanded; anterior patch strongly transverse and zigzag; Sumatra *P. funestus* Andrewes
- Elytral lateral border evenly curved; anterior patch round or slightly transverse, sometimes weakly zigzag.....12
- 12 Median lobe of aedeagus with apical orifice smaller, opened to the left side (Fig. 37); apical lamella long and narrow, length near two times the basal width (lateral view); elytral outer apical angles usually acuminate (Fig. 21); China (west to Salween River), N. Myanmar, S. Vietnam (Fig. 59)..... *P. acutidens* sp. n.
- Median lobe of aedeagus with apical orifice larger, opened to the left-dorsal side (Figs 38, 39); apical lamella short and wide, length a little greater than the basal width (lateral view); elytral outer apical angles usually acute or obtuse (Figs 22–25); China (east of Salween River), Myanmar, Thailand, Vietnam, Laos (Fig. 59).....13
- 13 Elytral anterior patch narrower, usually widely zigzag (Fig. 12); elytra third interval usually with two setigerous pores (the middle one absent); Taiwan... *P. ornatus formosanus* Dupuis
- Elytral anterior patch wider, usually nearly round (Figs 9–11); elytra third interval with three setigerous pores; other localities (Fig. 59)..... *P. ornatus ornatus* Schmidt-Göbel
- 14 Elytral posterior patch separate, composed of three to five small spots15
- Elytral posterior patch round, of single large spot17
- 15 Elytral posterior patch usually obsolete on the sixth interval, if present, adjacent to the spot on the fourth and fifth intervals (Fig. 12); third interval usually with two setigerous pores only; Taiwan..... *P. ornatus formosanus* Dupuis
- Elytral posterior patch with a small spot on the sixth interval, well separated from the larger spot on the fourth and fifth intervals (Figs 13–15); third interval always with three setigerous pores; other localities16

- 16 Elytral yellowish patches larger, usually longer than the interval width; pronotum usually narrower ($PW/PL = 1.55\text{--}1.60$); lateral margins distinctly sinuate before posterior angle; median lobe of aedeagus strongly dilated (Fig. 35, total length / greatest width = 3.7); Vietnam, China (Yunnan), Myanmar, India (Andaman, Sikkim) ***P. obtusipennis* Fedorenko**
- Elytral yellowish patches smaller, most of them equal or shorter than the interval width; pronotum usually wider ($PW/PL = 1.60\text{--}1.75$); lateral margins barely sinuate before posterior angle; median lobe of aedeagus a little dilated (Fig. 36, total length / greatest width = 4.8); China (Guizhou, Guangxi) ***P. obscuratus* sp. n.**
- 17 Larger size, 15.0–15.9 mm (largest in the subgenus); elytral posterior patch in intervals 4 to 7; elytra flat; Laos, China (Yunnan) ***P. dux* Andrewes**
- Smaller size, 7.2–8.5 mm (smallest in the subgenus); elytral posterior patch in intervals 2 to 5 or 3 to 4; elytra distinctly convex; Myanmar (Putao), China (Mêdog)..... ***P. gibbosus* sp. n.**

Pericalus aeneipennis Louwerens and *P. distinctus* Dupuis are not included in the key. Detailed discussions on these two very little known and dubious species are provided under remarks of their similar species (*P. elegans* and *P. obtusipennis*).

***Pericalus* (s. str.) *gibbosus* sp. n.**

<http://zoobank.org/58189BD2-F135-4471-A3FD-E3C34E3648E9>

Figs 1, 2, 19, 30, 33, 41, 52, 60

Type material. Holotype (IZAS): male, body length = 7.2 mm, card-mounted, genitalia dissected and placed in micro vial pinned under specimen, “Myanmar, Kachin state, Putao distr., way btw. Upper Shankhaung to Wasandum; rain forest; 1075 m”; “N27.4765, E97.2060, 2016.XII.11, SHI H.L. lgt. in dead log, CAS-SEABRI exp. 2016”; “HOLOTYPE ♂ *Pericalus gibbosus* sp. n., des. SHI & LIANG 2018” [red label] (Fig. 19). **Paratypes** (2 ex.): 1 female (IZAS): same data as holotype. 1 female (IZAS), “Xizang, Mêdog; alt 800–1200 m, Chinese Academy of Science”; “1983.11.5–10, Han Yinheng lgt.”; “IOZ (E) 1891857”.

Diagnosis. Smallest species in the subgenus, body length 7.2–8.5 mm; elytra black with four round yellowish spots, posterior patch in the third and fourth intervals, sometimes expanded onto part of the second and fifth. Pronotum cordiform, lateral margins strongly sinuate before posterior angles; disc with strong wrinkles. Elytra distinctly convex; outer apical angles rounded; sutural angles blunt; third interval with three setigerous pores; striae with large but shallow punctures. Median lobe of aedeagus with apical lamella very long, approximately one-fourth length of median lobe; endophallus with six thumb tack-like spines (Fig. 33).

Comparison. This species can be readily distinguished from other species in this subgenus. The elytral pattern is similar to that of *P. dux* and *P. longicollis*, all with four

round yellowish spots, but differs from both species by the elytral posterior patch in intervals 3–4, sometimes also part of 2 and 5 (versus in intervals 4–6 or 4–7); elytra much more convex; pronotum strongly sinuate before posterior angles (versus weakly or moderately sinuate); and much smaller body size.

This species is sympatric with *P. elegans* sp. n., *P. acutidens* sp. n., and *P. amplus*. It can be easily distinguished from these species by the different elytra pattern, smaller size, and very convex body.

Description. Body length 7.2–8.5 mm (male holotype 7.2 mm, female paratypes 8.2–8.5 mm). *Coloration.* Dorsal surface shiny blackish, with very faint violet hue on elytra; legs, antennae, mouthparts reddish brown; elytral anterior and posterior patches as single round spots, yellow or reddish yellow; the anterior one in intervals 4–7 or 4–6, the posterior one in intervals 2–5 or 3–4 (the male holotype with elytral spots smaller than those of the two females, Figs 1–2); ventral side black. *Microsculpture* faint and isodiametric on vertex and pronotal disc, distinct and linear on elytral intervals. *Head* with very strong and regular long wrinkles all through clypeus, frons and vertex, reaching or nearly reaching level of posterior margin of eyes, 6–8 wrinkles on each side; eyes strongly prominent; tempora abruptly constricted after eyes. *Pronotum* cordiform, PW/PL = 1.33–1.38, subequal to the width of head with eyes (PW/HW = 1.00–1.05); posterior margin a little narrower than anterior margin; lateral margins rounded in the middle, strongly sinuate and then straight before posterior angles; posterior angles sharp, nearly rectangular, projecting laterally, with a seta a little before posterior angles; lateral expansions wide; disc strongly convex and wrinkled, with a pair of faint pits on each side; sub-anterior impression distinct, median line strongly incised, not reaching posterior margin; basal fovea very deep, forming trifurcate incisions, extending medially forming W-shaped sub-posterior impression. *Elytra* ovate, strongly convex; EW/EL = 0.74–0.75; much wider than pronotum, EW/PW = 1.69–1.83; apical truncation weakly curved; outer apical angles rounded, sutural angles blunt, not pointed; striae deeply incised, with large but very shallow punctures; third interval with three setigerous pores, the first one at approximately basal tenth, the second near middle, the third one close to apex; the first one adjacent to the third stria, the other two close to the second stria; all intervals distinctly convex, seventh and eighth intervals tumid apically, eighth and ninth intervals with sparse fine setae aside of umbilical series; lateral expansions slightly widened at approximately basal third. *Male genitalia* (Fig. 33) with median lobe of aedeagus slender and bent, right margin slightly sinuate near middle; apical orifice very large, opened to the left; apical lamella very long, approximately one fourth length of median lobe, flat, in ventral view length approximately 2.8 times basal width, apex rounded; endophallus with six thumb tack-like spines, arranged in two groups, three near the base of apical orifice, the other three near base of median lobe. Right paramere short, apex truncate, not extended. *Female genitalia.* Internal reproductive system (Fig. 52): bursa copulatrix with a very long lobe (inferred to accommodate the large apical lamella of aedeagus); spermatheca digitiform, with weak whorl near middle, without basal pedicel, inserted on the joint of common oviduct and bursa copulatrix; spermathecal gland long, inserted near base of spermatheca, apex strongly dilated, base

forming long pedicel. Gonocoxite 2 of ovipositor (Fig. 41) scimitar-shaped, abruptly bent to the outer side at apical fifth; length approximately six times basal width; outer margin with three dorsolateral ensiform setae, the basal one finer and distant from the rest two; inner margin with one doromedial ensiform seta near apex.

Distribution. Only known from Putao (North Myanmar) and Mêdog (Southeast Xizang, China). (Fig. 60)

Etymology. The name *gibbosus* is Latin, meaning humped, referring to the strongly convex elytra of the new species, which are rather flat in all the other species of this subgenus.

Habitat. In north Myanmar (Putao), *P. gibbosus* sp. n. was collected under bark of a large fallen log next to a path in subtropical rainforest, elevation of 1075m. This species seems to be very rare, due to only two specimens were collected, cohabitates with *P. acutidens* and *P. amplus*. *Pericalus acutidens* was collected in exactly the same microhabitat together with the new species, but it has a wider elevational range and is much more common. *Pericalus amplus* is also rare in this area.

Remarks. The form of the male genitalia makes *P. gibbosus* the most unique member in the subgenus, and in the genus as well. Unlike all other examined species, *P. gibbosus* has the apical lamella very long, approximately one-fourth length of median lobe (less than one tenth in the other species); and the endophallus with thumb tack-like spines (only finely scaled in other species). This species may represent an isolated lineage in the genus; however, from the external characters, *P. gibbosus* perfectly agrees with the subgenus *Pericalus*. Moreover, we suspect that *Pericalus* (s. str.) could be paraphyletic, because all diagnostic characters for the subgenus seem to be plesiomorphic. Nevertheless, phylogeny is not the task of the present paper, and this new species is placed in *Pericalus* (s. str.).

***Pericalus* (s. str.) *dux* Andrewes, 1920**

Figs 3, 32, 43, 54, 60

Andrewes 1920: 25 (type locality: Laos [Xieng Khouang]; Holotype in NHML); Csiki 1932: 1369 (catalogue); Jedlička 1963: 378.

Material examined. 1 female (SNU), "China, Yunnan Prov., Nabanhe N.R., Bengsaihe, Alt.700 m, 20-XI-2008, HU Jia-Yao & TANG Liang leg."; 1 female (SNU), "Manfei, Nabanhe conv., Yunnan Prov., 10.I.2004, Li & Tang leg".

Diagnosis. Largest size of all species in the subgenus, body length 15.0–15.9 mm; dorsal surface black, elytra with four round yellowish spots; the anterior one in intervals 4–8, the posterior one in intervals 4–7. Pronotum transverse, PW/PL 1.47–1.50; lateral margins gently sinuate and then straight before nearly rectangular posterior angles; disc with fine wrinkles. Elytra flat; apex very faintly curved; outer apical angles rounded; sutural angles blunt or forming very short tooth; third interval with three setigerous pores, the middle one at approximately anterior third; striae shallow and impunctate; eighth and ninth interval with dense fine setae.

Comparison. This species can be easily distinguished from all other known species in the subgenus by its larger size and distinctive elytral pattern (Fig. 3). Two other species *P. longicollis* and *P. gibbosus* also have four round spots on elytra, but *P. dux* has wider spots placed laterally. This species is sympatric with *P. ornatus* in south Yunnan. These two species can be distinguished by the differences in body sizes, the elytra patterns, and the outer apical angle of the elytra.

Supplemental description. Male genitalia not studied. *Female genitalia.* Internal reproductive system (Fig. 54): spermatheca short and pedunculate, inserted on the bursa copulatrix; spermatheca tubular, approximately two times length of pedicel; pedicel short, branched near the joint; spermathecal gland absent. Gonocoxite 2 of ovipositor (Fig. 43) scimitar-shaped, gradually bent to the outer side after apical third; length approximately five times basal width; outer margin with two dorsolateral ensiform setae, the apical one placed near the middle, the basal one on the basal quarter, finer than the apical one; inner margin with one doromedial ensiform seta near apex.

Distribution. Laos (Xiang Khouang, Pon Bai, Ban Sai, Muong Pek), China (Yunnan) (Fig. 60).

***Pericalus* (s. str.) *elegans* sp. n.**

<http://zoobank.org/C5B8C2DF-DAD8-475A-A913-59AD66287FAB>

Figs 4, 5, 20, 31, 34, 42, 53, 60

Type material. **Holotype** (IZAS): male, body length = 10.6 mm, board mounted, left antenna wanting, genitalia dissected and deposited in micro vial pinned under specimen, “CHINA, Xizang, Mêdog, 96km at road Bomê to Mêdog, 1413 m, N29.5837, E95.4674, 2014.VII.20, daytime, YANG X.D. lgt., 14Y0158, CCCC.” [in Chinese]; “HOLOTYPE ♂ *Pericalus elegans* sp. n., des. SHI & LIANG 2018” [red label] (Fig. 20). **Paratypes** (4 ex.): 1 male (IZAS), left elytra broken: “China, Tibet, Mêdog county, close to township, N29.32687 E95.32975, broadleaf forest, 1300–1500 m, 2012.VII.30D, YANG G.Y. lgt.”; “IOZ(E)1700285”. 1 female (CCCC), “CHINA, Xizang, Mêdog, Phomshen village, 1846m, N29.5767, E95.3952, 2014.VII.12, light trap, YANG X.D. lgt., 14Y0460, CCCC”. 1 male, 1 female (IZAS), “China, Tibet, Zayü county, Xia Zayü Twonship, Gadui, 28.50226, 97.00425”; “1686 m, 2001.7.8D, Liu Ye collector, Institute of Zoology”. 1 male (CRS), “Tibet - Motuo co., Hanni, VI.2013”.

Diagnosis. Middle size in the subgenus, body length 10.6–11.6 mm; head and pronotum black, elytra unicolorous, cupreous green with a strong metallic hue. Pronotum strongly transverse, PW/PL = 1.65–1.80; lateral margins weakly sinuate before posterior angles; disc without transverse wrinkle. Elytra flat; outer apical angles rounded; sutural angles sharp, forming short tooth; third interval with three setigerous pores; striae shallow and impunctate. Median lobe of aedeagus evenly curved; apical orifice opened to the left side.

Comparison. Only three other species in the subgenus have no yellowish pattern on the elytra. This new species can be readily distinguished from *P. cicindeloides* and *P. fascinator* by the presence of three setigerous pores on the third elytral interval (vs. four

pores in the other two). From *P. aeneipennis*, which also has three setigerous pores according to the original description (further discussions, see below), this new species is distinguishable by all wrinkles long on vertex, reaching or nearly reaching level of posterior margin of eyes (vs. wrinkles short, only reaching a little beyond mid-eye level); pronotum much wider, PW/PL more than 1.65 (vs. approximately 1.30); pronotal lateral margins weakly sinuate before posterior angles (vs. strongly sinuate); posterior angles not projecting laterally (vs. projecting a little laterally); elytral outer apical angles completely rounded (vs. "hooked but not toothed"); and quite different distribution ranges.

Description. Body length 10.6–11.6 mm (no significant sexual differences).

Coloration. Head and pronotum shiny blackish, with very faint metallic hue; elytra cupreous green, with strong metallic hue; mouthparts, antennomeres 2–11 reddish brown; legs dark brown, trochanters and tarsi yellowish brown; ventral side black. **Microsculpture** faint and isodiametric on vertex and pronotal disc, distinct and isodiametric or slightly transversal on elytral intervals. **Head** with strong and irregular wrinkles; four to six short wrinkles on each side extending from clypeus to frons, middle area around frontoclypeal sulcus smooth; five to seven subparalleled long wrinkles along each side of inner margin of eye, reaching level of posterior margin of eyes; inner wrinkles forming concentric rings around the smooth vertex. Eyes very prominent; temporae gradually constricted after eyes. **Pronotum** strongly transverse, PW/PL = 1.65–1.80, subequal to width of head with eyes (PW/HW = 1.00–1.07); posterior margin a little narrower than anterior margin; lateral margins rounded in the middle, slightly sinuate before posterior angles; posterior angles a little more than rectangular angle, not projecting laterally, with a seta very close to the posterior angles; lateral expansions wide; disc weakly convex, with very faint wrinkles, with a pair of reniform shallow pits on each side; sub-anterior impression shallow, median line fine, not reaching anterior nor posterior margin; basal fovea shallow, extending medially merged with sub-posterior impression, extending posteriorly forming short oblique grooves. **Elytra** ovate, weakly convex; EW/EL = 0.73–0.78; wider than pronotum, EW/PW = 1.45–1.64; apical truncation weakly curved; outer apical angles rounded, sutural angles sharp, forming short tooth; striae shallowly incised, without punctures; third interval with three setigerous pores, the first one at approximately basal tenth, the second near middle, the third one close to apex; the first one adjacent to the third stria, the other two close to the second stria; intervals weakly convex, the eighth interval tumid apically, the eighth and ninth intervals with very sparse and fine setae aside of umbilical series; lateral expansions widely extended, strongly widened near basal third. **Male genitalia** (Fig. 34) with median lobe of aedeagus slender and bent, right margin almost straight, ventral margin evenly curved; apical orifice opened to the left; apical lamella short, a little flat, in ventral view length nearly same as basal width, in lateral view weakly constricted before apex; endophallus strongly folded, with fine scales all through length, without spines. Right paramere with apex extended and expanded, securiform. **Female genitalia.** Internal reproductive system (Fig. 53): spermatheca pedunculate, inserted on the base of common oviduct; spermatheca fusiform, longer than the pedicel; spermathecal gland inserted on the joint

of spermathecal pedicel, approximately twice as long as spermatheca (including the pedicel). Gonocoxite 2 of ovipositor (Fig. 42) scimitar-shaped, abruptly bent to the outer side at apical third; length approximately six times as basal width; outer margin with three dorsolateral ensiform setae, the basal one finer than the rest two; inner margin with one doromedial ensiform seta near apex.

Distribution. Only known from Mêdog and Zayü (Southeast Xizang, China). (Fig. 60).

Etymology. The name *elegans* refers to the beautiful metallic color of this new species.

Habitat. In southeast Tibet, this species occurs in montane rain forests, with the dominant trees being *Castanopsis* spp., *Machilus* spp., and *Elaeocarpus* spp. Elevation ranges between 1300 and 1850 m. Adults were collected on/in dead tree trunks, or attracted by light.

Remarks. According to the original description (Louwerens, 1964), *P. aeneipennis* from Borneo has only three setigerous pores on the third elytral interval and seems to be very similar to the new species *P. elegans*. However, we infer that Louwerens' species has four pores, as he either missed the last pore which is very close to elytra apex or confused it with the umbilical series, same as other species illustrated in the same paper (*P. longicollis*, *P. quadrimaculatus*, for example). Moreover, from the original description and illustration, in spite of the pores on the third elytral interval and coloration, *P. aeneipennis* is very similar to *P. cincidoides* which is also recorded in Borneo. We suspect these two species could be conspecific. Unfortunately, no determined material of *P. aeneipennis* from Borneo was available. Therefore, these two species are retained in their present status, but *P. aeneipennis* is not included in the key to species. Nevertheless, according to those diagnostic characters mentioned above, the new species *P. elegans* is quite different from *P. aeneipennis*.

Pericalus (s. str.) *amplus* Andrewes, 1937

Figs 6, 29, 40, 47, 58, 60

Andrewes 1937: 186 (type locality: Burma ["Ruby mines" = Mogok], holotype in NHML); Csiki 1932: 1369; Jedlička 1963: 377; Fedorenko 2017: 311 (Vietnam).

Material examined (7 ex.). **China:** 1 male (IZAS), "Yunnan, Xishuangbanna, Menglun town, W. reserve station, 2004.II.13, 720 m, Wu Jie leg". 2 females (CCCC), "Yunnan, Ruili, Bangda village, 1432 m, 2014.IX.16, night, Yang Xiaodong leg.". **Myanmar:** 1 male, 1 female (IZAS), "Myanmar, Kachin state, Putao distr., 5km NW of Upper Shankhaung; rain forest; 666 m, N27.4415, E97.2584, 2016.XII.21, SHI H.L. lgt., in dead log; CAS-SEABRI exp. 2016". 1 female (IZAS), "Myanmar, Kachin state, Putao distr., way btw. Upper Shankhaung to Wasandum; rain forest; 1075 m, N27.4765, E97.2060, 2016.XII.11, SHI H.L. lgt., in dead log; CAS-SEABRI exp. 2016". **Vietnam:** 1 male (IZAS), "TONKIN, Hoa-Binh, leg., A de Cooman".

Diagnosis. Medium size in the subgenus, body length 9.4–10.0 mm; dorsal surface black, elytra without metallic hue; anterior patch zigzag, five intervals wide, in the third to seventh intervals; posterior patch separate, composed of four small spots, in intervals 2–3, 4–5, 6, and 7–8 respectively. Pronotum transverse, PW/PL 1.56–1.65; lateral margins strongly sinuate before posterior angles. Elytral apex slightly curved, outer apical angles rounded; sutural angles blunt; third interval with four setigerous pores, the middle two at approximately anterior two-fifth and two-third; ninth interval with sparse fine setae. Median lobe of aedeagus strongly sinuate on ventral margin.

Comparison. Only three species in the subgenus have four setigerous pores in the third interval of the elytra, but the other two species *P. cicindeloides* and *P. fascinator* have no yellowish patches on the elytra. This species is very similar to *P. obtusipennis* in elytral pattern. For more detailed comparisons between them, see remarks of the latter species (p. 38).

Supplemental description. *Male genitalia* (Fig. 40). Median lobe of aedeagus fine, abruptly bent after base, forming a distinct angle on the ventral margin; ventral margin strongly sinuate near middle, dorsal margin concaved near base; apical orifice opened to the left; apical lamella small, a little flat, gradually narrowed to apex, slightly bent dorsally in lateral view; endophallus with fine scales only on basal half, without spines. *Female genitalia.* Internal reproductive system (Fig. 58): spermatheca pedunculate, inserted on the joint of common oviduct and bursa copulatrix; spermathecal body fusiform, apex pointed, longer than the pedicel, distinctly bent; spermathecal gland inserted on the joint of spermathecal pedicel, apex shortly dilated, approximately twice as long as spermatheca. Gonocoxite 2 of ovipositor (Fig. 47) scimitar-shaped, abruptly bent to the outer side at apical fifth; length approximately five times basal width; outer margin with three dorsolateral ensiform setae, the basal one finer than and a little distant from the other two; one doromedial ensiform seta near apex.

Distribution. China (Yunnan), Myanmar (Mogok, Putao), India (Assam), N Vietnam. This species is sympatric with *P. acutidens* sp. n. in north Myanmar and Yunnan, but much rarer. (Fig. 60)

***Pericalus* (s. str.) *acutidens* sp. n.**

<http://zoobank.org/C260316D-8B32-4B34-A740-6D50226B1816>

Figs 7, 8, 17, 21, 37, 45, 56, 59

Pericalus formosanus (in part); Fedorenko 2017: 311.

Type material. Holotype (IZAS): male, body length = 10.4 mm, board mounted, genitalia dissected and deposited in micro vial pinned under specimen, “Yunnan, Longchuan county, Mangdong, 1770 m, 2016.X.2, night, Yang Xiaodong leg., 16Y, CCCC” [in Chinese]; “HOLOTYPE ♂ *Pericalus acutidens* sp. n., des. SHI & LIANG 2018” [red label] (Fig. 17). **Paratypes** (36 ex.): **Yunnan:** 1 male, 2 females (CCCC), same data as holotype. 2 males, 1 female (CCCC), same data as holotype, but date 2016.IX.28. 4 males, 1 female (IZAS), same data as holotype, but date 2016.IX.30.

1 male, 3 females (CCCC), same data as holotype, but date 2016.VI.3. 1 female (CCCC), same data as holotype, but date 2016.IX.27, beating on vegetation. 1 female (IZAS), “Yunnan, Gongshan county, Dulongjiang, Maku, 1540m, 2015.VII.23, Yang Xiaodong leg”. 1 female (IZAS), “Yunnan Prov., Longyang, Mangkuan, Baihualing, on shrub, 25.30985, 98.79485, 1440 m, 2007.10.10 day, David Kavanaugh coll”. 1 female (IZAS), “Yingjiang county, Xima, Huihe power station, 1514 m, board leaf forest, 2013.IX.20, Yang Xiaodong leg”. 1 female (IZAS), “Yunnan, Nabang, 2013.IX.7 Zhu Xiaoyu leg”. 2 males (IZAS), “Yunnan, Ruili, Bangda village, 1432 m, 2014.IX.14, light trap, Yang Xiaodong leg”. 3 males, 1 female (CCCC), “Yunnan, Ruili, Bangda village, 1432m, 2014.IX.16, night, Yang Xiaodong leg”. 1 female (IZAS), “Yunnan, Ruili, Bangda Mt., 2014.IX.14, light trap, Cai Yinan leg”. 1 female (IZAS), “Yunnan, Ruili, Bangda Mt., 1450m, 2015.VIII.30, mixed forest, night, Lu Yanquan leg”. **Xizang:** 1 male (IZAS), “Xizang, Medog county, 850–900 m, 1987.II.19, Lin Zai leg”. **Myanmar:** 4 males, 1 female (IZAS), “Myanmar, Kachin state, Putao distr., way btw. Upper Shankhaung to Wasandum; rain forest; 1075 m, N27.4765, E97.2060, 2016.XII.11, SHI H.L. lgt., in dead log; CAS-SEABRI exp. 2016”. 1 male (IZAS), “Myanmar, Kachin state, Putao distr., 5 km NW. of Upper Shankhaung; rain forest; 666 m, N27.4415, E97.2584, 2016.XII.21, SHI H.L. lgt., in dead log; CAS-SEABRI exp. 2016”. 1 male (IZAS), “Myanmar, Kachin state, Putao distr., way btw. Ziradum and camp I; rain forest; in dead log; 27.5679, 97.1062 1022 m – 27.5991, 96.9948 1593 m, 2016.XII.14, SHI H.L. lgt. CAS-SEABRI exp. 2016”.

Diagnosis. Medium size in the subgenus, body length 9.2–12.0 mm; dorsal surface black, elytra usually with faint cyan hue; anterior patch round in form, usually slightly transverse and zigzag, three to five intervals wide; posterior patch separate, composed of three small spots, normally on intervals 2–3, 4–5, and 7 respectively. Pronotum lateral margins sinuate before posterior angles, posterior angles nearly rectangular. Elytra plain; apical truncation distinctly curved; outer apical angles acuminate, forming sharp tooth (Fig. 21); sutural angles blunt; third interval with three setigerous pores. Median lobe of aedeagus with apical orifice small, opened to the left side; apical lamella narrow and long, length near two times the basal width.

Comparison. The new species is very similar and close to *P. ornatus*, but can be distinguished by male genital characters: (1) in *P. acutidens*, the apical orifice of aedeagus is much smaller and opened exactly to the left side of median lobe; larger and opened to the left-dorsal side in *P. ornatus*; (2) in lateral view, median lobe of aedeagus a little narrower and less bent in the new species than in *P. ornatus*; (3) the apical lamella is a little narrower and longer in *P. acutidens*; (4) in ventral view, apical lamella of *P. acutidens* is almost straightly pointed to apex; in *P. ornatus*, the apical lamella is slightly bent to the right.

Externally, these two species are different in: elytral outer apical angles generally acuminate, projected outwards, forming short tooth in *P. acutidens* (Fig. 21); not or less pointed, acute, obtuse, or rarely rounded in *P. ornatus* (Figs 22–26). *P. acutidens* is also different from *P. o. ornatus* in elytral anterior patch usually a little transverse (versus usually nearly round), and from *P. o. formosanus* in elytral third interval with three setigerous pores (versus usually two pores). Generally, the difference on elytral outer

apical angles well distinguishes these two species for specimens from China. But in S. Vietnam, both species have the outer apical angles acuminate or acute (Figs 1-4, 6-7 in Fedorenko, 2017). Thus the differentiation of them through external characters can be difficult sometimes. For specimens from China, it is easier to diagnose *P. acutidens* n. sp. from *P. ornatus* by their allopatric distributions (Fig. 59), but they are sympatric in at least S. Vietnam.

The new species is sympatric with *P. obtusipennis* and *P. amplus* in SW. Yunnan, and they all have similar elytral patterns. From the latter two, *P. acutidens* can be easily distinguished by the acuminate elytral apical outer angles and the elytral posterior patches which do not have a separate small spot on the sixth interval.

Description. Body length 9.2–12.0 mm. *Coloration.* Dorsal surface black, elytra with faint cyan metallic hue, with yellowish patches; mouthparts, antennomeres 2–11 reddish brown; legs blackish, tarsus reddish brown; ventral side black. Elytral anterior patch round in form, generally a little transverse and zigzag, in the fourth to sixth intervals, sometimes also in parts of the third and seventh. Elytral posterior patch divided into three small spots, usually in intervals 2–3, 4–5, and 7 respectively; occasionally the first one only on the third interval, the second one only on the fifth interval or on the fourth, fifth, and sixth intervals. *Microsculpture* faint and nearly isodiametric on vertex and pronotal disc, strong and linear on elytral intervals. *Head* densely wrinkled; three or four wrinkles on each side extending from clypeus to frons; seven to ten fine wrinkles along each side of inner margin of eye, reaching level of posterior margins of eyes; wrinkles very weak on vertex, occiput almost smooth. Eyes strongly prominent; temporae gradually constricted after eyes. *Pronotum* strongly transverse, $PW/PL = 1.52\text{--}1.61$, subequal to the width of head with eyes ($PW/HW = 0.96\text{--}1.02$); posterior margin subequal to the width of anterior margin; lateral margins rounded in the middle, distinctly sinuate before posterior angles; posterior angles nearly rectangular, apex sharp, not projecting laterally; lateral expansions wide and rugose; disc a little convex, with fine wrinkles, with a pair of shallow pits on each side; sub-anterior impression barely visible, median line fine, not reaching anterior nor posterior margin; basal fovea shallow, extending medially merged with the shallow sub-posterior impression, extended posteriorly forming very shallow short oblique grooves. *Elytra* ovate, weakly convex; $EW/EL = 0.65\text{--}0.73$; much wider than pronotum, $EW/PW = 1.50\text{--}1.65$; apical truncation distinctly curved; outer apical angles generally acuminate, or rarely acute; sutural angles blunt; striae moderately incised, without punctures; third interval with three setigerous pores, the first one at approximately basal eighth, the second one at approximately middle, the third one close to apex; the first one adjacent to the third stria, the other two close to the second stria; intervals slightly convex, the eighth interval tumid apically, the eighth and ninth interval with sparse fine setae aside of umbilical series; lateral expansions narrowly extended, a little widened near basal third. *Male genitalia* (Fig. 37). Median lobe of aedeagus slender and bent, weakly sinuate in ventral and dorsal view; in lateral view, ventral margin evenly curved in the middle; apical orifice small, opened to the left; apical lamella narrow and long, sides parallel in ventral view, in lateral view gradually narrowed to apex, length near two times the basal width, apex rounded; endophallus simple, with

very fine scales all through length, without spines. Right paramere with apex extended and expanded, round in form. *Female genitalia*. Internal reproductive system (Fig. 56): spermatheca pedunculate, inserted on the base of common oviduct; spermathecal body fusiform, longer than the pedicel, distinctly bent; spermathecal gland inserted on the joint of spermathecal pedicel, apex not dilated (probably spermathecal gland apex missing), close to the length of spermatheca. Gonocoxite 2 of ovipositor (Fig. 45) scimitar-shaped, abruptly bent to the outer side at apical third; length approximately six times basal width; outer margin with three or four dorsolateral ensiform setae, the basal one finer than the other ones; inner margin with one doromedial ensiform seta near apex.

Distribution. A relatively widely distributed species, known from several localities west to Salween River: Myanmar: Putao, Shan States; China: Xizang (Mêdog), Yunnan (Nujiang, Dehong, Baoshan Prefectures), S. Vietnam (Fedorenko 2017); probably also in north India, Thailand, and Cambodia (Fig. 59).

Etymology. The name *acutidens* comes from Latin, referring to the generally acuminate elytral outer apical angles of the new species.

Habitat. According to the collecting data, this new species prefers tropical forests with the elevational range between 1000m and 1500m. Adults were collected on/in dead tree trunks, or attracted by light at night.

Remarks. This new species was recorded by Fedorenko (2017) as *P. formosanus* in south Vietnam. Based on the figures of male genitalia in Fedorenko (2017), we determined that his Vietnam *P. formosanus* is not the true *P. formosanus* of Dupuis, but is exactly identical to our new species.

From the examined materials in the present study, the new species is strictly allopatric with *P. ornatus* in China. The natural boundary in China between them seems to be the Salween River (Fig. 59). But we didn't examine any material from regions between the Salween River and Mekong River. These two species are sympatric in south Vietnam, and the new species is rarer than *P. ornatus* (Fedorenko, 2017).

Pericalus ornatus was previously recorded from North India (Assam, Sikkim, Garo Hills), Myanmar (North Shan States, Karin Chebà), Thailand, Laos, and Cambodia. We doubt some of these records are actually *P. acutidens* sp. n. The record from North Shan States (Andrewes 1923) is very close to Ruili (Yunnan) where *P. acutidens* sp. n. was recorded and *P. ornatus* does not occur. Thus this record should be confirmed to *P. acutidens* sp. n. According to the confirmed records (solid spots in Fig. 59) we inferred that these two species could be sympatric in S. Laos, S. Myanmar, Thailand, and Cambodia, and *P. ornatus* may not occur in N. India and N. Myanmar. The records from north India (Andrewes 1923) may refer to *P. acutidens* sp. n. or some other unknown species (empty red circles in Fig. 59).

Pericalus (*s. str.*) *ornatus ornatus* Schmidt-Göbel, 1846

Figs 9, 10, 11, 16, 22, 23, 24, 38, 48, 51, 59

Schmidt-Göbel 1846: 86 (type locality: Burma [Tenasserim]; syntypes in NMPC);
Bates 1892: 411 (Karin Chebà); Dupuis 1913: 83; Andrewes 1923: 49 (India,

Thailand, Laos, Cambodia); Csiki 1932: 1369 (catalogue); Andrewes 1937: 185; Jedlička 1963: 379 (Vietnam); Fedorenko 2017: 311.

Material examined (101 ex.). Syntype of *Pericalus ornatus*, 1 male (NMPC), "MUS. PRAGENSE TENASSERIM COLL. HELFER"; "*ornatus* Sch.g. COL. HELFER"; "Typus! Teste Dr. J.Obenberger" [red label] (Fig. 16). **Yunnan**: 5 ex (IZAS), "Yunnan, Jinghong, Ganlanba, 650 m, Wang Shuyong / Zang Lingchao leg., 1957.III.16". 1 male (IZAS), "Yunnan, Jinghong, Ganmanta, 580 m, Pu Fuji leg., 1957.IV.22". 1 male (IZAS), "Yunnan, Mengla county, Menglun town, W. reserve station, 2004.II.12, 720 m, Wu Jie leg". 1 female (IZAS), "Yunnan, Mengla county, Menglun town, W. reserve station, 2004.II.09, 560 m, Wu Jie leg". 1 male, 1 female (IZAS), "Yunnan, Menglun, Xishuangbanna tropical Botany Garden, 2009.IX.10, Zhu Xiaoyu leg.". 1 male (IZAS), "Yunnan, Mengla county, Wangtianshu, 2004.II.15, Wu Jie leg., 730 m". 1 male (IZAS), "Yunnan, Mengla county, Bubang, 2009.V.11, Li Hu leg". 2 females (IZAS), "Yunnan, Mengla county, 55km in Menglun town, 703 m, 2013.X.3, Yang Xiaodong leg". 1 male (IZAS), "Yunnan, Mengla county, 2999 km at G213 road, 2012.IX.22, Yang Xiaodong leg". 12 ex (IZAS), "China, Yunnan, Mengla, Biodiversity Corridor, N21.40482 E101.63035, 660m, Liang Hongbin & Li Kaiqian leg., 2011. IV.25D". 1 male (IZAS), "China, Yunnan, Mengla, Nanping, 765m, N27 17.206', E101 23.631', 2009.V.12, Li & Yang". 1 male (CCCC), "Yunnan, Hekou county, Huayudong, 150 m, 2010.IV.26 N, Lin Wensin leg". 37 ex (IZAS), "Yunnan, Jinping county, Mengla, 400 m, Huang Keren et. leg., 1956.IV.25". **Hainan**: 1 male 2 females (IZAS) "Hainan Prov., Yinggeling Nat. Res., Baisha, Hongxin, N19.07495, E109.52198, 429m, 2008.11.16, Shi H.L. coll. on dead log". 1 female (IZAS), "Hainan, Ledong, Jianfengling, Mingfenggu, N18.74393, E108.84453, 950 m, 2012. IV.20N, Shi H.L. Liu Y. leg". 1 male (IZAS), "Hainan, Ledong county, Jianfengling, Tianchi, 950 m, 2011.V.20–23, Lin Wensin". **Vietnam**: 29 ex (IZAS), "TONKIN, Hoa-Binh, leg. A de Cooman".

Diagnosis. Medium size in the subgenus, body length 8.4–12.5 mm; dorsal surface black, elytra usually with faint cyan hue; anterior patch usually nearly round, three to five intervals wide; posterior patch separate, composed of three small spots, in intervals 2–3, 4–6, and 7 respectively, the middle one variable, when narrowest, present on the fifth interval only. Pronotum transverse, PW/PL 1.53–1.63; lateral margins sinuate before posterior angles, posterior angles nearly rectangular; disc with fine wrinkles. Elytra flat; apical truncation distinctly curved; outer apical angles usually acute (Figs 22, 24), sometimes obtuse (Fig. 23) or acuminate (in S. Vietnam); sutural angles blunt; third interval with three setigerous pores, the second one near middle of elytron. Median lobe of aedeagus with apical orifice large, opened to left-dorsal side (Fig. 38).

Comparison. *P. o. ornatus* is distinguishable from similar taxa by the acute or obtuse elytral outer apical angles and elytral anterior patch usually round. *P. o. ornatus* is sympatric with *P. obtusipennis* and *P. amplius* in China, and all have similar elytral pattern. From the latter two species, *P. ornatus* can be easily distinguished by the elytral apical outer angles not rounded and without separate spot on the sixth interval.

Supplemental description. *Male genitalia* (Fig. 38). Median lobe of aedeagus slender and bent; in lateral view, ventral margin evenly curved in the middle; in ventral view, right margin barely sinuate near middle, apical lamella slightly bent to the right; apical orifice larger than *P. acutidens*, opened to left-dorsal side; apical lamella small, side paralleled in ventral view, in lateral view gradually narrowed to apex, length a little greater than the basal width, apex rounded; endophallus with very fine scales on some regions, without spines. *Female genitalia*. Internal reproductive system (Fig. 51): spermatheca pedunculate, inserted on the joint of common oviduct and bursa copulatrix; spermathecal body fusiform, a little longer than the pedicel, distinctly bent; spermathecal gland inserted on the joint of spermathecal pedicel, apex dilated, much longer than spermatheca. Gonocoxite 2 of ovipositor (Fig. 48) scimitar-shaped, abruptly bent to the outer side at apical fourth; length approximately six times as basal width; outer margin with three dorsolateral ensiform setae, the basal one a little distant from the other two; inner margin with one doromedial ensiform seta near apex.

Distribution. A relatively widely distributed species, known from localities east to Salween River: China: Yunnan (Xishuangbanna and Honghe Prefectures), Hainan; Myanmar (Tenasserim), Thailand, Vietnam, Laos, Cambodia (Fig. 59).

Remarks. We attribute above specimens to *P. ornatus* based on the descriptions (Schmidt-Göbel 1846; Andrewes 1923) and a photograph of one syntype we took in NMPC years ago (Figs 9, 16). The syntype of *P. ornatus* has an almost round elytral anterior patch and the outer apical angles acute, not acuminate. It agrees perfectly with the examined materials from southeast Yunnan and Tonkin. They are quite probably the same species, although the genitalia of syntype were not studied.

The specimens from Hainan are distinctive in having a slightly different elytral pattern: anterior patch generally smaller, usually three or four intervals wide (Fig. 11); specimens from other localities (Yunnan, Tonkin, and Myanmar) have the anterior patch generally larger, usually five intervals wide (Figs 9, 10). But all examined specimens of *P. ornatus ornatus* have the anterior patch nearly rounded (length subequal to the width).

Pericalus (s. str.) ornatus formosanus Dupuis, 1913

Figs 12, 25, 26, 39, 46, 57, 59

Dupuis 1913: 83 (type locality: Taiwan [Moozan, Sokutsu]; syntypes in IRSN); Jedlička 1963: 379; Kabak 2003: 437 (catalogue).

Type localities. “Moozan” is a misspelling of Hoozan (sometimes also Hozan), referring to Fengshan (N22.61, E120.35) in Kaohsiung county, south Taiwan. Sokutsu refers to Hsiaolin (N23.16, E120.64) in Kaohsiung county.

Material examined (13 ex.). 1 male (CCCC), “Taiwan, Pingtung County, Chunri, Dahanshan, 2009.V.3 D”. 1 male, 2 females (CCCC), “Taiwan, Kaohsiung County, Hsiaoguanshan, 1996.X.12, Chou Wen-I leg”. 1 female (CCCC), “Taiwan,

Kaohsiung, Tengjhih, 2008.V.24 N". 2 males, 2 females (CCCC), "Taiwan, Nantou county, Xitou, 1995.III.25". 1 male, 1 female (CCCC), "Taiwan, Miaoli county, Sanyi, Guandaoshan, 1995.VI.2". 1 female (CCCC), "Taiwan, Yilan county, Datong, Renze, 1998.IV.11". 1 female (CCCC), "Taiwan, Taichung county, Heping, Anmashan".

Diagnosis. Medium size species, body length 9.5–10.5 mm; dorsal surface black, elytra usually with faint cyan hue; anterior patch transverse, a little zigzag (more transverse and zigzag than *P. o. ornatus*), usually in the fourth to sixth intervals; posterior patch separate, composed of three small spots, in intervals 2–3, 4–5, and 7 respectively. Pronotum transverse, PW/PL 1.50–1.58; lateral margins sinuate before posterior angles, posterior angles nearly rectangular; disc with fine wrinkles. Elytra flat; apical truncation distinctly curved; outer apical angles usually obtuse (Fig. 25), occasionally rounded (Fig. 26) or acute; sutural angles blunt; third interval usually with two setigerous pores (occasionally three as other species), the middle one usually missing. Median lobe of aedeagus with apical orifice opened to left-dorsal side (Fig. 39).

Comparison. This subspecies is different from the nominate subspecies in: (1) elytral anterior patch generally more or less transverse (width a little more than length), and somewhat zigzag in *P. o. formosanus* (Fig. 12); nearly round (width subequal to the length) and not zigzag in *P. o. ornatus* (Figs 9–11). (2) *P. o. formosanus* generally with only two setigerous pores on the third elytral interval (occasionally three); in *P. o. ornatus* always with three setigerous pores; (3) in *P. o. formosanus*, the elytral outer apical angles obtuse in most examined specimens (Fig. 25); in *P. o. ornatus* usually acute (Figs 22, 24). But for some individuals, the shape of elytral outer apical angles cannot differentiate these two subspecies. The male genitalia of these two subspecies have no significant differences (Figs 38, 39).

Pericalus o. formosanus is very similar with *P. acutidens* in elytra pattern, but can be distinguished by two pores on elytral third interval, different male genitalia, and distribution. This subspecies is endemic and the only *Pericalus* species in Taiwan.

Distribution. Only known from Taiwan (Fig. 59).

Remarks. According to our examined specimens, the male genitalia of *P. formosanus* have no significant differences from those of *P. ornatus* from the Asian continent. Considering the external differences between *P. ornatus* as well as their allopatric distributions, it is preferable to assign *P. formosanus* as a subspecies of *P. ornatus* rather than synonymize them. Fedorenko (2017) recorded *P. formosanus* from S. Vietnam based on a misidentification of *P. acutidens* sp. n.

In most examined specimens have only two setigerous pores in the elytral third interval (the middle one missing), except for two specimens with three pores on right elytron only (Fig. 12). We consider the presence of the middle pore as individual aberration, and consider that the number of pores in third elytral interval is a good taxonomical character to distinguish between these two subspecies. For the elytral outer apical angles, most examined specimens have an obtuse angle (Fig. 25), but it is rounded in one specimen from Nantou (Fig. 26), and acute in one specimen from Kaohsiung and two of the five photographed syntypes (<http://digitmuse.nmns.edu.tw>).

***Pericalus (s. str.) obtusipennis* Fedorenko, 2017**

Figs 15, 27, 35, 49, 50, 60

Fedorenko 2017: 308 (type locality: Vietnam [Lao Cai]; holotype in ZMMU).

