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Two new genera of nematodes (Oxyurida, Hystrignathidae) parasites of Passalidae (Coleoptera) from the Democratic Republic of Congo

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Abstract

Two new genera and species parasitizing passalid beetles from the Democratic Republic of Congo are described. *Kongonema meyeri* **gen. n. sp. n**. is characterized by having females with the cervical cuticle unarmed, first cephalic annule cone-like and truncate, sub-cylindrical procorpus and genital tract didelphic-amphidelphic. The males of *K. meyeri* **gen. n. sp. n.** have the procorpus sub-cylindrical, the dorsal cuticle of the tail end thickened, a single large, median mammiform pre-cloacal papilla and a pair of small, pre-cloacal, sub-lateral papillae at a short distance before the level of the cloaca. *Lubanema decraemerae* **gen. n. sp. n.** is characterized by the body markedly fusiform, cuticle unarmed and strongly annulated, procorpus sub-cylindrical, isthmus as a constriction between procorpus and basal bulb, genital tract monodelphic-prodelphic and the posterior end rounded with a very short tail appendage.

Keywords

Nematoda, Hystrignathidae, *Kongonema*, *Lubanema*, Passalidae, Democratic Republic of Congo

Introduction

The family Hystrignathidae comprises 27 nominal genera with more than 100 species of monoxenous nematodes specific of the hind gut of passalid beetles. The family shows a mostly Gondwanian distribution, with taxa from North, Central and South America, West Indies, Africa and Australasia (Adamson and Van Waerebeke 1992). Of these areas, the Americas and West Indies present the highest generic and specific diversity.

In Africa, the group still remains neglected with most of the species restricted to their type localities. Théodoridès (1955) described the first African hystrignathids: *Artigasia pauliani* Théodoridès, 1955 and *A. geopetiti* Théodoridès, 1955 from Malagasian passalids. Later, Théodoridès (1958) described *A. pauliani* var. *joliveti* from the Democratic Republic of Congo. The status of this variety was analyzed by Adamson and Van Waerebeke (1992) who raised it to the rank of species. Baker (1967) recorded *Hystrignathus rigidus* Leidy, 1850 and *Xyo hystrix* Cobb, 1898 parasitizing three species of *Pentalobus* from Ghana. These two latter species had previously been described from North America and Australia, respectively. The main contribution to the knowledge of the family in the region was made by Van Waerebeke (1973), with the description of 14 species of *Artigasia* Christie, 1934 one of *Hystrignathus* Leidy, 1850 and the monotypic genus *Passalidophila* Van Waerebeke, 1973 all from Madagascar. The author also re-described *A. geopetiti* and recorded three types of males, unable to be assigned to their correct species. Van Waerebeke & Remillet (1982) described *Hystrignathus egalis* Van Waerebeke & Remillet, 1982 and *H. inegalis* Van Waerebeke & Remillet, 1982 from Ivory Coast.

This paper retakes the study on African hystrignathids, describing two new genera and species parasitizing passalid beetles from the Democratic Republic of Congo.

Material and methods

Several specimens of passalid beetles from the Democratic Republic of Congo (formerly Zaire) were examined in a parasitological survey during a research visit to the Royal Museum of Central Africa, Tervuren, Belgium. Eight specimens of *Didimus* sp. and two specimens of *Erionomus pilosus* Aurivillus, 1896 from Katale, Kivu region were included in this study, all collected during the Belgian expeditions to the Congo in the 1930´s and stored in 70% ethanol.

The hosts were dissected by practicing incisions in both pleural membranes and the intestines were extracted and kept in Petri dishes with 70% ethanol. The guts were excised and the parasites removed.

Nematodes were transferred and cleared in glycerine via slow evaporation method (Seinhorst 1959) and mounted in the same medium. The edges of the coverslips were sealed using nail polish. Measurements were made with a calibrated eyepiece micrometer attached to a compound microscope. De Man's ratios a, b, c and V% were calculated. Each variable is shown as the range followed by the mean plus standard deviation in parentheses; the number of measurements is also given. Micrographs were taken with an AxioCam digital camera attached to a Carl Zeiss AxioScop 2 Plus compound microscope. Line drawings were made with the softwares CorelDRAW X3 and Adobe Photoshop CS2 using the micrographs as templates. Scale bars of all plates are given in millimeters.