Material examined (7 ex.). 1 male (IZAS), “China, Yunnan prov., Nujiang, Lushui county, Pianma town, Gangfang vill., Xiaobadi; 2051 m, 2015.VI.9, light trap, Yang X.D. lgt.”; 2 males (IZAS), “China, Yunnan prov., Lushui county, Pianma township, 1900m”. 1 male (IZAS), “CHINA, Yunnan Prov., Lushui Co., Pianma, Ganheluo, riverside, 26.06210N, 98.61966E, 2100 m, 2005.V.13 day, Liang H.B. collector”. 1 male (IZAS), “CHINA, Yunnan Prov., Tengchong Co., Wuhe, Zhengding Forest station, 24.85458N, 98.73743E”; 1828 m, 2005.V.26 N, Liang H.B. collector”. 1 female (IZAS), “CHINA, Yunnan Prov., Longling Co., Longjiang, Xiaoheishan, riverside, 24.82888N, 98.76001E, 2020 m, 2005.V.26 N, Kavanaugh D. collector”. 1 female (IZAS), “Yunnan, Yingjiang county, Famuchang, 1770 m, 1980.IV.16, Li Hongxing leg”.

Diagnosis. Medium body size, length 8.8–10.8 mm; dorsal surface black, elytra with faint cupreous hue; anterior patch zigzag, three to five intervals in width; when widest, occupying the third to seventh intervals; posterior patch separated, composed of four small spots, in intervals 2–3, 4–5, 6, and 7–8 respectively. Pronotum transverse, PW/PL 1.55–1.60; lateral margins sinuate before posterior angles; disc with very fine wrinkles. Elytra flat; apex slightly curved; outer apical angles rounded; sutural angles blunt; third interval with three setigerous pores, the middle one at approximately anterior three-fifth; eighth and ninth intervals with sparse fine setae. Median lobe of aedeagus strongly dilated, total length / greatest width approximately 3.7 (Fig. 35).

Comparison. This species is most similar with *P. obscuratus* sp. n. in the genus. For comparisons between them, see Comparison section of that new species. *Pericalus obtusipennis* is also very similar to *P. distinctus* from India and Myanmar. Detailed discussions on these two species are provided below.

Pericalus obtusipennis might be confused with *P. ornatus* or *P. acutidens* due to their similar elytra pattern and sympatric distribution. But *P. obtusipennis* is different from the latter two species in several external characters: (1) elytral outer apical angles rounded in *P. obtusipennis*; acuminate, acute or obtuse in other two species; (2) elytral anterior patch zigzag in *P. obtusipennis*, always very narrow and strongly transverse (similar to that in *P. acutidens*); but rounded or nearly rounded in *P. ornatus*, rarely somewhat zigzag, but wider; (3) in *P. obtusipennis*, elytral posterior patches always with a separate small spot on the sixth interval, placed much beyond to that in the fourth and fifth intervals (Fig. 15); in the other two species, spot in sixth interval usually absent (Figs 9, 10); if present, adjacent to the larger spot in the fourth and fifth interval (Figs 11, 12); (4) all three species with very faint metallic hue on elytra, but cupreous in *P. obtusipennis* and cyan in the other two species. Moreover, *P. obtusipennis* has the median lobe of the aedeagus strongly dilated, very different from those of all other known species.

From the elytral pattern and outer angle, *P. obtusipennis* is also similar to *P. amplus* with which it is sympatric with in Yunnan and N. Vietnam. These two species can be

distinguished by: (1) *P. obtusipennis* with three setigerous pores in elytral third interval; *P. amplus* with four pores; (2) wrinkles along inner margin of eyes a little coarser and sparser in *P. obtusipennis*, with 7–8 wrinkles on each side; a little finer and denser in *P. amplus*, with 9–10 wrinkles on each side; (3) elytra a little more convex in *P. amplus*; (4) male genitalia very different (Figs 35, 40).

Supplemental description. *Male genitalia* (Fig. 35). Median lobe of aedeagus rather stout, total length / greatest width approximately 3.7 (in lateral view), strongly dilated after basal bend, and abruptly narrowed before apical lamella; ventral margin nearly straight in the middle, dorsal margin evenly curved; apical orifice large, reaching one third length of the median lobe, opened to the left; apical lamella small, digitiform, length approximately 1.5 times as basal width; endophallus with fine scales all through length, without spines. *Female genitalia*. Internal reproductive system (Fig. 50): spermatheca pedunculate, inserted on the joint of common oviduct and bursa copulatrix; spermathecal body fusiform, longer than the pedicel; spermathecal gland inserted on the joint of spermathecal pedicel, apex shortly dilated. Gonocoxite 2 of ovipositor (Fig. 49) scimitar-shaped, abruptly bent to the outer side at apical fourth; length approximately six times as basal width; outer margin with four dorsolateral ensiform setae, the basal one much finer than the other three; inner margin with one doromedial ensiform seta near apex.

Distribution. Vietnam (Lao Cai), China (Yunnan) (Fig. 60). This species is sympatric with *P. acutidens* sp. n. in west Yunnan, but seems to prefer a higher elevation (1700–2000 m) and is much rarer.

Remarks. The little known species *P. distinctus* Dupuis, recorded from India and Myanmar, is very similar to *P. obtusipennis*. From the very brief original description (Dupuis 1913) and comments added later (Andrewes 1937), diagnostic characters of *P. distinctus* can be summarized as follows: elytral outer apical angles rounded or obtuse; elytral anterior patch composed of a transverse band, in intervals third to sixth, slightly obliquely backwards on each side; posterior patch similar to that of *P. ornatus*; third interval with three setigerous pores; legs and antennae pale reddish brown, much lighter than *P. ornatus*. Most of these characters agree with those of *P. obtusipennis*, except for pale legs and antennae. We did not examine any confirmed material of *P. distinctus* in the present study and cannot compare it with *P. obtusipennis* further. But, with the very distinctive male genitalia, our examined specimens from Yunnan can be readily identified as *P. obtusipennis*.

***Pericalus* (s. str.) *obscuratus* sp. n.**

<http://zoobank.org/4154488C-C584-4004-83FE-2534E004AD09>

Figs 13, 14, 18, 28, 36, 44, 55, 60

Type material. **Holotype** (IZAS): male, body length = 11.1 mm, board mounted, genitalia dissected and deposited in micro vial pinned under specimen, “CHINA, Guizhou Prov., Jiangkou county, Fanjingshan Mt. S. slope, 4500 steps (Huixiangping) to 5300 steps (ropeway tower); N27.90180 E108.70372 – N27.90784 E108.70052; 1778–

1973m, 2012.VIII.24, night, on tree trunk, broadleaf forest; SHI Hongliang, HUANG Xinlei, LIU Yizhou leg., Inst. of Zoo., CAS”; “HOLOTYPE ♂ *Pericalus obscuratus* sp. n., des. SHI & LIANG 2018” [red label]. (Fig. 18) **Paratypes** (10 ex.): **Guizhou**: 1 male, 2 females (IZAS): same data as holotype. 2 females (IZAS): same data as holotype but date 2012.VIII.25. 1 female (IZAS), “CHINA, Guizhou Prov., Jiangkou county, Fanjingshan Mt. S. slope, 5300 steps to upper ropeway station); N27.90784 E108.70052 – N27.91027 E108.69846; 1973–2078 m, 2012.VIII.25, night, on dead log, broadleaf forest; SHI Hongliang, HUANG Xinlei, LIU Yizhou leg., Inst. of Zoo., CAS”. 2 males and 1 female (CCCC), “China, Guizhou prov., Fanjingshan mt., Huixiangping, N27.9018, E108.7037, 1775 m, 2009.VI.22, Lin W.S. lgt.”; **Guangxi**: 1 female (CCCC), “CHINA, Guangxi, Jinxiu, Dayaoshan, Fenzhanshan, 1050m, 2017.IV-13, J.-T. Zhao leg. CCCC”.

Diagnosis. Medium size, body length 9.9–11.5 mm; dorsal surface black, elytra with very faint cyan hue; anterior patch zigzag, three to five intervals in width, when widest, in the third to seventh intervals; posterior patch separate, composed of four small spots, in intervals 2–3, 4–5, 6, and 7; pronotum transverse, PW/PL 1.60–1.75; lateral margins barely sinuate before posterior angles; elytral outer apical angles rounded, sutural angles blunt; third interval with three setigerous pores; median lobe of aedeagus a little dilated.

Comparison. This new species is very similar to *P. obtusipennis*. It can be distinguished from the latter species by: (1) all elytral yellowish patches smaller than *P. obtusipennis*, most of patches equal or shorter than the interval width in *P. obscuratus* sp. n., usually longer than the interval width in *P. obtusipennis*; (2) elytra with very faint cyan metallic hue; with faint cupreous hue in *P. obtusipennis*; (3) pronotum usually wider (PW/PL = 1.60–1.75) than in *P. obtusipennis* (PW/PL = 1.55–1.60); (4) pronotal lateral margins barely sinuate before posterior angles (versus slightly but distinctly sinuate); (5) in *P. obscuratus* sp. n., median lobe of aedeagus only a little dilated, in lateral view total length / greatest width approximately 4.8 (Fig. 36); strongly dilated in *P. obtusipennis*, total length / greatest width approximately 3.7 (Fig. 35). In spite of the above characters, these two species are almost identical, but their different male genitalia support that they are distinct species.

Description. Body length 9.9–11.5 mm. *Coloration.* Dorsal surface black, elytra with very faint cyan hue, with yellowish patches; mouthparts, antennomeres 2–11 reddish brown; legs dark brown, tarsi yellowish brown; ventral side black. Elytral anterior patch zigzag, in the third to seventh intervals, pale markings in the third and seventh intervals sometimes faint; pale markings in odd intervals anteriorly placed, those in even intervals posteriorly placed; the zigzag patch narrow and a little oblique, usually subequal to single interval width, pale marking in the fifth interval a little anterior to that in the third. Elytral posterior patch separate, composed of four small spots in intervals 2–3, 4–5, 6, and 7; each spot usually shorter than single interval width; from anterior to posterior, the order of four spots: 6, 4–5, 7, 2–3. *Microsculpture* faint and isodiametric on vertex and pronotum disc, distinct and linear on elytral intervals. *Head* densely rugose; three to five shallow wrinkles on each side extending from clypeus to frons; eight to ten fine wrinkles along each side of inner margin of eye, reaching level of posterior margin of eyes; vertex and occiput almost

smooth. Eyes strongly prominent; temporae gradually constricted behind eyes. *Pronotum* strongly transverse, $PW/PL = 1.60\text{--}1.75$, sub-equal to the width of head with eyes ($PW/HW = 1.00\text{--}1.11$); posterior margin close to the width of anterior margin; lateral margins rounded in the middle, very weakly sinuate before posterior angles; posterior angles nearly rectangular, not or weakly projecting laterally, with a seta very close to the posterior angles; lateral expansions wide; disc weakly convex, nearly smooth, with very faint wrinkles, with a pair of very shallow pits on each side; sub-anterior impression barely visible, median line fine, not reaching anterior nor posterior margin; basal fovea shallow, extended medially merged with the shallow sub-posterior impression, extended posteriorly forming very shallow short oblique grooves. *Elytra* ovate, weakly convex; $EW/EL = 0.72\text{--}0.74$; much wider than pronotum, $EW/PW = 1.51\text{--}1.63$; apical truncation weakly curved; outer apical angles rounded, sutural angles blunt; striae moderately incised, impunctate; third interval with three setigerous pores, the first one at approximately basal eighth, the second at approximately apical two fifth, the third one close to apex; the first one adjacent to the third stria, the other two close to the second stria; intervals slightly convex, the eighth interval tumid apically, the eighth and ninth intervals with sparse fine seta aside of umbilical series; lateral expansions narrowly extended, a little widened near basal third. *Male genitalia* (Fig. 36). Median lobe of aedeagus a little dilated, total length / greatest width approximately 4.8 (in lateral view), gradually narrowed before apical lamella; ventral margin unevenly curved near middle, dorsal margin evenly curved; apical orifice large, reaching one fourth length of the median lobe, opened left-ventrally; apical lamella small, gradually narrowed to apex, length approximately 1.5 times as basal width; endophallus with fine scales all through length, without spines. Right paramere with apex extended and enlarged, securiform. *Female genitalia*. Internal reproductive system (Fig. 55): spermatheca pedunculate, inserted on the joint of common oviduct and bursa copulatrix; spermathecal body digitiform, longer than the pedicel, distinctly bent; spermathecal gland inserted on the joint of spermathecal pedicel, apex not dilated (probably spermathecal gland apex missing), nearly same length as spermathecal body. Gonocoxite 2 of ovipositor (Fig. 44) scimitar-shaped, abruptly bent to the outer side at apical fifth; length approximately six times as basal width; outer margin with three dorsolateral ensiform setae, the basal one finer than and a little distant from the rest two; inner margin with one dorsomedial ensiform seta near apex.

Distribution. Only known from two isolated localities in southern China: Fanjingshan (Guizhou) and Dayaoshan (Guangxi) (see Fig. 60).

Etymology. This name *obscuratus* means indistinct, referring to the elytral pattern of this new species which is much narrower than those of all other allied species, almost indistinct.

Habitat. In Fanjingshan, this species occurs in evergreen and deciduous broad-leaved mixed forests, with dominant trees of *Cyclobalanopsis* spp. and *Fagaus* spp., with an elevational range of 1775 to 2078 m. Adults were collected on or under bark of dead trees during the night.

Remarks. The new species is closest to *P. obtusipennis*. Their male genitalia, although different in thickness, are of the same form: somewhat dilated, large apical orifice, and small apical lamella.

Examined material of *Pericalus* (s. str.) species not recorded from China

Pericalus baehri Fedorenko: 1 male (IZAS), “Gunung Leser National Park, Sumatra, local collector, 2014”.

Pericalus cicindeloides Macleay: 22 males and females (IZAS), “Gunung Leser National Park, Sumatra, local collector, 2014”.

Pericalus cordicollis Andrewes: 1 male (IZAS), “Borneo: Sabah, Ranau distr., Kinabalu Park, Liwagu Trail, N6.0239, E116.5500, 1704m; Shi H.L. & Liu Y. leg. Dead log, 2016.V.5d”.

Pericalus funestus Andrewes: paratype, 1 male (NNML), “Gunung Singgalang, Sumatra’s Westkust, 1800M. VII 192, leg. E. Jacobson.”, “Cotype”, “*Pericalus funestus* Cotype Andr., H.E. Andrewes det.”, “Museum Leiden, *Pericalus funestus* andr., Det Andrewes”, “type”.

Pericalus guttatus Chevrolat: syntype, 1 male (OUM), “TYPE COL: 128 *Pericalus guttatus* Chevr., HOPE DEPT. OXFORD”, “Chevrolat Carabidae. Fr.V.d.Poll. Pres. 1909, E. B. Poulton.”

Pericalus longicollis Chaudoir: 3 males, 1 female (IZAS), “Gunung Leser National Park, Sumatra, local collector, 2014”; 2 males (IZAS), “Borneo: Sabah, Keningau district, Jungle Girl Camp, N5.4430, E116.4512; 1182m, Shi H.L. & Liu Y. leg., light trap, 2016.IV.25N”.

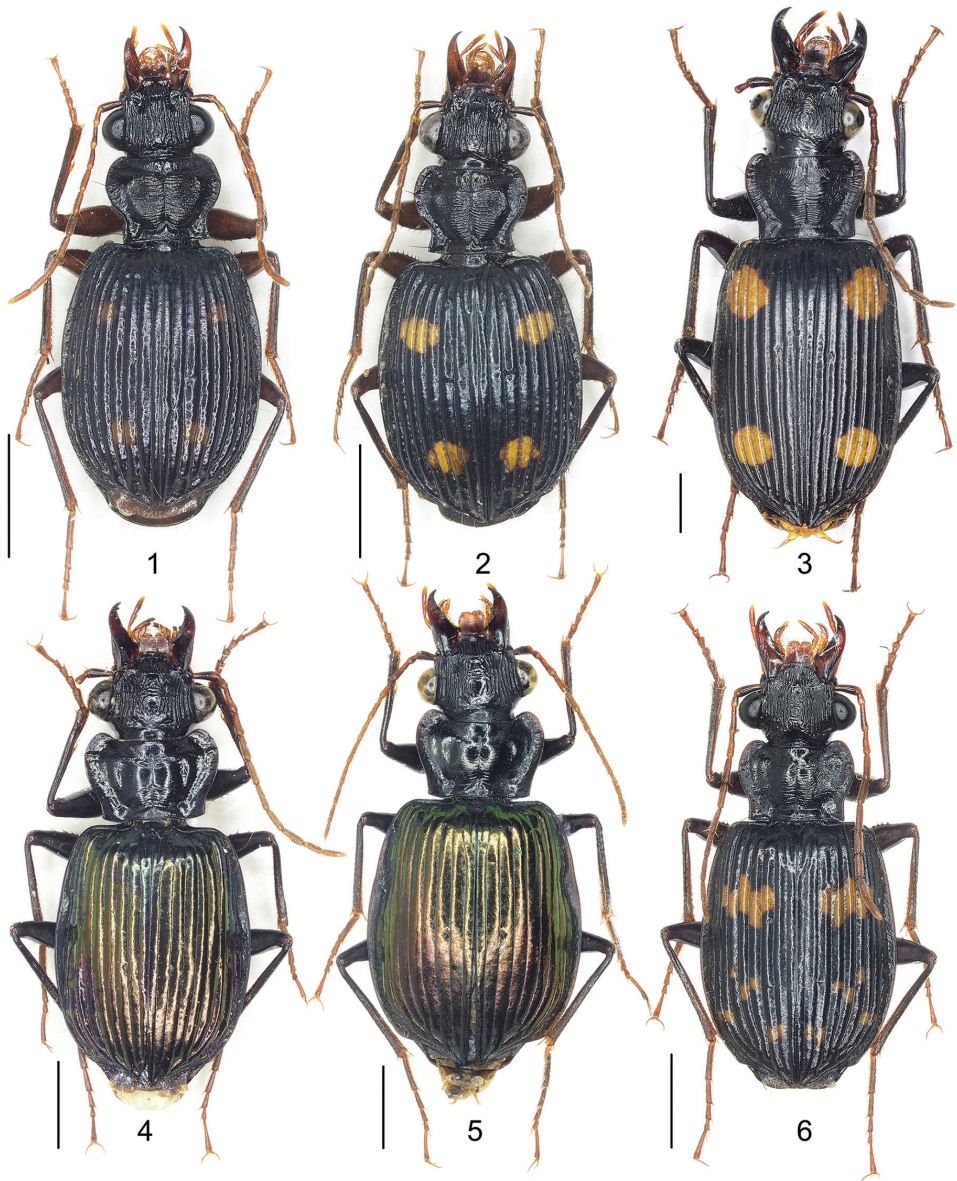
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Figures

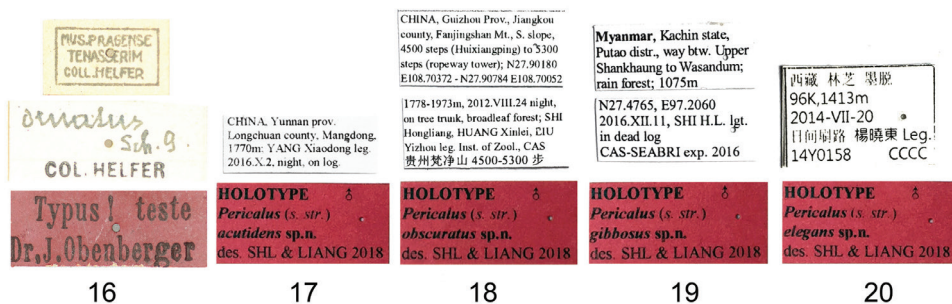
Figures 1–6. Habitus **1** *P. gibbosus* sp. n., holotype, Myanmar (Putao), male **2** *P. gibbosus* sp. n., paratype, Myanmar (Putao), female **3** *P. dux* Andrewes, Yunnan (Jinghong), female **4** *P. elegans* sp. n., holotype, Xizang (Mêdog), male **5** *P. elegans* sp. n. paratype, Xizang (Zayü), female **6** *P. amplus* Andrewes, Myanmar (Putao), male. Scale bars: 2 mm.



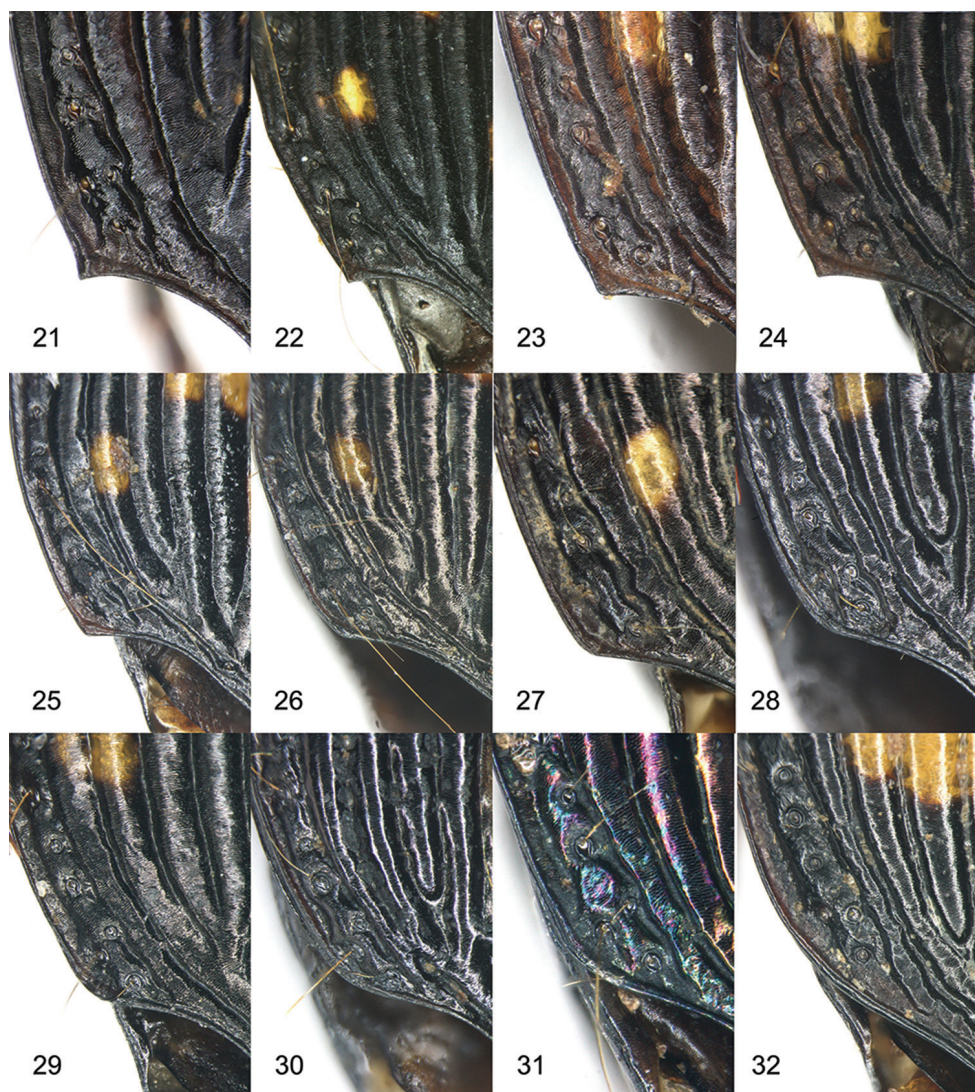
Figures 7–12. Habitus **7** *P. acutidens* sp. n., holotype, Yunnan (Longchuan), male **8** *P. acutidens* sp. n., paratype, Myanmar (Putao), female **9** *P. ornatus ornatus* Schmidt-Göbel, syntype, Myanmar (Tenasserim), male **10** *P. ornatus ornatus* Schmidt-Göbel, Yunnan (Hekou), male **11** *P. ornatus ornatus* Schmidt-Göbel, Hainan (Baisha), male; **12** *P. ornatus formosanus* Dupuis, Taiwan (Yilan), female. Scale bars: 2 mm.



Figures 13–15. Habitus **13** *P. obscuratus* sp. n., holotype, Guizhou (Fanjingshan), male **14** *P. obscuratus* sp. n., paratype, Guizhou (Fanjingshan), female **15** *P. obtusipennis* Fedorenko, Yunnan (Pianma), male. Scale bars: 2 mm.



Figures 16–20. Labels of types: **16** *P. ornatus ornatus* Schmidt-Göbel, syntype (NMPC) **17** *P. acutidens* sp. n., holotype (IZAS) **18** *P. obscuratus* sp. n., holotype (IZAS) **19** *P. gibbosus* sp. n., holotype (IZAS) **20** *P. elegans* sp. n., holotype (IZAS);



Figures 21–32. Elytral outer apical angle (left): **21** *P. acutidens* sp. n., Yunnan (Ruli) **22** *P. ornatus ornatus* Schmidt-Göbel, Yunnan (Mengla) **23** *P. ornatus ornatus* Schmidt-Göbel, Vietnam (Tonkin) **24** *P. ornatus ornatus* Schmidt-Göbel, Hainan (Baisha) **25** *P. ornatus formosanus* Dupuis, Taiwan (Miaoli) **26** *P. ornatus formosanus* Dupuis, Taiwan (Nantou) **27** *P. obtusipennis* Fedorenko, Yunnan (Pianma) **28** *P. obscuratus* sp. n., Guizhou (Fanjingshan) **29** *P. amplus* Andrewes, Myanmar (Putao) **30** *P. gibbosus* sp. n., Myanmar (Putao) **31** *P. elegans* sp. n., Xizang (Mêdog) **32** *P. dux* Andrewes, Yunnan (Jinghong).



Figures 33–34. Aedeagus: right-lateral, ventral, left-lateral, and dorsal views of median lobe, scale bars 0.5 mm. Right and left parameres, scale bars 0.2 mm. **33** *P. gibbosus* sp. n., holotype, Myanmar (Putao)
34 *P. elegans* sp. n., holotype, Xizang (Médog).



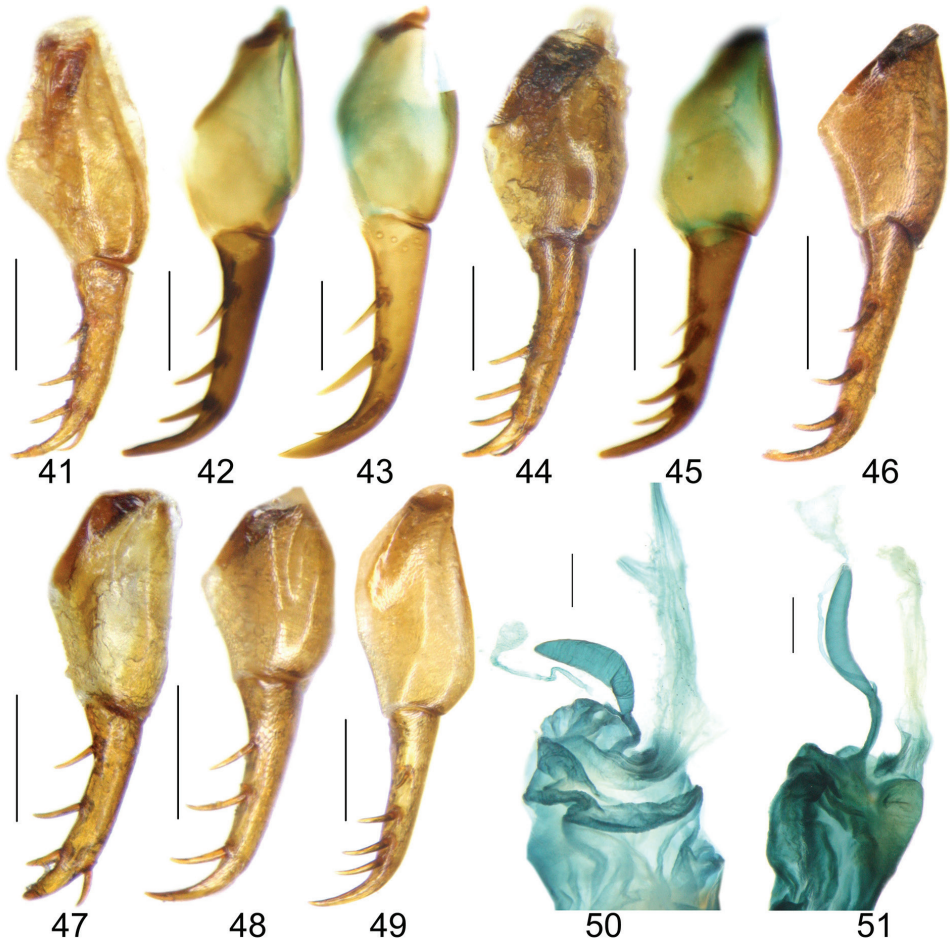
Figures 35–36. Aedeagus: right-lateral, ventral, left-lateral, and dorsal views of median lobe, scale bars 0.5 mm. Right and left parameres, scale bar 0.2 mm. **35** *P. obtusipennis* Fedorenko, Yunnan (Pianma) **36** *P. obscuratus* sp. n., holotype, Guizhou (Fanjingshan).



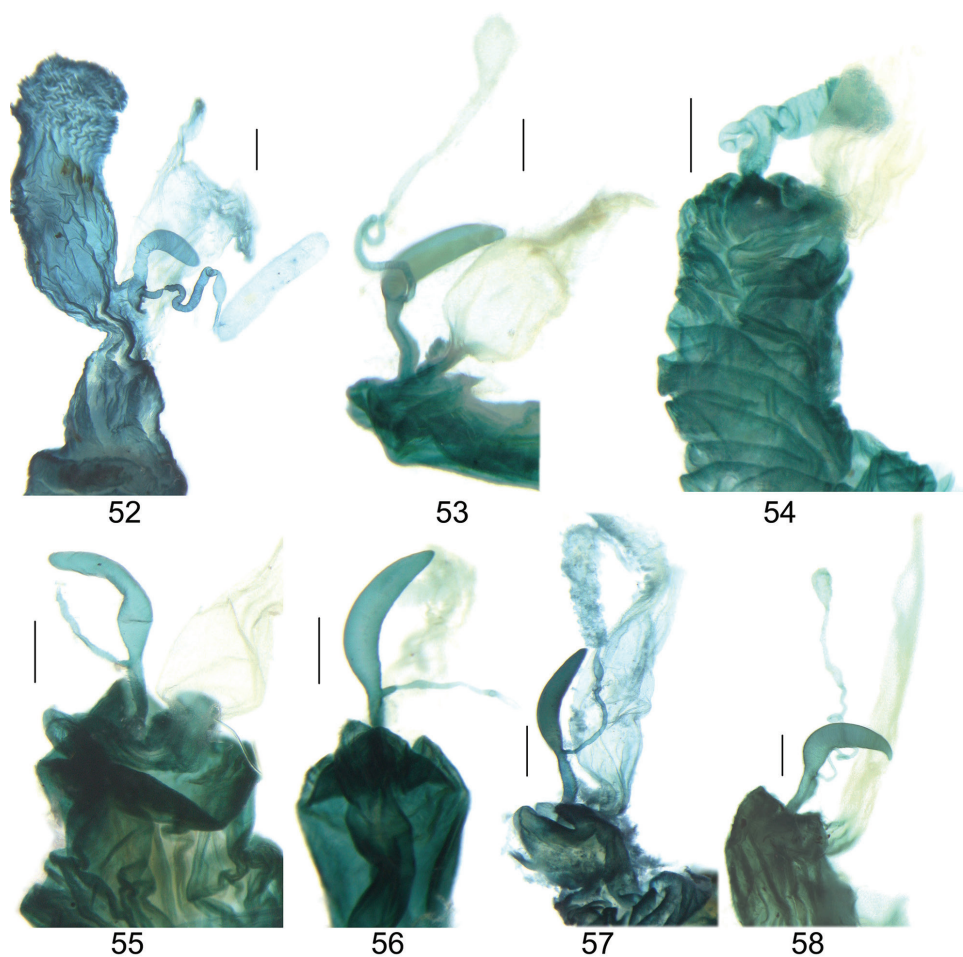
Figures 37–38. Aedeagus: right-lateral, ventral, left-lateral, and dorsal views of median lobe, scale bars 0.5 mm. Right and left parameres, scale bar 0.2 mm. **37** *P. acutidens* sp. n. Holotype, Yunnan (Longchuan) **38** *P. ornatus ornatus* Schmidt-Göbel, Yunnan (Mengla).



Figures 39–40. Median lobe of aedeagus, right-lateral, ventral, left-lateral, dorsal views **39** *P. ornatus formosanus* Dupuis, Taiwan (Miaoli) **40** *P. amplus* Andrewes, Myanmar (Putao). Scale bars: 0.5 mm.



Figures 41–51. 41–49. Stylomere of right ovipositor, ventral view, **41** *P. gibbosus* sp. n., Xizang (Mêdog) **42** *P. elegans* sp. n., Xizang (Mêdog) **43** *P. dux* Andrewes, Yunnan (Jinghong) **44** *P. obscuratus* sp. n., Guizhou (Fanjingshan) **45** *P. acutidens* sp. n., Yunnan (Longchuan) **46** *P. ornatus formosanus* Dupuis, Taiwan (Miaoli) **47** *P. amplus* Andrewes, Myanmar (Putao) **48** *P. ornatus ornatus* Schmidt-Göbel, Hainan (Baisha) **49** *P. obtusipennis* Fedorenko, Yunnan (Longling) **50–51** Female reproductive system **50** *P. obtusipennis* Fedorenko, Yunnan (Longling) **51** *P. ornatus ornatus* Schmidt-Göbel, Yunnan (Mengla). Scale bars: 0.2 mm.



Figures 52–58. Female reproductive system, **52** *P. gibbosus* sp. n., Xizang (Mêdog) **53** *P. elegans* sp. n., Xizang (Mêdog) **54** *P. dux* Andrewes, Yunnan (Jinghong) **55** *P. obscuratus* sp. n., paratype, Guizhou (Fanjingshan) **56** *P. acutidens* sp. n., Yunnan (Longchuan) **57** *P. ornatus formosanus* Dupuis, Taiwan (Yilan) **58** *P. amplius* Andrewes, Myanmar (Putao). Scale bars: 0.2 mm.

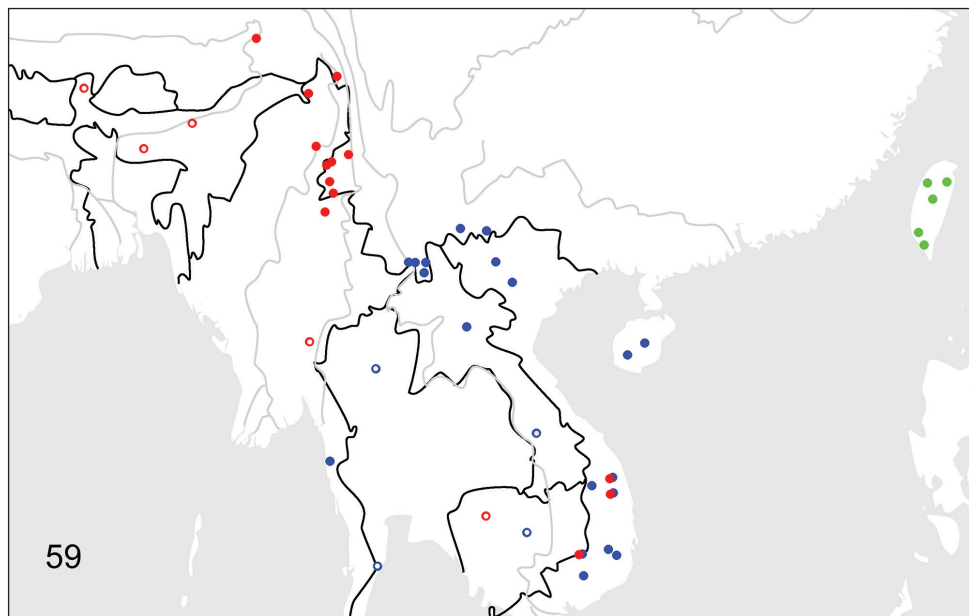


Figure 59. Distribution map for *P. acutidens* sp. n. (red); *P. ornatus ornatus* Schmidt-Göbel (blue); *P. ornatus formosanus* Dupuis (green); dubious records marked by hollow spots.

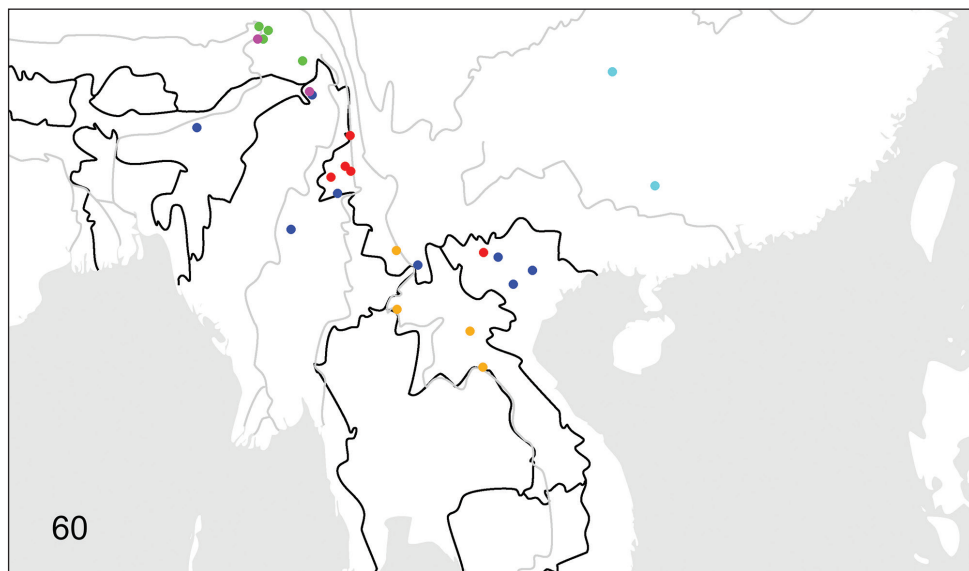


Figure 60. Distribution map for *P. obtusipennis* Fedorenko (red); *P. obscuratus* sp. n. (cyan); *P. amplus* Andrewes (blue); *P. gibbosus* sp. n. (magenta); *P. elegans* sp. n. (green); *P. dux* Andrewes (orange).

A multi-access identification key based on colour patterns in ladybirds (Coleoptera, Coccinellidae)

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Abstract

An identification key based on French ladybird colouration is proposed for the tribes Chilocorini, Coccinellini, and Epilachnini. These tribes were chosen based on their relatively limited species diversity, as well as their large size and high colour diversity, making them easy to observe and collect. The identification key runs on Xper³ software, which allows the building of structured knowledge bases and online free-access keys. The online interactive Xper key is available at <http://french-ladybird.identificationkey.fr>.

Keywords

Citizen science, Coccinellidae, Coccinellini, Chilocorini, Epilachnini, France, interactive identification keys, ladybirds, Xper

Introduction

The identification of species is central in ecology, conservation biology, systematics, and related disciplines (species inventories and community studies, ecosystem management, establishment and improvement of environmental public policies, taxonomic

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reviews, and management of natural history collections) (Oliver 1988, Hebert et al. 2003, Smith et al. 2008, Vander Zanden et al. 2010). Europe is one of the best-known parts in the world in terms of biodiversity (Fontaine et al. 2012), especially concerning distribution patterns at the country scale. This has been highlighted by the release of the Fauna Europaea database since 2004 (de Jong et al. 2014), which gathers the scientific names and distributions of all living European animal species and is assembled by a large network of specialists. However, most new species are described by non-professional taxonomists (Fontaine et al. 2012) and the distribution of a majority of organisms remains poorly known. Citizen science programs aim to fill that gap (Silvertown 2009), thanks to the participation of amateurs and the general public to the inventory and description of life (e.g., National Biodiversity Network in the UK, Swedish Species Gateway in Sweden, Chicago Wilderness Project in the USA, Vigie-Nature in France; see Silvertown 2009). From this perspective, visual and interactive identification of species offers tremendous potential for the general public.

If the identification of large and charismatic animals may be easy, the majority of organisms require expert skills for accurate identification and the inability to identify species represents a major challenge known as the Taxonomic Impediment (SCBD 2010). The most basic requirement for people studying and working on biodiversity aspects is the availability of species identification guides. However, easy-to-use identification guides for non-taxonomists and the general public are scarce and available for relatively few taxonomic groups (SCBD 2010). Consequently, the other features of organisms (such as distribution, ecology, biology) remain poorly known (Costello et al. 2006, SCBD 2010).

Coccinellidae is a family of beetles popular and appreciated by naturalists and the general public. Because these animals have ecological and economic values as predators of pest insects (e.g. aphids, scale insects), their identification may be of importance for naturalists, amateurs and professionals (Hemptinne et al. 2005, Hodek and Honěk 2009, Ali et al. 2014). Several citizen science programs aim to describe the distribution patterns of this group: we can mention for instance the Harlequin Ladybird Survey (<http://www.harlequin-survey.org>) and the Ladybird Survey (<http://www.ladybird-survey.org>) in the UK, the Lost Ladybug Project (<http://www.lostladybug.org>) and the Buckeye Lady Beetle Blitz (<https://entomology.osu.edu/about-us/multi-media/buckeye-lady-beetle-blitz>) in the US, and the Coccinula Recording Scheme in Belgium (Bagnée et al. 2011). The data collected led to a significant number of scientific works that have been published (e.g., Brown et al. 2008, Comont et al. 2012, 2014, Gardiner et al. 2012, Purse et al. 2015).

Single-access identification keys consist of a series of identification steps that form a single and unique identification path for a given taxon. Although it is a very powerful tool for identifying species, the user cannot choose the character to be observed (the answer for every single step must be known), and the identification is impossible if some characters are missing (e.g., if the specimen is poorly preserved). Moreover, this type of keys cannot be modulated or adapted to various kinds of publics, environmental conditions, season, or geographical location.

Most North American or European ladybird identification keys are single-access and difficult to use for non-specialists (Dauguet 1949, Iablokoff-Khnzorian 1982, Gordon 1985, Chapin and Brou 1991). Others are mainly based on shape and colour, but most characters need specific vocabulary, which makes the key still too complicated for the general public in the perspective of citizen science programs (Belgium: Baugnée and Branquart 2000; West of France: Le Monnier and Livory 2003; British Isles: Roy et al. 2013; North of France: Declercq et al. 2014).

Modern tools developed along with digital technologies and data processing make identification easier for the user. In this perspective, several interactive identification keys (IIK) are available online (e.g., <http://www.ladybird-survey.org/bbc/spotter.php>, <http://www.discoverlife.org/20/q?guide=Ladybug>), but most of them are only digital versions of single-access keys and maintain the same difficulties for the user.

A multi-access interactive key is a computer-aided identification tool that makes it possible to find correct names of species where the user enters attributes (character-state values) of the specimen (Dallwitz et al. 2013). The advantages compared to conventional keys are as follows: characters can be used in any order, characters are ordered to start with the one that best separates the remaining taxa, keys can be completed with illustrations (pictures, drawings) and texts explaining the terminology used, correct identifications can be obtained despite errors made by the user (FloraBase – <https://florabase.dpaw.wa.gov.au/keys>; Dallwitz et al. 2013). The software also includes the possibility to print a single-access key for field identification if needed, and to weight characters according to the user skills and abilities (students, general public, naturalists...). Despite the advantages provided by multi-access interactive keys, none has been produced for ladybirds so far.

This study aims to i) release the first multi-access digital interactive identification key for French ladybirds based on colour that takes into account intraspecific variability; and ii) study and discuss the discriminating power of the characters: can we identify species by colour pattern only? What are the most discriminating characters?

Materials and methods

Taxonomic coverage

As the aim of the key is to provide an identification tool for the general public in the perspective of citizen science programs, we have restricted the taxonomic coverage to the tribes Chilocorini, Coccinellini and Epilachnini (Table 1). Members of these tribes are relatively large (3–9 mm) and display a great diversity of colours, making them easily detectable in their environment and identifiable by non-specialists. We also included the most common colour forms, trying to cover most of the intraspecific variability of these species.

The current taxonomy (Seago et al. 2011) and the species list follow Tronquet (2014) and include native, introduced, and acclimated species. Sixty-six taxa are in-

Table 1. Taxonomic coverage of the study.