Some specimens were prepared for SEM as follows: they were dehydrated in a graded ethanol series, critical point-dried, mounted in aluminum stubs and coated in gold. SEM micrographs were taken at an acceleration voltage of 22-25 kV.

Classification at generic level was followed after Adamson & Van Waerebeke (1992). For comparison, one paratype of *Passalidophila exceptionalis* Van Waerebeke, 1973; deposited in the Nematode Collection of the Museum of Natural History, Paris (MNHN) was reviewed. The type material and vouchers of the next taxa are deposited in the Colección Helmintológica de las Colecciones Zoológicas (CZACC), Instituto de Ecología y Sistemática, Havana, Cuba; the Collection of the Royal Museum of Central Africa (RMCA), Tervuren, Belgium; the Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium and the Coleçao Helmintologica do Instituto Oswaldo Cruz (CHIOC), Rio de Janeiro, Brazil.

Systematics

Family Hystrignathidae Travassos, 1920

Genus *Kongonema* gen. n.

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http://species-id.net/wiki/Kongonema

Generic diagnosis. Female. Body comparatively robust. Cervical cuticle unarmed. Lateral alae present, from the oesophageal region to a short distance beyond the level of the anus. Posterior ends of the lateral alae rounded, forming lobes. Head bearing eight paired papillae. First cephalic annule cone-like, truncate, barely inflated, about two head-lengths long. Oesophagus consisting of a muscular sub-cylindrical procorpus, its base well set-off from the isthmus. Nerve ring encircling procorpus at its midpoint. Excretory pore post-bulbar. Reproductive system didelphic-amphidelphic. Eggs ovoid, ridged-shelled. Tail filiform and subulate.

Male. Body shorter and more slender than female. Cervical cuticle unarmed. Lateral alae present, from the oesophageal region to the level of the single median mammiform papilla. First cephalic annule inconspicuous. Stoma scarcely developed. Oesophagus with a sub-cylindrical procorpus, well set-off from the short isthmus. Nerve ring encircling procorpus at its posterior half. Excretory pore post-bulbar. Monorchic. Testis outstretched. Spicule absent. Posterior end ventrally curved, tapering abruptly, forming a very short, rounded tail appendage. Dorsal cuticle of the tail end thickened. A single large, median mammiform pre-cloacal papilla present. A pair of small, pre-cloacal, sub-lateral papillae located at a short distance before the level of the cloaca.

Type species. *Kongonema meyeri* Morffe & García gen. n. sp. n. (monotypic genus).

Distribution. Democratic Republic of Congo.

Etymology. The generic name (neuter) is a combination of Kongo, after the main ethnic group in the country of this taxon, and the suffix –nema.

Kongonema meyeri sp. n.

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http://species-id.net/wiki/Kongonema_meyeri
Figs 1 A-G, 2 A-D, 3 A-E

Type material. ♀ holotype, Democratic Republic of Congo, Kivu Region, Katale, 1°19'S, 29°22'E; in *Didimus* sp.; 4.V.1939; Hautmann coll.; CZACC 11.4653. Paratypes: 10♀♀, same data as holotype, CZACC 11.4654-11.4663; 10♀♀, same data as holotype, RMCA; 4♀♀, same data as holotype, CHIOC; ♂, same data as holotype, CZACC 11.4664; ♂, same data as holotype, RMCA.

Additional material. Vouchers: 2♀♀, Democratic Republic of Congo, Kivu Region, Katale, 1°19'S, 29°22'E; in *Didimus* sp.; 4.V.1939; Hautmann coll., RBINS. 2♀♀, Democratic Republic of Congo, Kivu Region, Katale, 1°19'S, 29°22'E; in *Erionomus pilosus*; 4.V.1939; Hautmann coll.; CZACC 11.4665-11.4666; 2♀♀, same data as the latter, RMCA;

Measurements. Holotype (female) a = 12.15, b = 5.06, c = 7.26, V% = 58.08, total length = 1.670, maximum body width = 0.138, first cephalic annule (length×width) = 0.013×0.038, stoma length = 0.050, procorpus length = 0.260, isthmus length = 0.020, diameter of basal bulb = 0.058, total length of oesophagus = 0.330, nerve ring to anterior end = 0.185, excretory pore to anterior end = 0.440, vulva to posterior end = 0.700, anus to posterior end = 0.230, eggs = 0.123×0.050 (n = 1).

Paratypes (females) (n = 24) a = 8.65-13.08 (10.68 ± 0.90 n = 23), b = 4.30-5.03 (4.71 ± 0.71 n = 21), c = 5.65-7.45 (6.43 ± 0.37 n = 23), V% = 53.02-58.82 (55.91 ± 1.43 n = 23), total length = 1.400-1.670 (1.530 ± 0.075 n = 23), maximum body width = 0.120-0.170 (0.144 ± 0.012 n = 24), first cephalic annule (length×width) = 0.013-0.025×0.038-0.043 (0.016 ± 0.003×0.041 ± 0.002 n = 19), stoma length = 0.033-0.050 (0.045 ± 0.005 n = 19), procorpus length = 0.210-0.270 (0.244 ± 0.013 n = 20), isthmus length = 0.020-0.033 (0.024 ± 0.003 n = 22), diameter of basal bulb = 0.053-0.070 (0.061 ± 0.004 n = 24), total length of oesophagus = 0.283-0.350 (0.324 ± 0.014 n = 21), nerve ring to anterior end = 0.148-0.190 (0.172 ± 0.011 n = 21), excretory pore to anterior end = 0.320-0.490 (0.402 ± 0.046 n = 23), vulva to posterior end = 0.620-0.750 (0.674 ± 0.038 n = 23), anus to posterior end = 0.200-0.280 (0.239 ± 0.019 n = 23), eggs = 0.120-0.133×0.043-0.063 (0.125 ± 0.004×0.051 ± 0.006 n = 26).

Paratypes (males) (n = 2) a = 15.67-17.33 (16.50 ± 1.18 n = 2), b = 3.47-3.58 (3.52 ± 0.08 n = 2), c = 121.33-125.33 (123.33 ± 2.83 n = 2), total length = 0.910-0.940 (0.925 ± 0.021 n = 2), maximum body width = 0.053-0.060 (0.056 ± 0.005 n = 2), procorpus length = 0.250 (n = 2), isthmus length = 0.018-0.020 (0.019 ± 0.002 n =