	Chilocorini Mulsant, 1846	<i>Chilocorus bipustulatus</i> Linnaeus, 1758
		<i>Chilocorus renipustulatus</i> Scriba, 1791
		<i>Exochomus octosignatus</i> Gebler, 1830
		<i>Exochomus quadripustulatus</i> Linnaeus, 1758
		<i>Parexochomus nigromaculatus</i> Goeze, 1777
Coccinellinae Latreille, 1807	Coccinellini Latreille, 1807	<i>Halysia sedecimguttata</i> Linnaeus, 1758
		<i>Psyllobora vigintiduopunctata</i> Linnaeus, 1758
		<i>Vibidia duodecimguttata</i> Poda, 1761
		<i>Anisosticta novemdecimpunctata</i> Linnaeus, 1758
		<i>Coccinula quatuordecimpustulata</i> Linnaeus, 1758
		<i>Coccinula sinuatoimarginata</i> Faldermann, 1837
		<i>Tytthaspis sedecimpunctata</i> Linnaeus 1761 – f. <i>duodecimpunctata</i>
		<i>Adalia bipunctata</i> Linnaeus, 1758 – f. <i>annulata</i>
		<i>Adalia bipunctata</i> Linnaeus, 1758 – f. <i>pantherina</i>
		<i>Adalia bipunctata</i> Linnaeus, 1758 – f. <i>quadrimaculata</i>
		<i>Adalia bipunctata</i> Linnaeus, 1758 – f. <i>sexpustulata</i>
		<i>Adalia bipunctata</i> Linnaeus, 1758 – f. <i>typica</i>
		<i>Adalia conglomerata</i> Linnaeus, 1758 – f. <i>decas</i>
		<i>Adalia decempunctata</i> Linnaeus, 1758 – f. <i>decempustulata</i>
		<i>Adalia decempunctata</i> Linnaeus, 1758 – f. <i>guttatopunctata</i>
		<i>Adalia decempunctata</i> Linnaeus, 1758 – f. <i>lutea</i>
		<i>Adalia decempunctata</i> Linnaeus, 1758 – f. <i>quadripunctata</i>
		<i>Adalia decempunctata</i> Linnaeus, 1758 – f. <i>scribai</i>
		<i>Adalia decempunctata</i> Linnaeus, 1758 – f. <i>subpunctata</i>
		<i>Adalia decempunctata</i> Linnaeus, 1758 – f. <i>terna</i>
		<i>Adalia decempunctata</i> Linnaeus, 1758 – f. <i>typica</i>
		<i>Anatis ocellata</i> Linnaeus, 1758
		<i>Aphidecta oblitterata</i> Linnaeus, 1758 – f. <i>typica</i>
		<i>Calvia decemguttata</i> Linnaeus, 1767
		<i>Calvia quatuordecimguttata</i> Linnaeus, 1758
		<i>Calvia quindecimguttata</i> Fabricius, 1777
		<i>Ceratomegilla alpina</i> Villa A. & Villa G. B., 1835
		<i>Ceratomegilla notata</i> Laicharting, 1781
		<i>Ceratomegilla rufocincta</i> Mulsant, 1850
		<i>Ceratomegilla undecimnotata</i> Schneider D.H. 1792
		<i>Coccinella venusta</i> Weise, 1879
		<i>Coccinella hieroglyphica</i> Linnaeus, 1758
		<i>Coccinella magnifica</i> Redtenbacher, 1843
		<i>Coccinella quinquepunctata</i> Linnaeus, 1758
		<i>Coccinella septempunctata</i> Linnaeus, 1758
		<i>Coccinella undecimpunctata</i> Linnaeus, 1758
		<i>Harmonia axyridis</i> Pallas, 1773 – f. <i>conspicua</i>
		<i>Harmonia axyridis</i> Pallas, 1773 – f. <i>novemdecimsignata</i>
		<i>Harmonia axyridis</i> Pallas, 1773 – f. <i>spectabilis</i>
		<i>Harmonia conformis</i> Boisduval, 1835
		<i>Harmonia quadripunctata</i> Pontoppidan, 1763 – f. <i>sedecimpunctata</i>
		<i>Harmonia quadripunctata</i> Pontoppidan, 1763 – f. <i>typica</i>
		<i>Hippodamia septemmaculata</i> DeGeer, 1775 – f. <i>cestiva</i>
		<i>Hippodamia tredecimpunctata</i> Linnaeus, 1758
		<i>Hippodamia variegata</i> Goeze, 1777 – f. <i>quinquemaculata</i>
		<i>Hippodamia variegata</i> Goeze, 1777 – f. <i>undecimpunctata</i>
		<i>Hippodamia variegata</i> Goeze, 1777 – f. <i>carpini</i>
		<i>Hippodamia variegata</i> Goeze, 1777 – f. <i>constellata</i>

Coccinellinae Latreille, 1807	Coccinellini Latreille, 1807	<i>Hippodamia variegata</i> Goeze, 1777 – f. <i>velox</i>
		<i>Myrrha octodecimguttata</i> Linnaeus, 1758
		<i>Myzia oblongoguttata</i> Linnaeus, 1758
		<i>Oenopia conglobata</i> Linnaeus, 1758
		<i>Oenopia dublieri</i> Mulsant, 1846
		<i>Oenopia impustulata</i> Linnaeus, 1767
		<i>Oenopia lyncea</i> Olivier, 1808
		<i>Propylea quatuordecimpunctata</i> Linnaeus, 1758 – f. <i>weisei</i>
		<i>Sospita vigintiguttata</i> Linnaeus, 1758
		<i>Henosepilachna argus</i> Geoffroy in Fourcroy, 1785
	Epilachnini Chevrolat in Dejean, 1837	<i>Henosepilachna elaterii</i> Rossi, 1794
		<i>Subcoccinella vigintiquatuorpunctata</i> Linnaeus, 1758 – f. <i>limbata</i>
		<i>Subcoccinella vigintiquatuorpunctata</i> Linnaeus, 1758 – f. <i>typica</i>

cluded in the key (47 species and 19 intraspecies colour forms). Several species were removed from this list: introduced and non-acclimated species (*Chilocorus kuwanae* Silvestri, 1909; *C. nigritus* Fabricius, 1798; *C. stigma* Say, 1835; *Hippodamia convergens* Guérin-Ménéville, 1842; *Olla v-nigrum* Mulsant, 1866), or doubtful records (*Anisosticta strigata* Thünberg, 1795; *Cynegetis impunctata* Linnaeus, 1767). *Platynaspis luteorubra* Goeze, 1777 (Chilocorinae, Platynaspini) was also removed due to its small size (2.5–3.5mm). Since only a few discriminating characters are known that are not reliable with colour patterns, *Henosepilachna angusticollis* Reiche, 1862 is not discriminated from its congener *H. argus* Geoffroy in Fourcroy, 1785 in the key.

Specimens were examined in the collection of the Muséum national d'Histoire naturelle, Paris, France (MNHN) and their data are available at <https://science.mnhn.fr/institution/mnhn/collection/ec/search>.

Characters used in the key

A list of 21 morphological characters based on colour and shape is defined, mainly from existing identification keys (Iablokoff-Khnzorian 1982, Baugnée and Branquart 2000, Roy et al. 2013, Declercq et al. 2014) (Table 2). Only characters that are visible to the naked eye or with a ×10 hand lens are included. The character nomenclature follows Roy et al. (2013), except for characters #10, 11, 15, 16, 17, and 18. All characters were treated as discrete.

Interactive identification key construction and statistics

Digitalization of the 47 species was performed using Xper² v.2.3.2 (Ung et al. 2010) and transferred to Xper³ (Vignes-Lebbe et al. 2016). These softwares are dedicated to manage structured taxonomic descriptions, to analyse these descriptions and to produce keys (Kerner et al. 2011, Corvez and Grand 2014, Martin et al. 2015). A wiki and a documentation of Xper³ are available at <http://wiki.xper3.fr/index.php/UserManualXper3>.

Table 2. List of descriptors used in this study.

Pronotum
1. Pronotum colours
2. Pattern on pronotum
3. Number of pronotum patterns
4. Type of pronotum patterns
Elytra
5. Elytra main colour (background)
6. Elytra markings
7. Colour of elytra markings
8. Number of elytra markings
9. Type of elytra markings
10. Number of lateral lines in the elytra markings
11. Number of longitudinal lines in the elytra markings
12. A spot in the first third of the elytra
13. One of the spots reaches the rim of the elytra
14. Cream ring around dots
15. Dark sutural elytra band
16. Scutellar spot
17. Shape of the scutellar spot
18. White marks between the scutellar spot and the elytra basis
19. Distinct rim around the edge of the elytra
20. Elytra covered with short hairs
Underside
21. Small white triangular marks on the underside below both the middle and front legs

An Xper knowledge base is a set of items described using the same model and terminology, and documented by texts and images. In this key there are 66 items covering 47 species and 19 intraspecies colour forms. The descriptive model consists of a hierarchy of descriptors and a chosen terminology for expressing different possible values (states). The descriptors are the 21 morphological characters previously described. Some of them are consistent only if some conditions are true for another descriptor and these dependencies define a hierarchical structure of descriptors (Table 2). The complete terminology (descriptors and states) is documented by images and texts in order to avoid misinterpretation, a crucial point for relevant identifications with the key. Figure 1 presents the description of the species *Coccinella quinquepunctata* following these model and terms.

Xper³ was also used to compare species and genera. For each descriptor, the comparison tests are able to distinguish a pair of items. Three different measures are available (Burguière et al. 2013). The result is displayed as a table with different colours to separate three cases: (1) items have the same values for a given descriptor (= no discrimination), (2) one pair of items is completely distinct for a given descriptor (= total discrimination), (3) at least one pair of items has not equal values for the descriptor, but these values overlap (= partial discrimination). For a given descriptor the sum of the comparison for all pairs of items is a measure of its ability to distinct taxa (discriminatory power).

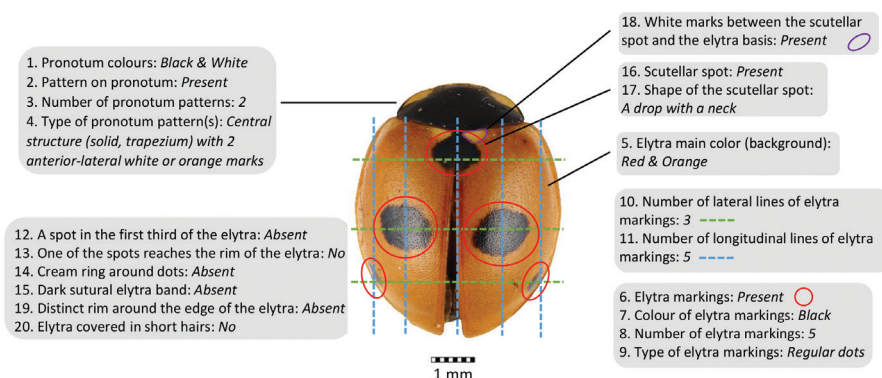


Figure 1. Description of *Coccinella quinquepunctata* following the list of terms used in this study.

The discriminatory power, which represents the quantitative assessments of the ability of a descriptor to distinguish taxa, is measured with the Xper original index (Lebbe 1991) implemented in the Xper² software. This index is based on the incompatibility between descriptions. Two taxa are incompatible (or dissimilar or discriminated) if for one given descriptor there are no states of descriptors in common. For each descriptor the index value ranges between 0 (null discriminatory power of the descriptor) and 1 (the descriptor can distinguish all taxa).

Comparisons within and between genera are made with the “compare groups” and “compare items” options of Xper³. For the comparison between genera, we estimated the number of discriminating characters, weighted or not by the number of colour forms. A subset of descriptors sufficient to discriminate the total of descriptors with the same efficiency was also calculated with the “minset” tool (Lebbe and Vignes 1992, Ziani et al. 1994).

Comparison with standard keys

Two types of keys are available: free-access keys and single-access keys (Hagedorn et al. 2010). A free-access key is a very flexible identification key allowing the user to choose the characters he or she wants to describe. Another web service (Ikey+) (Burguière et al. 2013) is a single-access key builder. A single-access key is a classical key in which descriptors are ordered steps. The topology of the key is a tree and it is possible to compute some indices on the tree: number of maximal steps, length of the paths, etc.

A single-access identification key was generated by IKey+ under Xper³ with the default option and the Xper score method. In this case we show four statistics by taxon: the number of steps, the length of the shortest and the longest paths, and the average length of paths. This key was then compared with five single-access keys for European ladybirds (Dauguet 1949, Baugnée and Branquart 2000, Le Monnier and Livory 2003, Roy et al. 2013, Declercq et al. 2014).

Results

Structure and analysis of the key

The consistency of the knowledge base has been tested with the “Checkbase” functionality of Xper³: no items share the same description and all items are described. The base is 100% complete. Twenty-one descriptors are used: five do not have any dependence (either father or son), four are parent descriptors (for which two are also child descriptors) and 14 are child descriptors (for which two are also parent descriptors). Ninety-eight states are described (minimal/maximal/average number of states: 2/12/4.67).

Discriminatory power of descriptors (Table 3)

The four most discriminating characters (XPER index >0.8) are the type of pronotum patterns (#5), the number of elytra markings (#8), and the number of lateral (#10) and longitudinal (#11) lines of elytra markings. These characters can separate taxa in 7 to 13 groups. For example, the two most discriminating characters (#5 and #8) split all the remaining taxa in 10–13 different groups including 2–13 taxa per group.

The characters #14 and #21 are the least discriminating as they both have an XPER index below 0.8. These characters are binary and split all taxa in two unequal groups (60 vs 2 for the character #14, 65 vs 1 for the character #21). Despite its weak discriminating power, the character #21 is the only one that can distinguish the two species *Coccinella septempunctata* and *C. magnifica*. Eleven descriptors are sufficient to separate all taxa (Table 3, in bold).

Comparison within and between genera

Comparison within a genus: *Coccinella* (Table 4)

Among the 21 characters, 12 are informative (in blue) whereas the other nine are constant and cannot discriminate within this genus (in red). The intersection column shows what is constant in *Coccinella*, therefore helping with the description of the genus: black and white pronotum with two patterns (Central structure - solid, trapezium with two anterior-lateral white or orange marks), elytra with different markings, but always devoid of rim around the edge, short down hairs, cream rings around dots, or dark sutural band.

Comparison between the 24 genera included in the study (Table 5)

Among the genera with at least two species studied, the most constant are *Coccinula* (5% of discriminating characters), *Henosepilachna* (14%) and *Chilocorus* (19%); the most variable are *Adalia* (76%) and *Harmonia* (67%). If weighted by the number of described colour forms per genera, the most constant are still *Coccinula* and *Henosepilachna*; whereas the most variable genera are *Ceratomegilla* and *Exochomus*.

Table 3. List of the discriminating power efficiency of descriptors. Those written in bold are sufficient for discriminating all taxa.

Category	Descriptor	XPER index	Number of descriptor states
Pronotum	4. Type of pronotum pattern(s)	0.85	10
Elytra	8. Number of elytra markings	0.85	12
Elytra	10. Number of lateral lines of elytra markings	0.83	8
Elytra	11. Number of longitudinal lines of elytra markings	0.82	7
Pronotum	3. Number of pronotum patterns	0.71	9
Elytra	17. Shape of the scutellar spot	0.68	4
Elytra	5. Elytra main colour (background)	0.53	7
Elytra	7. Colour of elytra markings	0.52	6
Elytra	13. One of the spots reaches the rim of the elytra	0.49	2
Elytra	18. White marks between the scutellary spot and the elytra basis	0.47	2
Elytra	16. Scutellar spot	0.46	2
Elytra	12. A spot in the first third of the elytra	0.4	2
Elytra	9. Type of elytra markings	0.32	6
Elytra	15. Dark sutural elytra band	0.18	2
Elytra	19. Distinct rim around the edge of the elytra	0.14	2
Elytra	6. Elytra markings	0.12	2
Elytra	20. Elytra covered in short hairs	0.12	2
Pronotum	2. Pattern on pronotum	0.11	2
Pronotum	1. Pronotum colours	0.09	7
Elytra	14. Cream ring around dots	0.06	2
Underside	21. Small white triangular marks on the underside below both the middle and front legs	0.03	2

Single-access identification key and comparison with standard keys

For each identification, the descriptive statistics of the generated key (Appendix 1) are: mean 4.2 steps (2–7), 1–4 paths leading to a taxon (mean 1.5). Unlike many other single-access keys, lots of steps for identifying a taxon do not follow the taxonomy. This is the case in the three tribes: for instance, the user can follow five different paths for identifying an *Epilachnini* species (in green). The same reasoning applies to *Coccinella* species (in red) with six different paths, and the colour forms of *A. decempunctata* (marked with a yellow star) with six different paths (Figure 2).

In comparison to other standard keys (Table 6), this newly generated key is more efficient for finding the taxon, despite its highest number of included species, except for *Coccinula quatuordecimpustulata* and the key of Dauguet (1949). For example, only five steps are required in the generated key for identifying *Coccinella septempunctata*, whereas 8–14 steps are needed in the other keys.

Table 4. Comparison within genus: *Coccinella* (six species), showing informative characters (in bold) and constant characters (in regular). The intersection column shows what is constant within the genus.

	<i>Coccinella venusta</i>	<i>Coccinella hieroglyphica</i>	<i>Coccinella magnifica</i>	<i>Coccinella quinquepunctata</i>	<i>Coccinella septempunctata</i>	<i>Coccinella undecimpunctata</i>	UNION	INTERSECTION
1. Pronotum colours					Black; White			
2. Elytra main colour (background)	Black; Orange	Black; Orange	Red; Orange	Red; Orange	Red; Orange	Red; Orange	Black; Orange; Red	Orange
3. Pattern on pronotum					Present			
4. Number of pronotum patterns					2			
5. Type of pronotum patterns					Central structure (solid, trapezium) with 2 anterior-lateral white or orange marks			
6. Elytra markings					Present			
7. Colour of elytra markings	Red; Orange; Black	Black	Black	Black	Black	Black	Red; Orange; Black	Black
8. Number of elytra markings	1; 2	7	7	5	7	10–14	1; 2; 5; 7; 10–14	
9. Type of elytra markings	Other	Ovoid shape spot; Other	Regular dots	Regular dots	Regular dots	Regular dots	Ovoid shape spot; Regular dots; Other	
10. Number of lateral lines of elytra markings	not applicable	3	3	3	3	3	3	
11. Number of longitudinal lines of elytra markings	not applicable	4	5	5	5	5	4; 5	
12. Scutellar spot	Absent	Absent	Present	Present	Present	Present	Absent; Present	
13. Distinct rim around the edge of the elytra					absent			
14. Elytra covered in short hairs					No			

	<i>Coccinella venusta</i>	<i>Coccinella hieroglyphica</i>	<i>Coccinella magnifica</i>	<i>Coccinella quinquepunctata</i>	<i>Coccinella septempunctata</i>	<i>Coccinella undecimpunctata</i>	UNION	INTERSECTION
15. Small white triangular marks on the underside below both the middle and front legs	Absent	Absent	Present	Absent	Absent	Absent	Absent; Present	
16. Cream ring around dots	Absent							
17. Dark sutural elytra band	Absent							
18. Shape of the scutellar spot	not applicable	not applicable	A drop (spot with a neck)	A drop (spot with a neck)	A drop (spot with a neck)	A drop (spot with a neck)	A drop (spot with a neck)	
19. White marks between the scutellar spot and the basis of elytra	not applicable	not applicable	Present	Present	Present	Present	Present	
20. One of the spots reaches the rim of the elytra	No	Yes	No	No	No	No	Yes; No	
21. A spot in the first third of the elytra	Absent	Present	Present	Absent	Present	Present	Absent; Present	

Table 5. Comparison between the 24 genera included in the study, showing the most constant or variable genus, weighted or not by the intraspecific variability taken into account in this study (number of colour forms).

	Number of species studied	Number of colour forms studied	Number of discriminating characters within genus	
			with all colours forms	weighted by the number of colour forms
<i>Adalia</i>	3	14	16 (76%)	1.1
<i>Calvia</i>	3	3	5 (23%)	1.7
<i>Ceratomegilla</i>	4	4	13 (62%)	3.3
<i>Chilocorus</i>	2	2	4 (19%)	2
<i>Coccinella</i>	6	6	11 (52%)	1.8
<i>Coccinula</i>	2	2	1 (5%)	0.5
<i>Exochomus</i>	2	2	7 (33%)	3.5
<i>Harmonia</i>	3	6	14 (67%)	2.3
<i>Henosepilachna</i>	2	2	3 (14%)	1.5
<i>Hippodamia</i>	3	7	10 (48 %)	1.4
<i>Oenopia</i>	4	4	10 (48%)	2.5
<i>Subcoccinella</i>	1	2	–	–
<i>Anatis</i>	1	1	–	–
<i>Anisosticta</i>	1	1	–	–
<i>Aphidecta</i>	1	1	–	–
<i>Halysia</i>	1	1	–	–
<i>Myrrha</i>	1	1	–	–
<i>Myzia</i>	1	1	–	–
<i>Parexochomus</i>	1	1	–	–
<i>Propylea</i>	1	1	–	–
<i>Psyllobora</i>	1	1	–	–
<i>Sospita</i>	1	1	–	–
<i>Tytthaspis</i>	1	1	–	–
<i>Vibidia</i>	1	1	–	–

Discussion

The work presented in this study led to the release of the first multi-access interactive digital identification key for French ladybirds. The adaptability and great number of possibilities provided by this new generation tool are unparalleled for this group, and make the key very flexible and abundantly illustrated and described, thanks to images and texts. Since it is available online and open to experts for modification, the identification key can easily be improved. It will be possible to add ladybird taxa and to extend the geographic area (e.g., a key to all European ladybirds).

Most classical and single-access keys share characters that are quite difficult to observe for students, naturalists and the general public (e.g. for ladybirds in Dauguet 1949 or Roy et al. 2013: mandibles, tooth on tibia, tarsal claws, mesosternal epimera, abdominal post-coxal lines). Here, all taxa are distinguishable with only 11 characters focusing on markings (number and shape). All characters used in this new key are visible to the naked eye or with a x10 hand lens; therefore this tool is designed for non-

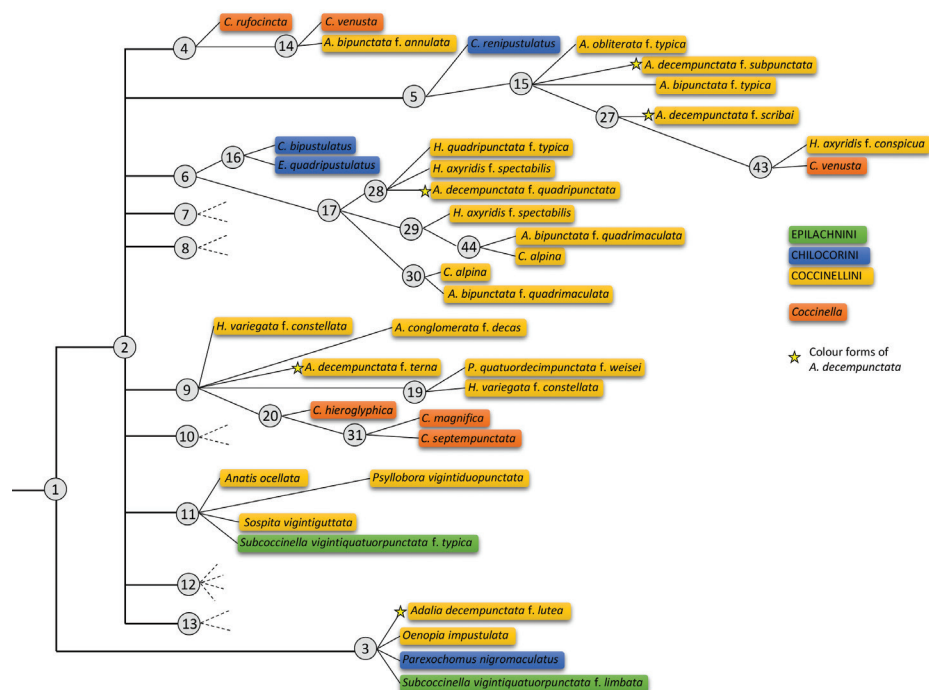


Figure 2. Representation of a part of the single-access identification key generated by IKey+ under Xper³ and the Xper score method (statistics detailed in Appendix 1). The taxonomy is highlighted (the three tribes included in this study, the genus *Coccinella* and the colour forms of *Adalia decempunctata*). Numbers in the circles represent the number of steps in the generated key.

specialists. Using this key, most species can be identified through pictures only, as it is already the case in the identification key for the photographic survey of flower visitors (Spipoll citizen science program, www.spipoll.org), also built with Xper³.

Identification in the field is traditionally realised with paper-printed keys, but recent developments of mobile devices make it possible to use portable version of digital keys. In this perspective, the project “KeyToNature” (www.keytonature.eu) aims to develop new, more convenient and paper-free identification tools, for use within schools and universities across Europe and available on a variety of mobile platforms (laptops, smartphones). However these keys are single access, e.g., MobileKey (Weber and Hagedorn 2010) or the iRecord Ladybirds mobile application, and do not support all the possibilities provided by the free-access keys. Recently, a set of software and applications for transferring the information present in a local Xper database to an Android application has been developed (Troudet 2012). For example, the Malaco-fr application provides an interactive way to identify French snails in the field and without internet connection (Gargominy and Ripken 2011). The free-access key of French ladybirds described in this study will soon be transferred to such a mobile application,

Table 6. Comparison between five single-access keys from bibliography and the generated key by IKey+ under Xper³ for 13 ladybird species: average number of steps (number of paths, length of the shortest and the longest paths).

	Generated Key - this study 47 species	Dauguet (1949) 35 species	Baugnée and Branquart (2000) 37 species	Le Monnier and Livory (2003) 35 species	Roy et al. (2013) 26 species	Derolez et al. (2014) 35 species
<i>Adalia bipunctata</i> f. <i>typica</i>	4 (1)	5 (1)	8 (1)	11 (1)	7 (1)	9 (1)
<i>Anatis ocellata</i>	3 (2)	6 (1)	4.6 (3, 3–7)	4 (1)	8 (3, 6–10)	8 (2, 7–9)
<i>Anisosticta novemdecimpunctata</i>	3 (1)	5 (1)	9 (1)	5 (1)	10 (1)	5.5 (2, 3–8)
<i>Calvia quatuordecimguttata</i>	5 (1)	11 (1)	12 (1)	10 (1)	8 (1)	11 (1)
<i>Chilocorus bipustulatus</i>	4 (1)	-	7 (1)	4 (1)	4 (1)	8 (1)
<i>Coccinella hieroglyphica</i>	4 (2)	10 (1)	6.5 (4, 4–9)	-	8 (1)	8 (2, 7–9)
<i>Coccinella quinquepunctata</i>	3 (1)	12 (1)	8 (1)	-	10 (1)	13 (1)
<i>Coccinella septempunctata</i>	5 (1)	13 (1)	8 (1)	12 (1)	11 (1)	14 (1)
<i>Coccinella undecimpunctata</i>	5 (1)	11 (1)	8.5 (2, 8–9)	11 (1)	10 (1)	10.5 (2, 10–11)
<i>Coccinula quatuordecimpustulata</i>	6 (2)	10 (1)	5 (1)	14 (1)	-	11 (1)
<i>Myzia oblongoguttata</i>	5.5 (2, 5–6)	6 (1)	6 (1)	6 (1)	7 (1)	7 (1)
<i>Oenopia conglobata</i>	4 (1)	10 (1)	11 (1)	9 (1)	-	6 (1)
<i>Psyllobora vigintiduopunctata</i>	3 (1)	8 (1)	11 (1)	12 (1)	12 (1)	7 (1)

which will make it possible to use this tool in educative programs such as “Vigie-nature école” (<https://www.vigienature-ecole.fr>).

Both experienced and inexperienced users are likely to succeed in identifying problematic species (Morse et al. 1996, Drinkwater 2009) if they use convenient, multi-access interactive digital keys. The general public can discriminate species and several colour forms only with colour/form characters and a ×10 lens. Moreover, Xper³ provides possibilities for collaborative work and editing through its website. All the online features make it possible to update the knowledge base easily (e.g. adding numerous colour forms or acclimated species, or new characters such as ecological data). This kind of key aims to increase the curiosity of the general public, and to collect more data on the biology and distribution of species.

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Appendix I

STATISTICS				
Taxon	Number of paths leading to taxon	Length of the shortest path leading to taxon	Average length of paths leading to taxon	Length of the longest path leading to taxon
<i>Adalia bipunctata</i> f. <i>annulata</i>	1	4	4	4
<i>Adalia bipunctata</i> f. <i>pantherina</i>	1	4	4	4
<i>Adalia bipunctata</i> f. <i>quadrinaculata</i>	2	5	5.5	6
<i>Adalia bipunctata</i> f. <i>sempustulata</i>	2	3	3.5	4
<i>Adalia bipunctata</i> f. <i>typica</i>	1	4	4	4
<i>Adalia conglomerata</i> f. <i>decas</i>	1	3	3	3
<i>Adalia decempunctata</i> f. <i>decempustulata</i>	2	7	7	7
<i>Adalia decempunctata</i> f. <i>guttatopunctata</i>	4	7	7	7
<i>Adalia decempunctata</i> f. <i>lutea</i>	1	2	2	2
<i>Adalia decempunctata</i> f. <i>quadripunctata</i>	1	5	5	5
<i>Adalia decempunctata</i> f. <i>scribai</i>	1	5	5	5
<i>Adalia decempunctata</i> f. <i>subpunctata</i>	1	4	4	4
<i>Adalia decempunctata</i> f. <i>terna</i>	1	3	3	3
<i>Adalia decempunctata</i> f. <i>typica</i>	2	6	6	6
<i>Anatis ocellata</i>	2	3	3	3
<i>Anisosticta novemdecimpunctata</i>	1	3	3	3
<i>Aphidecta oblitterata</i> f. <i>typica</i>	2	2	3	4
<i>Calvia decemguttata</i>	2	6	6	6
<i>Calvia quatuordecimguttata</i>	1	5	5	5
<i>Calvia quindecimguttata</i>	2	6	6	6
<i>Ceratomegilla alpina</i>	2	5	5.5	6
<i>Ceratomegilla notata</i>	2	6	7	8
<i>Ceratomegilla rufocincta</i>	1	3	3	3
<i>Ceratomegilla undecimnotata</i>	1	8	8	8
<i>Chilocorus bipustulatus</i>	1	4	4	4
<i>Chilocorus renipustulatus</i>	1	3	3	3
<i>Coccinella hieroglyphica</i>	2	4	4	4
<i>Coccinella magnifica</i>	1	5	5	5
<i>Coccinella quinquepunctata</i>	1	3	3	3
<i>Coccinella septempunctata</i>	1	5	5	5
<i>Coccinella undecimpunctata</i>	1	5	5	5
<i>Coccinella venusta</i>	2	4	5	6
<i>Coccinula quatuordecimpustulata</i>	2	6	6	6
<i>Coccinula sinuatomarginata</i>	1	5	5	5
<i>Exochomus octosignatus</i>	1	2	2	2
<i>Exochomus quadripustulatus</i>	1	4	4	4

STATISTICS				
Taxon	Number of paths leading to taxon	Length of the shortest path leading to taxon	Average length of paths leading to taxon	Length of the longest path leading to taxon
<i>Halysia sedecimguttata</i>	1	5	5	5
<i>Harmonia axyridis</i> f. <i>conspicua</i>	2	6	6	6
<i>Harmonia axyridis</i> f. <i>novemdecimsignata</i>	2	4	4.5	5
<i>Harmonia axyridis</i> f. <i>spectabilis</i>	2	5	5	5
<i>Harmonia conformis</i>	3	3	4	5
<i>Harmonia quadripunctata</i> f. <i>sedecimpunctata</i>	2	3	3	3
<i>Harmonia quadripunctata</i> f. <i>typica</i>	1	5	5	5
<i>Henosepilachna argus</i>	2	4	5	6
<i>Henosepilachna elaterii</i>	1	4	4	4
<i>Hippodamia septemmaculata</i> f. <i>cestiva</i>	2	3	3.5	4
<i>Hippodamia tredecimpunctata</i>	1	4	4	4
<i>Hippodamia variegata</i> f. <i>undecimpunctata</i>	2	5	6	7
<i>Hippodamia variegata</i> f. <i>quinquemaculata</i>	1	3	3	3
<i>Hippodamia variegata</i> f. <i>carpini</i>	1	4	4	4
<i>Hippodamia variegata</i> f. <i>constellata</i>	2	3	3.5	4
<i>Hippodamia variegata</i> f. <i>velox</i>	2	5	5.5	6
<i>Myrrha octodecimguttata</i>	1	5	5	5
<i>Myzia oblongoguttata</i>	4	5	5.5	6
<i>Oenopia conglobata</i>	1	4	4	4
<i>Oenopia dublieri</i>	1	4	4	4
<i>Oenopia impustulata</i>	1	2	2	2
<i>Oenopia lyncea</i>	4	5	5.5	6
<i>Parexochomus nigromaculatus</i>	1	2	2	2
<i>Propylea quatuordecimpunctata</i> f. <i>weisei</i>	2	4	4	4
<i>Psyllobora vigintiduopunctata</i>	1	3	3	3
<i>Sospita vigintiguttata</i>	1	3	3	3
<i>Subcoccinella vigintiquatuorpunctata</i> f. <i>limbata</i>	1	2	2	2
<i>Subcoccinella vigintiquatuorpunctata</i> f. <i>typica</i>	1	3	3	3
<i>Tythraps sedecimpunctata</i> f. <i>duodecimpunctata</i>	2	5	5.5	6
<i>Vibidia duodecimguttata</i>	1	5	5	5
AVERAGE	1.53	4.197	4.364	4.53

Revision of the Hawaiian psyllid genus *Swezeyana*, with descriptions of seven new species (Hemiptera, Psylloidea, Triozidae)

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Abstract

The endemic Hawaiian genus *Swezeyana* Caldwell, 1940 is highly distinctive due to the extremely long genal processes. In addition, some of the immatures are ornamented with extraordinary tubercles and tentacles. Two *Swezeyana* species are redescribed, and seven new species are described, bringing the total number of species in the genus to nine. All species are hosted by a single, endemic host plant, *Planchonella sandwicensis* (Sapotaceae), which is distributed across all major islands in the archipelago. The majority of *Swezeyana* species are single island endemics. A sister taxon pair is found sympatrically on the same individual plants on Kauai, and putative sister or at least closely related species are also found sympatrically on Oahu and Hawaii, suggesting these taxa may have diversified in sympatry. However, there is no observed ecological niche partitioning, despite some striking morphological diversity, as all *Swezeyana* species have free-living immatures that are found on the leaf surface, and therefore no apparent biological shifts are coincident with occupying the same host plant. Two species groups are represented by strikingly different female terminalia structure and endoskeletal development, although ovipositor structure is very similar between the two groups. Mitochondrial DNA barcodes (COI and cytB) are provided for eight of the nine species. A phylogenetic analysis of the mitochondrial barcode regions indicates species relationships within *Swezeyana* and provides a comparison of genetic divergence with other Hawaiian endemic genera.

Keywords

jumping plant lice, mitochondrial DNA barcode, *Planchonella*, Sapotaceae, taxonomy

Introduction

The Hawaiian Islands are one of the most isolated terrestrial landscapes on earth with high levels of endemism reflecting both limited immigration and in situ diversification (Gillespie et al. 2012). Because these islands are relatively young geologically, they provide a snap shot of evolutionary processes occurring early in lineage diversification that are often obscured over time in older landscapes. We can witness processes such as early burst adaptive radiation for which there is rarely evidence in continental landscapes (Losos and Ricklefs 2009). One can also see these patterns replicated across different islands in an archipelago adding support to interpretations of early speciation processes (Gillespie 2004).

The Hawaiian psyllid fauna is relatively well known compared to other tropical faunas (Zimmerman 1948). The native species and most of the described genera are endemic with a number of exemplary cases of adaptive radiations on endemic host plants (e.g., *Pariaconus* Enderlein, 1926 on *Metrosideros* (Myrtaceae), *Hevaheva* Kirkaldy, 1902 on *Melicope* (Rutaceae), and *Megatrioza* Crawford, 1915 on *Pritchardia* (Arecaceae)) (Zimmerman 1948, Uchida and Beardsley 1988, Percy 2017a). Increasingly, molecular data on these species radiations is contributing additional information required to interpret evolutionary processes, but there remains considerably more work to do to reveal whether common dynamics are driving evolution across these different psyllid groups, as well as to determine the origins of the closest relatives outside the Hawaiian Islands (Percy 2017a). In addition, there are pressing conservation issues related to documenting psyllid diversity and species that are host specific on native plants in a rapidly eroding and threatened native flora (Percy 2017b).

Swezeyana Caldwell, 1940 is an endemic Hawaiian genus with two previously described species, *Swezeyana elongagena* Caldwell, 1940 and *Swezeyana reticulata* Caldwell, 1940, which are here redescribed and seven new species are added. All *Swezeyana* species occur on a single, endemic host plant, *Planchonella sandwicensis* (Sapotaceae). *Planchonella sandwicensis* is scattered in abundance, and only occasionally locally common in some areas of the archipelago. However, *Swezeyana* species are only rarely encountered, and where found, abundances are usually low with only a few individuals collected; although in a short note on *Swezeyana*, Tuthill (1966) remarked that immatures of two species were observed to be abundant on Maui in 1965, but he also remarked that this represented the first collection of the genus since the type material was collected in the 1920s and 1930s (Caldwell 1940). Immatures and adults are found on the leaf surface, and all species for which the biology is known have free-living immatures. There is relatively little morphotypic variation in the host plant across the different islands, compared, for instance, to the morphotypic variation found in the host plant of *Pariaconus*, *Metrosideros polymorpha* (Percy et al. 2008, Percy 2017a). The absence of observed differences in immature biologies and habitats, and the lack of host variation make it therefore difficult to interpret the drivers of the often striking morphological diversity, particularly in the immatures (Tuthill 1966).

The adult morphology is most obviously characterized by the extremely long genal processes and some unusual structural features of the fore wing. The fore wing has a more or less extended “pseudopterostigma” which appears as a thickened anterior fore margin extending from a position parallel to the trifurcation of R, M and Cu₁ to approximately 1/3 to 1/2 the length of vein Rs. In reference to this feature, Zimmerman (1948) referred to the radius (R) becoming “obsolete” beyond the origin of vein Rs. In addition, often present are few to many partial or fully developed cross veins in cell r₁ traversing between vein Rs and the anterior wing margin. Further adult variation is provided by the presence or absence of wing patterns and the striking differences in the structure of the female terminalia.

The objective of this study is to detail the diversification and distribution of this unusual and uncommon Hawaiian endemic genus, which provides yet another example of in situ psyllid diversification within the Hawaiian Islands. Understanding parallel processes of potential sympatric diversification in *Swezeyana* will contribute to our knowledge of speciation processes in Psylloidea more broadly.

Materials and methods

Field collections were made in May–July 2002, August 2003, February 2011, May–July 2014. Adults were preserved in 95% ethanol. For morphological examination, ethanol-preserved material was macerated and cleared in 10% potassium hydroxide followed by clove oil, and slide mounted in Canada balsam as described in Hodkinson and White (1979). Morphological terminology follows Hodkinson and White (1979), Hollis (1984), and Percy (2003a, 2017a). The DNA barcodes provided here were sequenced from two mitochondrial gene regions, cytochrome oxidase subunit 1 (COI), and cytochrome B (cytB). DNA was obtained from material preserved in ethanol, and protocols for DNA extraction, polymerase chain reaction and sequencing follow those described in Percy (2003b); polymerase chain reaction primers for COI and cytB, respectively, are given in Simon et al. (1994) and Timmermans et al. (2010), see also Percy et al. (2018). Genetic distances reported here and the phylogenetic analysis with bootstrap support (1000 replicates) were obtained using neighbour-joining (NJ) analyses with uncorrected (p) distances in PAUP* (Swofford 2003). For comparison of topology and node support the following analyses were run on the CIPRES Science Gateway (Stamatakis 2014, Miller et al. 2010): a Maximum likelihood (ML) analysis using RAxML (v. 8.2.4) with GTRCAT, 1000 rapid bootstraps, and Gamma optimization of tree space; and a Bayesian analysis using MrBayes (v. 3.2.6) with two independent runs with four coupled MCMC chains run for 20 million generations, sampling every 1000th generation, and visualized using a 50% majority-rule consensus tree with 25% of topologies discarded as burn-in (Ronquist and Huelsenbeck 2003). The molecular analysis includes eight of the nine *Swezeyana* species and 16 other taxa from Trioziidae, mostly representing other Hawaiian genera for comparative divergence analysis; and one species from Carsidaridae as an outgroup (*Mesohomotoma hibisci*

Table 1. Additional taxa sampled for the mitochondrial DNA analysis, with GenBank accession numbers.

Species	Locality	GenBank COI/cytB (publication)
Family: Carsidaridae		
<i>Mesohomotoma hibisci</i> (Froggatt, 1901)	Society Islands (Moorea)	KY294174/KY294658 (Percy 2017a)
	Society Islands (Raiatea)	KY294171/KY294655 (Percy 2017a)
	New Caledonia	KY294170/KY294654 (Percy 2017a)
	Singapore	KY294176/KY294660 (Percy 2017a)
Family: Triozidae		
<i>Anomocephala unica</i> Tuthill, 1942	Austral Islands (Rapa)	KY293698/KY294177 (Percy 2017a)
<i>Bactericera cockerelli</i> (Šulc, 1909)	California	KY011201/KY011296 (Percy 2017a)
<i>Hemischizocranium aloha</i> (Caldwell, 1940)	Hawaiian Islands (Kauai)	MG988755/MG989062 (this study)
<i>Hemischizocranium bessi</i> Tuthill, 1956	Hawaiian Islands (Hawaii)	MG988756/MG989063 (this study)
<i>Hevaheva maculata</i> Caldwell, 1940	Hawaiian Islands (Kauai)	KY293702/KY294181 (Percy 2017a)
<i>Hevaheva minuta</i> Crawford, 1925	Hawaiian Islands (Kauai)	KY293703/KY294182 (Percy 2017a)
<i>Hevaheva perkinsi</i> Kirkaldy, 1902	Hawaiian Islands (Oahu)	KY293704/KY294183 (Percy 2017a)
<i>Hevaheva silvestris</i> Kirkaldy, 1908	Hawaiian Islands (Oahu)	KY293705/KY294184 (Percy 2017a)
<i>Pariaconus iolani</i> (Kirkaldy, 1902)	Hawaiian Islands (Kauai)	KY293820/KY294297 (Percy 2017a)
<i>Pariaconus proboscideus</i> Percy, 2017	Hawaiian Islands (Hawaii)	KY294095/KY294573 (Percy 2017a)
<i>Pariaconus pyramidalis</i> Percy, 2017	Hawaiian Islands (Hawaii)	KY294124/KY294607 (Percy 2017a)
<i>Pariaconus mauianensis</i> Percy, 2017	Hawaiian Islands (Maui)	KY293841/KY294316 (Percy 2017a)
<i>Stevekenia aiea</i> Percy, 2017	Hawaiian Islands (Kauai)	KY971542/KY971544 (Percy 2017b)
<i>Stevekenia nothocestri</i> Percy, 2017	Hawaiian Islands (Oahu)	KY971541/KY971543 (Percy 2017b)
<i>Trioza remota</i> Foerster, 1848	England	KY294162/KY294646 (Percy 2017a)
<i>Trioza urticae</i> (Linné, 1758)	England	KY011191/KY011286 (Wonglersak et al. 2017)
<i>T. urticae</i>	Greece	KY011122/KY011219 (Wonglersak et al. 2017)
	Norway	KY011175/KY011270 (Wonglersak et al. 2017)
	Poland	KY011114/KY011212 (Wonglersak et al. 2017)

(Froggatt, 1901)) (Table 1). The DNA sequences are deposited in GenBank. Type material is deposited in the Natural History Museum, London, UK (BMNH).

Abbreviations used in the descriptions and given in Tables 2–4 are as follows (all measurements are recorded in mm). Adults: WL, fore wing length; WW, fore wing width; HW, head width; VW, vertex width; AL, antennal length; PB, distal proboscis segment length; WL:WW, ratio fore wing length:width; WL:Rs, ratio fore wing length:vein Rs length; CUR, ratio fore wing cell cu_1 width:height; MR, ratio fore wing cell m_2 width:height; HW:VW, ratio head width:vertex width; VL:GP, ratio vertex length:genal process length; VL:VW, ratio vertex length:width; AL:HW ratio antennal length:head width; HW:HT ratio head width:hind tibia length; HT:HF, ratio hind tibia length:femur length. Adult male terminalia: MP, proctiger length; PL, paramere length; AEL, distal aedeagus segment length; PL:HW, ratio paramere length:head width; MP:PL, ratio proctiger length:paramere length; PL:AEL, ratio paramere

Table 2. Adult *Suezeyana* measurements (mm).