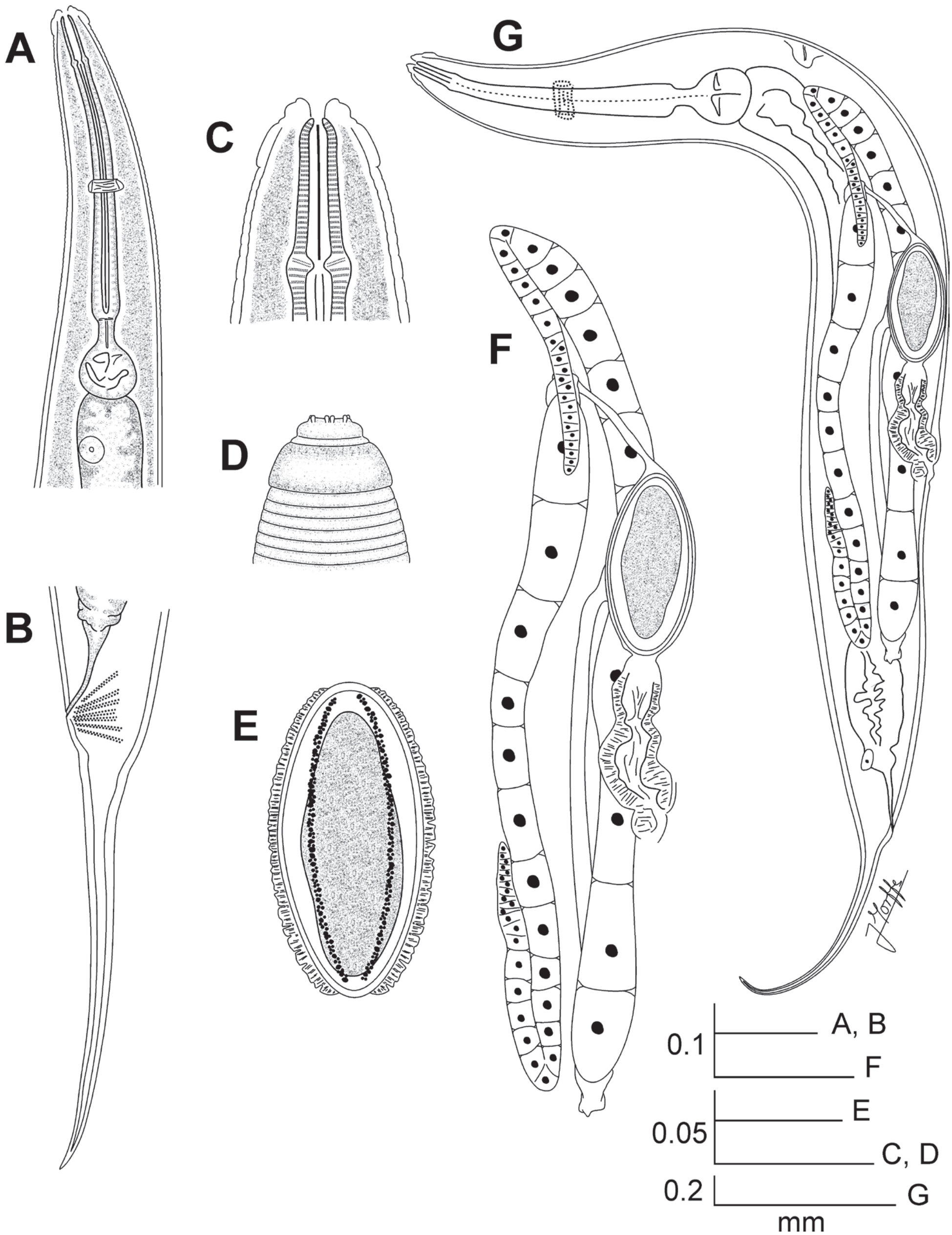

Figure 1. *Kongonema meyeri* gen. n. sp. n. Female. **A** Oesophageal region, ventral view **B** Tail, lateral view **C** Cephalic end, internal view **D** Cephalic end, external view **E** Egg **F** Reproductive system, lateral view **G** Entire nematode, lateral view.

2), diameter of basal bulb = 0.035 (n = 2), total length of oesophagus = 0.263 (n = 2), nerve ring to anterior end = 0.138-0.148 (0.143 ± 0.007 n = 2), excretory pore to anterior end = 0.290-0.330 (0.310 ± 0.028 n = 2), cloacae to posterior end = 0.008 (n = 2).