Group	Species	n	WL	WW	HW	VW	AL	GP	PB	MP	PL	AEL	FP	FSP	RL	EL
<i>elongagena</i>	<i>elongagena</i>	4m 3f	2.33–2.82	0.67–0.80	0.55–0.60	0.32–0.36	0.82–0.97	0.41–0.48	0.08	0.05–0.07	0.15–0.17	0.10–0.11	0.33–0.34	0.23–0.26	0.17–0.23	0.18–0.20
	<i>atra</i>	2m 2f	1.91–2.58	0.55–0.71	0.50–0.55	0.27–0.32	0.64–0.65	0.32–0.35	0.05–0.06	0.05–0.06	0.09	0.08–0.10	0.26–0.31	0.23–0.24	0.13–0.15	–
	<i>hawaiiensis</i>	0m 2f	2.33–2.38	0.73–0.76	0.55–0.58	0.30–0.35	0.55	0.31–0.33	0.06	–	–	–	0.32	0.30	0.18	–
	<i>magna</i>	1m 0f	3.38	0.92	0.70	0.39	1.12	0.52	0.08	0.13	0.17	0.15	–	–	–	–
	<i>odhuensis</i>	4m 3f	2.09–2.88	0.61–0.85	0.49–0.58	0.28–0.33	0.68–0.88	0.35–0.36	0.06–0.07	0.05	0.12–0.13	0.08–0.10	0.27–0.30	0.20–0.24	0.14–0.16	–
<i>reticulata</i>	<i>rubra</i>	2m 7f	1.79–2.30	0.61–0.79	0.50–0.57	0.29–0.33	0.52–0.56	0.27–0.33	0.07	0.10–0.11	0.11	0.10–0.11	0.33–0.39	0.23–0.28	0.17–0.21	0.16–0.21
	<i>reticulata</i>	5m 5f	1.91–2.58	0.55–0.79	0.45–0.53	0.26–0.30	0.61–0.71	0.30–0.38	0.06	0.09–0.10	0.09–0.10	0.11–0.14	0.34–0.43	0.22–0.30	0.14–0.19	0.12–0.21
	<i>tentaculata</i>	4m 4f	1.94–2.53	0.58–0.77	0.47–0.55	0.27–0.32	0.76–0.77	0.35–0.44	0.07–0.08	0.10–0.12	0.11–0.12	0.13–0.14	0.46–0.52	0.36–0.38	0.18–0.23	0.20
	<i>magnaccai</i>	4m 0f	1.55–1.76	0.45–0.52	0.41–0.42	0.24	0.58	0.26–0.32	0.05–0.06	0.08–0.10	0.10	0.10–0.13	–	–	–	–

Table 3. Adult *Suezeyana* ratios.

Group	Species	WL:WW	CUR	MR	HW:VW	HW:GP	VL:GP	VL:VW	AL:HW	HW:HT	HT:HF
<i>elongagena</i>	<i>elongagena</i>	3.42–3.66	1.71–2.06	0.75–0.90	1.64–1.71	1.20–1.32	0.54–0.63	0.74–0.82	1.54–1.78	1.63–1.65	0.79–0.92
	<i>atra</i>	3.40–3.68	1.59–1.82	0.78–0.86	1.70–1.83	1.43–1.64	0.57–0.73	0.72–0.76	1.30	1.79–1.94	0.77–0.83
	<i>hawaiiensis</i>	3.14–3.21	1.35–1.61	0.75–0.83	1.65–1.80	1.73–1.76	0.78–0.82	0.78–0.80	0.95–1.00	2.00–2.11	0.75–0.82
	<i>magna</i>	3.66	2.18	0.85	1.77	1.35	0.59	0.77	1.61	1.64	0.85
	<i>oahuensis</i>	3.36–3.57	1.63–2.08	0.78–0.93	1.68–1.79	1.40–1.58	0.64–0.75	0.77–0.84	1.39–1.53	1.74–1.90	0.72–0.86
<i>reticulata</i>	<i>rubra</i>	2.88–3.06	1.15–1.32	0.77–0.92	1.65–1.76	1.69–1.89	0.69–0.87	0.68–0.75	0.93–1.03	1.82–2.09	0.75–0.87
	<i>reticulata</i>	3.27–3.55	1.50–1.71	0.58–0.93	1.65–1.78	1.39–1.60	0.60–0.76	0.75–0.82	1.25–1.40	1.53–1.88	0.74–0.83
	<i>tentaculata</i>	3.16–3.39	1.33–1.64	0.83–1.00	1.67–1.72	1.15–1.35	0.56–0.63	0.76–0.83	1.40–1.61	1.41–1.80	0.71–0.86
	<i>magnaccai</i>	3.29–3.50	1.58–1.73	0.80–0.90	1.69–1.73	1.31–1.59	0.62–0.76	0.81	1.41	1.73–2.25	0.63–0.76

Table 4. Adult *Swezeyana* ratios for male and female terminalia.

Group	Species	PL:HW	MP:PL	PL:AEL	AEL:AELH	PL:SH	FP:HW	FP:RL	FP:SP
<i>elongagena</i>	<i>elongagena</i>	0.29–0.31	0.31–0.43	1.46–1.56	2.00–2.33	0.95–1.05	0.55–0.56	1.41–1.95	1.24–1.45
	<i>atra</i>	0.18	0.59–0.73	0.92–1.10	2.00–2.18	0.67–0.85	0.51–0.57	2.05–2.06	1.10–1.34
	<i>hawaiiensis</i>	–	–	–	–	–	0.59	1.82	1.05
	<i>magna</i>	0.24	0.76	1.14	2.64	1.05	–	–	–
	<i>oahuensis</i>	0.25–0.26	0.38	1.19–1.60	2.00–2.17	0.94–1.00	0.53	1.90–2.05	1.27–1.36
	<i>rubra</i>	0.22	0.96–1.00	1.04–1.08	2.25–2.27	0.80	0.61–0.69	1.71–2.19	1.20–1.41
<i>reticulata</i>	<i>reticulata</i>	0.19	1.00–1.18	0.65–0.79	2.27–2.80	0.79–0.92	0.69–0.78	2.17–2.45	1.34–1.56
	<i>tentaculata</i>	0.25–0.26	0.93–1.03	0.81–0.88	2.25–2.57	0.78–0.93	0.86–0.95	2.24–2.59	1.27–1.42
unplaced	<i>magnaccai</i>	0.24–0.25	0.76–0.92	0.78–1.08	2.18–2.67	0.83–1.00	–	–	–

length:distal aedeagus segment length; AEL:AELH, ratio distal aedeagus segment length:aedeagus apical head length; PL:SH, ratio paramere length:subgenital plate height. Adult female terminalia: FP, proctiger length; FSP, subgenital plate length; RL, anal ring length; EL, egg length; FP:HW, ratio female proctiger:head width; FP:RL, ratio female proctiger:anal ring length; FP:SP: ratio female proctiger:subgenital plate length. Immatures: BL, body length; BW, body width; WPL, fore wing pad length; CPL, caudal plate length; CPW, caudal plate width; RW, circumanal ring width; HW, head width; AL, antennal length; BL:BW ratio body length:width; HW:AL ratio head width:antennal length; CPW:RW ratio caudal plate width:circumanal ring width.

Taxonomic treatment

Triozidae Löw, 1879

***Swezeyana* Caldwell, 1940**

Swezeyana Caldwell, 1940: 389. Type species: *Swezeyana elongagena* Caldwell, 1940, by original designation.

Description. Adult. General colour variable ranging from pale yellow-brown, to green or yellow-green, to almost black; often with pink or reddish highlights on the fore wing as well as on the body, especially genal processes, legs, and abdomen. Fore wing membrane either with distinct darker patches or clouds of pigmentation, these range from dark brown to red, and in some cases are limited to termination of veins at wing margins and around cross veins between Rs and wing margin, if without distinct patterns

of pigmentation, appearing uniformly clear, opaque yellow or fuscous; wing veins pale to red or dark brown, cross veins between Rs and ventral wing margin with or without pigmentation. Adult length including fore wing from 2–5 mm. Fore wing elongate and usually narrow (ratio WL:WW > 2.80, often > 3), acute to bluntly acute apically, either with trifurcation of veins R, M and Cu₁, or with vein R branching anterior of bifurcation of M and Cu₁; vein Rs long, reaching wing margin distad of M fork, but either with or without complete extension of Rs to wing margin, incomplete termination of Rs usually marked by pigmentation; vein R shorter than Cu₁ and terminating at base of Rs, a pseudopterostigma is present between base of Rs and wing margin, and a more or less thickened wing margin (C+Sc) is present from the wing base to the pseudopterostigma, in some cases occupying part or entire area of cell c+sc; with or without one or more partial or complete cross veins traversing cell r₁ between vein Rs and ventral wing margin; a single, broadly shaped marginal cluster of radular spines (Figs 3O, 6J) in cells cu₁, m₁, and m₂; surface spinules either present in all cells, dense or sparsely distributed, or few to absent from c+sc, r₂ and r₁, often relatively sparsely distributed but becoming denser towards wing margin. Hind wing narrow and elongate (> 0.5 length of fore wing), clear or slightly fuscous in basal half. Head moderately deflexed downwards, vertex more or less flat dorsally, with lateral ocelli lying on small tubercles, medial epicranial suture distinct; genal processes extremely long, often upturned at apices, with scattered long setae and usually a single, long subapical seta on each process. Antennae short; antennal segments 10, either entirely dark, or more usually with terminal 3(-7) segments darker, or distal part of segments 3-8 darker; a single rhinarium apically on each of segments 4, 6, 8, 9; 1-2 long setae on each of segments 3-9, terminal segment with two unequal length apical setae. Distal proboscis segment short, darker apically. Thorax somewhat flattened to only moderately arched; vertex and thorax with scattered short to moderately long setae. Legs short, hind legs robust with femur longer than tibia; hind leg with meracanthus reduced to almost absent; metafemur with several stout setae apically; metatibia with or without distinct genual spine basally and typically with 1+2 (occasionally 1+3) sclerotized apical spurs; pro- and mesotarsi subequal in length, metatarsi unequal with extremely long basal tarsus slightly expanded with concave, ridged underside (Fig. 3M). Male terminalia with somewhat elongate subgenital plate; proctiger with pronounced posterior lobes medially, 1-2 long setae usually present on posterior apices of each lobe, length shorter, subequal or longer than paramere; paramere shape variable, generally broad basally and tapering to apex, with two stout setae on the interior apex (sometimes appearing as one from lateral view); distal aedeagus segment apex hooked. Female terminalia with medium to long dorsal and ventral setae; proctiger either truncate and markedly convex apically, with apex broad, blunt, bearing small medial cleft and fringed with stout setae, or dorsal surface more or less straight, apex tapering, lacking medial cleft and distinct fringe of setae; proctiger longer than subgenital plate; anal ring hour-glass shaped (with or without a head compartment at proximal end) and composed of a, usually, uninterrupted, double row of cells, posterior/distal portion of ring margin either smooth or convoluted; subgenital plate ventral surface either convex or more or

less straight, apex terminating in a variably shaped beak often bearing a short or more pronounced medial cleft spanned by a short or extended membrane; ovipositor valves small, without serrations (Fig. 9O).

Egg. Known for four species. Pale or light brown, oblong-ovoid with a short, laterally positioned pedicel sub-basally on underside; distinctly hexagonal, honeycomb-like, sculpturing, to semi-hexagonal or rounded indentations dorsally; underside unsculptured, tail apparently lacking.

Immature. Known for four species. 5th instar oblong-ovoid, ventro-dorsally flattened with slightly protruding wing buds and distinct humeral lobes; antennae with 3(-4) segments bearing 3(-4) rhinaria (1 on segments 2-3, and 2 on apical segment) and two long, terminal, simple setae of unequal length; tarsi with broad crescent arolia and extremely small, reduced claws; each terminal tarsus bearing a long capitate seta; anus situated ventrally, circumanal ring broad and composed of a single row of elongate cells; dorsum either with wax producing pores (see Tuthill 1966), or non-wax producing tubercles and tentacles (Fig. 12). Chaetotaxy: 5th instar with either continuous or interrupted coverage of marginal setae; overall setal types, even between closely related species (e.g., *S. reticulata* and *S. tentaculata*), highly variable (Fig. 12). Smaller instars only known for *S. reticulata* and *S. tentaculata*, in which tubercles are apparent from 2nd instar (Fig. 13).

Biology. All species for which the biology is known have free-living immatures on the surface of leaves (either lower, or both upper and lower surfaces). Those species with immatures described here with protruding tubercles and tentacles were mostly found on the lower leaf surface among dense indumentum and often close to the mid-rib (Fig. 12N).

Host plant. All *Swezeyana* are host specific on a single Hawaiian endemic host plant species, *Planchonella sandwicensis* (Sapotaceae).

Comments. Two species groups are recognized, *elongagena* group and *reticulata* group, based primarily on the strikingly different forms of female terminalia. The *elongagena* group has broad, truncate female terminalia with a strongly convex proctiger apex; the proctiger and subgenital plate bear a small to pronounced medial cleft at the apex. In contrast, the *reticulata* group has tapering terminalia without a medial cleft in the proctiger apex. In both species groups the subgenital plate terminates in a more or less well developed beak with small to pronounced cleft spanned by a membrane. The underlying endoskeleton of the two different forms of female terminalia indicate distinctly different development of the apodemes in the two species groups: broad and short in *elongagena* group (Fig. 4P), and long and narrow in *reticulata* group (Fig. 10I). However, not all species treated here are known for both sexes, therefore current assignment to these groups relies on other characteristics and DNA barcode data (see Discussion). Due to the unknown female morphology and inconclusive placement in the molecular phylogeny, *S. magnaccai* is not placed within a species group. Fore wing characteristics such as wing membrane colouration and pseudoveins/cross veins are found in both groups. The 5th instar immatures may also be diagnostic, with *elongagena* group having wax producing pores dorsally (illustrated in Tuthill 1966 for *S. elongagena*) and

continuous ring of marginal setae (illustrated in Caldwell 1940 for *S. elongagena*); while in contrast, the *reticulata* group are characterized by non-wax producing tubercles and tentacles and lack a contiguous marginal ring of setae (Figs 12–13). However, currently immatures are known for these three species only, so it remains to be tested whether these highly distinct immature morphologies reflect species group assignments.

Note on adult assignment to species group. The two species groups (*elongagena* group and *reticulata* group) are most easily recognized by the shape of the female terminalia, e.g., extremely convex apex of female proctiger in the *elongagena* group, versus more or less dorsally straight and tapering in the *reticulata* group. The *elongagena* group females have a FP:HW ratio typically < 0.70 (range 0.51–0.69), and FP:RL ratio typically < 2.18 (range 1.41–2.19); whereas in the *reticulata* group FP:HW ratio is typically > 0.70 (range 0.69–0.95), and FP:RL ratio is typically > 2.18 (range 2.17–2.59). *Swezeyana* males are less easily assigned to a species group, but *elongagena* group males have a distal aedeagus segment that is typically shorter than the paramere (PL:AEL ratio range 0.92–1.60), whereas *reticulata* group males have a distal aedeagus segment that is longer than the paramere (PL:AEL ratio range 0.65–0.88). Notably, the fore wing characters used by Zimmerman (1948) to key out the two species described by Caldwell (*S. elongagena* and *S. reticulata*), such as presence/absence of cross veins in cell r_1 and presence/absence of distinct patterns of pigmentation are found in both species groups. The key below does not key to species group, rather it employs characters useful in distinguishing species, in particular those co-occurring on the same island.

Note on molecular analyses. The neighbour-joining analysis of two mitochondrial DNA regions is presented in Fig. 2. Strong support is recovered for the *reticulata* group, but not for the *elongagena* group. The topologies recovered in comparative ML and Bayesian analyses differ only at weakly or unsupported nodes. The three nodes that group same island sister taxon pairs (on Kauai, Oahu, and Hawaii) are recovered in all analyses but with variable support (much stronger support in the Bayesian than NJ or ML analyses) (see Fig. 2 and Discussion). Maximum genetic divergence (uncorrected p-distances) among *Swezeyana* species is 19.9%; maximum intraspecific divergence (3%) was found in *S. magnaccai* on Oahu.

Key to Swezeyana adults

- 1 Fore wings with distinct darker patches or clouds of pigmentation, in some cases only around termination of veins at wing margins and around cross veins between R_s and wing margin in cell r_1 (Fig. 1E–I) **2**
- Fore wings without distinct darker patches or clouds of pigmentation, appearing uniformly clear or opaque, cross veins between R_s and wing margin in cell r_1 , if present, unpigmented (Fig. 1A–D) **6**
- 2 Antennae short, subequal to head width (ratio AL:HW < 1.1), ratio HW:GP > 1.65 , female proctiger strongly convex apically with apex extremely broad and blunt, ratio FP:HW < 0.70 , on Hawaii **3**

- Antennae longer ($AL:HW > 1.1$), ratio $HW:GP < 1.65$, female proctiger more or less straight dorsally with apex bluntly acute, on other islands **4**
- 3 Fore wings with extensive patches and clouds of red-brown pigmentation, particularly across the central area of wing, and numerous cross veins (typically more than 5) between R_s and wing margin in cell r_1 , smaller species with broader wings (ratio $WL:WW < 3.1$) and wing cell cu_1 relatively narrow and high (ratio $CUR < 1.33$) (Figs 1I, 8A–W)..... ***S. rubra* sp. n.**
- Fore wings with only indistinct fuscous brown on membrane and distinct small darker brown patches around termination of veins at wing margins and around cross veins between R_s and wing margin in cell r_1 , cross veins fewer (typically less than 5), larger species with narrower wings (ratio $WL:WW > 3.1$) and wing cell cu_1 relatively wide and low (ratio $CUR > 1.33$) (Figs 1E, 5I–K) ***S. hawaiiensis* sp. n.**
- 4 Larger species ($WL > 1.9$ mm), paramere shape more triangular with a broader base, on Kauai (possibly other islands for *S. reticulata*) **5**
- Smaller species ($WL < 1.9$ mm), paramere shape more slender with a narrower base, on Oahu (Figs 1F, 11)..... ***S. magnaccai* sp. n.**
- 5 Fore wing with fewer cross veins (typically less than 6) between R_s and wing margin, head with shorter genal processes (ratio $HW:GP > 1.36$) and shorter antennae ($AL < 0.75$ mm, ratio $AL:HW \leq 1.40$), paramere shorter and broader (ratio $PL:HW < 0.20$, ratio $PL:AEL < 0.80$), female terminalia shorter (ratio $FP:HW < 0.80$) with posterior margin of anal ring less convoluted and incised (Figs 1G, 9A–T; immatures Figs 12A–G, 13A–F) ***S. reticulata* Caldwell, 1940**
- Fore wing with more cross veins (typically more than 6) between R_s and wing margin, head with longer genal processes (ratio $HW:GP < 1.36$) and longer antennae ($AL > 0.75$ mm, ratio $AL:HW \geq 1.40$), paramere longer and narrower (ratio $PL:HW > 0.20$, ratio $PL:AEL > 0.80$), female terminalia longer (ratio $FP:HW > 0.80$) with posterior margin of anal ring more convoluted and incised (Figs 1H, 10A–S; immatures Figs 12H–N, 13G–J)
..... ***S. tentaculata* sp. n.**
- 6 Smaller species ($WL < 3$ mm, $AL < 1$ mm), wing cell cu_1 relatively narrow and high (ratio $CUR < 2.1$), on Oahu, Molokai, Maui..... **7**
- Larger species ($WL > 3$ mm, $AL > 1$ mm), wing cell cu_1 relatively wide and low (ratio $CUR > 2.1$), on Kauai (Figs 1D, 6A–K) ***S. magna* sp. n.**
- 7 Genal processes shorter ($GP < 0.40$ mm, ratio $HW:GP > 1.35$), paramere shorter (ratio $PL:HW < 0.27$) and with less extended anteriorly directed apex, on Oahu **8**
- Genal processes longer ($GP > 0.40$ mm, ratio $HW:GP < 1.35$), paramere longer (ratio $PL:HW > 0.27$) and with more extended anteriorly directed apex, on Molokai and Maui (Figs 1A, 3A–P) ***S. elongagena* Caldwell, 1940**
- 8 Paler species (generally yellow-brown to green), fore wing vein R_s typically longer relative to wing length (ratio $WL:R_s$ 1.57–1.82) resulting in shorter distance between terminations of R_s and M_{1+2} , antennae longer

- (AL > 0.65 mm), paramere longer (ratios PL:HW > 0.20, PL:AEL > 1.15, PL:SH > 0.90) (Figs 1B, 7A–R) ***S. oahuensis* sp. n.**
- Darker species (generally dark brown to black), fore wing vein Rs typically shorter relative to wing length (ratio WL:Rs 1.76–2.03) resulting in longer distance between terminations of Rs and M₁₊₂, antennae shorter (AL ≤ 0.65 mm), paramere shorter (ratios PL:HW < 0.20, PL:AEL < 1.15, PL:SH < 0.90) (Figs 1C, 4A–T) ***S. atra* sp. n.**

Note on species descriptions. *Swezeyana* is a small genus with, in general, considerable morphological homogeneity. The species descriptions below provide details of species specific characteristics not supplied in the generic description above.

Species group: *elongagena*

Swezeyana elongagena Caldwell, 1940

Figures 1A, 3

Swezeyana elongagena Caldwell, 1940: 390.

Description. Adult. General body colour green to yellow-green or yellow-brown, last 3–5 antennal segments darker brown to black, apices of genae sometimes pinkish-red. Fore wing membrane uniformly pale fuscous (Fig. 1A). Fore wing apex acute to bluntly acute; pseudoptero stigma relatively short to medium long (Fig. 3P), none to few (1–3) cross pseudoveins in cell r₁; surface spinules sparsely distributed, apparently absent from c+sc (Fig. 3O); medium long setae on ventral margin and medium short to short setae on veins and dorsal margin. Antennae medium long (ratio AL:HW 1.54–1.78) (Fig. 3D); genal processes long (GP > 0.40 mm, ratio HW:GP < 1.35) and often upturned at apices (Fig. 3A–B); short to medium short setae on vertex and thorax. Meracanthus small (Fig. 3N), genual spine reduced (Fig. 3L). Male terminalia (Fig. 3G–I): paramere slender, long (ratio PL:HW > 0.27), tapering to anteriorly projecting apex with two short stout setae; distal aedeagus segment short relative to paramere (ratio PL:AEL 1.46–1.56), apex developed into a large rounded hook with blunt apex. Female terminalia (Fig. 3E–F): proctiger dorsal surface strongly convex apically, apex broad, blunt, bearing medial cleft and fringed with stout setae, anal ring long (ratio FP:RL 1.41–1.95), with reduced head compartment at proximal end, distal portion of ring margin smooth; subgenital plate convex with medial cleft pronounced (almost half length of subgenital plate).

Egg. Pale with well-defined hexagonal (honeycomb-like) sculpturing dorsally (Fig. 3J).

Immature. Described and illustrated by Caldwell (1940) and Tuthill (1966). Although Caldwell refers to marginal “sectasetae” in his description, he illustrates distinctly fan-shaped and apparently unbisected setae. Tuthill provides an image of an immature with long “wax filaments” produced by dorsal pores, and notes that free-

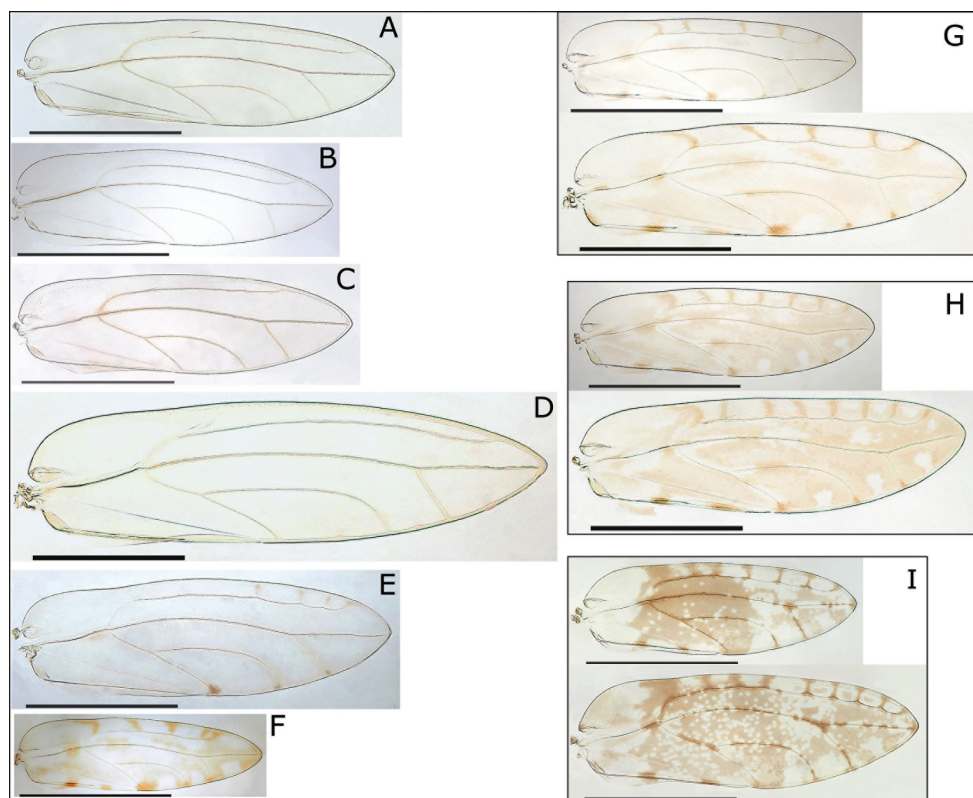


Figure 1. Fore wings of nine *Swezeyana* species: **A** *S. elongagena* (male) **B** *S. oahuensis* (male) **C** *S. atra* (male) **D** *S. magna* (male) **E** *S. hawaiiensis* (female) **F** *S. magnaccai* (male) **G** *S. reticulata* (male above, female below) **H** *S. tentaculata* (male above, female below) **I** *S. rubra* (male above, female below). Scale bars: 1 mm.

living immatures were observed mostly on the upper, but also lower, leaf surfaces. Both descriptions suggest notable morphological differences to immatures described here for *S. reticulata* and *S. tentaculata* sp. n.

Host plant. *Planchonella sandwicensis*.

Distribution. Maui, Molokai (a single female specimen recorded from Kauai, and apparently now missing, is queried in Zimmerman (1948), and may have been *S. magna* sp. n.). Specimens from Molokai are close to the type specimens from Maui, and currently this species is considered to be restricted to these two islands.

Comments. Although Caldwell's (1940) illustration only indicates a single cross pseudovein, examination of the type specimen revealed three unpigmented pseudoveins. A single female paratype collected from Kalalau Trail, Kauai, is likely to be *S. magna* sp. n. (see also assignment in error comment in Zimmerman 1948)

Material examined. Holotype female (slide mounted), Haelaau, Maui, USA, ex *Planchonella* sp., 19 December 1928 (BPBM). Paratypes: 10m 5f, same data as holotype (not located). Other material: 5m 4f, Kamakou Preserve, Molokai, USA,

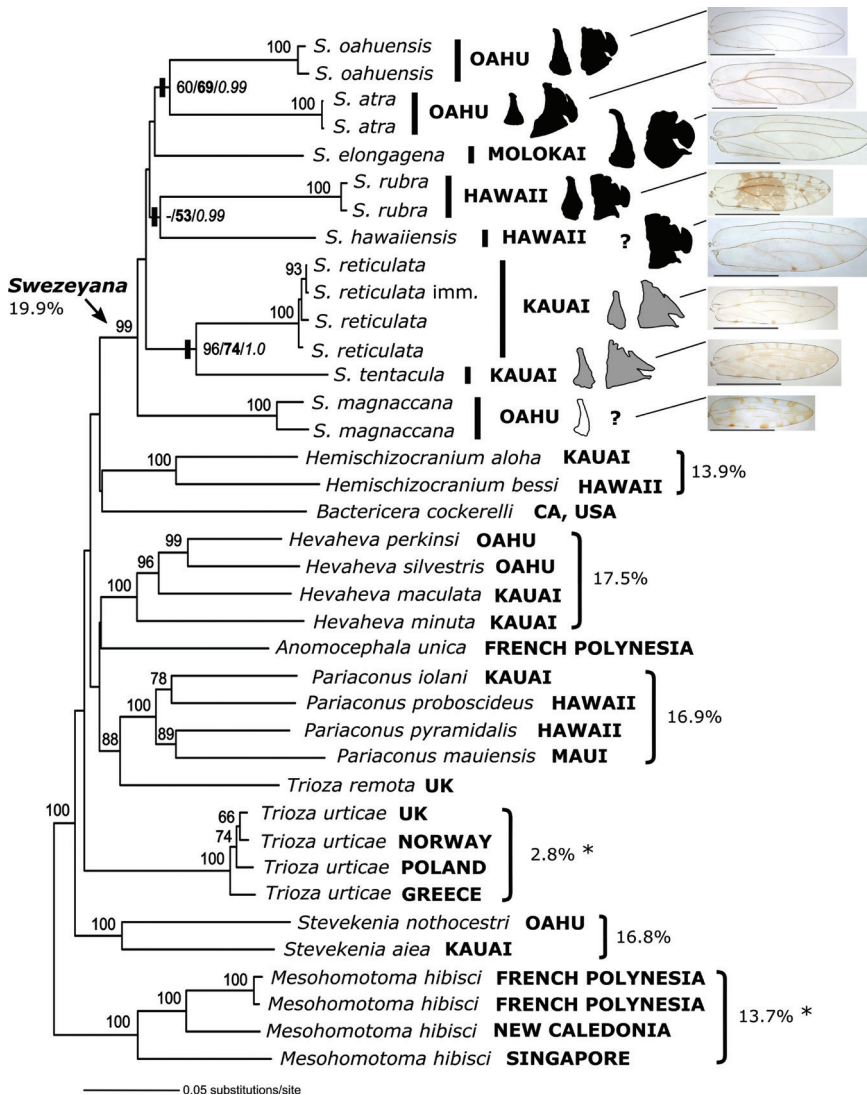


Figure 2. Neighbour-joining (NJ) analysis (combined COI and cytB data) with 1000 bootstrap replicates in PAUP*. Eight of the nine *Swezeyana* species are included and 16 other taxa from Triozidae, mostly representing other Hawaiian genera for comparison of divergence; and one species from Carsidaridae as an outgroup (*Mesohomotoma hibisci*) (Table 1). Outlines of parameres and female terminalia illustrate the two recognized species groups (*elongagena* group in black, *reticulata* group in grey, *S. magnaccana* unplaced), and fore wing images (Fig. 1) show the distribution of patterned/pigmented wings. Regional localities of sample are given, and “imm.” indicates an immature sampled for *S. reticulata*. NJ bootstrap support values $\geq 60\%$ are indicated for all nodes, and comparative node support from ML and Bayesian analyses are shown for the three same island sister taxa pairs (NJ/ML[bold]/Bayesian[italic]) (see Discussion). Maximum genetic divergence (uncorrected p-distances) is shown for *Swezeyana* and four other endemic Hawaiian genera; also shown are maximum intraspecific distances (indicated with an asterisk) for two widespread non-Hawaiian species with multiple individuals sampled across terrestrial (*T. urticae*) or oceanic (*M. hibisci*) landscapes (see Discussion).

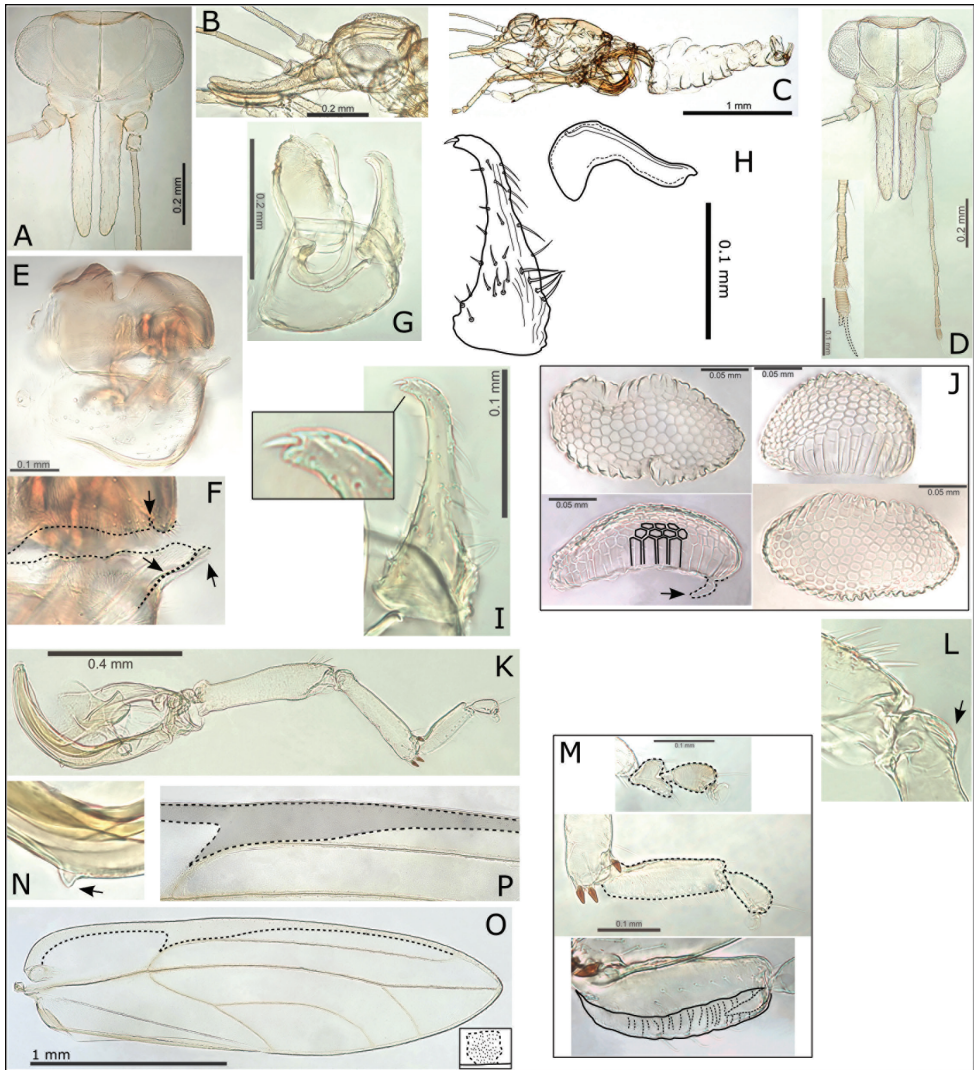


Figure 3. *Swezeyana elongagena*. **A** head **B** head (lateral view) **C** male **D** head and antenna, inset detail of terminal antennal segments (terminal setae outlined) **E** female terminalia **F** detail of apex of female terminalia indicating beak and position of medial clefts in proctiger and subgenital plate (outlined) **G** male terminalia **H** paramere and distal aedeagus segment **I** paramere, inset detail of apex **J** eggs (distinctly hexagonal sculpturing and pedicel outlined and indicated) **K** hind leg **L** base of hind tibia with reduced genual spine indicated **M** mesotarsi and metatarsi (outlined), concave and ridged underside of basal metatarsus (outlined) **N** small but distinct meracanthus (indicated) **O** fore wing with interior edge of ventral margin outlined, inset illustrating broad shape of marginal radular spine cluster **P** extent of fore wing pseudopterostigma (shaded).

N21.1236, W-156.9108, ex *Planchonella sandwicensis*, 17 August 2003, “Hi20-03” D. Percy leg. (BMNH).

Gene sequences. MG988832 (COI) MG989153 (cytB) (Hi20-03).

***Swezeyana atra* sp. n.**

<http://zoobank.org/3BA915C9-4A1D-4910-A5A7-F7F130BF1314>

Figures 1C, 4

Diagnosis. Medium sized, dark coloured species, with fore wing membrane unpatterned, antennae medium short, genal processes long, paramere short, and female proctiger strongly convex apically.

Description. Adult. General body colour brown to black, particularly dark on the dorsum of head and thorax. Fore wing membrane generally uniformly clear or slightly fuscous, with fuscous-brown cloud usually present around vein R and basal dorsal claval margin (Fig. 1C). Fore wing apex acute; pseudopterostigma relatively long (Fig. 4S), typically no cross pseudovein in cell r_1 (one individual seen with partial cross vein); surface spinules relatively sparsely distributed but denser towards wing margin, few or absent from c+sc; medium long setae on ventral margin and medium short to short setae on veins and dorsal margin. Antennae medium short (ratio AL:HW 1.30) (Fig. 4B–C); genal processes medium long (GP < 0.40 mm, ratio HW:GP > 1.40) and slightly upturned at apices (Fig. 4B); medium short to short setae on vertex and thorax. Meracanthus extremely small (Fig. 4Q), genual spine reduced or absent (Fig. 4R). Male terminalia (Fig. 4F–I): paramere short (ratio PL:HW < 0.20), tapering to slightly anteriorly projecting apex with two short stout setae; distal aedeagus segment long relative to paramere (ratio PL:AEL 0.92–1.10), apex developed into a large rounded hook with blunt apex. Female terminalia (Fig. 4J–P): proctiger dorsal surface strongly convex apically, apex broad, blunt, bearing medial cleft and fringed with stout setae, anal ring medium long (ratio FP:RL > 2.00), without or with reduced head compartment at proximal end, distal portion of ring margin smooth; subgenital plate slightly convex with short medial cleft (Fig. 4N–O).

Egg. Unknown.

Immature. Unknown.

Host plant. *Planchonella sandwicensis*.

Distribution. Oahu. Only known from the Waianae Mountains.

Etymology. Named for the dark body colouration, especially the head and thorax (adjective in the nominative singular).

Comments. This is the darkest of the *Swezeyana* species. It has the shortest paramere in the *elongagena* group, with the shape more similar to those in the *reticulata* group. The distribution in the Waianae Mountains is shared with *S. oahuensis*, and the molecular topology places these two species as sister taxa but with weak bootstrap support (Fig. 2).

Material examined. Holotype male (slide mounted), Waianae Mnts, Oahu, USA, N21.4585, W-158.0973, ex *Planchonella sandwicensis*, 5 July 2014, “Hi65-14” D. Percy leg. (BMNH). Paratype (slide mounted) 1f, as for holotype (BMNH). Other material: 1m 1f, Puu Hapapa, Central Waianae Mnts, Oahu, USA, N21.4666, W-158.1029, ex *Planchonella sandwicensis*, 17 May 2014, “KM14-14” K. Magnacca leg. (BMNH).

Gene sequences. MH001521 (COI) MH001527 (cytB) (Hi65-14); MH001522 (COI) MH001528 (cytB) (KM14-14).

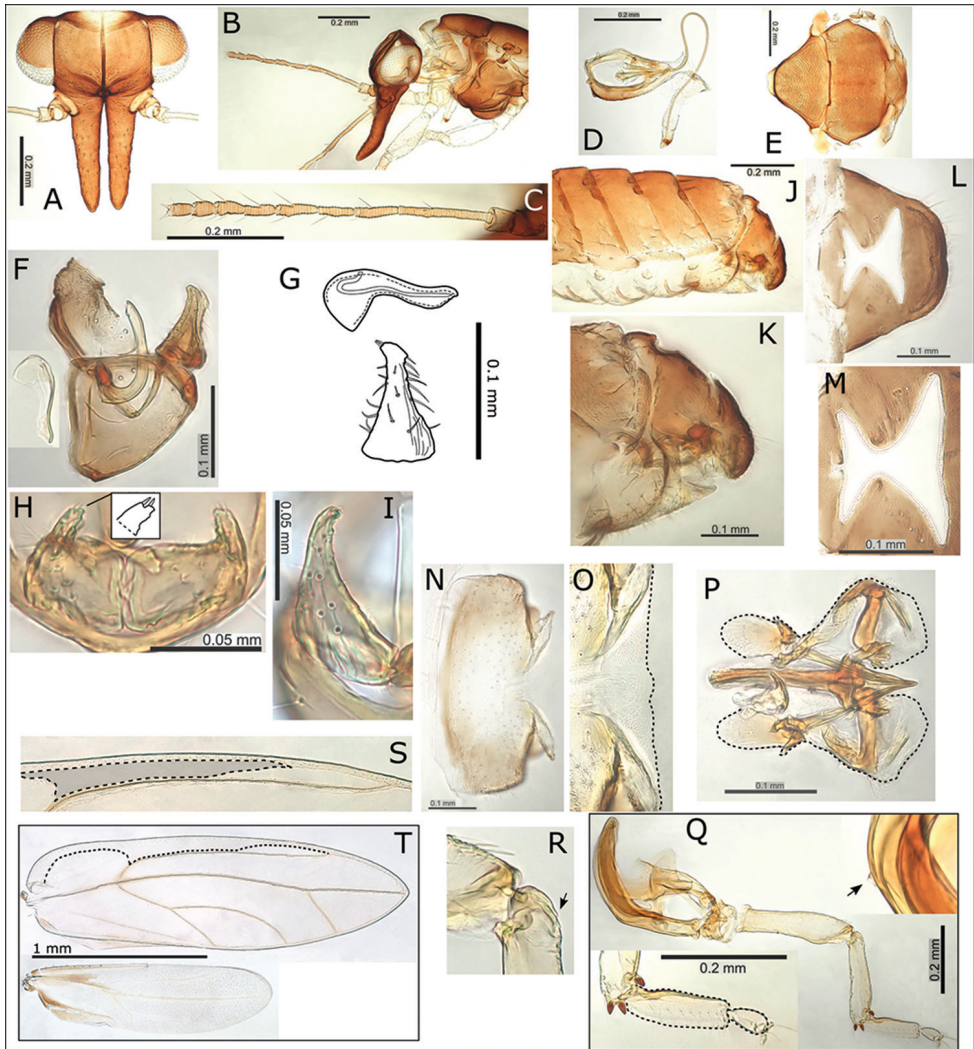


Figure 4. *Swezeyana atra* sp. n. **A** head **B** head and antenna (lateral view) **C** antenna **D** proboscis **E** dorsum of thorax **F** male terminalia, inset distal aedeagus segment **G** paramere and distal aedeagus segment **H** parameres (dorsal view), inset illustrating paramere apex **I** paramere (posterior view) **J** female abdomen **K** female terminalia **L** female proctiger (dorsal view) **M** detail of anal ring **N** female subgenital plate (ventral view) **O** detail of posterior apex of female subgenital plate with membrane (outlined) **P** female terminalia endoskeleton (dorsal view, outlined) **Q** hind leg, inset reduced meracanthus (indicated) and metatarsi (outlined) **R** base of hind tibia with highly reduced genual spine (indicated) **S** extent of fore wing pseudopterostigma (shaded) **T** fore wing (above) with interior edge of ventral margin outlined, hind wing (below).

***Swezeyana hawaiiensis* sp. n.**

<http://zoobank.org/68663D7C-532C-4158-9A58-FF189893B6D3>

Figures 1E, 5

Diagnosis. Medium sized, light coloured species, with fore wing membrane unpatterned, antennae and genal processes relatively short, and female proctiger strongly convex apically.

Description. Adult. General body colour green to yellow-green. Fore wing membrane generally slightly fuscous, darker fuscous clouds around cross pseudoveins towards apex of cell r_1 , and distinct brown patches at termination of veins Cu_{1a} , Cu_{1b} , and M_{3+4} (Figs 1E, 5K). Fore wing apex acute to bluntly acute; pseudopterostigma short (Fig. 5K), 2-3 cross pseudoveins present in apical portion of cell r_1 ; surface spinules sparsely distributed and reduced in distribution, few or absent from r_1 , r_2 , and $c+sc$; medium long setae on ventral margin and medium short to short setae on veins and dorsal margin. Antennae short (ratio AL:HW 0.95–1.00), terminal 3 segments darker brown (Figs 5A–B); genal processes relatively short (GP < 0.35 mm, ratio HW:GP > 1.70), not or only slightly upturned at apices (Fig. 5A); short to minute setae on vertex and thorax. Meracanthus small (Fig. 5H), genual spine reduced or absent (Fig. 5I). Female terminalia (Fig. 5D–F): proctiger dorsal surface strongly convex apically, apex broad, blunt, bearing medial cleft and fringed with stout setae (Fig. 5E), anal ring long (ratio FP:RL 1.82), with head compartment at proximal end, distal portion of ring margin smooth; subgenital plate slightly convex with short medial cleft with beak and membrane extended (Fig. 5F).

Egg. Unknown.

Immature. Free-living immatures were observed mostly on the upper, but also on the lower, leaf surfaces. Specimens collected were unfortunately lost during specimen shipping.

Host plant. *Planchonella sandwicensis*.

Distribution. Hawaii. Only known from PuuWaaWaa area.

Etymology. Named for its distribution on the island of Hawaii (adjective in the nominative singular).

Comments. This species was collected from the same individual host tree as *S. rubra*; both species are in the *elongagena* group but are easily separated in the field due to general body colour and a distinctly patterned fore wing in *S. rubra*; both species have comparatively short genal processes as well as the shortest antennae in the genus (subequal to head width). The molecular topology places these as sister taxa, but without bootstrap support. Males with the same collection data as females were unfortunately lost during specimen shipping.

Material examined. Holotype female (slide mounted), PuuWaaWaa, Hawaii, USA, N19.784, W-155.833, 820m, ex *Planchonella sandwicensis*, 29 July 2002, “440A-02” D. Percy leg. (BMNH). Paratype (slide mounted) 1f, as for holotype (BMNH).