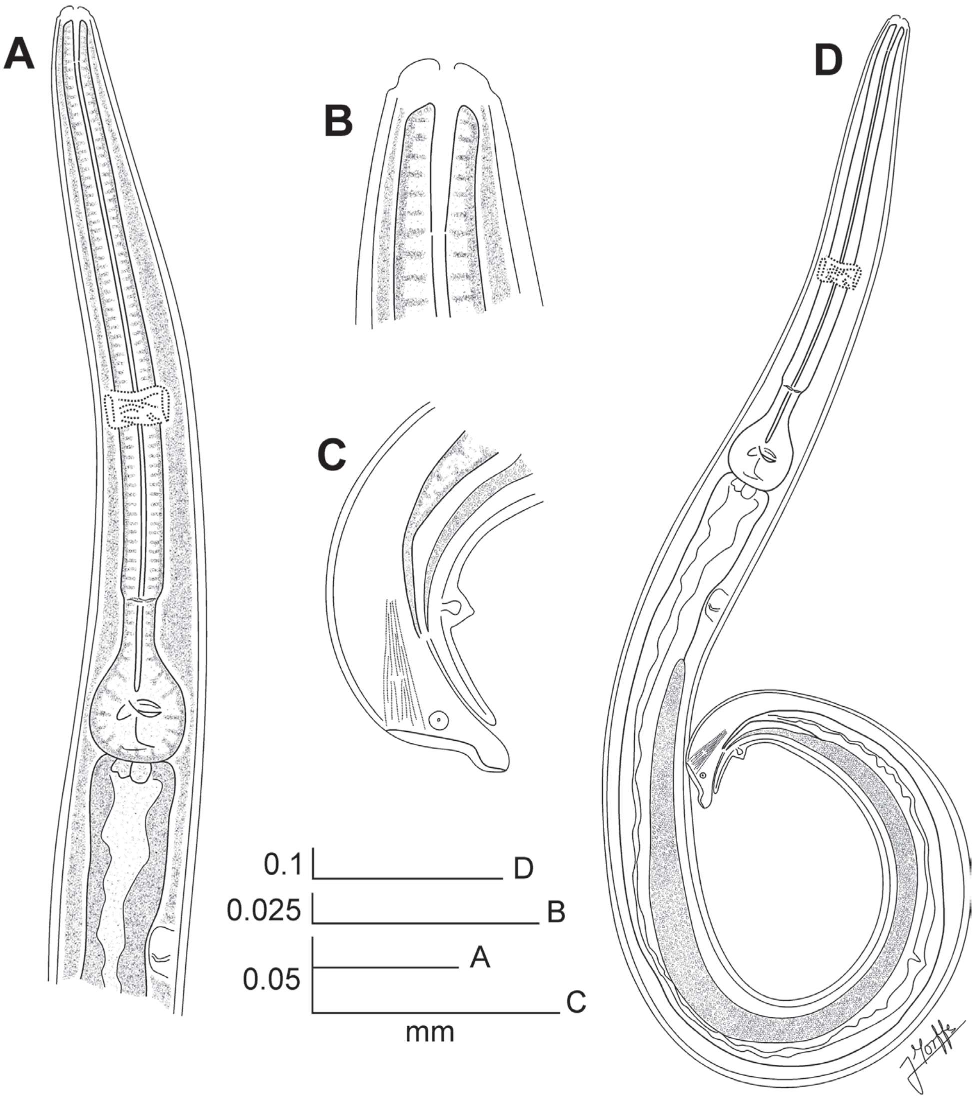

Figure 2. *Kongonema meyeri* gen. n. sp. n. Male. **A** Oesophageal region, lateral view **B** Cephalic end, internal view **C** Posterior end, lateral view **D** Entire nematode, lateral view.

Specimens from *Erionomus pilosus*. Females (n = 4) a = 9.46-10.75 (10.06 ± 0.68 n = 4), b = 4.75-4.97 (4.87 ± 0.09 n = 4), c = 6.58-7.13 (6.82 ± 0.23 n = 4), V% = 55.56-61.59 (57.75 ± 2.72 n = 4), total length = 1.640-1.750 (1.703 ± 0.046 n = 4), maximum body width = 0.153-0.185 (0.170 ± 0.015 n = 4), first cephalic annule (length×width) = 0.018-0.020×0.043-0.048 (0.019 ± 0.001×0.045 ± 0.002 n = 4), stoma length = 0.048-0.053 (0.050 ± 0.003 n = 4), procorpus length = 0.255-0.275 (0.267 ± 0.009 n = 4), isthmus length = 0.020-0.025 (0.023 ± 0.002 n = 4), diameter of basal bulb = 0.068-0.075 (0.071 ± 0.004 n = 4), total length of oesophagus = 0.330-0.360

(0.350 ± 0.014 n = 4), nerve ring to anterior end = 0.185-0.195 (0.189 ± 0.004 n = 4), excretory pore to anterior end = 0.420-0.510 (0.475 ± 0.040 n = 4), vulva to posterior end = 0.630-0.760 (0.720 ± 0.61 n = 4), anus to posterior end = 0.230-0.260 (0.250 ± 0.014 n = 4), eggs = 0.120-0.130×0.048-0.065 (0.126 ± 0.004×0.058 ± 0.007 n = 7).

Description. Female. Body comparatively robust, widening from the base of the first cephalic annule, maximum body diameter at level of the vulva, then tapering towards anus. Cervical cuticle unarmed, markedly annulated (annuli *ca.* 5-7 µm). Rest of the body with marked annuli decreasing their width towards the level of the anus. Subcuticular longitudinal striae present. Lateral alae *ca.* 9 µm wide, from the oesophageal region (*ca.* 30 µm before the level of the nerve ring) to a very short distance beyond the level of the anus. Posterior ends of the lateral alae rounded, forming short lobes. Head well developed, set-off from body by a single, deep groove and bearing eight rounded, paired papillae. Amphids pore-like, laterally situated. Mouth sub-triangular in shape. First cephalic annule cone-like, truncate, barely inflated, about two head-lengths long. Stoma comparatively long, about three first cephalic annule lengths long, surrounded by an oesophageal collar. Oesophagus consisting of a muscular, sub-cylindrical procorpus, its base slightly wider and well set-off from the short isthmus. Basal bulb subspherical, valve plate well developed. Intestine simple, sub-rectilinear, anterior portion dilated. Rectum short, anus not prominent, as a crescent-like slit. Nerve ring encircling procorpus at about its midpoint. Excretory pore situated at about half of a body width posterior to basal bulb. Genital tract didelphic-amphidelphic, both ovaries reflexed. Anterior ovary reflexed behind the excretory pore, posterior ovary reflexed at about a body width before the anus. Distal flexures of ovaries about one body width-length long. Oöcytes in single rows. Vulva a median transverse slit slightly displaced to the posterior half of body, lips prominent. Vagina muscular, forwardly directed. Eggs ovoid, bearing eight longitudinal, rough, ridges on the shell. Tail comparatively long, filiform, subulate, ending in a sharp point.