Gene sequences. MG988835 (COI) MG989155 (cytB) (440A-02).

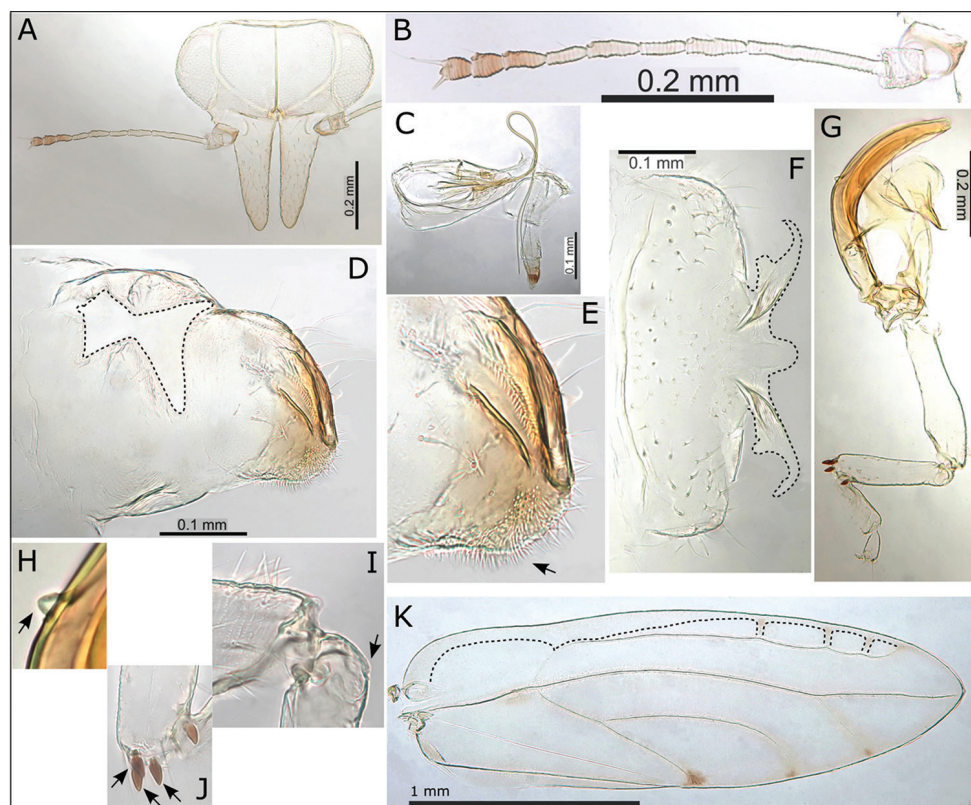


Figure 5. *Swezeyana hawaiiensis* sp. n. (female). **A** head and antenna **B** antenna **C** proboscis **D** proctiger, dorso-lateral view showing anal ring (outlined) **E** detail of apex of proctiger showing medial cleft and fringe of apical setae (indicated) **F** female subgenital plate (ventral view) with apical beak and membrane outlined **G** hind leg **H** small but distinct meracanthus (indicated) **I** base of hind tibia (highly reduced genual spine indicated) **J** detail of atypical 1+3 (indicated) arrangement of sclerotized apical metatibia spurs **K** fore wing, with interior edge of ventral margin outlined.

***Swezeyana magna* sp. n.**

<http://zoobank.org/8168F0F6-C89C-4488-B637-4D017FA8154A>

Figures 1D, 6

Diagnosis. Large, light coloured species, with fore wing membrane unpatterned, antennae and genal processes long, and paramere short.

Description. Adult. General body colour yellow-green to yellow-brown, last 7-8 antennal segments darker brown. Fore wing membrane uniformly pale fuscous (Fig. 1D). Fore wing apex acute; pseudopterostigma medium long (Fig. 6I), 0-1 cross pseudoveins in basal portion of cell r_1 ; surface spinules sparsely distributed, apparently absent from c+sc; medium long setae on ventral margin and medium short setae on veins and dorsal margin. Antennae long (AL > 1 mm, ratio AL:HW 1.61) (Fig. 6A); genal processes long (GP > 0.50 mm, ratio HW:GP < 1.40) and slightly upturned at

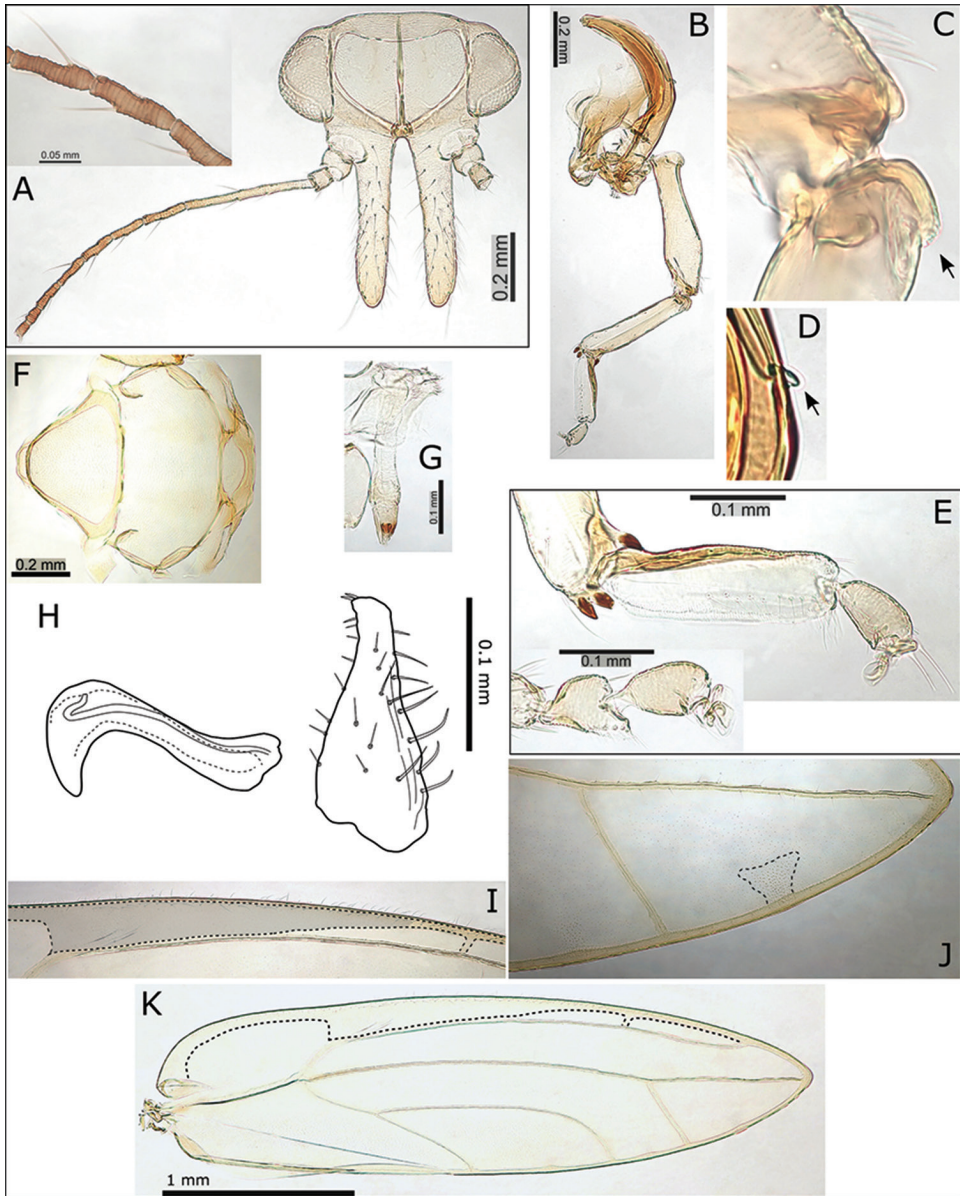


Figure 6. *Swezeyana magna* sp. n. **A** head and antenna, inset antenna detail **B** hind leg **C** base of hind tibia (reduced genual spine indicated) **D** small but distinct meracanthus (indicated) **E** metatarsi, inset comparative size of mesotarsi **F** dorsum of thorax **G** proboscis **H** aedeagus and paramere **I** extent of pseudopterostigma (shaded) **J** broad shape of marginal radular spine cluster (outlined) **K** fore wing, with interior edge of ventral margin outlined.

apices (Fig. 6A); short to minute setae on vertex and thorax. Meracanthus small (Fig. 6D), genual spine reduced (Fig. 6C). Male terminalia (Fig. 6H): paramere short (ratio PL:HW 0.24), tapering to small, anteriorly projecting apex with two short stout setae;

distal aedeagus segment long relative to paramere (ratio PL:AEL 1.14), apex developed into a large rounded hook with bluntly acute apex.

Egg. Unknown.

Immature. Unknown.

Host plant. *Planchonella sandwicensis*.

Distribution. Kauai. Only known from one location in Kokee State Park.

Etymology. Named for the large body size (adjective in the nominative singular).

Comments. This is the largest *Swezeyana* species and is only known from a single male; fore wing type suggests it is part of the *elongagena* species group, but the paramere shape is somewhat similar to other *reticulata* group species on Kauai. As no molecular sequences are available for this species, the group affiliation remains uncertain, but this species and the other Kauai species may represent early divergence of the *elongagena* and *reticulata* species groups.

Material examined. Holotype male (slide mounted), Kokee State Park, Kauai, USA, N22.1444, W-159.6477, ex *Planchonella sandwicensis*, 29 October 2005, “Hi01-05” D. Percy leg. (BMNH).

***Swezeyana oahuensis* sp. n.**

<http://zoobank.org/50F9E50B-DA6D-4DD9-BAA5-3B8347B49E16>

Figures 1B, 7

Diagnosis. Medium sized, light coloured species, with fore wing membrane unpatterned, antennae medium long, genal processes long, paramere medium long, and female proctiger strongly convex apically.

Description. Adult. General body colour green to yellow-green or yellow-brown, last 5–7 antennal segments darker brown, apices of genae sometimes pinkish-red. Fore wing membrane uniformly pale fuscous (Fig. 1B). Fore wing apex acute; pseudoptero stigma medium to long (Fig. 7R), no cross pseudoveins in cell r_1 ; surface spinules sparsely distributed, reduced or absent from r_1 and r_2 , and apparently absent from $c+sc$ which is partly to almost entirely composed of a thickened ventral wing margin ($C+Sc$); medium long setae on ventral margin and medium short to short setae on veins and dorsal margin. Antennae medium long (ratio AL:HW 1.39–1.53) (Fig. 7B, D); genal processes medium long ($GP \geq 0.35$ mm, ratio HW:GP ≥ 1.40) and often upturned at apices (Fig. 7A–B, G); short to medium short setae on vertex and thorax. Meracanthus small (Fig. 7E), genual spine reduced or absent (Fig. 7E). Male terminalia (Fig. 7M–Q): paramere slender, medium long (ratio PL:HW ≥ 0.25), tapering to anteriorly projecting apex with two short stout setae; distal aedeagus segment short relative to paramere (ratio PL:AEL 1.19–1.60), apex developed into a large rounded hook with bluntly acute apex. Female terminalia (Figs 7H–L): proctiger dorsal surface strongly convex apically, apex broad, blunt, bearing medial cleft and fringed with stout setae, anal ring medium long (ratio FP:RL 1.90–2.05),

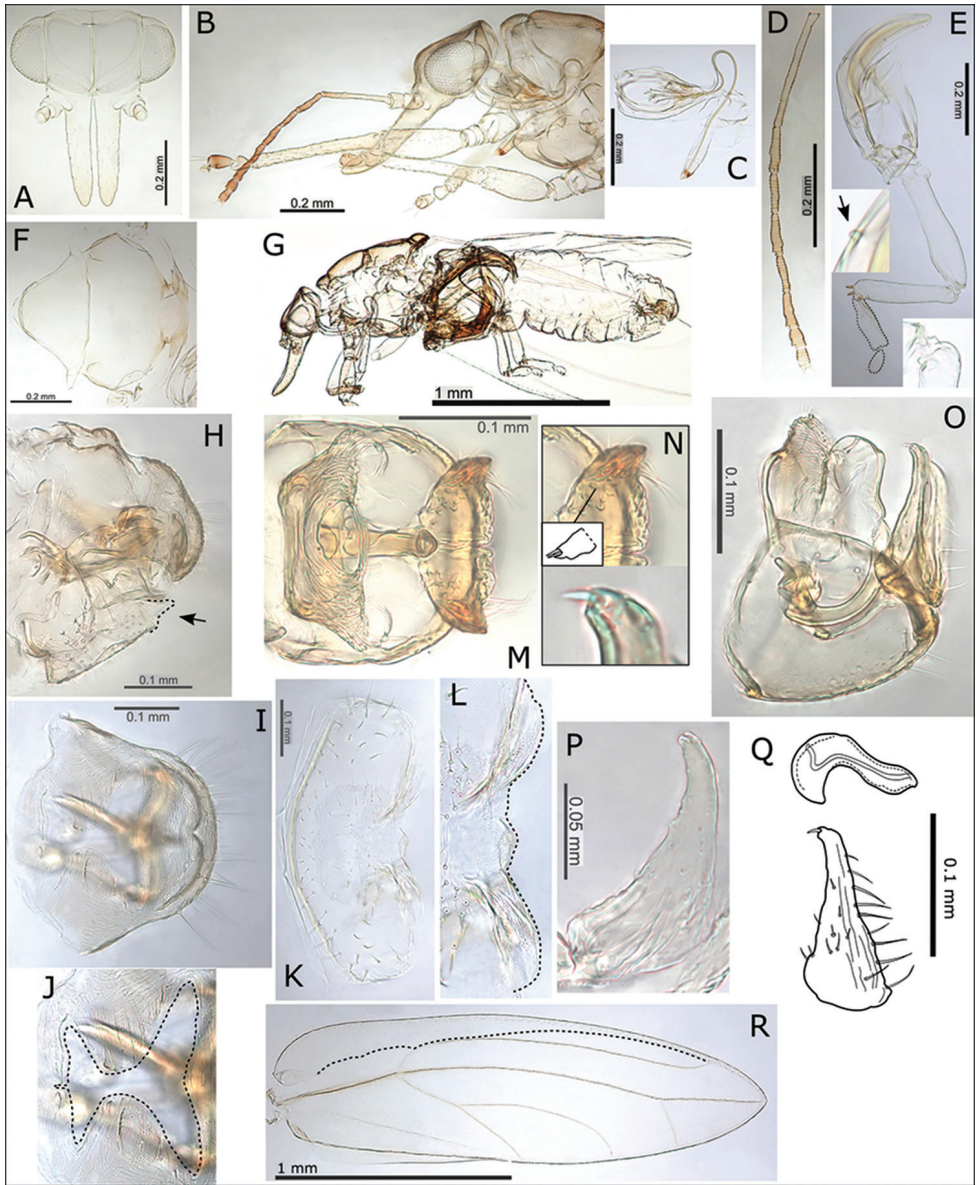


Figure 7. *Swezeyana oahuensis* sp. n. **A** head **B** head and antenna (lateral view) **C** proboscis **D** antenna **E** hind leg, inset detail of reduced meracanthus (indicated) and genual spine **F** dorsum of thorax **G** female **H** female terminalia (truncate subgenital plate indicated, apex outlined) **I** female terminalia (dorsal view) **J** detail of anal ring (outlined) **K** female subgenital plate (ventral view) **L** detail of posterior apex of female subgenital plate with beak and membrane (outlined) **M** male terminalia (dorsal view) **N** paramere apex (dorsal view above and outlined, lateral view below) **O** male terminalia **P** paramere (posterior view) **Q** aedeagus and paramere **R** fore wing, with interior edge of ventral margin outlined.

with reduced head compartment at proximal end, distal portion of ring margin smooth; subgenital plate slightly convex with short medial cleft with beak and membrane extended (Fig. 7K–L).

Egg. Unknown.

Immature. Unknown.

Host plant. *Planchonella sandwicensis*.

Distribution. Oahu. Only known from the Waianae Mountains.

Etymology. Named for its distribution on the island of Oahu (adjective in the nominative singular).

Comments. This species and *S. atra* may represent insular diversification on Oahu (see comments for *S. atra*).

Material examined. Holotype male (slide mounted), Mnt Kaala road (culvert 32), Waianae Mnts, Oahu, USA, ex *Planchonella sandwicensis*, 26 August 2003, “Hi57-03” D. Percy leg. (BMNH). Paratypes (slide mounted) 2f, as for holotype (BMNH). Paratypes (slide mounted) 2m, Pahole NAR, Waianaea Mnts, Oahu, USA, N21.5364, W-158.1919, ex *Planchonella sandwicensis*, 14 August 2003, “Hi06-03” D. Percy leg. (BMNH). Other material: 1m 2f, South Mohiakea, Central Waianae Mnts, Oahu, USA, N21.4821, W-158.1247, ex *Planchonella sandwicensis*, 29 January 2014, “KM16-14” K. Magnacca leg. (BMNH).

Gene sequences. KY294142 (COI) KY294626 (cytB) (KM16-14) [previously submitted to GenBank as *Swezeyana elongagena* Caldwell, 1940 (in Percy 2017a)]; KY294143 (COI) KY294627 (cytB) (Hi57-03) [previously submitted to GenBank as *Swezeyana elongagena* Caldwell, 1940 (in Percy 2017a)].

***Swezeyana rubra* sp. n.**

<http://zoobank.org/19F21190-095C-4B30-9CF7-FEF2EFA58EE6>

Figures 1I, 8

Diagnosis. Medium small, red-brown species, with fore wing membrane distinctly patterned, antennae and genal processes relatively short, paramere short, and female proctiger strongly convex apically.

Description. Adult. General body colour red or red-brown, last 2-3 antennal segments darker brown. Fore wing distinctly patterned with irregular clouds of red pigmentation, mottled red-brown pattern in apical 2/3 of fore wing, with basal portion either clear (males) or slightly mottled (females), males have a darker almost solid red-brown area of pigmentation across middle of wing membrane, wing veins variably brown to speckled brown with darker brown patches indicating position of cross pseudoveins, intersections of veins and wing margin, as well as two brown patches on the dorsal claval wing margin, and on vein R+M+Cu₁ just basal to vein trifurcation, there are distinctly unpigmented areas surrounding marginal clusters of radular spines (Fig. 1I). Fore wing apex bluntly acute, shape shorter and broader than other *Swezeyana* (WL:WW < 3.10); pseudopterostigma long (Fig. 8V), 5-7 cross pseudoveins in cell r₁ (Fig. 8W); surface

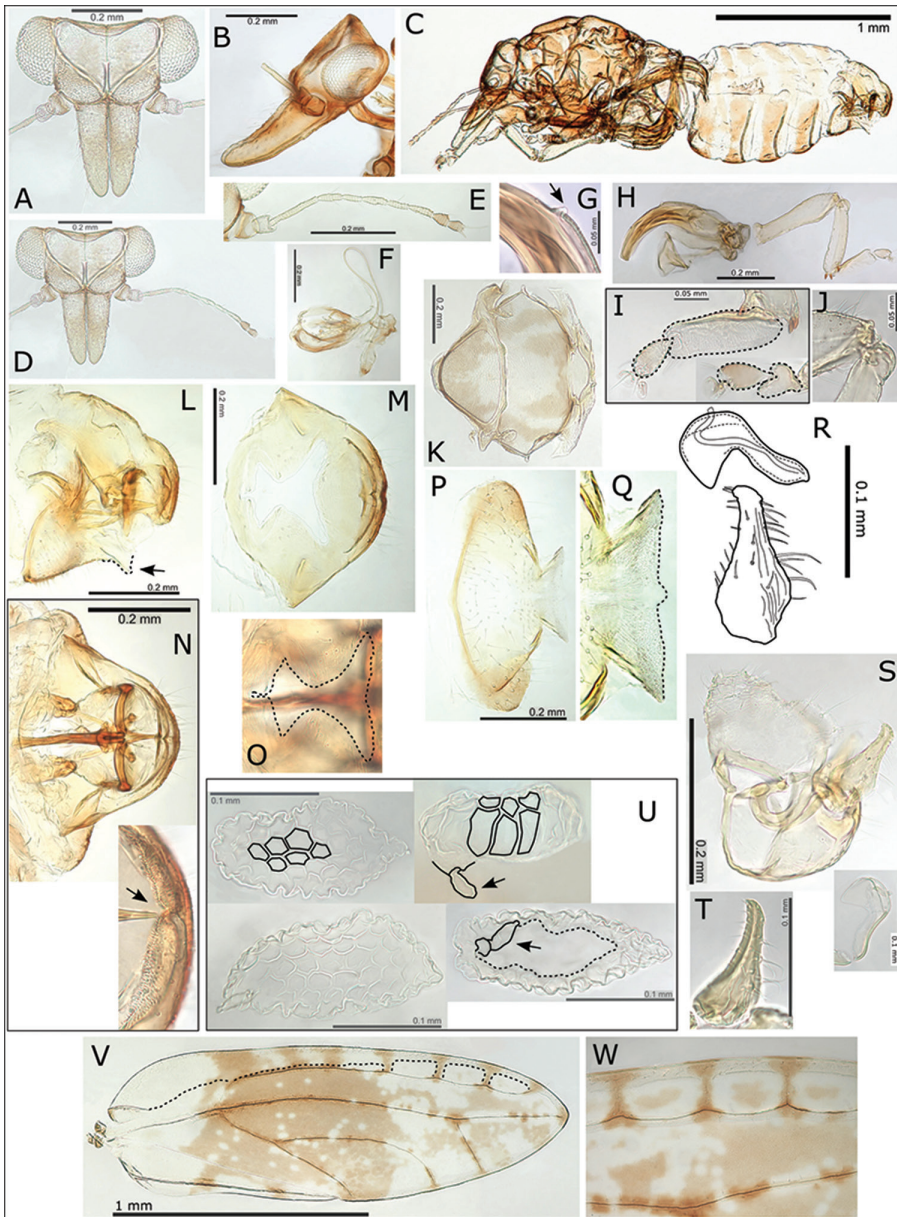


Figure 8. *Swezeyana rubra* sp. n. **A** head **B** head (lateral view) **C** female **D** head and antenna **E** antenna **F** proboscis **G** reduced meracanthus (indicated) **H** hind leg **I** metatarsi (outlined), inset comparative size of mesotarsi (outlined) **J** base of hind tibia **K** dorsum of thorax **L** female terminalia (subgenital beak indicated, apex outlined) **M** female proctiger (dorsal view) **N** female terminalia (dorsal view), inset apex of proctiger (ventral view, cleft indicated) **O** detail of anal ring (outlined) **P** female subgenital plate (ventral view) **Q** detail of posterior apex of female subgenital plate with beak and membrane (outlined) **R** aedeagus and paramere **S** male terminalia, inset aedeagus **T** paramere (posterior view) **U** eggs (semi-hexagonal sculpturing, pedicel and unsculptured underside outlined and indicated) **V** fore wing, with interior edge of ventral margin outlined **W** fore wing detail of pigmented cross veins.

spinules densely distributed in all cells, but cell c+sc often partly to almost entirely composed of a thickened ventral wing margin (C+Sc); medium long setae on ventral margin and medium short to short setae on veins and dorsal margin. Antennae short (ratio AL:HW 0.93–1.03) (Fig. 8C–D); genal processes relatively short (GP < 0.35 mm, ratio HW:GP > 1.65) and not or slightly upturned at apices (Fig. 8A–C); medium short to short setae on vertex and thorax. Meracanthus small (Fig. 8G), genual spine reduced or absent (Fig. 8J). Male terminalia (Fig. 8R–T): paramere short (ratio PL:HW < 0.25), tapering to slightly anteriorly projecting apex with two short stout setae; distal aedeagus segment short relative to paramere (ratio PL:AEL < 1.10), apex developed into a large rounded hook with acute apex. Female terminalia (Fig. 8L–Q): proctiger dorsal surface strongly convex apically, apex broad, blunt, bearing medial cleft and fringed with stout setae, anal ring medium long (ratio FP:RL 1.71–2.19), with reduced head compartment at proximal end, distal portion of ring margin smooth; subgenital plate slightly convex with little or no medial cleft but with beak and membrane extended (Fig. 8P–Q).

Egg. Pale with loosely structured hexagonal sculpturing dorsally (Fig. 8U).

Immature. Unknown.

Host plant. *Planchonella sandwicensis*.

Distribution. Hawaii. Only known from PuuWaaWaa area.

Etymology. Named for the generally red body colouration (adjective in the nominative singular).

Comments. This species was collected from the same individual host tree as *S. hawaiiensis* (see comments for *S. hawaiiensis*).

Material examined. Holotype male (slide mounted), PuuWaaWaa, Hawaii, USA, N19.784, W-155.833, 820m, ex *Planchonella sandwicensis*, 29 July 2002, “440B-02” D. Percy leg. (BMNH). Paratypes (slide mounted) 2f, as for holotype (BMNH). Other material: 2m 8f, PuuWaaWaa Forest Reserve, Hawaii, USA, 2600 ft, ex *Planchonella sandwicensis*, 23 February 2011, “JG5B” J. Giffin leg. (BMNH).

Gene sequences. MH001523 (COI) MH001529 (cytB) (JG5B); MG988834 (COI) MG989156 (cytB) (440B-02).

Species group: *reticulata*

Swezeyana reticulata Caldwell, 1940

Figures 1G, 9

Swezeyana reticulata Caldwell, 1940: 390.

Description. Adult. General body colour yellow-brown to darker brown, last 2-3 antennal segments darker brown. Fore wing patterned with irregular clouds of brown pigmentation (although less distinctly than in *S. rubra* and *S. tentaculata*), darker brown patches indicate position of cross pseudoveins, intersections of veins and wing margin, as well as 1-2 brown patches on the dorsal claval wing margin, and a more or

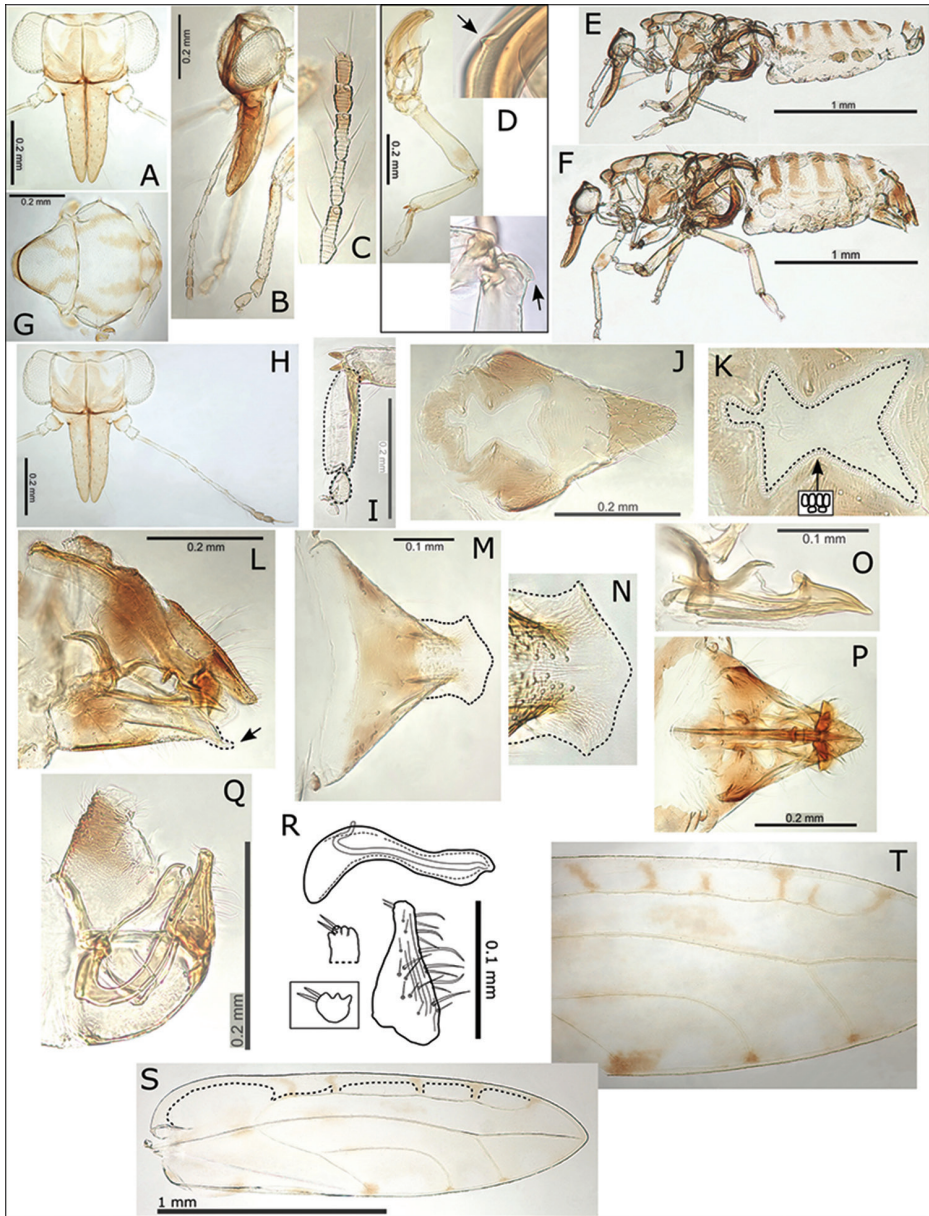


Figure 9. *Swezeyana reticulata*. **A** head **B** head and antenna (lateral view) **C** detail of antenna **D** hind leg, inset highly reduced meracanthus (indicated) and base of hind tibia with genual spine (indicated) **E** male **F** female **G** dorsum of thorax **H** head and antenna **I** metatarsi (outlined) **J** female proctiger (dorsal view) **K** detail of anal ring (outlined), illustrating circumanal ring pores **L** female terminalia (subgenital beak indicated, apex outlined) **M** female subgenital plate (ventral view, apex outlined) **N** detail of posterior apex of female subgenital plate with beak and membrane (outlined) **O** ovipositor **P** female terminalia (dorsal view), lateral valves extending beyond proctiger **Q** male terminalia **R** aedeagus and paramere, with details of paramere apex (above interior view, below dorsal view) **S** fore wing, with interior edge of ventral margin outlined **T** fore wing detail of pigmented cross veins.

less distinct patch on vein R+M+Cu₁ just basal to vein trifurcation, unpigmented areas surround the marginal clusters of radular spines (Fig. 1G). Fore wing apex acute to bluntly acute; pseudopterostigma short (Fig. 9S), 3–4 cross pseudoveins in cell r₁ (Fig. 9T); surface spinules densely distributed in all cells; medium long setae on ventral margin and short setae on veins and dorsal margin. Antennae medium short (ratio AL:HW 1.25–1.40) (Fig. 9B, I); genal processes medium long (GP < 0.40 mm, ratio HW:GP < 1.65) and slightly upturned at apices (Fig. 9A–B, E–F); medium short to short setae on vertex and thorax. Meracanthus small, genual spine developed (Fig. 9D). Male terminalia (Fig. 9Q–R): paramere short (ratio PL:HW < 0.25), tapering to apex with two short stout setae; distal aedeagus segment long relative to paramere (ratio PL:AEL < 0.80), apex developed into a large rounded hook with bluntly acute apex. Female terminalia (Fig. 9J–P): proctiger dorsal surface more or less straight, tapering to bluntly acute apex without medial cleft, anal ring relatively short (ratio FP:RL 2.17–2.45), with well-developed head compartment at proximal end, distal portion of ring margin slightly convoluted; subgenital plate more or less straight ventrally with little or no medial cleft and with beak and membrane slightly extended (Fig. 9L–N).

Egg. Pale with shallow hexagonal indentations dorsally.

Immature. Colour: Mottled, cream and red-brown. Structure: 5th instar with circumanal ring wide, and more or less straight, with a single row of uninterrupted elongate cells (Fig. 13G). Chaetotaxy: 5th instar with marginal, narrow, blunt sectasetae, and sub-marginal longer acute, simple setae on enlarged, ridged annuli or pediments (Fig. 13A–C); dorsal surface rugose, with small acute, simple setae on bulbous, ridged pediments, and with distinct arrangement of 28 protruding tubercles (13 on head and thorax, 15 on abdomen, of these 10 are medial, and 18 are lateral or sub-marginal), tubercles bearing scattered small, blunt, simple setae (Fig. 13D–F). 1st instar with marginal narrow, blunt sectasetae (Fig. 12A); 2nd instar with marginal narrow, blunt sectasetae, sub-marginal longer acute simple setae on enlarged and ridged annuli or pediments, and 7 sub-marginal tubercles, with 3 on thorax bearing 1–2 acute simple setae, and a marginal sub-apical pair of long simple setae on abdomen (Fig. 12B–D); 3rd – 4th instar chaetotaxy and tubercle arrangement similar to 5th instar (Fig. 12E–F). In 4th and particularly 5th instar, 4 of the dorsal tubercles are more darkly pigmented (these are the distal medial tubercles on thorax and abdomen, and the proximal lateral tubercles on abdomen; Fig. 13E–F).

Immature measurements (mm) and ratios: 5th instar (n = 4): BL 1.67–1.71; BW 1.06–1.15; WPL 0.85–0.88; CPL 0.73–0.79; CPW 0.62–0.97; RW 0.17–0.18; HW 0.52–0.57; AL 0.19–0.20; BL:BW 1.49–1.57; HW:AL 2.60–2.96; CPW:RW 3.70–5.77.

Host plant. *Planchonella sandwichensis*.

Distribution. Kauai (possibly also on Maui, see comments). Appears to be the most common of the three *Swezeyana* species found on Kauai.

Comments. Tuthill (1966) notes the co-occurrence of two species on Maui, and refers to these as *S. elongagena* and *S. reticulata*; but *S. reticulata* is here considered endemic to Kauai and the observed species on Maui may be an as yet undescribed species. The immatures as noted by Tuthill have “a remarkable armament of large protuberances [sic] on the dorsal surface” and therefore fit within the *reticulata* group.

Material examined. Holotype female (BPBM, not located). Other material: 1f, Nualolo Trail, Kokee State Park, Kauai, USA, on *Polyscias waimeae*, 25 May 2002, “370-02” D. Percy leg. (BMNH). 10m 4f 7i, Kokee State Park, Kauai, USA, N22.1444, W-159.6477, ex *Planchonella sandwicensis*, 29 October 2005, “Hi01-05” D. Percy leg. (BMNH). 5m 1f, Kokee State Park, Kauai, USA, N22.1503, W-159.6453, ex *Planchonella sandwicensis*, 29 October 2005, “Hi02-05” D. Percy leg. (BMNH). 12m 7f, Kokee State Park, Kauai, USA, N22.1309, W-159.6388, ex *Planchonella sandwicensis*, 30 October 2005, “Hi05-05” D. Percy leg. (BMNH). 1m 10f, Kokee State Park, Kauai, USA, N22.0948, W-159.6953, ex *Planchonella sandwicensis*, 30 October 2005, “Hi11-05” D. Percy leg. (BMNH).

Gene sequences. MG988833 (COI) MG989154 (cytB) (Hi01-05); MH001524 (COI) MH001530 (cytB) (Hi05-05 adult); MH001525 (COI) MH001531 (cytB) (Hi05-05 immature); MH001526 (COI) MH001532 (cytB) (Hi11-05).

***Swezeyana tentaculata* sp. n.**

<http://zoobank.org/6605B22E-FEFD-4EA5-A501-5E2D094A877A>

Figures 1H, 10

Diagnosis. Medium sized, red-brown species, with fore wing membrane patterned, antennae medium long, genal processes long, paramere short, and female proctiger more or less straight dorsally.

Description. Adult. General body colour red to red-brown, last 2-3 antennal segments darker brown. Fore wing distinctly patterned with irregular clouds of red-brown pigmentation, darker brown patches indicate position of cross pseudoveins, intersections of veins and wing margin, as well as two brown patches on the dorsal claval wing margin, and on vein $R+M+Cu_1$ just basal to vein trifurcation, there are distinctly unpigmented areas surrounding marginal clusters of radular spines (Figs 1H, 10S). Fore wing apex bluntly acute; pseudopterostigma short (Fig. 10R), 4-6 cross pseudoveins in cell r_1 (Fig. 10R-S); surface spinules densely distributed in all cells; long setae on ventral margin and medium short to short setae on veins and dorsal margin. Antennae medium long (ratio AL:HW 1.40–1.61) (Fig. 10C, E-F); genal processes long ($GP \geq 0.35$ mm, ratio HW:GP ≤ 1.35) and upturned at apices (Figs 10A-C); medium short to short setae on vertex and thorax. Meracanthus reduced, almost absent, genual spine developed (Fig. 10H). Male terminalia (Fig. 10P-Q): paramere short (ratio PL:HW < 0.30), tapering to apex with two short stout setae; distal aedeagus segment long relative to paramere (ratio PL:AEL < 0.90), apex developed into a large rounded hook with acute apex. Female terminalia (Fig. 10I-N): proctiger dorsal surface more or less straight, tapering to bluntly acute apex without medial cleft, anal ring relatively short (ratio FP:RL 2.24–2.59), with well-developed head compartment at proximal end, distal portion of ring margin convoluted; subgenital plate more or less straight ventrally with little or no medial cleft and with beak and membrane slightly extended (Fig. 9L-N).

Egg. Pale, sculpturing consisting of rounded indentations dorsally (Fig. 10O).

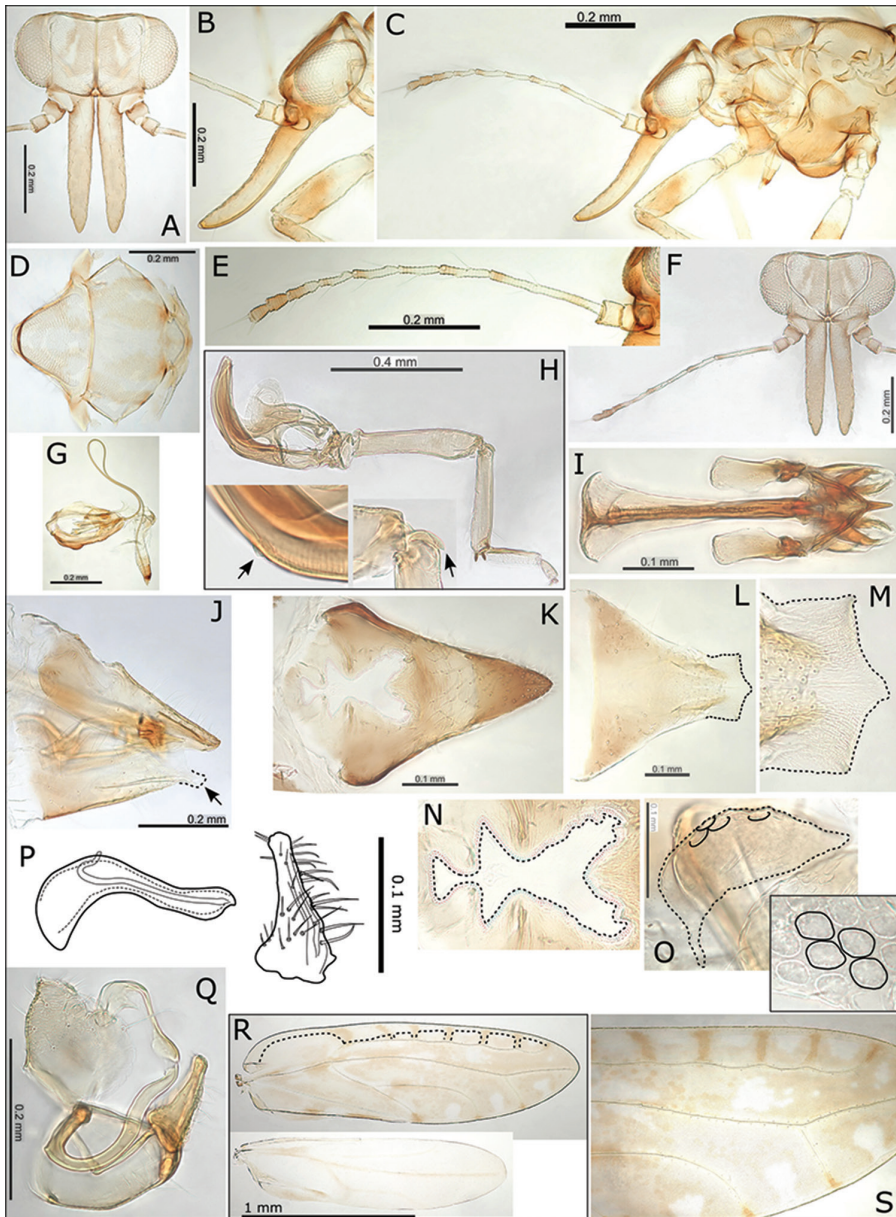


Figure 10. *Swezeyana tentaculata* sp. n. **A** head **B** head (lateral view) **C** head and antenna (lateral view) **D** dorsum of thorax **E** antenna **F** head and antenna **G** proboscis **H** hind leg, inset highly reduced meracanthus (indicated) and base of hind tibia with genual spine (indicated) **I** female terminalia endoskeleton (dorsal view) **J** female terminalia (subgenital beak indicated, apex outlined) **K** female proctiger (dorsal view) **L** female subgenital plate (ventral view, apex outlined) **M** detail of posterior apex of female subgenital plate with beak and membrane (outlined) **N** detail of anal ring (dorsal view, outlined) **O** egg (outlined), inset detail of sculpturing on dorsal surface **P** aedeagus and paramere **Q** male terminalia **R** fore wing (above), with interior edge of ventral margin outlined, hind wing (below) **S** fore wing detail of pigmented cross veins and unpigmented membrane surrounding marginal radular spine clusters.

Immature. Colour: Mostly red-brown, some cream mottling. Structure: 5th instar with circumanal ring wide, slightly constricted medially and lateral apices upturned, with a single row of uninterrupted elongate cells (Fig. 13I). Chaetotaxy: 5th instar with marginal, pointed sectasetae, and sub-marginal longer acute, simple setae on enlarged, ridged annuli or pediments (Fig. 13H, J–K); dorsal surface rugose, with small club setae, and with distinct arrangement of 28 protruding tubercles and tentacles (13 on head and thorax, 15 on abdomen, of these 10 are medial, and 18 are lateral or sub-marginal), all but 4 of the dorso-medial protuberances (on abdomen) are developed into elongate tentacles bearing scattered small, blunt, simple setae on the apical portion, and small club setae on the basal portion, tentacle apices bear 1–2 acute simple setae (Fig. 13L). 3rd – 4th instar chaetotaxy and tubercle/tentacle arrangement similar to 5th instar (Fig. 12G–J); in 3rd instars the lateral and submarginal tubercles bear 2 club setae at the apices (Fig. 12I), and the dorso-medial tubercles destined to become tentacles are larger and bear several club setae (Fig. 12H), by 4th instar elongation into tentacles is already evident. Somewhat more darkly pigmented tentacles are found in the same position as described for *S. reticulata* (the distal medial tentacles on thorax and abdomen, and the proximal lateral tentacles on abdomen; Fig. 13H, K). The tentacles are also evident in photographs of immatures on the leaf surface (Fig. N).

Immature measurements (mm) and ratios: 5th instar (n = 3): BL 1.48–1.52; BW 0.91–0.97; WPL 0.73–0.76; CPL 0.64; CPW 0.76; RW 0.16–0.17; HW 0.48–0.52; AL 0.18; BL:BW 1.56–1.63; HW:AL 2.61–2.95; CPW:RW 4.51–4.92.

Host plant. *Planchonella sandwicensis*.

Distribution. Kauai. Only known from Kokee State Park.

Etymology. Named for the distinctly long tentacles on the dorsum of immatures (adjective in the nominative singular).

Comments. Found sympatrically with *S. reticulata* and *S. elongagena* on the same individual plants. Immatures were observed among the ferruginous trichomes on the undersides of leaves, often along the leaf mid-rib (Fig. 13N).

Material examined. Holotype male (slide mounted), Kokee State Park, Kauai, USA, N22.1444, W-159.6477, ex *Planchonella sandwicensis*, 29 October 2005, “Hi01-05” D. Percy leg. (BMNH). Paratypes (slide mounted) 3f 7i, as for holotype (BMNH). Other material: 2m 2f, Kokee State Park, Kauai, USA, N22.1309, W-159.6388, ex *Planchonella sandwicensis*, 30 October 2005, “Hi05-05” D. Percy leg. (BMNH).

Gene sequences. MG989157 (cytB) (Hi01-05).

Species group: unplaced

Swezeyana magnacai sp. n.

<http://zoobank.org/5DA970DA-2E09-495A-9EF0-9654946E5348>

Figures 1F, 11

Diagnosis. Small, red- to yellow-brown species, with fore wing membrane patterned, antennae and genal processes medium long, and paramere short.