Male. Body shorter than female, comparatively slender, posterior region ventrally curved. Cervical cuticle unarmed. Sub-cuticular longitudinal striae present. Lateral alae from the oesophageal region (about three body-widths posterior to the cephalic end) to the level of the single mammiform papilla (about a body-width before the level of anus). Head not set-off from body. First cephalic annule not developed. Stoma not defined. Oesophagus consisting of a sub-cylindrical procorpus, well set-off from the short isthmus. Basal bulb rounded, valve plate well developed. Intestine simple, anterior portion slightly dilated. Nerve ring encircling procorpus at its posterior half, about 65% of its length. Excretory pore situated at about 1.5 body-widths posterior to basal bulb. Monorchic. Testis outstretched, arising at a short distance behind the excretory pore. Spicule absent. Dorsal cuticle of the tail region thickened. A single, large, pre-cloacal ventromedian mammiform papilla situated at about a body width before the posterior end. A pair of small, pre-cloacal, sub-lateral papillae situated at a short distance before the level of the cloaca. Tail region becoming sharp visibly from the beginning of the cuticular thickening, until forming a very short tail appendage, its tip rounded.

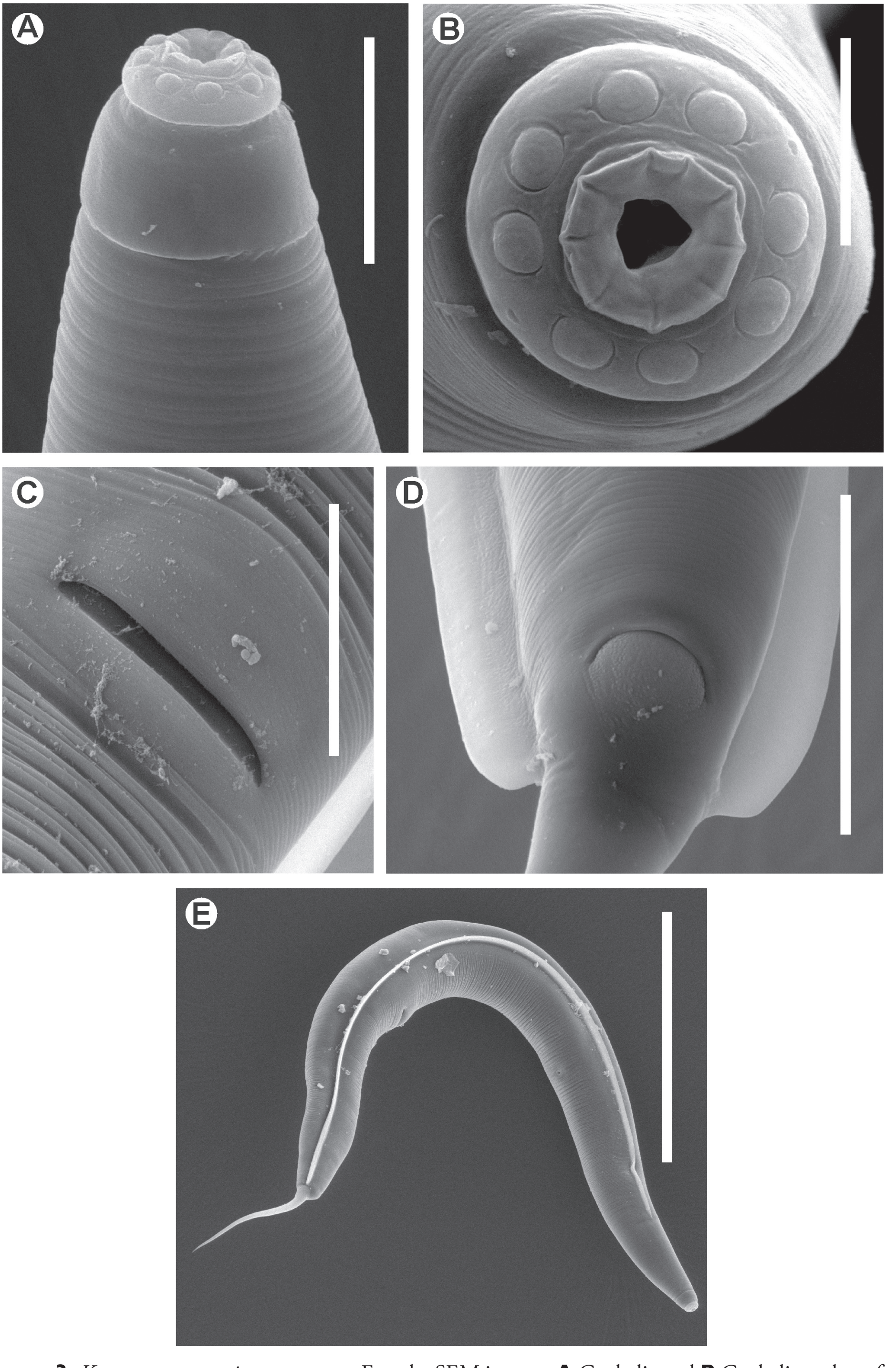

Figure 3. *Kongonema meyeri* gen. n. sp. n. Female. SEM images. **A** Cephalic end **B** Cephalic end, *en face* view **C** Vulva **D** Anus and end of lateral alae **E** Habitus, lateral view. Scale lines: A. 0.025 mm, B. 0.01 mm, C, D. 0.04 mm, E. 0.3 mm.

Discussion. There are three genera of hystrignathids the female of which present the cervical cuticle unarmed, procorpus sub-cylindrical and reproductive system digonant: *Anomalostoma* Cordeira, 1981; *Coynema* (Coy, García & Alvarez, 1993) Morffe & García, 2011 and *Ventelia* Travassos & Kloss, 1958. The first differs by having the anterior region of the procorpus strongly swollen, surrounding the stoma (Cordeira 1981). The stoma of *Kongonema* gen. n. is surrounded only by an oesophageal collar, as occur in many hystrignathids. *Anomalostoma* lacks an evident first cephalic annule *vs.* conspicuous first cephalic annule of *Kongonema* gen. n.

Females of *Coynema* can be segregated by the basal dilatation of its procorpus and the anterior region of the intestine notably inflated, forming a saccular structure (Morffe and García 2011). Both traits are absent in *Kongonema* gen. n., which procorpus increases its diameter slightly and gradually towards its base and the fore region of the intestine is only moderately inflated, without the saccular structure mentioned above. The oviduct next to the vagina forms a loop in *Coynema*, instead of the straight oviduct of the present genus.

The males of *Kongonema* gen. n. resemble their counterparts of *Coynema* (only close genus where the male is known) by lacking of spicule and by having a similar arrangement of the copulatory papillae: the ventromedian pre-cloacal papilla (typical of Hystrignathidae) and another pair of small sub-lateral pre-cloacal papillae. *Kongonema* gen. n. differs by having a sub-cylindrical procorpus, without the basal dilation and by lacking the saccular region of the intestine characteristic of *Coynema*. The posterior end of *Kongonema* gen. n. forms a short, rounded tail appendage *vs.* the sharp tail of *Coynema.*

On the other hand, *Ventelia* has the procorpus barely set-off from the isthmus, since the posterior third of the procorpus decreases its diameter. The hind procorpus of *Kongonema* gen. n. increases its diameter slightly and is well differentiated from the isthmus.

Type host. *Didimus* sp. (Coleoptera: Passalidae).

Other host. *Erionomus pilosus* Aurivillus, 1896 (Coleoptera: Passalidae).

Site. Gut caeca.

Type locality. Katale, Kivu region, Democratic Republic of Congo.