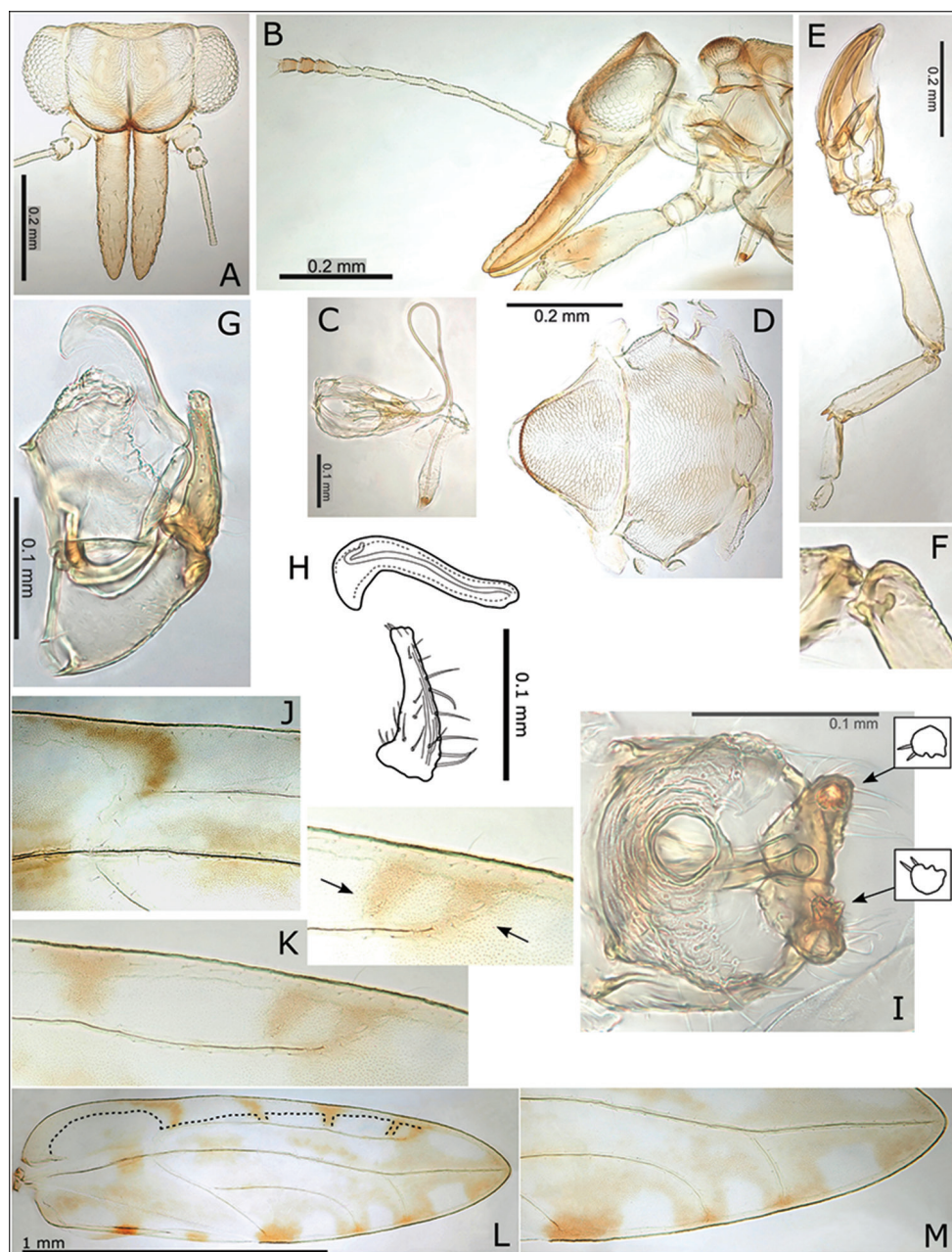


Figure 11. *Swezeyana magnaccai* sp. n. **A** head **B** head and antenna (lateral view) **C** proboscis **D** dorsum of thorax **E** hind leg **F** base of hind tibia **G** male terminalia **H** aedeagus and paramere **I** male terminalia (dorsal view), inset details of paramere apices **J** fore wing detail of termination of vein R at base of pseudopterostigma **K** fore wing detail of incomplete termination of vein Rs at wing margin (inset incomplete veins indicated) **L** fore wing, with interior edge of ventral margin outlined **M** fore wing detail of unpigmented membrane surrounding marginal radular spine clusters.

Description. Adult. General body colour orange-red to yellow-brown, last 2-3 antennal segments darker brown. Fore wing patterned with irregular clouds of orange-brown pigmentation, darker patches indicate position of cross pseudoveins, intersections of veins and wing margin, as well as 1-2 darker patches on the dorsal claval wing margin, and a more or less distinct patch on vein R+M+Cu₁ just basal to vein trifurcation, unpigmented areas surround the marginal clusters of radular spines (Figs 1F, 11M). Fore wing apex bluntly acute; pseudopterostigma relatively long (Fig. 11J, L), 2-3 cross pseudoveins in cell r₁ (Fig. 11L); surface spinules densely distributed in all cells; medium long setae on ventral margin and medium short to short setae on veins and dorsal margin. Antennae medium long (ratio AL:HW 1.41) (Fig. 11B); genal processes medium long (GP < 0.35 mm, ratio HW:GP < 1.65) and not or only slightly upturned at apices (Fig. 11A–B); medium short to short setae on vertex and thorax. Meracanthus extremely small to almost absent, genual spine reduced or absent (Fig. 11E–F). Male terminalia (Fig. 11H–I): paramere short (ratio PL:HW < 0.30), tapering to apex with two short stout setae; distal aedeagus segment long relative to paramere (ratio PL:AEL < 1.10), apex developed into a large rounded hook with acute apex.

Egg. Unknown.

Immature. Unknown.

Host plant. *Planchonella sandwicensis*.

Distribution. Oahu. Only known from the Waianae Mountains.

Etymology. Named for Karl Magnacca, a talented biologist who contributed several specimens for this study (noun in the genitive case).

Comments. Currently only known from males, it may belong in the *reticulata* species group based on fore wing characters and paramere shape, but is currently unplaced.

Material examined. Holotype male (slide mounted), Mokuleia Forest Reserve, Pahole, N Waianae Mnts, Oahu, USA, N21.53208, W-158.1786, ex *Planchonella sandwicensis*, 6 July 2014, “Hi74-14” D. Percy leg. (BMNH). Paratypes (slide mounted) 2m, as for holotype (BMNH). Other material: 1m, Puu Hapapa, Central Waianae Mnts, Oahu, USA, N21.4666, W-158.1029, ex *Planchonella sandwicensis*, 17 May 2014, “KM14-14” K. Magnacca leg. (BMNH).

Gene sequences. KY294144 (COI) KY294628 (cytB) (Hi74-14) [previously submitted to GenBank as *Swezeyana reticulata* Caldwell, 1940 (in Percy 2017a)]; KY294145 (COI) KY294629 (cytB) (KM15-14) [previously submitted to GenBank as *Swezeyana reticulata* Caldwell, 1940 (in Percy 2017a)].

Discussion

All *Swezeyana* species are hosted by a single, endemic Hawaiian host plant, *Planchonella sandwicensis* (Sapotaceae); and this long lived woody plant is distributed across all major islands in the archipelago. Co-occurrence of two or more *Swezeyana* species

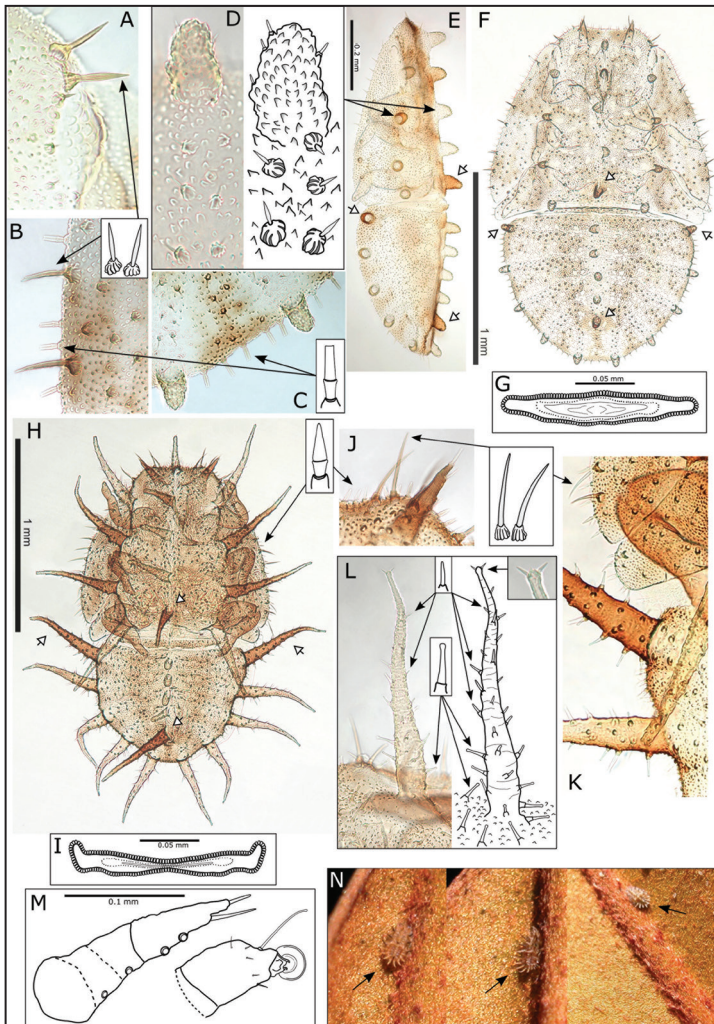


Figure 12. *Swezeyana reticulata* and *Swezeyana tentaculata* 5th instar immatures. **A–G, M** *S. reticulata*: **A** detail of dorsal lanceolate setae with inflated and ridged bases anterior of eye **B** detail of dorsal sub-marginal lanceolate setae with inflated and ridged bases on margin of wing pads **C** detail of tubercles on margin of abdomen, and marginal narrow, blunt sectasetae **D** detail of dorsal tubercle bearing small simple setae, and small lanceolate setae with greatly inflated and ridged bases on surrounding surface **E** lateral view showing arrangement of dorsal tubercles, open arrows indicate position of thoracic and abdominal tubercles typically more darkly pigmented **F** dorsal view, open arrows indicate position of thoracic and abdominal tubercles typically more darkly pigmented **G** anal ring **H–L, N** *S. tentaculata*: **H** dorsal view, open arrows indicate position of thoracic and abdominal tentacles typically more darkly pigmented, inset detail of marginal pointed sectasetae **I** anal ring **J, K** detail of dorsal sub-marginal long, simple setae with narrowly inflated and ridged bases, **K** also shows different pigmentation for 1st and 2nd tentacle on abdomen margin **L** detail of long tentacle with simple setae towards the apex and a pair of small simple setae apically, and longer slightly capitate rod setae towards the base and on surrounding surface **M** tarsus and antenna (similar for both species) **N** red-brown *S. tentaculata* immatures found along the midribs on undersides of leaves among the red-brown leaf trichomes.

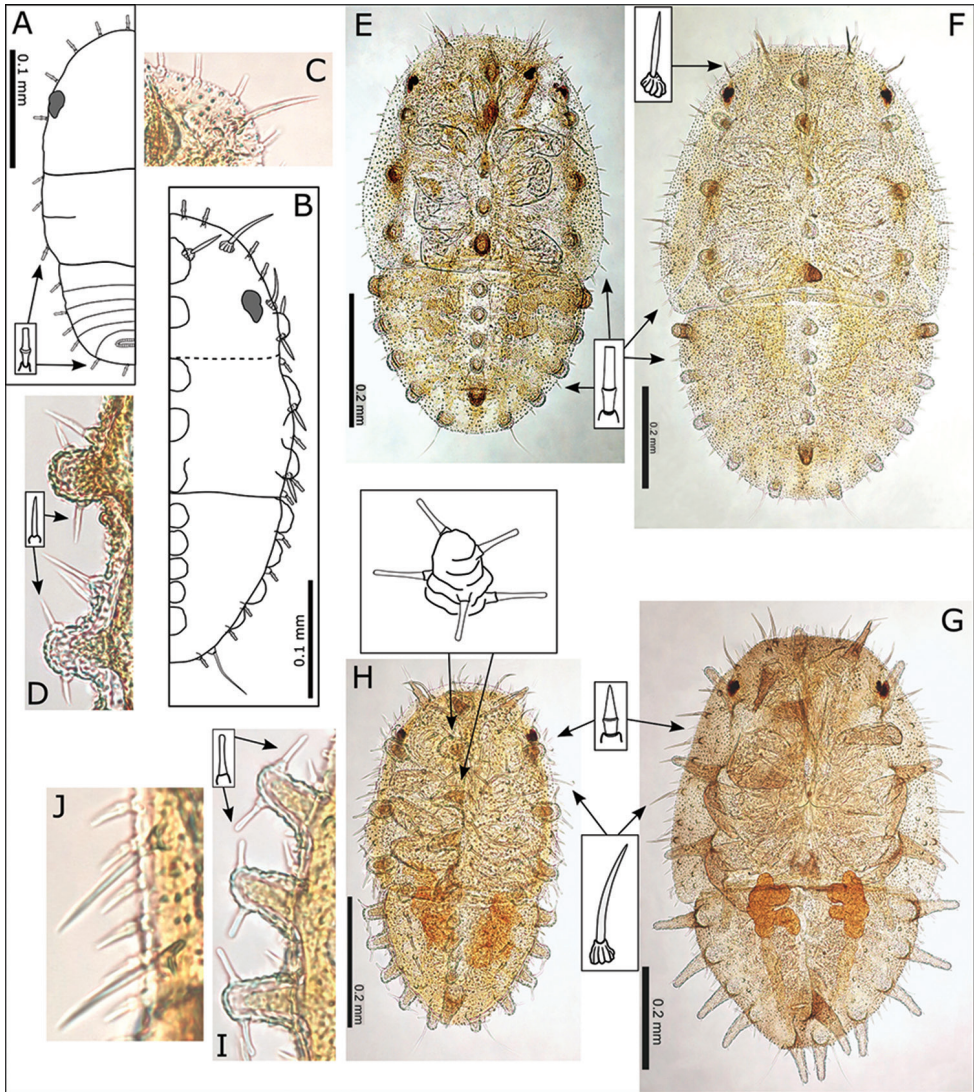


Figure 13. *Swezeyana reticulata* and *Swezeyana tentaculata* 1st-4th instar immatures. **A-F** *S. reticulata*: **A** 1st instar, inset detail of marginal narrow, blunt sectasetae **B** 2nd instar with appearance of tubercles **C** detail of 2nd instar anterior marginal and sub-marginal head setae **D** detail of 2nd instar marginal tubercles on the thorax bearing simple setae towards apices **E** 3rd instar, inset detail of marginal narrow, blunt sectasetae **F** 4th instar, inset detail of dorsal and sub-marginal lanceolate setae with inflated and ridged bases **G-J** *S. tentaculata*: **G** 4th instar, with details of marginal pointed sectasetae, and dorsal and sub-marginal simple setae with narrowly inflated and ridged bases **H** 3rd instar, with detail of larger dorso-medial tubercles bearing spiral of slightly capitate rod setae; marginal pointed sectasetae, and dorsal and sub-marginal simple setae with narrowly inflated and ridged bases as for 4th instar **I** detail of 3rd instar pairs of slightly capitate rod setae near the apices of marginal tubercles on the abdomen **J** detail of 3rd instar marginal pointed sectasetae, and dorsal sub-marginal simple setae.

collected from the same tree are known for at least four islands, Kauai, Oahu, Maui, and Hawaii (Caldwell 1940, Tuthill 1966, and this study). In reference to two species found on Maui, Tuthill (1966) remarked that “the occurrence of the two distinct species in the same ecological niche is unusual”, and this is a striking pattern in the genus. Expectations are that, in close sympatry, specialization for different niches on the host plant will, at some scale, contribute to driving diversification, particularly if the species represent sympatric speciation (Matsubayashi et al. 2010). The morphological, ecological and molecular evidence for sympatric speciation in *Swezeyana* provides some interpretive challenges.

Supporting the possibility of sympatric speciation is the single island endemism of most *Swezeyana* species that are known to co-occur, as well as some support from the molecular data. Due to a lack of backbone resolution in the phylogeny based on the two region DNA barcode data, short branches and variably supported nodes for the three putative same island species pairs, indicate these two gene regions are most effective for confirmation of species assignment, but less effective for resolving relationships between species. Nevertheless, of the three co-occurring species pairs, those on Oahu and Hawaii (*S. atra* and *S. oahuensis* on Oahu; and *S. hawaiiensis* and *S. rubra* on Hawaii) represent putative sister pairs, while a species pair on Kauai (*S. reticulata* and *S. tentaculata*) provides an unequivocal example (with stronger phylogenetic support likely due to a more recent speciation event) for a sister taxon relationship for these co-occurring species. The Kauai species pair have repeatedly been found co-occurring on the same individual leaves and both species are likely endemic to Kauai. Therefore, in the Kauai example, geography and molecular data provide strong evidence for diversification in sympatry.

The Hawaiian psyllids in the genus *Pariaconus* that feed on *Metrosideros polymorpha* also show similar evidence of divergence in sympatry, but these *Metrosideros*-feeding species often exhibit clear niche partitioning of the host species by different galling and non-galling biologies and/or occupation of different parts of the plant and/or different plant morphotypes (Percy 2017a). In contrast, *Swezeyana* species, as far as we know, all have free-living immatures found on the leaf surface, and there are no clearly apparent biological or microhabitat shifts coincident with occupying or partitioning the host plant. Most studies that have looked at species pairs in ecologically equivalent systems (e.g., same host plant) have concluded that in the absence of ecologically driven divergence (e.g., host races), allopatry must be important for either incomplete or complete non-ecological speciation (Jordal et al. 2006, Nyman et al. 2010). There is no evidence for past allopatry in co-occurring *Swezeyana*, but within island microgeographic allopatry may or may not have been more prevalent in the past when there was less forest disturbance, and more abundance of *Planchonella* trees.

Other than the sister taxon pair on Kauai, all *Swezeyana* species sampled for the DNA analysis are highly divergent from one another, and the lack of backbone resolution in the genus suggests there may have been a modest but rapid early radiation after colonization of the Hawaiian Islands, with little more recent divergence. Alternatively, more recent divergence events may have been obscured by extinction, or

not yet discovered. Molecular divergence provides a comparison with other Hawaiian psyllid lineages, and suggests that *Swezeyana*, is another relatively old endemic genus in the Hawaiian Islands (Percy 2017a,b). Maximum pairwise molecular distances within *Swezeyana*: 19.9%, can be compared with *Hevaheva* Kirkaldy, 1902: 17.5%, *Pariaconus*: 16.9%, *Stevekenia* Percy, 2017: 16.8%, and *Hemischizocranium* Tuthill, 1956: 13.9% (Fig. 2). In addition, it is interesting to compare maximum intraspecific divergence for two widespread non-Hawaiian taxa, *Trioza urticae* (Linné, 1758) (the common nettle psyllid): 2.8%, sampled from across Europe (southern Greece to arctic Norway, ~3500 km) (Wonglersak et al. 2017), and *Mesohomotoma hibisci*: 13.7%, a Pacific-wide species sampled from Singapore, New Caledonia, and French Polynesia (~7000 km and ~4500 km) (Percy 2017a); these two extremely widespread taxa are distributed over similarly large distances, but one is an almost entirely terrestrial landscape, whereas the other is an oceanic island landscape. The data indicates there is surprisingly efficient dispersal over large terrestrial distances (in this case facilitated by a highly abundant host plant, the common nettle, *Urtica dioica*), and in contrast relatively poor dispersal across oceans (despite the host plant, in this instance, *Hibiscus tiliaceus*, being abundant in nearly all Pacific regions). The different challenges to dispersal and gene flow across these landscapes are the most likely cause of the different levels of intraspecific molecular divergences observed, and similar processes (i.e., reduced dispersal and gene flow) probably also contribute to the high degree of single island endemism generally found in the Hawaiian psyllid fauna. Understanding the role of varying genetic landscapes in newly forming species and island speciation has been exemplified in studies of Darwin's finches in the Galapagos (Petren et al. 2005, Han et al. 2017), but obtaining adequate sampling to test similar hypotheses in psyllids will always be challenging.

Recognition of the two species groups in *Swezeyana* (*elongagena* group and *reticulata* group) is based primarily on the strikingly different structures of the female terminalia. This morphology is characterized by different development of the apodemes giving rise to distinct endoskeletons in the two species groups, and these different female terminalia structures imply traits related to oviposition that could be important in diversification, although the ovipositor itself is more or less invariant. However, because taxa in different species group, and taxa in the same species group, co-occur on the same individual plants, seemingly without any observable niche partitioning, it is particularly difficult to understand what may have initially driven this striking differentiation in female terminalia structure. Although the two species groups are recovered in the molecular topology, there is little to no bootstrap support for the *elongagena* group, emphasizing again the effectiveness of these barcode regions for identifying individuals to species but not for providing resolution at deeper nodes for higher classification. Nevertheless, the molecular data does serve to emphasise that the presence and number of cross veins and wing patterning varies within species groups. For instance, the two species with the greatest degree of wing patterning, as well as highest number of cross veins between Rs and the wing margin, *S. rubra* and *S. tentaculata*, are in different species groups, *elongagena* group and *reticulata* group respectively, and the more patterned

wings with a greater number of cross veins appear to have resulted from convergence in these characteristics. A wing type with numerous cross veins may be the ancestral state, but at present more sampling and analysis are required to test this hypothesis. Some of the fore wing and other unusual morphological traits in the genus may point to different dimensions of niche specialization among species. For instance, the often striking reddish to pink colouration/highlights found in many *Swezeyana* may provide camouflage against the rusty coloured trichomes on the host plant leaves, and variation in body and wing colouration may be involved in different strategies for predator avoidance or mate selection; the notably thickened anterior fore wing margin is another unusual characteristic of the genus that is as yet unexplained, but may play a role in acoustic communication (Percy et al. 2006). Other unusual characters such as the extremely long genal processes and long basal metatarsi are likewise unexplained. Variation in both colour and communication traits may represent additional niche dimensions (Jiggins 2008, Nosil and Sandoval 2008) in which selection and adaptation could have driven divergence in these species. The strikingly different immature morphology among co-occurring species also suggests that, despite no observable niche partitioning, immature morphologies may have arisen in response to different selection pressures, and therefore immatures may indeed be utilizing the host environment differently.

Swezeyana species are not generally abundant, for instance in comparison to some of the *Metrosideros*-feeding *Pariaconus* (Percy 2017a). During this study, typically not more than a handful of *Swezeyana* individuals were captured from one location/tree, although Tuthill (1966) recorded the two Maui species as locally abundant, as did Swezey (1954) for *S. elongagena* on Maui. Generally low abundance may partly be due to the scattered distribution of *Planchonella* trees, which are less common than *Metrosideros*. In addition, there is an increasing lack of new regeneration of *Planchonella*, which may preclude the establishment and growth of larger psyllid populations. However, it is possible sampling bias plays a role because large *Planchonella* trees are not easily accessible and the new leaf growth is mostly in the canopy. In addition, *Planchonella sandwicensis*, as with much of the native Hawaiian flora, was likely much more abundant, but habitat disturbance and clearing have impacted both plant and host specific taxa such as psyllids (Percy 2017b).

The taxonomic affiliations of *Swezeyana* to other genera within the family Trioziidae is uncertain due to the lack of a robust phylogenetic framework for the family, but it is worth noting that the immatures of *Hemischizocranium*, which are also free-living on the leaf surface, have a distinct medial (anterior-posterior) linear row of small dorsal tubercles (Tuthill 1956), similar in size to those illustrated here for 3rd instars of *S. reticulata*. Furthermore, in a recent phylogenomic analysis, using the most comprehensive sampling to date of the Psylloidea (Percy et al. 2018), a major clade of predominantly non-galling trioziid species includes three Hawaiian endemic genera *Swezeyana*, *Hemischizocranium*, and *Stevekenia* Percy, 2017. Additional sampling within this clade would be useful in determining the relationships of these genera and their source origins outside the Hawaiian Islands.

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Larva and pupa of *Ctesias* (s. str.) *serra* (Fabricius, 1792) with remarks on biology and economic importance, and larval comparison of co-occurring genera (Coleoptera, Dermestidae)

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Abstract

Updated descriptions of the last larval instar (based on the larvae and exuviae) and first detailed description of the pupa of *Ctesias* (s. str.) *serra* (Fabricius, 1792) (Coleoptera: Dermestidae) are presented. Several morphological characters of *C. serra* larvae are documented: antenna, epipharynx, mandible, maxilla, ligula, labial palpi, spicisetae, hastisetae, terga, frons, foreleg, and condition of the antecostal suture. The paper is fully illustrated and includes some important additions to extend notes for this species available in the references. Summarised data about biology, economic importance, and distribution of *C. serra* are also provided. The comparison of larval characteristics for some of the genera of Dermestidae co-occurring with *Ctesias* is presented. A key for identification of these genera is also provided.

Keywords

exuvia, immature stage, larva, pupa, seta, terga

Introduction

The genus *Ctesias* Stephens, 1830 is placed in the tribe Megatomini in the subfamily Megatominae. According to the world catalogue of Dermestidae, the genus contains only 26 species (Háva 2018) distributed mainly in the Palearctic and Afrotropical zone (Háva 2015, 2018). They all have been divided into four subgenera, *Ctesias* Stephens (four species), *Decemctesias* Háva (fourteen species), *Novemctesias* Háva (two species) and *Tiresiomorpha* (Pic) (six species) (Háva 2018). The genus seems to be closely related to genera such as *Globicornis* Latreille, 1829, *Megatoma* Herbst, 1791, *Trogoderma* Dejean, 1821 and *Reesa* (Milliron, 1939), but can be distinguished in the adult phase by the following characteristics: sharply defined antennal cavity and well developed antennal club with subtriangular antennomeres, giving the male antennal club a serrate appearance (Mroczkowski 1975, Peacock 1993). The larval features that distinguish *Ctesias* from related genera like *Globicornis*, *Megatoma*, *Trogoderma* and *Reesa* were given by Peacock (1993) and are mainly expressed by location of tufts of the hastisetae (= dense brushes of hastisetae) on the abdominal terga. In *Ctesias* these are located on each side of a membrane behind the tergum and moreover abdominal segment VIII lacks tufts. In comparison in *Globicornis*, *Megatoma*, *Trogoderma* and *Reesa*, tufts of hastisetae are situated on sclerotised areas of terga and never on membranes behind the terga (i.e., hastisetae are concentrated on the lateral portions of the posterior abdominal terga, behind the row of stout spicisetae); abdominal segment VIII with tufts of hastisetae. Due to the presence of the tufts of hastisetae on membranous emarginations of the terga, larvae of *Ctesias* are similar to *Anthrenus* Geoffroy, 1762 with the main difference between these genera being the shape of the body. In *Ctesias* the body is constricted behind the abdominal terga I–III, which are each longer than tergum IV, while in *Anthrenus* the body is not constricted and usually widened evenly from the pronotum (broadest at abdominal terga IV–VI (Beal 1991)), according to Peacock (1993) II–V. Moreover, in *Ctesias* there are four tufts of hastisetae (on membranous areas behind the abdominal terga IV–VII), while in *Anthrenus* there are only three (on the membranous areas behind the abdominal terga V–VII).

Interestingly, of the 21 species of *Ctesias*, the larval stages of only one, *Ctesias serra* (Fabricius, 1792), are referred to in the literature (compare with Table 1). In this paper, an updated description of larva of *Ctesias serra* (Fabricius, 1792) is given. This species represents the nominal subgenus *Ctesias* s. str. and is widely distributed in Europe. It has been also recorded from Algeria, Russia, and Caucasus (Háva 2015). The species is widely distributed through most European countries and is associated with areas of mature trees such as old parks, ancient woodlands, pasture woodlands, hedgerow trees, and forests (Peacock 1993). The paper presents some additions to extend notes for this species available in the references. The following set of larval characters are described and illustrated for the first time: foreleg, frons, pronotum, abdominal segment I, abdominal segments VII–IX. Additionally, the pupa is described and illustrated for the first time. Summarised data about the biology, economic importance, and distribution of *C. serra* are also provided.

Table 1. List of *Ctesias* species with references related to larval morphological characters.

Taxa	References	Available data
<i>Ctesias</i> Stephens, 1830	Lepesme and Paulian 1939	Short sentence in key (p. 167)
	Beal 1967	Short sentence in key (p. 290)
	Klausnitzer 1978	Short sentences in key (p. 168) [in German]
	Peacock 1993	Short sentences in key (p. 37)
	Klausnitzer 2001	Short sentences in key (p. 31–32) [in German]
<i>Ctesias</i> (s. str.) <i>serra</i> (Fabricius, 1792)	Perris 1846	Brief description of larval morphology (p. 339) [in French], illustration of larval habitus, antenna, setae (p. 345, pl. IX, fig. 4f)
	Dcaux 1891	Short description of larval morphology (p. 27) [in French] and illustration of habitus (p. 27)
	Donisthorpe 1897	Brief description of larval morphology (p. 162), pupa (p. 162)
	Böving and Craighead 1931	Illustration of apex of maxilla (p. 267), mouthparts (ventral, p. 267), habitus (lateral view, p. 267)
	Lepesme and Paulian 1939	Illustration of antenna (p. 163)
	Rees 1943	Short sentence in key (p. 7), brief description of larval morphology (p. 12), and illustration of antenna (p. 15), epipharynx (p. 18)
	Korschefsky 1944	Short description in key (p. 150), illustration of habitus (p. 154, pl. II)
	Klausnitzer 1978	Short sentence in key (p. 168) [in German], illustration of habitus (p. 169)
	Peacock 1993	Short description in key (p. 37) and on pages 43, 60, illustration of larval habitus (p. 120), epipharynx (p. 128) [epipharynx shown after Rees (1943)]
	Klausnitzer 2001	Illustration of habitus (dorsal, lateral view, p. 34), antenna (p. 34), epipharynx (p. 34) [habitus and epipharynx shown after Peacock (1993)]

The current work is a continuation of the previous articles devoted to study the morphology of the immature stages of Dermestidae (Beal and Kadej 2008, Kadej 2012a, b, c, Kadej and Jaroszewicz 2013, Kadej et al. 2013a, b, Kadej and Guziak 2017a, b, Kadej 2017, Kadej et al. 2017).

Materials and methods

For morphological examination of larvae and exuviae of the last-stage, specimens stored in ethanol were used. The material came from the collection of the Department of Invertebrate Biology, Evolution and Conservation, University of Wrocław (DIBEC). Larva/exuvium were boiled for 3–10 minutes in 10% solution of KOH, and then rinsed with distilled water. They were then placed in distilled water for ~1 hour to clean and soften the material. All structures were put in glycerin on slides. The morphological structures were studied under a Nikon Eclipse E 600 phase contrast microscope with a drawing tube attached, and a Nikon SMZ-800 binocular microscope;

examination was done using transmitted light. Photos were taken with Canon 500D and Nikon Coolpix 4500 cameras under Nikon Eclipse 80i and/or Nikon SMZ-800. In addition to the description provided herein, plates of the larval habitus/pupa as well as drawings of selected elements are also provided.

The terminology used in this paper follows Kiselyova and McHugh (2006), Kadej and Jaroszewicz (2013), and Kadej et al. (2013a, b).

Figure abbreviations

ac	acrotergite;	mp	mesal pair of labor-epipharyngeal setae;
as	antecostal suture (ridge);	ms	mesonotum;
asg	abdominal segments;	msr	mesal row of setae on lacinia;
br	transverse row of placoid sensillae on epipharynx;	mt	metanotum;
c	claw;	mxp	maxillary palp(i);
cs	campaniform sensilla;	p2	second pair of labor-epipharyngeal setae;
dst	distal epipharyngeal sensillae;	pls	placoid sensilla;
dmr	dorsomesal row of setae on lacinia;	pr	pretarsus;
er	epipharyngeal rods;	pro	pronotum;
f	femur;	prs	processes;
fe	fore wing;	s	sensorium (accessory sensory papillae);
g	galea;	sbp	subproximal epipharyngeal sensillae;
hw	hind wing;	st	stipes;
l	lacinia;	t	tibia;
lp	labial palp(i);	tr	tubercula.

Taxonomy

Subfamily Megatominae Leach, 1815

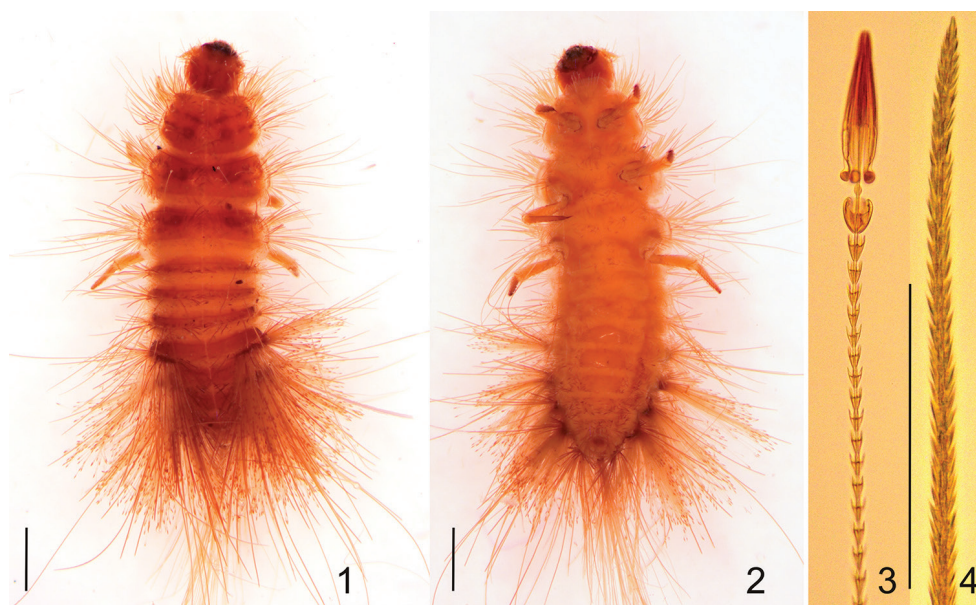
Tribe Megatomini Ganglbauer, 1904

Genus *Ctesias* Stephens, 1830

***Ctesias* (s. str.) *serra* (Fabricius, 1792)**

Figs 1–21

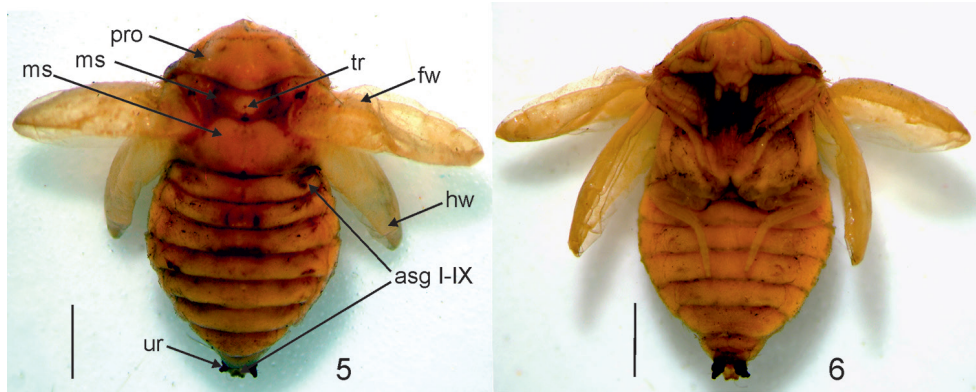
Material examined. (2 larvae) Polonia, Brzóza distr. Kozienice 7.VII.1956, w próchnie pnia lipy [inside the mould of the trunk of linden *Tilia* spp.], leg. B. Burakowski, det. M. Mroczkowski 1956; (2 larvae) Polonia, Maciejowice distr. Kozienice 6.VII.1956, w próchnie (bielu) dębu koło chodników Anobiidae [inside the mould of the oak *Quercus* spp. next to corridors of Anobiidae], leg. B. Burakowski, det. M. Mroczkowski 1956; (1 larva) Polonia, Maciejowice distr. Kozienice 6.VII.1956, pod korą olchy [under the



Figures 1–4. Mature larva of *Ctesias* (s. str.) *serra* (Fabricius, 1792). **1** Dorsal view **2** Ventral view **3** Head (apex) of hastiseta **4** Spiciseta. Scale bars: 0.1 mm.

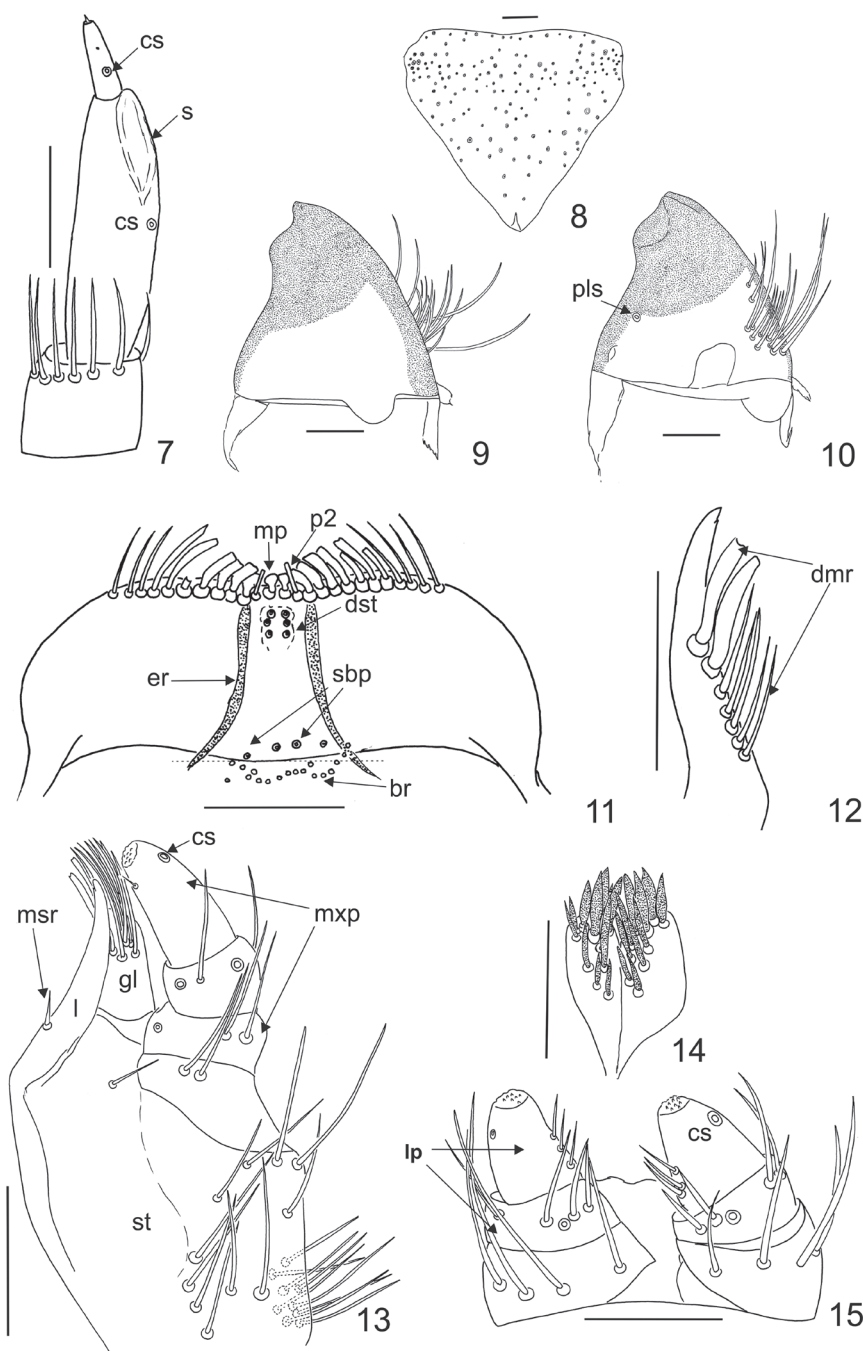
bark of alder *Alnus* spp.], leg. B. Burakowski, det. M. Mroczkowski 1956; (7 larvae) Puszcza Kampinoska, Sieraków, 31.X.1952, pod kora dębu [under the bark of the oak *Quercus* spp., leg. M. Mroczkowski]; (1 exuvia, 1 pupa) Warszawa, Saska Kępa pod korą wierzby [under the bark of willow *Salix* spp.] 10.V.1955, leg. M. Mroczkowski; (1 exuvia, 4 larvae) Polonia, Dojlidy ad. Białystok 19.III.1959 leg. R. Bielawski, det. M. Mroczkowski 1959; (1 larva) Germania: Brandenburg, Berlin, Schorfheide, 1.IV.1994. leg. A. Herrmann, coll. A. Herrmann. All materials (except for the last larva) are deposited in the Department of Invertebrate Biology, Evolution and Conservation, University of Wrocław, Przybyszewskiego 65, PL–51–148 Wrocław, Poland.

Description. Larva, last instar. Length 5.0–7.0 mm. Body fusiform, relatively long, rather flattened, not hunchbacked. Integument of head, nota and terga yellowish brown to brown; tergal plates sclerotised (Fig. 1), sterna only partially hyaline (= sterna I–VIII with central median line with strongly sclerotised and shiny strip (Fig. 2)), femora and tibiae light yellowish (Figs 1–2). On thoracic terga (= nota I–III) there are darker spots or patches present. Setae (spicisetae and hastisetae) on tegra brown (Fig. 1). On sterna only brown scaly-like spicisetae present (Fig. 2). Head protracted and hypognathous. Six stemmata present on the head (four + two other below). Frons triangular, without frontal, median tubercle (Fig. 8). On the frons two kinds of spicisetae present: lanceolate (= nudiseta) and scale-like. Lanceolate setae situated along anterior margin and on the central area, while scaly spicisetae along lateral margins and in the posterior part of the plate; several also present on the central area among lanceolate setae. Antennae orientated anterolaterally; composed of three antennomeres



Figures 5–6. Pupa of *Ctesias* (s. str.) *serra* (Fabricius, 1792). **5** Dorsal view **6** Ventral view Scale bars: 0.1 mm.

(Fig. 7). Terminal antennomere 4.0 times as long as wide, with one small sensory sensillum (appendage) on apex and two campaniform sensillae (upper one small, lower one bigger). Ratio of length of terminal antennomere to length of penultimate and antepenultimate antennomeres combined nearly 1.0:5.0. Sensorium in ventral position not extending above apex of segment 2. One campaniform sensillum present on antennomere 2 under sensorium. Antennomere 1 with 6–7 long setae (Fig. 7). Gula separate from postmentum; epicranial stem present. Median endocarina absent. Labro-epipharyngeal margin with 8 to 11 setae in the outer series. Mesal labro-epipharyngeal setae (mp) spatulate (broad) while second pair (p2) stout (narrow). On ventral side of epipharynx basal transverse row (br) of placoid sensillae present (13 to 18 sensory cups in the proximal transverse series (br)). Epipharyngeal rods (er) present and diverging proximally. Four sensory cups in the subproximal epipharyngeal sensilla (sbp), two large and two small ones. Distal epipharyngeal sensillae (dst) arranged in one group of six (in two longitudinal series of three sensillae, Fig. 11). Lateral setae on epipharynx absent (Fig. 11). Dorsal surface of labro-epipharynx with many setae. Mandible brown with dark brown (almost black) apex; apical teeth and ventral accessory process absent. Apical half of mandible heavily sclerotised and sharply delineated from basal half (Figs 9, 10). Mandibular mola and pseudomola absent. Hyaline lobe at ventral base of mandible absent. Prostheca perhaps absent, brush of setae absent mesally near mandibular base. Placoid sensillae (pls) present in approximately one-third of the basal dorso-lateral length of mandible (Fig. 10). Maxillary palp composed of three palpomeres with terminal palpomere longest. Ratio length of terminal palpomere to length of the two proceeding palpomeres combined 1.0:1.5. First palpomere with variable combination of setae and campaniform sensilla; two setae (one campaniform sensillum) or four setae (one campaniform sensillum). Second palpomere with 2–3 setae and 1–4 campaniform sensillae. Third palpomere with one campaniform sensillum, one short seta subapical and group of small sensillae situated in the apical area. Lacinia with one heavily sclerotised lacinial tooth, straight at apex. Lacinia sclerotisation separated from stipes. Seven straight thick to slender setae present in a dorsomesal row

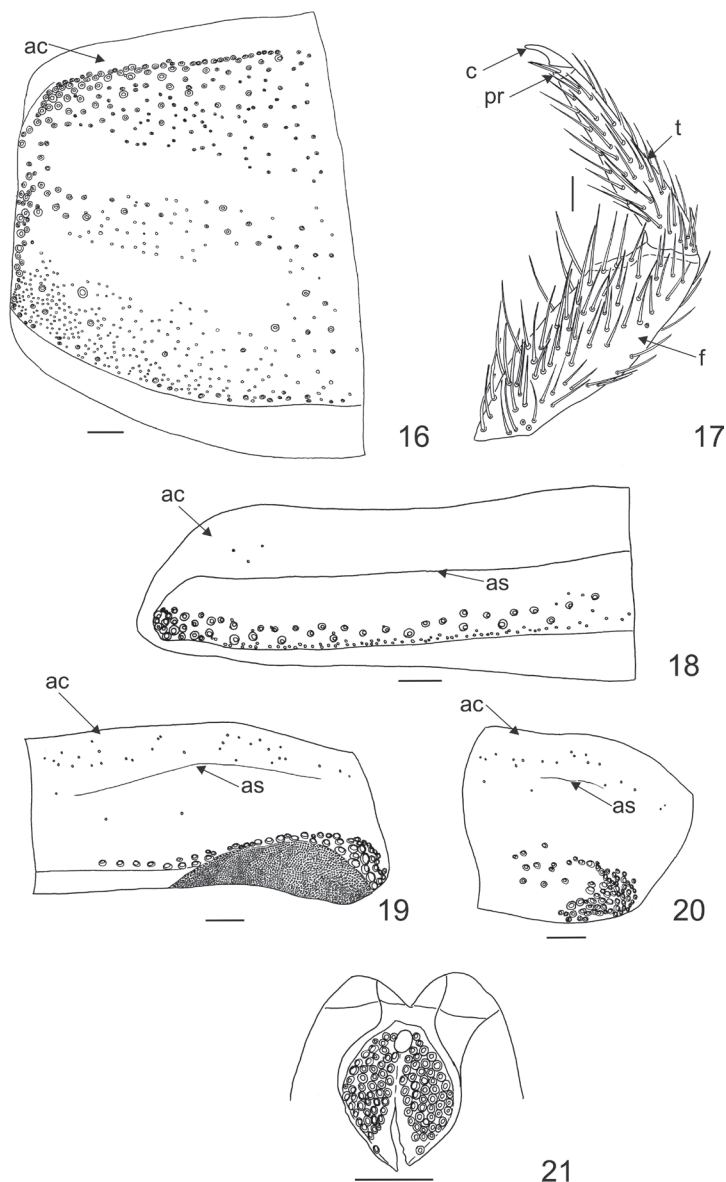


Figures 7–15. Mature larva of *Ctesias* (s. str.) *serra* (Fabricius, 1792). **7** Antenna (dorso-fronto-lateral) **8** Frons (dorsal; large circles with rings represent points of insertion of large scaly-like spicisetae, small circles represent points of insertion of nudisetae (= lanceolate spicisetae) **9** Mandible (dorsal) **10** Mandible (lateroventral) **11** Epipharynx (ventral) **12** Apex of lacinia (dorsal) **13** Maxilla (ventral) **14** Labium (ventral) **15** Labial palpi (ventral). Scale bars: 0.1 mm.

on lacinia (dmr) (Fig. 12). Mesal row of setae on lacinia (msr) composed of a basally thickened seta (Fig. 13). Galea arising from stipes, ending close to the apex of lacinia. The apical area of galea covered densely with setae. Stipes with 18–20 long setae placed mainly near the antero-lateral margin, one to two setae present near the inner margin (under the first palpomere) (Fig. 13). Hypopharynx hyaline. Bridge sclerite (central part of the distal element of the hypopharyngeal sclerome) appearing jointed medially. Anterior arms of bridge sclerite and distal lateral sclerites of hypopharynx absent. Ligula with approximately 21 lanceolate setae (Fig. 14). Labial palp with 2 palpomeres. First segment wider than second segment; 2.0 times as wide as long, with four setae on the disc (sometimes setae absent – they can be lost during dissection – then resembling campaniform sensillae). Terminal labial palpomere with group of small sensillae in the apical area, one campaniform sensillum (cs) close to external margin and three setae on inner margin (Fig. 15).

Antecostal suture on notum I absent, but distinct on nota II–III and abdominal terga I–VII (Figs 18 and 19); abdominal segment VIII without suture or only remnant remaining (Fig. 20). Acrotergites of notum I without setae, while acrotergites of nota II–III and abdominal terga I–VIII with short setae (Figs 18–20). Notum I with long, stout, large spicisetae along anterior (here directed anteriorly under the head), lateral and posterior margin (here directed latero-posteriorly and vertically - upright). Setae on posterior margin situated near the latero-posterior angle, some additionally near suture, some also present on central area of disc of notum I (Fig. 16). Nota II, III with median row of large spicisetae, and along lateral margins of terga. Abdominal terga I–VII with posterior rather than median row of large spicisetae, and along lateral margins of terga (Figs 18–19). These mainly directed latero-posteriorly and vertically (upright). Hastisetae are present both on nota as well as abdominal terga (Figs 16, 18–20). Hastisetae of abdominal terga IV–VII forming dense lateral brushes (longest and thickest on V–VII). Setal patterns of abdominal tergum I with numerous large spicisetae in posterior row; lateral margin bearing also spicisetae; hastisetae on posterior half of tergite more numerous than spicisetae (Fig. 18). Abdominal tergum VII with short, stout setae along anterior margin; large spicisetae in posterior row above the membranous area bearing densely situated hastisetae (Fig. 19). Abdominal tergum VIII without pair of abdominal pits (oval apertures); setal patterns as illustrated (Fig. 20) - short, stout setae along anterior margin; large spicisetae in posterior part. Abdominal tergum IX reduced with numerous long scaly-like spicisetae (Fig. 21). Legs (tibia, femur and trochanter) covered with many lanceolate setae as illustrated on Fig. 17. Claws dark brown. Ratio tibial to femoral length 4.0:5.0. Pretarsus with two narrow lanceolate setae inserted at base. Length of posterior pretarsal seta subequal to length of anterior pretarsal seta (Fig. 17), anterior pretarsal seta perhaps slightly longer.

Pupa (Figs 5–6): length 4.0–5.0 mm. Integument yellowish brown with erect, brown coloured spicisetae distributed rather uniformly on head, dorsum and wings. Head directed downwards (not visible from above). Antennae long, reaching lateral margin of pronotum. Antenna with 11 antennomeres (the boundaries of individual segments not sharply delimited); antennal club with 3 antennomeres (Fig. 6). Anten-



Figures 16–21. Mature larva of *Ctesias* (s. str.) *serra* (Fabricius, 1792). **16** Pronotum (dorsal, left half, denuded; large circles represent points of insertion of large spicisetae, small circles along the suture represent points of insertion of hastisetae) **17** Right protosternal leg (dorsal) **18** Abdominal tergum I (dorsal, left half, denuded; large circles represent points of insertion of large spicisetae, small circles represent points of insertion of hastisetae) **19** Abdominal tergum VII (dorsal, right half, denuded; large circles represent points of insertion of large spicisetae, small circles along the suture represent points of insertion of short setae, small circles below large circles represents points of insertions of hastisetae) **20** Abdominal tergum VIII (dorsal, right half, denuded; large circles represent points of insertion of large spicisetae, small circles along the suture represent points of insertion of short setae) **21** Abdominal tergum IX (dorsal, denuded; circles represent points of insertion of large spicisetae). Scale bars: 0.1 mm.

nal club serrated, shorter than flagellum. Eyes clearly visible, convex, oval; situated just behind upper margins of antennae. Pronotum transverse, widest near mesonotum (between posterior angles), with the anterior part narrowed; posterior border of pronotum distinctly elongated in the middle; posterior angles slightly rounded. Mesonotum half as long as metanotum. Mesonotum and metanotum slightly convex. Mesonotum with distinct tubercula in the central part of the disc. Hind wings shorter than fore wings, reaching posterior margin of abdominal segment IV (Fig. 5). The width of abdominal segments I–IV gradually broadened, while V–VIII narrowed posteriorly (Fig. 5). Abdominal segment IX with two black processes (Figs 5–6) (from lateral view these processes slightly curved upward). Abdominal segment IX emarginated in the middle. Legs visible, well developed. Gin traps absent (Fig. 5). Pupa remains within the last exuvium (= larval skin) which is interrupted from head to last abdominal terga (Donisthorpe 1897, 1920). Probably pupa anchored by two clusters of long fine setae inserted on each side of the abdominal tergum VIII.

Biology. Knowledge of the biology of the species is limited, with only a small amount of published information (Donisthorpe 1920, Mroczkowski 1975, Peacock 1993). There is probably only one generation a year. In Poland, adults occur from May to July and sometimes August. Beetles have been recorded from under bark, from tree cavities, by sap flows, and on flowers (where they usually copulate). The eggs are laid under the bark of trees and usually number ca. 20–40. The larvae hatch after 2–3 weeks, passing through usually five instars. Pupation takes place in Autumn or Spring (in April). Since both larvae of the last instar and pupae have been observed under bark throughout the winter, it appears that the species can overwinter as either a pupa or larva. It is known that larvae live under the bark of the mature trees (of different species such as: oak, poplar, elm, sycamore, hawthorn, fir, beech, horse and sweet chestnut, maple, redwood, cherry and willow), close to spiders' webs, where they feed on dead insects (Rees 1946, Burakowski et al. 1986, Peacock 1993, Kadej 2005). They also feed on clutches of butterflies eggs (Mroczkowski 1975, Peacock 1993). Occasionally, larvae have been observed in the nests of Aculeata, where they feed on the larval exuviae. They have also been found in insect galleries (e.g. cerambycid *Nothorhina punctata* (Fabricius, 1798)), in old fungus, and in rotting trees and stumps of mainly deciduous trees (Hämäläinen and Mannerkoski 1984, Peacock 1993). Due to a secretive life they are usually observed as immature stages. The larvae, when disturbed by predators, can erect and vibrate the abdominal brushes of hastisetae (Donisthorpe 1897, Joy 1920, Rees 1946). This specific way of defence is facilitated by a well-developed supra-anal organ on the last abdominal segment (Mroczkowski 1975, Peacock 1993).

Economic importance. Probably because of its rarity, this species has no serious economic importance. However, it is likely that in its natural habitat it can play a positive role in reducing the number of eggs of butterflies classified as pest of forests (Mroczkowski 1975). Harding (1986) classified the species as an old forest indicator.

Distribution. Widely distributed in Europe (from the Mediterranean region to the UK and the southern province of Fennoscandia). It has been also recorded from Algeria, Caucasus and Russia (Stavropol) (Háva 2015).

Discussion

Most of the larval morphological characteristics presented here are shown for the first time for *C. serra*. In comparison with previous papers of Perris (1846), Böving and Craighead (1931), and Lepesme and Paulian (1939), the current graphics illustrate much more detailed larval morphology. Some of the graphics used by previous authors are reproduced images (e.g. Rees (1943) or Peacock (1993)). Thus based on the available data, only superficial comparisons were possible. Moreover, some characteristics were mistakenly interpreted by previous workers. For instance, Perris (1846, p. 310) wrote that the antenna of *C. serra* has 4 segments, while actually there are only 3.

However, the morphology of epipharynx is quite interesting. Structures shown by Rees (1943, p. 18), Peacock (1993, p. 128) and Klausnitzer (2001, p. 34) are similar to those studied by me (compare with Fig. 11, current paper) with the exception of complexes of the sensillae (sbp) and (br). I have observed more placoid sensillae in the basal transverse row (br). There were 13 to 18 sensory cups in the proximal transverse series (br), whilst in abovementioned papers there were only 10. I also recorded four sensory cups in the subproximal epipharyngeal sensilla (sbp) – two big and two small ones, while Rees (1943, p. 18), Peacock (1993, p. 128) and Klausnitzer (2001, p. 34) observed only two.

It is difficult to compare larval characters of *C. serra* with congenetics because of a lack of larval morphological descriptions for the other species. For this reason I decided to collect and summarise larval data for the genera which co-occur with *Ctesias* (see Table 2). The aim was to focus on these larval characteristics which allow for easy identification at the generic level.

Moreover, because *Ctesias serra* inhabits quite similar habitats (= in or near spider webs, under loose bark, in old decayed wood) as some of the representatives of the genera *Anthrenus* (e.g. *A. fuscus* Olivier, 1789 or *A. museorum* (Linnaeus, 1761)), *Globicornis* (e.g. *G. corticalis* (Eichhoff, 1863) or *G. emarginata* (Gyllenhal, 1808)), *Megatoma* (e.g. *M. undata* (Linnaeus, 1758)) or *Trinodes* (e.g. *T. hirtus* (Fabricius, 1781)), I have identified morphological characters that could aid precise determination. The first characteristic that is useful in distinguishing *Ctesias serra* from other species is body shape. In *C. serra* it is constricted at abdominal terga I–III, and the body is broadest at notum III (ratio length to width 1.0:3.0), while in the rest of the genera there is no constriction. The body is broadest at abdominal segments IV–VI in *Anthrenus*, at notum III or abdominal segment I in *Globicornis* and *Megatoma* (ratio length to width 1.0:4.5), and at abdominal segment I in *Trinodes* (ratio length to width 1.0:2.5).

Also the integument colour is distinctly different in *Globicornis* (dark brown to black) and *Trinodes* (greyish with a sclerotised brown strip along the anterior and posterior margin of the tergite, enclosing a transverse membranous area on each side), while in *Ctesias* it is yellowish brown to brown (and thoracic terga (= nota I–III) sometimes with darker spots or patches). *Megatoma* is also yellowish brown (in some species have thoracic terga I–III with distinctly dark brown patches at sides, sometimes extending to middle on terga II and III). Only in *Ctesias* do the sterna I–VIII have a central median line with a strongly sclerotised and shiny strip.

Table 2 Comparison of larval characteristics for some of the genera of Dermestidae co-occurring with *Ctesias serna*.

Character	Body shape	Colour of integument	Tegites/Sternites	Urogomphi	Abdominal tufts of hastisetae
<i>Dermestes</i> Linnaeus, 1758	Elongate, cylindrical (gradually tapering to last abdominal segment; ratio length to width 1.0:4.5); broadest at notum III; without caudal brush of long, slender setae	Usually dark brown to black, but sometimes yellowish and sometimes with median yellowish strip from anterior margin of pronotum	Tegites usually strongly sclerotised. Sternites membranous (= hyaline), but those of abdominal segments IX–X, and occasionally VII–X, entirely sclerotised	Present on abdominal tergite IX dorsally	Absent
<i>Thyrodrias</i> Motschulsky, 1839	Compact and C-shaped, cyphosomatic (ratio length to width 1.0:3.0); broadest at abdominal segment I; without caudal brush of long, slender setae	Light golden brown	Tegites sclerotised. Sternites membranous (= hyaline)	Absent	Absent
<i>Trinodes</i> Dejean, 1821	Relatively short (= compact, ratio length to width 1.0:2.5); broadest at abdominal segment I; without caudal brush of long, slender setae	Greyish with sclerotised brown strip along anterior and posterior margin of tergite, enclosing a transverse membranous area on each side	Tegites sclerotised. Sternites membranous (= hyaline)	Absent	Absent
<i>Attagenus</i> Latreille, 1802	Elongate, cylindrical, orthosomatic (gradually tapering to last abdominal segment; ratio length to width 1.0:6.0); broadest at notum I; with caudal brush of long, slender setae	Yellowish brown to brown	Tegites sclerotised. Sternites membranous (= hyaline)	Absent	Absent
<i>Anthrenus</i> Geoffroy, 1762	Relatively short (= compact, ratio length to width 1.0:2.5); broadest at abdominal terga IV–VI; flattened, not hunchbacked and not constricted; slender setae present on tergum IX, but not so long as in <i>Attagenus</i> , <i>Ctesias</i> , <i>Megatomus</i> , <i>Reesa</i> , <i>Trogoderma</i>	Yellowish brown to dark brown; sometimes with darker spots or patches on terga	Tegites sclerotised. Sternites sometimes sclerotised	Absent	On membranous area behind terga V–VII
<i>Ctesias</i> Stephens, 1830	Fusiform, and relatively long, sub-oblong (ratio length to width 1.0:3.0); broadest at notum III; rather flattened, not hunchbacked; constricted behind abdominal terga I–III; with caudal brush of long, slender setae	Yellowish brown to brown; thoracic terga (= nota I–III) sometimes with darker spots or patches	Tegites sclerotised. Sterna I–VIII with central median line with strongly sclerotised and shiny strip	Absent	On membranous area behind terga IV–VII

1 According to Beal (1991) body of *Anthrenus* larvae is broadest at abdominal segments IV–VI, while according to Peacock (1993) at abdominal segments II–V.

Character	Body shape	Colour of integument	Tegites/Sternites	Urogomphi	Abdominal tufts of hastisetæ
Genus					
<i>Globicornis</i> Latreille, 1829	Fusiform, and relatively long, sub-oblong (ratio length to width approx. 1.0:4.5); broadest at notum III; slightly hunchbacked; with caudal brush of long, slender setae	Brown to dark brown	Tegites sclerotised. Sternites membranous (= hyaline)	Absent	On terga V–VIII ² (never on membranes behind terga)
<i>Megatomia</i> Herbst, 1792	Fusiform, and relatively long (ratio length to width 1.0:4.5); broadest at notum III; flattened, not hunchbacked; with caudal brush of long, slender setae	Yellowish brown (in some species thoracic terga I–III with distinctly dark brown patches at sides, sometimes extending to middle on terga II and III)	Tegites sclerotised. Sternites membranous (= hyaline)	Absent	On terga VI–VIII (never on membranes behind terga)
<i>Reesa</i> Beal, 1967	Fusiform, and relatively long (ratio length to width 1.0:4.0); broadest at notum III; rather flattened, not hunchbacked, orthosomatic; with caudal brush of long, slender setae	Yellowish brown to dark brown (then strongly pigmented)	Tegites sclerotised. Sternites membranous (= hyaline)	Absent	On terga I–VIII (but the longest and thickest on VI–VIII) (never on membranes behind terga)
<i>Trogoderma</i> Dejean, 1821	Fusiform, and relatively long (ratio length to width 1.0:2.0); broadest at notum III; rather flattened, not hunchbacked, orthosomatic; with caudal brush of long, slender setae	Yellowish brown to dark brown	Tegites sclerotised. Sternites membranous (= hyaline)	Absent	On terga V(VI)–VIII (longest and thickest on VI–VIII) (never on membranes behind terga)

² In *G. corticalis* and *G. emarginata*, but it is likely that this feature is similar also in *G. nigripes*.

Table 2.2 Continuation of the comparison of larval characteristics for some of the genera of Dermestidae co-occurring with *Ctesias serna*.

Character	Genus	Body setation	Ratio length to width of head of hastiseta	Antecostal suturae	Epipharynx	Setae Mp/p2 on labro-epipharyngeal margin
<i>Dermestes</i> Linnaeus, 1758		Hastisetae absent (only spicisetae present, occasionally modified into ramous setae or club-shaped setae)	N/A	Distinct, present on nota II–III and abdominal terga I–X	No distal epipharyngeal sensilla (dst)	Middle 4 setae of labro-epipharyngeal margin consisting of 2 spatulate, broad inner (Mp) and 2 stout, narrow (p2) outer setae
<i>Thyodrias</i> Motschulsky, 1839		Hastisetae absent (club-shaped setae present ³ ; spinulate setae only on transverse membranous areas of each tergite, not on pronotum)	N/A	Distinct, present on nota II–III and abdominal terga I–VIII	No distal epipharyngeal sensilla (dst)	Middle 4 setae of labro-epipharyngeal margin consisting of 4 spatulate, broad setae both in inner (Mp) and (p2) outer setae
<i>Trinodes</i> Dejean, 1821		Hastisetae absent (black, erect spicisetae present)	N/A	Distinct, present on nota II–III and abdominal terga I–VIII	No distal epipharyngeal sensilla (dst)	Middle 4 setae of labro-epipharyngeal margin consisting of 2 spatulate, broad inner (Mp) and no setae (p2) in outer series ⁴
<i>Attagenus</i> Latreille, 1802		Hastisetae absent (only spinulate (= lanceolate) and in some species also scale-like setae present)	N/A	Distinct, present on nota II–III and abdominal terga I–VIII	Usually 2 distal epipharyngeal sensilla (dst) present, but not enclosed by furrow (sometimes dst absent)	Middle 4 setae of labro-epipharyngeal margin consisting of 2 spatulate, broad inner (Mp) and 2 stout, narrow (p2) outer setae
<i>Anthrenus</i> Geoffroy, 1762		Both hastisetae and spicisetae present	Head of hastisetae variable: 3 to more than 5 times as long as wide at the widest point	Present on nota II–III, incomplete on abdominal tergites I–IV; sometimes slightly visible on tergum V	Distal epipharyngeal sensillae (dst) arranged in one group of 6, but not enclosed by furrow (usually sensillae are in a faintly defined fusiform area)	Middle 4 setae of labro-epipharyngeal margin consisting of 2 spatulate, broad inner (Mp) and 2 stout, narrow (p2) outer setae

³ But only in late instar larvae (Zhantiev 2000)

⁴ According to Peacock (1993, p. 125, fig. 209)

Character	Body setation	Ratio length to width of head of hastiseta	Antecostal suturae	Epipharynx	Setae Mp/p2 on labro-epipharyngeal margin
Genus					
<i>Ctesias</i> Stephens, 1830	Both hastisetae and spicisetae present	Head of hastisetae more than 3 times as long as wide at the widest point	Absent on notum I, but distinct on nota II–III and abdominal terga I–VII (Figs 18 and 19); abdominal segment VIII without the suture or only remains of it can be observed	Distal epipharyngeal sensillae (dst) arranged in one group of 6 (in two longitudinal series of 3 sensillae), not enclosed by distinct furrow	Middle 4 setae of labro-epipharyngeal margin consisting of 2 spatulate, broad inner (Mp) and 2 stout, narrow (p2) outer setae
<i>Globicornis</i> Latreille, 1829	Both hastisetae and spicisetae present	Head of hastisetae less than 3 (e.g. <i>G. corticalis</i> and <i>G. emarginata</i>), or more than 3 times as long as wide at the widest point (e.g. <i>G. nigripes</i>)	Absent on notum I, but distinct on nota II and III as well as abdominal terga I–VIII (on segment VIII its form reminds thread-like carina)	Distal epipharyngeal sensilla arranged in two groups: one of two sensillae, and second of four sensillae; both groups completely enclosed/encircled by a furrow (except <i>G. nigripes</i> in which six distal sensillae are enclosed in one ring); besides in <i>G. corticalis</i> and <i>G. emarginata</i> apices of the epipharyngeal rods are joined by a sclerotised transverse bar	Middle 4 setae of labro-epipharyngeal margin consisting of 2 spatulate, broad inner (Mp) and 2 stout, narrow (p2) outer setae
<i>Megatoma</i> Herbst, 1792	Both hastisetae and spicisetae present	Head of hastisetae more than 3 times as long as wide at the widest point	Smooth and distinct, present on nota I–III and abdominal terga I–VIII (absent on segment VIII in subgenus <i>Pseudohadrotoma</i>)	Distal epipharyngeal sensillae arranged in one group of 6 in two rows	Middle 4 setae of labro-epipharyngeal margin consisting of 4 spatulate, broad sense both in inner (Mp) and (p2) outer setae
<i>Reesa</i> Beal, 1967	Both hastisetae and spicisetae present	Head of hastisetae more than 3 times as long as wide at the widest point	Absent on notum I, but distinct and denticulate on nota II–III and abdominal terga I–IX	Distal epipharyngeal sensillae arranged in one group (enclosed in distinct ring) of 6	Middle 4 setae of labro-epipharyngeal margin consisting of 2 spatulate, broad inner (Mp) and 2 stout, narrow (p2) outer setae
<i>Trogoderma</i> Dejean, 1821	Both hastisetae and spicisetae present	Head of hastisetae less than 3 times as long as wide at the widest point	Not always well defined; if present usually absent on abdominal segment VIII, but in those rare instances when it is present, it is weak and interrupted at several points	Distal epipharyngeal sensillae arranged in one group (enclosed in distinct ring) of 4-6(7) or sometimes in two rings of 2 and 4	Middle 4 setae of labro-epipharyngeal margin consisting of 2 spatulate, broad inner (Mp) and 2 stout, narrow (p2) outer setae

Table 2.3 Continuation of the comparison of larval characteristics for some of the genera of Dermestidae co-occurring with *Ctesias serm*.

Character	# of stemmata	Antenna	Maxillary palp	Pretarsal setae
Genus				
<i>Dermestes</i> Linnaeus, 1758	6 ⁵	Antennal segment 2 more than twice (3–4x) as long as segment 3; sensorium arising from apex of segment 2 and never terminates at apex of segment 3	4 segments	Equal
<i>Thylodrias</i> Motschulsky, 1839	3	Antennal segment 2 much narrower and shorter than segment 1 and half as long as segment 3; sensorium arising from apex of segment 2 and terminates at middle of segment 3	4 segments	Unequal (anterior seta shorter than posterior one)
<i>Trinodes</i> Dejean, 1821	6	Antennal segment 2 nearly as long and broad, as segment 1 and less than half as long as segment 3; sensorium arising from basal third of segment 2 and terminates almost at apex of segment 3	4 segments	Unequal (anterior seta shorter than posterior one)
<i>Attagenus</i> Latreille, 1802	4–5 ⁶	Antennal segment 2 more than twice (3–4x) as long as segment 3; sensorium arising from apex of segment 2 and never terminates at apex of segment 3	4 segments	Probably variable – depends on species
<i>Anthrenus</i> Geoffroy, 1762	6	Antennal segment 2 more than twice as long as segment 3; sensorium arising from apex of segment 2 and never terminates at apex of segment 3	3 segments	Variable – depends on species
<i>Ctesias</i> Stephens, 1830	6	Antennal segment 2 more than twice as long as segment 3; sensorium in ventral position – only sometimes slightly extending above apex of segment 2	3 segments	Subequal
<i>Globicornis</i> Latreille, 1829	6	Antennal segment 2 twice as long as segment 3; sensorium in ventral position, below the apex of segment 2	3 segments	Equal (e.g. <i>G. corticalis</i> , <i>G. emarginata</i> and <i>G. nigripes</i>)
<i>Megatoma</i> Herbst, 1792	5(?) ⁸	Antennal segment 2 twice as long as segment 3; sensorium in ventral position, below the apex of segment 2	3 segments	Equal
<i>Reesa</i> Beal, 1967	4	Antennal segment 2 not more than half as long as segment 3; sensorium in ventral position, below the apex of segment 2; antennal segment 2 with at least one seta (sometimes two setae)	3 segments	Subequal
<i>Trogoderma</i> Dejean, 1821	5	Antennal segment 2 not more than half as long as segment 3; antennal segment 2 either without setae or with one-two setae(c)	3 segments	Variable – depends on species

⁵ According to Zhantiev (2000) *Dermestes depressus* lacks stemmata.

⁶ According to Beal (1991)

⁷ After Peacock (1993: p. 37)

⁸ According to Kadej (2017)

Other differences involve morphology and the location of abdominal tufts of hastisetæ. In *Ctesias* and *Anthrenus* they are situated behind abdominal terga and always on membranous areas, while in *Globicornis* and *Megatoma* they are located on sclerotised areas on abdominal terga (and never on membranes behind the terga). *Trinodes* do not have hastisetæ. In *Ctesias* there are four tufts of hastisetæ (on the membranous area behind the abdominal terga IV–VII), while in *Anthrenus* there are only three (on the membranous area behind the abdominal terga V–VII). Additionally, in *Trogoderma*-like Megatomini such as *Megatoma*, dense brushes of hastisetæ are dark brown and compact (hastisetæ are shorter and densely packed under the terga), while in *Ctesias* the hastisetæ are lighter (= brown or yellowish brown), longer, and are loosely packed. For other features see Table 2. A key for identification of the genera of Dermestidae co-occurring with *Ctesias* is presented below.

A separate comment is required regarding pupae since, as for the larvae, there are no detailed descriptions of the morphology of this stage for *Ctesias* except for a brief description at the generic level by Donisthorpe (1897, p. 162, cf. Table 1). This genus now contains 26 species (Háva 2018). Here, for the first time, the morphological characteristics of the pupae of *C. serra* is presented. Lack of additional data for other species does not allow for any comparison with other representatives of that genus. Nevertheless, it is worthy to compare some pupal characteristics with available data of other pupa known within the Dermestidae.

Pupae of *C. serra* lack gin-traps. These occur in Dermestini Latreille, 1804 or Attagenini Laporte de Castelnau, 1840 and are thought to protect soft-bodied pupae from predators or parasites, like mites (Zhantiev 1976, Kiselyova and McHugh 2006). For this reason *C. serra* is similar to some pupae of Trinodini Casey, 1900, Thylodriini Semenov-Tian-Shanskiy, 1909 and Anthrenini Gistel, 1848, in which the gin-traps are either poorly developed or lacking. The pupae of the abovementioned taxa retain their larval exuviae to which they remain firmly attached via anchor setae. The same behavior was observed by Donisthorpe (1897, 1920) who reported that pupae of *C. serra* remain within the last exuvium which is interrupted from head to the last abdominal terga. The part of the dorsum that remains exposed is usually covered in long, soft or stiff hairs. The same can be seen on the dorsal side of the pupae of *Megatoma undata* (Linnaeus, 1758) shown by Kadej (2017, p. 65). Long hairs have not been observed on the dorsum of *C. serra* but these could have been lost before examination of material.

It is noteworthy that the pupae of *C. serra* have two urogomphi-like processes on the IX abdominal segment. Typical urogomphi are mainly known from the larval stages of *Dermestes* Linnaeus, 1758, *Orphilus* Erichson, 1846 and *Thorictodes* Reitter, 1875 (Beal 1991). These characters are also present in pupae of *Dermestes*. However, it is also known that there are some genera that do not possess urogomphi as larvae, but do so as pupae (Kiselyova and McHugh 2006). Such situation has been observed in the larval and pupal stages of *Attagenus* Latreille, 1802 and *Novelsis* Casey, 1900. The presence of urogomphi in the pupa is probably an ancestral character. According to Kiselyova and McHugh (2006) their presence in *Dermestes* and in some Attagenini Laporte de Castelnau, 1840 may be a retained plesiomorphic trait. It is difficult to distinguish whether

these two processes I have reported in pupa of *C. serra* are typical urogomphi and they may only a deformation of the pupa. To exclude atypical morphology or to confirm the presence of urogomphi, longer series of individuals are required to answer this question. If these processes are indeed typical urogomphi, than this observation in *Ctesias* contradicts the statement of Kiselyova and McHugh (2006) that the rest of Dermestidae lack urogomphi and pupate within the last larval exuvium. Regardless, the example of *C. serra* sheds new light on our knowledge of pupal stages and indicates the need for further studies of these unexplored stages. Kiselyova and McHugh's analysis demonstrates how useful pupal characteristics can be in the investigation of phylogenetic relationships between genera. The need for further research is also justified by the example of the recently described pupae of *M. undata* (Kadej 2017). The pupae here do not have either urogomphi or processes, although as in *C. serra*, this species is classified within the Megatomini Leach, 1815. Therefore, it is also likely that pupal characteristics would be an excellent taxonomic tool for the Dermestidae. There is a great need to discover characteristics which may be useful taxonomic features for distinguishing genera or even enabling species identification. Thus, more taxonomic studies are needed in order to assess the value of different morphological characters of pupae in the Dermestidae.

Key to identification genera co-occurring with *Ctesias* Stephens, 1830

- 1 Urogomphi on IX abdominal tergite dorsally.....***Dermestes* L., 1758**
- Urogomphi on IX abdominal tergite dorsally absent.....**2**
- 2 Abdominal tufts of hastisetae absent**3**
- Abdominal tufts of hastisetae present.....**5**
- 3 Body cylindrical, broadest at notum I; with caudal brush of long, slender setae.....***Attagenus* Latreille, 1802**
- Body compact, broadest at abdominal segment I, without caudal brush of long, slender set**4**
- 4 Body uniformly light golden brown; posterior margin of terga with club-shaped setae; antennal segment 2 much narrower and shorter than segment 1 and half as long as segment 3; sensorium arising from apex of segment 2 and terminates at middle of segment 3 ***Thyodrias* Motschulsky, 1839**
- Body brown or greyish with sclerotised brown strip along anterior and posterior margin of tergite, enclosing a transverse membranous area on each side; posterior margin of terga without club-shaped setae – black, long, stout spicisetae present; antennal segment 2 nearly as long and broad, as segment 1 and less than half as long as segment 3; sensorium arising from basal third of segment 2 and terminates almost at apex of segment 3..... ***Trinodes* Dejean, 1821**
- 5 Abdominal tufts of hastisetae on membranous area behind terga**6**
- Abdominal tufts of hastisetae on terga (never on membranous area behind terga)**7**

- 6 Body broadest at notum III and constricted behind abdominal terga I–III; caudal brush of long, slender setae present; abdominal tufts of hastisetae on membranous area behind terga IV–VII; sterna I–VIII with central median line with strongly sclerotised and shiny strip ***Ctesias* Stephens, 1830**
- Body broadest at abdominal terga IV–VI and not constricted; slender setae present on terga IX, but not so long as it is in *Ctesias*; abdominal tufts of hastisetae on membranous area behind terga V–VII ***Anthrenus* Geoffroy, 1762**
- 7 Antennal segment 2 twice as long as segment 3 **8**
- Antennal segment 2 not more than half as long as segment 3 **9**
- 8 Terga brown to dark brown; abdominal tufts of hastisetae on terga V–VIII
..... ***Globicornis* Latreille, 1829**
- Terga yellowish brown (in some species thoracic terga I–III with distinctly dark brown patches at sides, sometimes extending to middle on terga II and III); abdominal tufts of hastisetae on terga VI–VIII ***Megatoma* Herbst, 1792**
- 9 Abdominal tufts of hastisetae on terga I–VIII; antecostal suture absent on notum I, but distinct and denticulate on nota II–III and abdominal terga I–IX; head of hastisetae more than 3 times as long as wide at the widest point
..... ***Reesa* Beal, 1967**
- Abdominal tufts of hastisetae on terga V (VI)–VIII; antecostal suture not always well defined; if present usually absent on abdominal segment VIII, but in those rare instances when it is present, it is weak and interrupted at several points head of hastisetae less than 3 times as long as wide at the widest point...
..... ***Trogoderma* Dejean, 1821**

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Porifera collection of the Italian National Antarctic Museum (MNA), with an updated checklist from Terra Nova Bay (Ross Sea)

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Abstract

This new dataset presents occurrence data for Porifera collected in the Ross Sea, mainly in the Terra Nova Bay area, and curated at the Italian National Antarctic Museum (MNA, section of Genoa). Specimens were collected in 331 different sampling stations at depths ranging from 17 to 1,100 meters in the framework of 17 different Italian Antarctic expeditions funded by the Italian National Antarctic Research Program (PNRA). A total of 807 specimens, belonging to 144 morphospecies (i.e., 95 taxa identified at species level and 49 classified at least at the genus level) is included in the dataset. Nearly half (45%) of the species reported here correspond to species already known for Terra Nova Bay. Out of the remaining 55% previously unknown records,

under a third (~29%) were classified at the species level, while over a quarter (~26%) were ascribed to the genus level only and these would require further study. All vouchers are permanently curated at the MNA and are available for study to the scientific community. A 3D model of an uncommon species from the Ross Sea, i.e. *Tethyopsis brondstedti* (Burton, 1929), is also presented and will be made available for outreach purposes.

Keywords

Antarctica, Italian National Antarctic Museum, Porifera, Ross Sea, Terra Nova Bay, 3D models

Purpose

Since the very beginning of the Italian expeditions in the Ross Sea, which started in 1985, sponges have been one of the most studied taxa, due both to the high number of species found in the Terra Nova Bay area (where Italy has its coastal station “Mario Zucchelli”, 74°41'42"S, 164°7'23"E), and to the strong community of Italian taxonomists specialized in Antarctic sponges. This sponge collection has been progressively growing each year, with new collections of specimens at each expedition of the Italian National Antarctic Research Program (PNRA) in the Terra Nova Bay area. These specimens have been studied and exchanged among different researchers for comparisons and publications for years, they represented the base of a PhD thesis (Sarà 2002), and then the whole collection was finally acquired by the Italian National Antarctic Museum (MNA, section of Genoa, Italy) in 2010. Since then the sponge collection has been restored, crosschecked for distributional data with the original labels, matched with a collection of permanent glass slides of spicules and updated in terms of taxonomy or new identifications of specimens.

This study aims at publishing and valorising occurrence data of the Porifera collected during several scientific expeditions of the Italian National Antarctic Program (PNRA) in the Ross Sea.

This collection is amongst the largest for Antarctic sponges and despite it being mainly focused on the Terra Nova Bay area, it represents a *unicum* given the amount of permanent glass slides with spicules available and the large database of images of sponges documented *in situ*, or freshly collected.

This distributional dataset is the fifth MNA contribution to the Antarctic Biodiversity Portal (www.biodiversity.aq), which is the thematic Antarctic node for both the Ocean Biogeographic Information System (AntOBIS) and the Global Biodiversity Information Facility (ANTABIF), based on materials stored at the MNA. The previous contributions were: Ghiglione et al. (2013), Piazza et al. (2014), Selbmann et al. (2015) and Cecchetto et al. (2017).

Project description

Project title: Antarctic Porifera in the collection of the Italian National Antarctic Museum (MNA)

Curator and Promoter: Stefano Schiaparelli

Personnel: Claudio Ghiglione, Maria Chiara Alvaro, Matteo Cecchetto, Simone-pietro Canese, Rachel Downey, Alice Guzzi, Claudio Mazzoli, Paola Piazza, Hans Tore Rapp, Antonio Sarà, Stefano Schiaparelli

Funding: The specimens were collected during different Antarctic expeditions funded by the Italian National Antarctic Research Program (PNRA). The complete list of research projects is reported here (in *italic* is the project name or category under the PNRA program, followed by the project code, the expedition number, and the corresponding year):

- *Necton e risorse da pesca* 2.1.4.6, III expedition (1987/1988)
- *Oceanografia & Benthos* 2.1.4.3, III expedition (1987/1988)
- *Benthos* 3.2.1.2.5, V expedition (1989/1990)
- *Oceanografia geologica* 3.2.1.4, V expedition (1989/1990)
- *Ecologia e biogeochimica dell'Oceano Meridionale* 2d.2, IX expedition (1993/1994)
- *Ecologia e biogeochimica dell'Oceano Meridionale* 2d.2, X expedition (1994/1995)
- *Ecologia e biogeochimica dell'Oceano Meridionale – ROSSMIZE* 2d.2, XI expedition (1995/1996)
- *Ecologia e biogeochimica dell'Oceano Meridionale* 2b.3, XIII expedition (1997/1998)
- *Struttura e dinamica delle cenosi marine di Baia Terra Nova* 2b.3.1, XIV expedition (1998/1999)
- *L'area marina protetta di Baia Terra Nova: struttura e variazioni a breve e lungo termine* 8.5, XV expedition (1999/2000)
- *Processi genetici e significato paleoclimatico e paleoceanografico dei CARBONati marini biogenici in ANTartide – CARBONANT* 4.7, XVII expedition (2001/2002)
- *L'area marina protetta di Baia Terra Nova: struttura e variazioni a breve e lungo termine* 8.5, XVII expedition (2001/2002)
- *The costal ecosystem of Victoria Land coast: distribution and structure along the latitudinal gradient* 2002/8.6, XVIII expedition (2002/2003)
- *The costal ecosystem of Victoria Land coast: distribution and structure along the latitudinal gradient* 2002/8.6, XIX expedition (2003/2004)
- *Batteri e cianobatteri antartici: biodiversità e produzione di composti con potenzialità applicative in biotecnologia* 2004/1.6, XX expedition (2004/2005)
- *Variabilità della ventilazione polare abissale e suo impatto sulla circolazione globale – PolarDOVE* 2004/8.2, XXI expedition (2005/2006)
- *L'ecosistema costiero di Baia Terra Nova – Latitudinal Gradient Project* 2006/08.01, XXV expedition (2009/2010)
- *Ecologia e ciclo vitale di specie ittiche costiere del Mare di Ross* 2004/08.04, XXV expedition (2009/2010)
- *Barcoding of Antarctic Marine Biodiversity – BAMBi* 2010/A1.10, XXVII expedition (2011/2012)
- *Diversità genetica spazio temporale di endoparassiti delle regioni polari: uno studio per la valutazione dell'impatto dei cambiamenti globali sulle reti trofiche marine* 2009/A1.09, XXVIII expedition (2012/2013)

- *Barcoding of Antarctic Marine Biodiversity – BAMBi 2010/A1.10, XXVIII expedition (2012/2013)*
- *Vulnerabilità dei pesci polari al cambiamento climatico: ciclo vitale, habitats e relazione con il ghiaccio marino in *Pleuragramma antarcticum* 2010/A1.11, XXVIII expedition (2012/2013)*
- *Barcoding of Antarctic Marine Biodiversity – BAMBi 2010/A1.10, XXIX expedition (2013/2014)*
- *Integrità dell'ecosistema marino antartico come presupposto per lo studio dell'interazione parassita-ospite: un approccio genetico, molecolare ed immunologico 2013/AZ1.09, XXIX expedition (2013/2014)*

Study area description: The specimens were collected in the Ross Sea sector of the Southern Ocean in a bathymetric range from 17 to 1,100 meters of depth (Fig. 1).

Design description: Data were assembled by revising all the distributional records of the specimens deposited in the collections of the Italian Antarctic National Museum (MNA, section of Genoa, Italy). The samples were collected in the framework of several expeditions of the Italian National Antarctic Research Program (PNRA) from 1987 to 2014.

Methods

Method step description: See sampling description below and flowchart of Fig. 2.

Study extent description: The distributional data considered here originated from 331 different sampling stations ranging between 17 and 1,100 metres of depth (Figs 1, 3, 4, 5).

Sampling description: Sampling was performed on a total of 331 different sampling stations (Figs 1, 3, 4, 5) through the deployment of a variety of sampling gears, mainly dredges (Charcot dredge, Naturalist dredge, Triangular dredge and Picard dredge) and Van Veen grabs of different volumes. Some samples were also opportunistically collected by long fishing lines, mid water trawls (that touched the bottom due to a failure of the winches), trammel nets, and other fishing nets that provided additional material to standard techniques. Some samples, from the XIV, XV, XVII, XVIII, XXIII, and XXV PNRA expeditions, were hand-collected by SCUBA diving. In one case (i.e., *Sycetta antarctica* (Brøndsted, 1931), MNA 8847) the specimen was collected beached and sampling coordinates refer to the coastline. In another case, i.e., *Lycopodina* cf. *vaceleti* (van Soest and Baker 2011), the specimen record is based on a georeferenced ROV video frame (Fig. 6) and no physical samples are available.

Once the material has been acquired by the MNA after sorting and shipment activities, all the specimens were classified to the lowest possible taxonomical resolution. In the years, different researchers have contributed to the classification of the specimens: Homoscleromorpha were studied by Maurizio Pansini and Antonio Sarà; Demospongiae and Hexactinellida were studied by Rachel Downey, Antonio Sarà, Marco Bertolino, Maurizio Pansini and Barbara Calcinai; Calcarea were studied by Hans Tore Rapp.

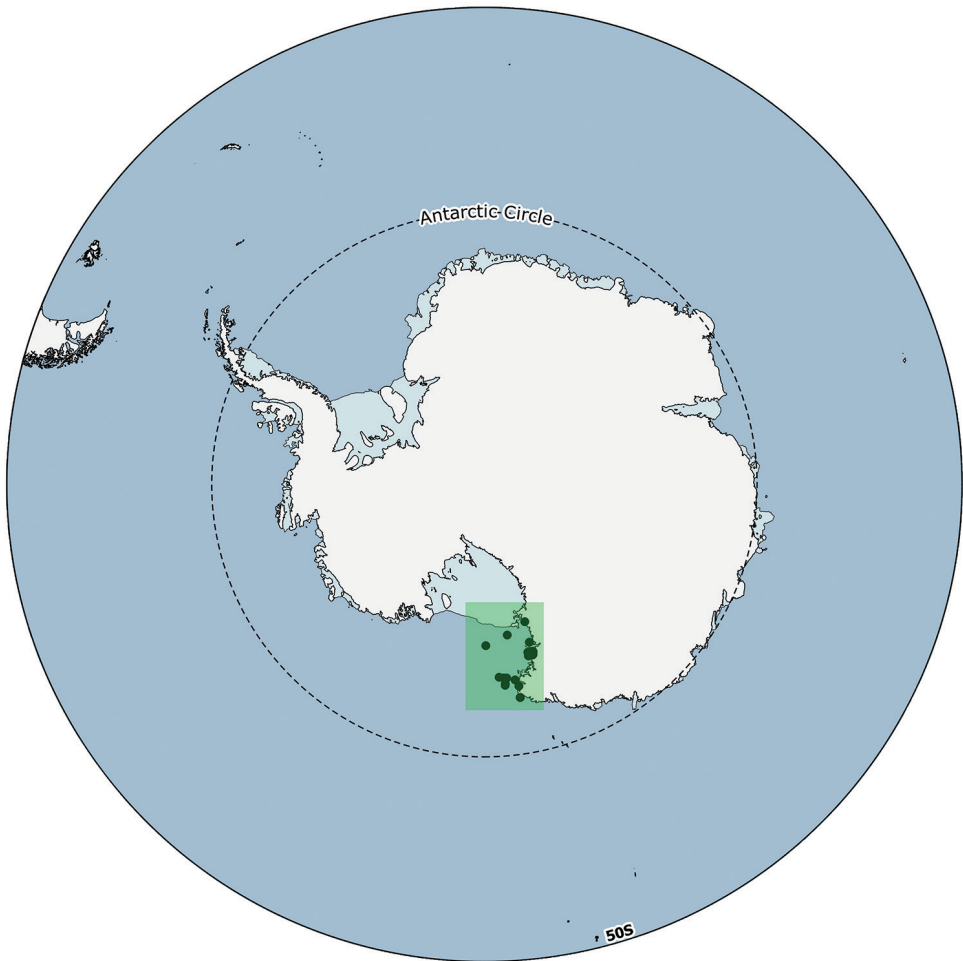


Figure 1. General map of Antarctica with the study area highlighted (green box). Detailed maps of the sampling areas are provided in Figs 3, 4, and 5.

The present dataset has been formatted in order to fulfil the Darwin Core standard protocol required by the OBIS scheme (<http://www.iobis.org/manual/lifewatchqc/>) and according to the SCAR-MarBIN Data Toolkit (available at <http://www.scarmarbin.be/documents/SM-FATv1.zip>). The dataset was uploaded in the ANTOBIS database (the geospatial component of SCAR-MarBIN).

Vouchers are now preserved in 90% ethanol (~53% of the entire collection), frozen (~23%), or dried (~24%). The data flow chart illustrating the sampling, sorting, and storing procedures for specimens, data, and image availability is reported in Fig. 2.

Quality control description: Specimens were identified at the finest possible taxonomic resolution and only those that have been classified at least at the genus level were included in the present dataset. During all the phases of sorting, classification, and storage of samples at the MNA, quality control and data cleaning have been un-

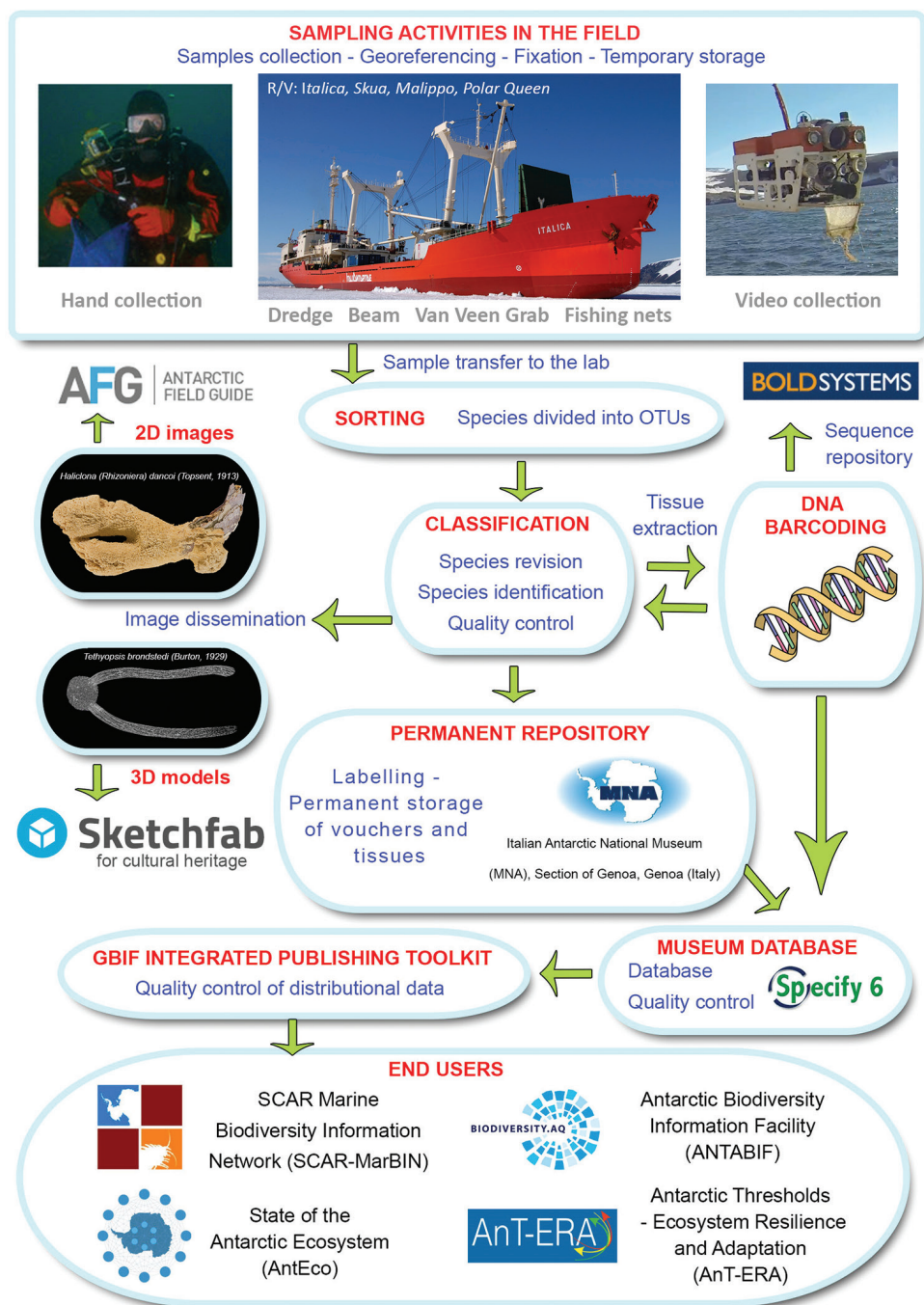


Figure 2. Flowchart depicting major stages in dataset development and publishing.

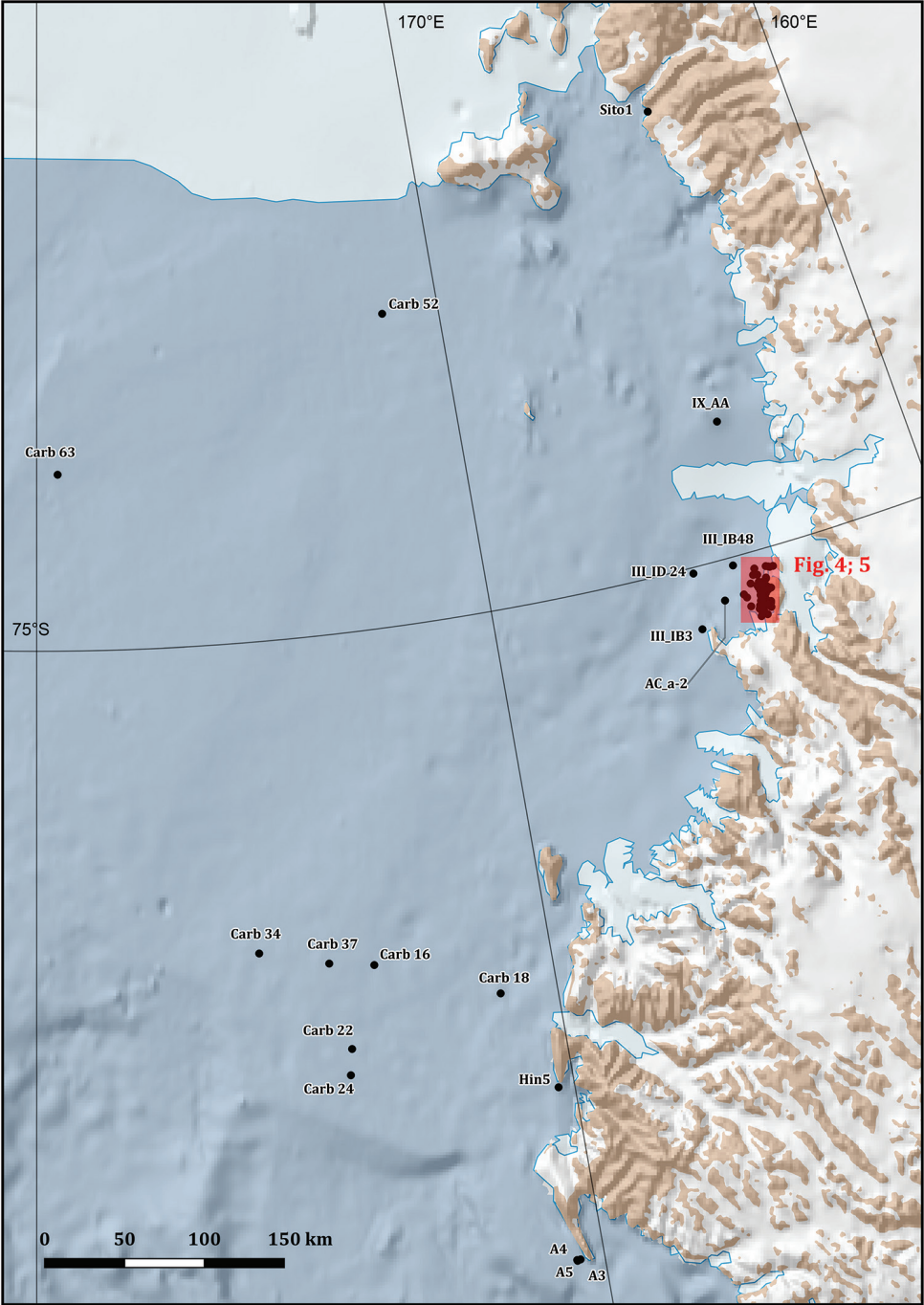


Figure 3. Sampling stations map in the Ross Sea area, Antarctica. The area in the red box is depicted, at a finer spatial scale, in Figs 3, 4.

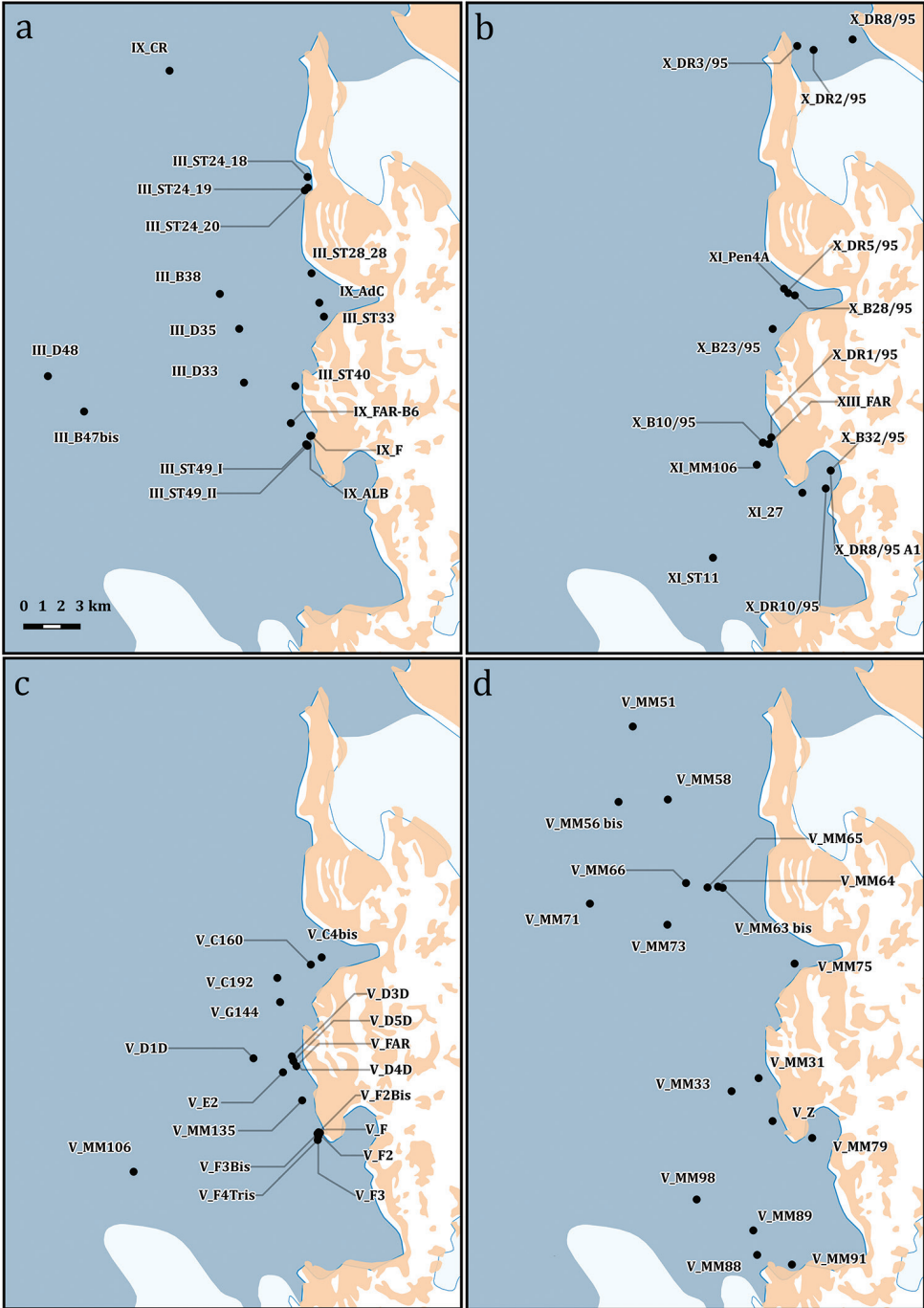


Figure 4. Detailed map of the sampling stations of the PNRA expeditions III, V, IX, X, XI, XIII.

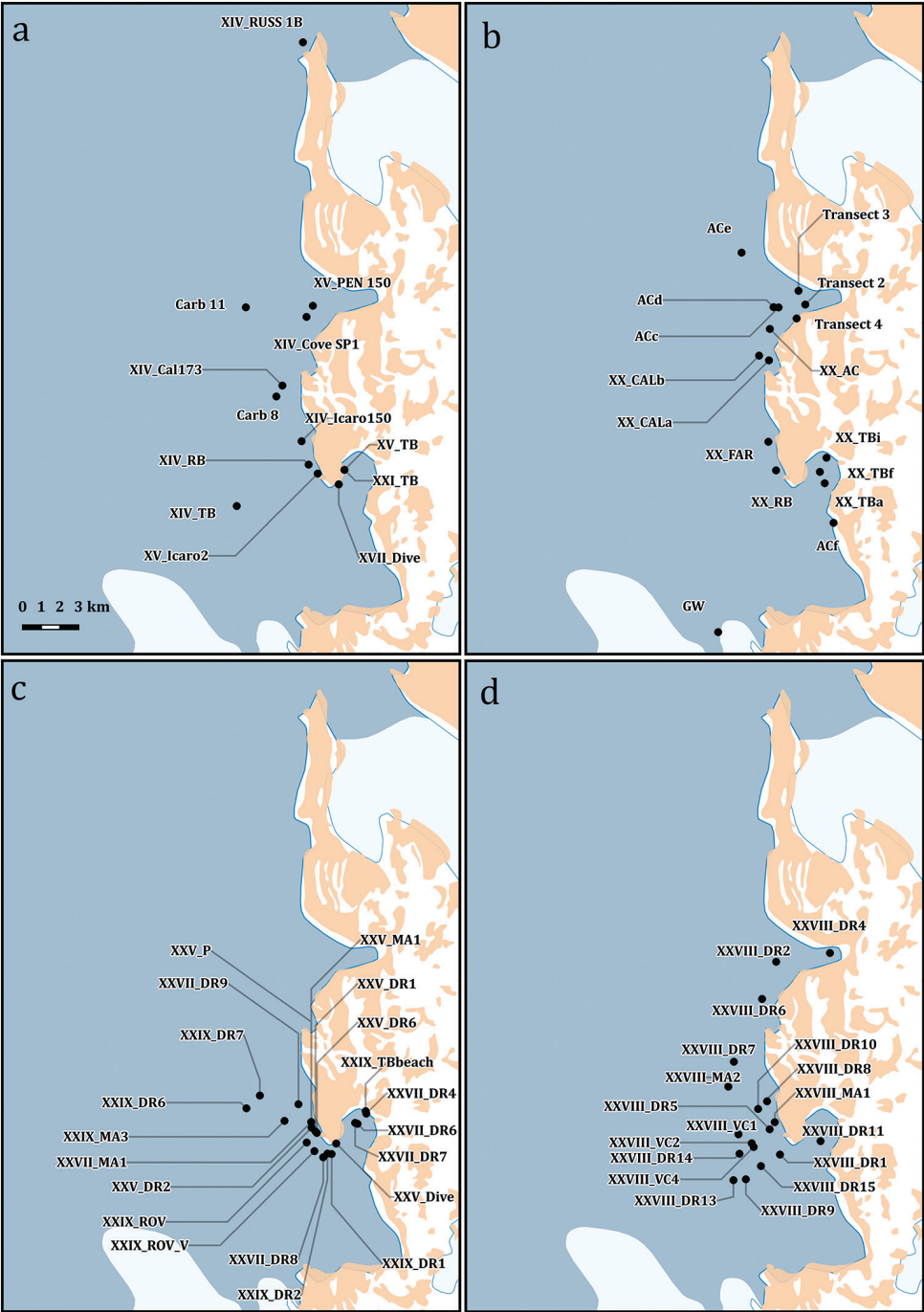


Figure 5. Detailed map of the sampling stations of the PNRA expeditions II XIV, XV, XVII, XX, XXI, XXV, XXVII, XXVIII, XXIX.

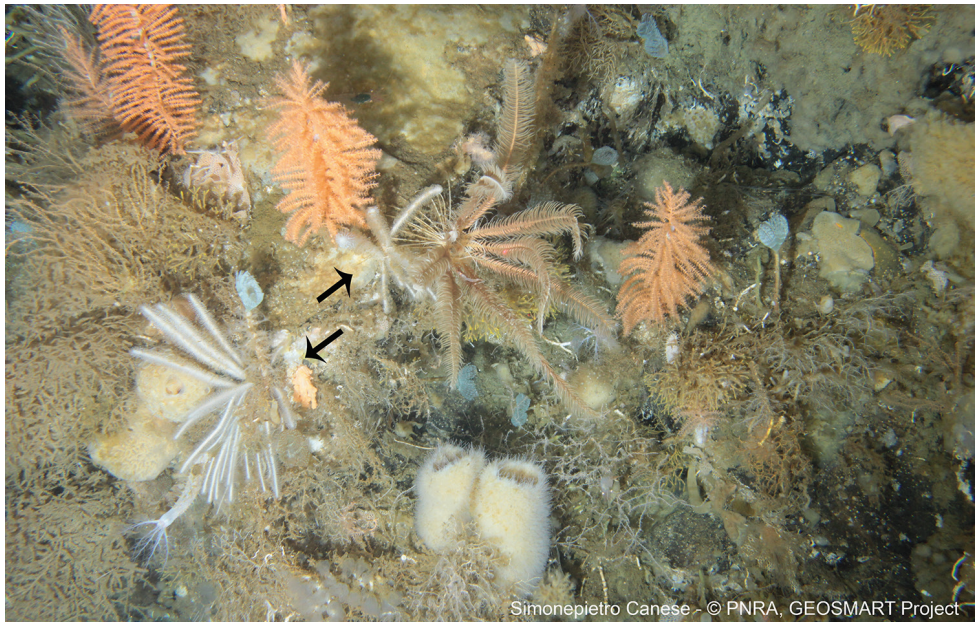


Figure 6. ROV video frame reporting the presence (arrows) of the species *Lycopodina* cf. *vaceleti* (van Soest & Baker, 2011) at Terra Nova Bay.

dertaken at various stages in order to produce high quality data and make consistent cross-references between the database and sample labels. The MNA uses an SQL-based database (Specify 6) and a R-Shiny web application to manage its collections and link all the data (photos, glass slides, etc.) to the physical samples.

Due to the large amount of researchers that managed the material before the acquisition of the collection by the MNA, all the specimens and distributional records were rechecked and then imported in the museum database. During this phase it emerged that only ~75% of the Porifera collection fulfilled the expected minimum set of data fields to be included in GBIF. The remaining ~25% of the material present in the MNA collection can be divided in a ~7%, represented by material not yet classified, and another ~18% represented by old materials that cannot be ascribed to a specific sampling station due to missing labels or incomplete information about sampling.

Georeferencing on board each of the different research vessels is based on the interpolation of GPS satellite receivers and a gyrocompass. Station coordinates and sampling events were recorded during sampling activities based on various GPS systems.

Taxonomic coverage

General taxonomic coverage description: This dataset focuses on all classes (Calcarea, Demospongiae, Hexactinellida, and Homoscleromorpha) of the Phylum Porifera (Kingdom Animalia), and includes a total of 807 specimens belonging to 144 mor-

phospecies (with 95 taxa classified at species level and 49 at genus level), and representing 12 orders and 30 families (Fig. 7). Nearly half (~45%; 65 species) of the collected taxa correspond to records already known for the Terra Nova Bay area (Cattaneo et al. 2000; Cerrano et al. 2000; Sarà et al. 1990, 1992), about one third (~29%; 42 species) correspond to new records classified at specific level, and just over a quarter (~26%; 37 species) to new records classified at the genus level. The new records for Terra Nova Bay are reported with the acronym 'NR' immediately after the species name in the following taxonomic ranks section.

Permanent glass slides with the spicules are available for ~88% of the species of the MNA collection while SEM pictures are available for ~31% of the species (some of which are already available on the Antarctic Field Guide project at: <http://afg.biodiversity.aq/pdfs/144164-a-field-guide-to-antarctic-sponges.pdf>).

In a few cases (i.e. *Plakina monolopha* Schulze, 1880, MNA 1715, MNA 1753; *Plakina trilopha* Schulze, 1880, MNA 1504; *Eurypon miniaeum* Thiele, 1905, MNA 9106), there is no voucher and only glass slides with spicules are available. Another species, i.e., *Lycopodina* cf. *vaceleti* (van Soest & Baker, 2011), is without a MNA collection code, as it was identified from an ROV video frame (Fig. 6), and represents the first record of this carnivorous sponge at Terra Nova Bay and, globally, the second record of this species (Van Soest and Baker 2011). This species was identified thanks to Rob Van Soest and Claire Goodwin and represents an important “visual record” because only a few pictures of carnivorous sponges *in situ* are available. In the case of the species *Tedania* (*Tedaniopsis*) *oxeata* Topsent, 1916 (MNA 8244), the specimen record was obtained by using the ROV arms (Fig. 8).

The MNA collection also includes several sponge holotypes (Table 1). Some species (i.e. *Haliclonissa verrucosa* Burton, 1932 with vouchers MNA 915, MNA 916, MNA 917, MNA 918; *Anoxycalyx* (*Scolymastra*) *joubini* (Topsent, 1916) with voucher MNA 928; *Lissodendoryx* (*Ectyodoryx*) *nobilis* (Ridley & Dendy, 1886) with voucher MNA 863) were previously published in other manuscripts (i.e. Fondi et al. 2014;

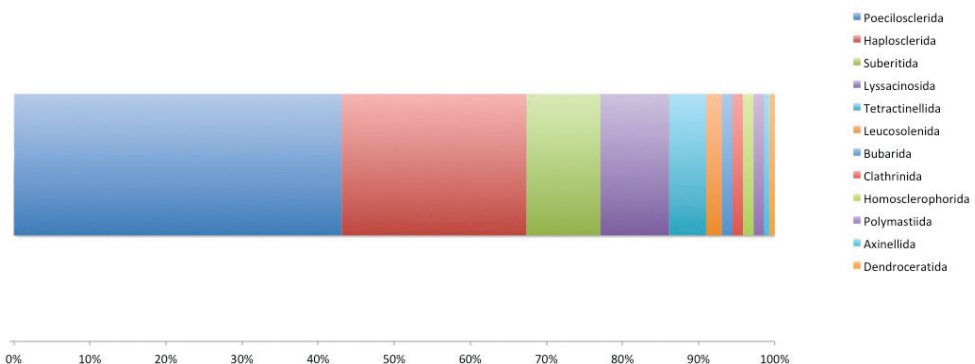


Figure 7. Taxonomic coverage (reported in percentage of specimens per Order) of MNA Porifera collection. Poecilosclerida cover ~43% of the collection specimens, followed by Haplosclerida (~24%), Suberitida (~10%) and Lyssacinoida (~9%). The remaining orders cover less than ~14%.



Figure 8. ROV video frame of the species *Tedania (Tedaniopsis) oxeata* Topsent, 1916 (MNA 8244) found at 250 meters of depth before the use of the ROV arm to obtain a fragment.

Table 1. Sponge holotypes stored at the MNA.

MNA	Species
MNA 832	<i>Microxina sarai</i> Calcinai & Pansini, 2000
MNA 833	<i>Microxina lanceolata</i> Calcinai & Pansini, 2000
MNA 834	<i>Lissodendoryx (Ectyodoryx) minuta</i> Calcinai & Pansini, 2000
MNA 835	<i>Iophon terranova</i> Calcinai & Pansini, 2000
MNA 865	<i>Crella (Crella) aurantiaca</i> Bertolino, Calcinai & Pansini, 2009
MNA 888	<i>Mycale (Aegogropila) denticulata</i> Bertolino, Calcinai & Pansini, 2009

Orlandini et al. 2014; Papaleo et al. 2013; 2012; Mangano et al. 2009; Romoli et al. 2011) without an MNA catalogue number which have been assigned after the publication. In the collection is also present an uncommon sponge (i.e. *Tethyopsis brondstedii* (Burton, 1929), MNA 2839) which was previously sampled as a single specimen during the Terra Nova expedition in 1910, in the eastern sector of the Ross Sea, in particular in the regions of McMurdo Sound and Terra Nova Bay and at depth range of 402–965 meters (Burton 1929). According to records obtained from the Ocean Biogeographic Information System (OBIS 2018), this species had not been re-found for close to a century, until the NIWA (New Zealand National Institute of Water and Atmospheric Research) campaigns of 2004 and 2008 in the Ross Sea. During these recent expeditions, 17 specimens of this species were obtained. Two additional speci-

mens of this small, idiosyncratic species have now been identified also from the 2002 MNA Carbonant expeditions in the Terra Nova Bay region. *Tethyopsis* Stewart, 1870, is a genus containing only nine known species, with the vast majority of these distinctive species occurring in the Southern Hemisphere, in particular, New Zealand and Antarctica (Van Soest et al. 2018). Online records of the global distributions of this genus from OBIS (2018) indicate that only ca. 200 specimens of this genus have been previously found prior to this publication.

Taxonomic ranks

Kingdom: Animalia

Phylum: Porifera

Class: Calcarea

Orders: Clathrinida, Leucosolenida

Families: Achramorphidae, Grantiidae, Leucettidae, Sycettidae

Genera: *Leucetta*, *Leucandra*, *Megapogon*, *Sycetta*

Species: *Leucandra* cf. *gausapata* (NR), *Leucettidae* sp.1 (NR), *Leucetta antarctica* (NR), *Megapogon raripilus* (NR), *Sycetta antarctica* (NR)

Kingdom: Animalia

Phylum: Porifera

Class: Demospongiae

Orders: Axinellida, Bubarida, Dendroceratida, Haplosclerida, Poecilosclerida, Polymastiida, Suberitida, Tetractinellida

Families: Acanthidae, Ancorinidae, Bubaridae, Chalinidae, Cladorhizidae, Coelosphaeridae, Crellidae, Darwinellidae, Dendrocellidae, Halichondriidae, Hymedesmiidae, Isodictyidae, Latrunculiidae, Microcionidae, Mycalidae, Myxillidae, Niphatiidae, Phloedictyidae, Polymastiidae, Raspailiidae, Stylocordylidae, Suberitidae, Tedaniidae, Tetillidae

Genera: *Acanthorhabdus*, *Antarctotetilla*, *Artemisina*, *Asbestopluma*, *Bubaris*, *Calyx*, *Cinachyra*, *Clathria*, *Crella*, *Dendrilla*, *Eurypon*, *Fibulia*, *Halichondria*, *Haliclona*, *Haliclonissa*, *Hemigellius*, *Homaxinella*, *Hymeniacidon*, *Inflatella*, *Iophon*, *Isodictya*, *Kirkpatrickia*, *Latrunculia*, *Lissodendoryx*, *Lycopodina*, *Microxina*, *Mycale*, *Myxilla*, *Myxodoryx*, *Phorbis*, *Plicatellopsis*, *Plocamionida*, *Polymastia*, *Pseudosuberites*, *Sphaerotylus*, *Stylocordyla*, *Suberites*, *Tedania*, *Tethyopsis*

Species: *Acanthorhabdus fragilis* (NR), *Antarctotetilla leptoderma*, *Artemisina apollinis* (NR), *Artemisina* cf. *tubulosa*, *Artemisina* sp.1 (NR), *Artemisina tubulosa*, *Asbestopluma* (*Asbestopluma*) *belgicae*, *Asbestopluma* (*Asbestopluma*) sp. (NR), *Bubaris* cf. *vermiculata* (NR), *Bubaris vermiculata* (NR), *Calyx arcuarius*, *Calyx* cf. *arcuarius*, *Calyx kerguelensis* (NR), *Cinachyra antarctica* (NR), *Cinachyra barbata*, *Cinachyra* cf. *antarctica* (NR), *Cinachyra* cf. *barbata*, *Cinachyra* sp.1 (NR), *Clathria* (*Axosuberites*) *nidificata*, *Clathria* (*Clathria*) cf. *toxipraedita*, *Clathria* (*Clathria*) *toxipraedita*,

Clathria (Microciona) antarctica (NR), *Clathria (Thalysias) flabellata* (NR), *Crella (Crella) aurantiaca* (NR), *Crella (Pytheas) stylifera* (NR), *Dendrilla membranosa*, *Eurypon miniaceum*, *Fibulia cribriporosa* (NR), *Fibulia maeandrina* (NR), *Halichondria (Halichondria) panicea* (NR), *Haliclona (Gellius) cf. flagellifera* (NR), *Haliclona (Gellius) cf. glacialis* (NR), *Haliclona (Gellius) cf. spongiosa* (NR), *Haliclona (Gellius) glacialis* (NR), *Haliclona (Gellius) tylotoxa* (NR), *Haliclona (Haliclona) cf. penicillata*, *Haliclona (Haliclona) penicillata*, *Haliclona (Rhizoniera) cf. dancoi*, *Haliclona cf. divulgata* (NR), *Haliclona cf. scotti* (NR), *Haliclona (Rhizoniera) dancoi*, *Haliclona divulgata* (NR), *Haliclona (Soestella) cf. chilensis* (NR), *Haliclona sp.* (NR), *Haliclona sp.1* (NR), *Haliclona sp.2* (NR), *Haliclona sp.3* (NR), *Haliclona sp.4* (NR), *Haliclona virens* (NR), *Haliconissa verrucosa* (NR), *Hemigellius bidens* (NR), *Hemigellius calyx* (NR), *Hemigellius cf. fimbriatus*, *Hemigellius fimbriatus*, *Hemigellius pilosus*, *Homaxinella balfourensis*, *Homaxinella cf. balfourensis*, *Homaxinella cf. flagelliformis*, *Homaxinella flagelliformis*, *Hymeniacidon insutus* (NR), *Inflatella belli*, *Inflatella cf. coelosphaeroides* (NR), *Inflatella sp.1* (NR), *Iophon terranova*, *Iophon unicorn*, *Isodictya conulosa*, *Isodictya erinacea*, *Isodictya kerguelenensis*, *Isodictya microchela* (NR), *Isodictya setifera*, *Isodictya sp.1* (NR), *Isodictya sp.2* (NR), *Isodictya toxophila* (NR), *Kirkpatrickia coulmani* (NR), *Kirkpatrickia variolosa*, *Latrunculia (Latrunculia) biformis*, *Lissodendoryx sp.1* (NR), *Lissodendoryx (Ectyodoryx) anacantha* (NR), *Lissodendoryx (Ectyodoryx) antarctica*, *Lissodendoryx (Ectyodoryx) minuta*, *Lissodendoryx (Ectyodoryx) nobilis*, *Lissodendoryx (Ectyodoryx) ramilobosa*, *Lissodendoryx (Lissodendoryx) flabellata*, *Lycopodina cf. vacaleti* (NR), *Microxina benedeni*, *Microxina cf. simplex* (NR), *Microxina charcoti*, *Microxina lanceolata*, *Microxina sarai*, *Microxina simplex* (NR), *Microxina sp.1* (NR), *Mycale (Aegogropila) denticulata* (NR), *Mycale (Aegogropila) magellanica*, *Mycale (Mycale) tridens*, *Mycale (Oxymycale) acerata*, *Mycale fibrosa*, *Mycale sp.1* (NR), *Myxilla (Burtonanchora) asigmata*, *Myxilla (Myxilla) elongata*, *Myxilla (Myxilla) mollis* (NR), *Myxilla sp.1* (NR), *Myxodoryx cf. hanitschi*, *Myxodoryx hanitschi*, *Phorbas glaberrimus*, *Phorbas nexus* (NR), *Plicatellopsis antarctica*, *Plocamionida gaussiana* (NR), *Polymastia invaginata*, *Pseudosuberites montiniger*, *Pseudosuberites nudus*, *Sphaerotylus antarcticus*, *Stylocordyla cf. chupachups*, *Stylocordyla chupachups*, *Suberites caminatus*, *Suberites mollis* (NR), *Suberites sp.1* (NR), *Tedania (Tedaniopsis) cf. charcoti*, *Tedania (Tedaniopsis) charcoti*, *Tedania (Tedaniopsis) massa* (NR), *Tedania (Tedaniopsis) oxeata* (NR), *Tedania (Tedaniopsis) tantula*, *Tedania sp.1* (NR), *Trachytodania spinata* (NR), *Tethyopsis brondstedti* (NR)

Kingdom: Animalia

Phylum: Porifera

Class: Hexactinellida

Order: Lyssacinoida

Family: Rossellidae

Genera: *Anoxycalyx*, *Rossella*

Species: *Anoxycalyx (Scolymastra) joubini*, *Rossella antarctica* (NR), *Rossella cf. antarctica* (NR), *Rossella cf. longstaffi* (NR), *Rossella cf. villosa* (NR), *Rossella fibulata* (NR),

Rossella levis (NR), *Rossella nuda* (NR), *Rossella* cf. *nuda* (NR), *Rossella racovitzae* (NR), *Rossella* sp.1 (NR), *Rossella* sp.2 (NR), *Rossella* sp.3 (NR)

Kingdom: Animalia

Phylum: Porifera

Class: Homoscleromorpha

Order: Homosclerophorida

Family: Plakinidae

Genus: *Plakina*

Species: *Plakina monolopha*, *Plakina trilopha*

Spatial coverage

General geographic description:

Ross Sea, Antarctica (Figs 1, 3, 4, 5)

Coordinates:

PNRA III expedition: -74.64833, -74.96667; 164.00000, 164.61167

PNRA V expedition: -74.63450, -74.90400; 164.02433, 164.47500

PNRA IX expedition: -74.71667, -75.76333; 164.04280, 164.19058

PNRA X expedition: -74.68557, -74.89367; 163.78557, 164.14752

PNRA XI expedition: -74.66833, -74.78333; 164.03333, 164.29167

PNRA XIII expedition: -74.71357, 164.13772

PNRA XIV expedition: -74.69405, -74.89950; 163.93748, 164.28620

PNRA XV expedition: -74.69667, -74.77658; 164.05327, 164.12868

PNRA XVII expedition: -72.51267, -76.76817; 164.09721, 179.50533

PNRA XVIII expedition: -77.56570, 163.61163

PNRA XIX expedition: -71.30667, -72.28667; 170.29833, 170.48667

PNRA XX expedition: -74.63347, -74.80570; 164.00194, 164.98583

PNRA XXI expedition: -74.69667, 164.08000

PNRA XXV expedition: -74.69027, -74.70348; 164.10255, 164.13762

PNRA XXVII expedition: -74.68562, -74.71337; 164.03502, 164.14903

PNRA XXVIII expedition: -74.68090, -74.77737; 163.95400, 164.23640

PNRA XXIX expedition: -74.68602, -74.72242; 164.03486, 164.24206

Temporal coverage:

PNRA III expedition: January 6, 1988 - February 2, 1988

PNRA V expedition: December 24, 1989 - February 1, 1990

PNRA IX expedition: December 27, 1993 - January 29, 1994

PNRA X expedition: January 21, 1995 - February 8, 1995

PNRA XI expedition: February 5, 1996 - February 8, 1996

PNRA XIII expedition: February 19, 1998

PNRA XIV expedition: January 6, 1999 - March 3, 1999

PNRA XV expedition: January 25, 2000 - April 25, 2000

PNRA XVII expedition: January 8, 2002 - February 7, 2002

PNRA XVIII expedition: November 11, 2002

PNRA XIX expedition: February 14, 2004 - February 16, 2004

PNRA XX expedition: January 17, 2005 - February 11, 2005

PNRA XXI expedition: January 23, 2006

PNRA XXV expedition: December 13, 2009 - January 11, 2010

PNRA XXVII expedition: January 10, 2012 - February 3, 2012

PNRA XXVIII expedition: January 9, 2013 - January 31, 2013

PNRA XXIX expedition: January 16, 2014 - February 1, 2014

Natural collections description

Parent collection identifier: Italian National Antarctic Museum (MNA, section of Genoa, Italy)

Collection name: Porifera collection of the Italian National Antarctic Museum (MNA) - Data

Specimen preservation method: Part of the material collected during the expeditions was fixed in formalin and then transferred in ethanol (samples between 1985 and 2006), or was frozen immediately after collection and kept in the same condition in order to preserve the DNA quality and integrity. All samples are now stored in the collections of the Italian National Antarctic Museum (MNA, section of Genoa, Italy).

Virtual collection of vouchers and 3D models: The species used in the 3D model, *Tethyopsis brondstedti* (Burton, 1929) (MNA 2839, Fig. 9) presents a spherical body from which 2 fragile oscular tubes protrude from the upper part of the main sponge body, reminiscent of a bull head with horns. The long oscular tubes are believed to serve as both inhalant and exhalant orifices for the sponge (Hajdu et al. 1994). The surface of the sponge's main body is often found covered in small pebbles and other sandy debris, indicating that this species may live partially buried within the seabed sediment. The main sponge body is radial and is composed of oxeas (long spicules which are pointed at both ends) and triaenes (long spicules which are pointed at one end and the other is composed of three equal rays, reminiscent of a wind turbine). These triaenes can be bifurcated at each end of the ray (dichotriaene), the rays can be curved backwards (anatriaene), or are a triaene with only two rays, that are usually bifurcated at each end (orthodiaene). The oscular tubes of the sponge are composed of intricate layers of orthodiaenes. The main body of the sponge also contains tiny asters (star-shaped spicules, with rays radiating equally from a central point), which are composed of strongylasters (blunt-tipped or slightly bulbous ended rays) and oxyasters (with sharply pointed rays).

The model of the sponge was obtained through micro-CT imaging performed at the Department of Geosciences (University of Padova) by CM. A bench-top Skyscan 1172 micro-CT system (Bruker®), equipped with a Hamamatsu 100/250 microfocus X-ray

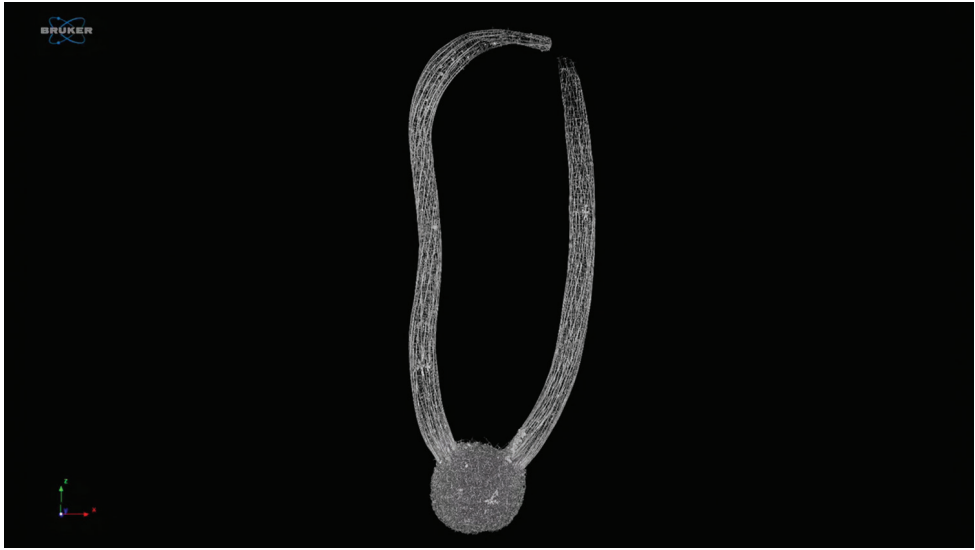


Figure 9. Video of the 3D model of *Tethyopsis brondstedii* (Burton, 1929) (MNA 2839), a very uncommon sponge only occurring in the Ross Sea. The diameter of the main spherical body is ~10 mm and the length/width of the oscular tubes are respectively ~30 mm and ~5 mm.

source (80 kV, 124 μ A) and a Hamamatsu C9300 11 megapixel camera (with a pixel size of 8.68 μ m) filtered by a 0.5 mm Aluminium foil was used. Projection images were acquired with 1200 ms exposure time, 2x2 binning mode, 0.30° rotation step over 360° rotation, averaged over 10 frames and in vertical random movement mode to minimise noise, providing an image pixel size of 13.2 μ m. An oversized sample option was applied with 4 connected scans, leading to a total acquisition time of about 1170 min. Post-acquisition reconstruction was performed using the NRecon (Bruker microCT®) software package, starting from raw projection images, and applying thermal correction, misalignment compensation, ring artefact reduction and beam hardening correction. Segmentation was then performed with CT Analyser (Bruker microCT®) software package, using a 3D adaptive thresholding procedure (mean of minimum and maximum value) within spherical kernels of radius 8 pixels, starting from a pre-determined pre-thresholding value. Resulting images were saved as monochrome (1 bit) bitmaps and imported in the CT-Vox (Bruker microCT®) software package to perform 3D rendering and animations. The model will be available on the MNA web site (www.mna.it) and on Sketchfab (<https://sketchfab.com/MNA>). The species chosen for the model corresponded to one of the few specimens collected in the Ross Sea area after the species description (Burton 1929).

Datasets

Dataset description: This dataset contains data about all four classes (Calcarea, Demospongiae, Hexactinellida and Homoscleromorpha) of the Phylum Porifera, based on

vouchers from the Ross Sea (with a special focus on Terra Nova Bay) curated at the MNA. In total, the dataset includes 144 different morphospecies, and a total of 807 specimens. Several studies were based on this dataset: Alvizu et al. (in press); Bertolino et al. 2009; Calcinai et al. 2000; Cattaneo-Vietti et al. 2000; Fondi et al. 2014; Mangano et al. 2009; Orlandini et al. 2014; Papaleo et al. 2012, 2013; Romoli et al. 2011; Sarà 2002; Sarà et al. 1992. The validity and synonyms of each species name were checked in WORMS (World Register of Marine Species; <http://www.marinespecies.org>; last check made on 2018-03-28). The Darwin Core elements included in the dataset are: ID, Institution code (i.e. the name of the institution where the samples are kept), basis of record, occurrence ID, catalogue number (i.e. MNA catalogue number), individual count, preparation (preservation method and more info about the sample, e.g., ETOH, dry, glass slides, etc.), event ID (i.e. original sampling station code), sampling protocol (sampling gear), event date, year, month, day, verbatim event date, field number (sampling station code as showed in the maps), event remarks (i.e., expedition), maximum depth meters, decimal latitude, decimal longitude, taxon ID, scientific name ID, scientific name, kingdom, phylum, class, order, family, genus, subgenus, specificEpithet, infraspecificEpithet, scientific name authorship, and taxon remarks. Some of the sampling stations are dredge stations, which have two sets of coordinates: the starting and end points. In these cases the coordinates reported in the dataset refer to the starting point of the dredge station.

Object name: Porifera collection of the Italian National Antarctic Museum (MNA) - Data

Character encoding: UTF-8

Format name: Darwin Core Archive format

Format version: 1.0

Distribution: http://ipt.biodiversity.aq/resource.do?r=mna_antarctic_porifera

Language: English

Metadata language: English

License of use: This dataset [Porifera collection of the Italian National Antarctic Museum (MNA) - Data] is made available under the Creative Commons Attribution License (CC-BY) 4.0: <http://www.creativecommons.org/licenses/by/4.0/legalcode>

Date of metadata creation: 2018-03-28

Hierarchy level: Dataset

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