Etymology. Specific epithet dedicated to Dr. Marc de Meyer, curator of the Entomological Collection of the Royal Museum of Central Africa, Tervuren, Belgium. In appreciation of his kind help by permitting access to the material assessed.

Genus *Lubanema* gen. n.

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http://species-id.net/wiki/Lubanema

Generic diagnosis. Female. Body notably robust and fusiform. Posterior end strongly rounded, bearing a terminal, very short, conical tail appendage. Cuticle unarmed, markedly annulated until the level of the anus. Lateral alae wide, from the oesophageal region to the level of the anus. Posterior ends of the alae almost forming a straight angle with the body axis, slightly convex and with short lobes in their margins. First cephalic annule cone-like, slightly inflated, its margins convex. Oesophagus with a sub-cylindrical, muscular procorpus. Isthmus as a constriction between the procorpus and basal bulb. Nerve ring encircling procorpus at its posterior half. Excretory pore post-bulbar. Reproductive system monodelphic-prodelphic. Ovary stout. Eggs markedly ovoid, smooth-shelled.

Type species. *Lubanema decraemerae* Morffe & García gen. n. (monotypic genus).

Distribution. Democratic Republic of Congo.

Etymology. The generic name (neuter) is a combination of Luba, after one of the ethnic groups in the country, and the suffix –nema.

Lubanema decraemerae sp. n.

urn:lsid:zoobank.org:act:D480D872-86F3-4920-B9A7-550925CCD97A
http://species-id.net/wiki/Lubanema_decraemerae
Figs 4 A-G, 5 A-D

Type material. ♀ holotype, Democratic Republic of Congo, Kivu Region, Katale, 1°19'S, 29°22'E; in *Didimus* sp.; 4.V.1939; Hautmann coll.; CZACC 11.4667. Paratypes: ♀, same data as holotype, CZACC 11.4668; ♀, same data as holotype, RMCA.

Measurements. Holotype (female) a = 6.70, b = 5.97, c = 40.18, V% = 57.92, total length = 2.210, maximum body width = 0.330, first cephalic annule (length×width) = 0.020×0.070, stoma length = 0.048, procorpus length = 0.268, diameter of basal bulb = 0.108, total length of oesophagus = 0.370, excretory pore to anterior end = 0.520, vulva to posterior end = 0.930, anus to posterior end = 0.055, eggs = 0.168-0.173×0.075-0.080 (0.170 ± 0.004×0.078 ± 0.004 n = 2).

Paratypes (females) (n = 2) a = 4.44-6.36 (5.40 ± 1.36 n = 2), b = 3.66-5.68 (4.67 ± 1.43 n = 2), c = 34.45-38.18 (36.31 ± 2.64 n = 2), V% = 56.67 (n = 1), total length = 2.100-2.400 (2.250 ± 0.212 n = 2), maximum body width = 0.330 (n = 2), first cephalic annule (length×width) = 0.020×0.063-0.065 (0.020×0.064 ± 0.002 n = 2), stoma length = 0.043-0.045 (0.044 ± 0.002 n = 2), procorpus length = 0.275-0.300 (0.288 ± 0.018 n = 2), diameter of basal bulb = 0.108 (n = 2), total length of oesophagus = 0.370-0.400 (0.385 ± 0.021 n = 2), nerve ring to anterior end = 0.223 (n = 1), excretory pore to anterior end = 0.410-0.600 (0.505 ± 0.134 n = 2), vulva to posterior end = 1.040 (n = 1), anus to posterior end = 0.043-0.055 (0.049 ± 0.009 n = 2), eggs = 0.183×0.078 (n = 1).

Description. Female body large, notably robust and fusiform, widening gradually from the base of the first cephalic annule, reaching maximum width near mid-body, then tapering softly towards the posterior end that rounds off abruptly. A comparatively very short, conical tail appendage with its tip rounded arises terminally from the posterior end. Cervical cuticle unarmed, with marked annule (*ca.* 13 µm wide), extending to the rest of body, until level of the anus. Lateral alae thick, *ca.* 55 µm wide, extending from the hind third of the procorpus to the level of the anus. Posterior ends of lateral alae almost forming a straight angle with the body axis, slightly convex, their external margins forming a very short lobe. Head bearing eight rounded, paired papillae, set-

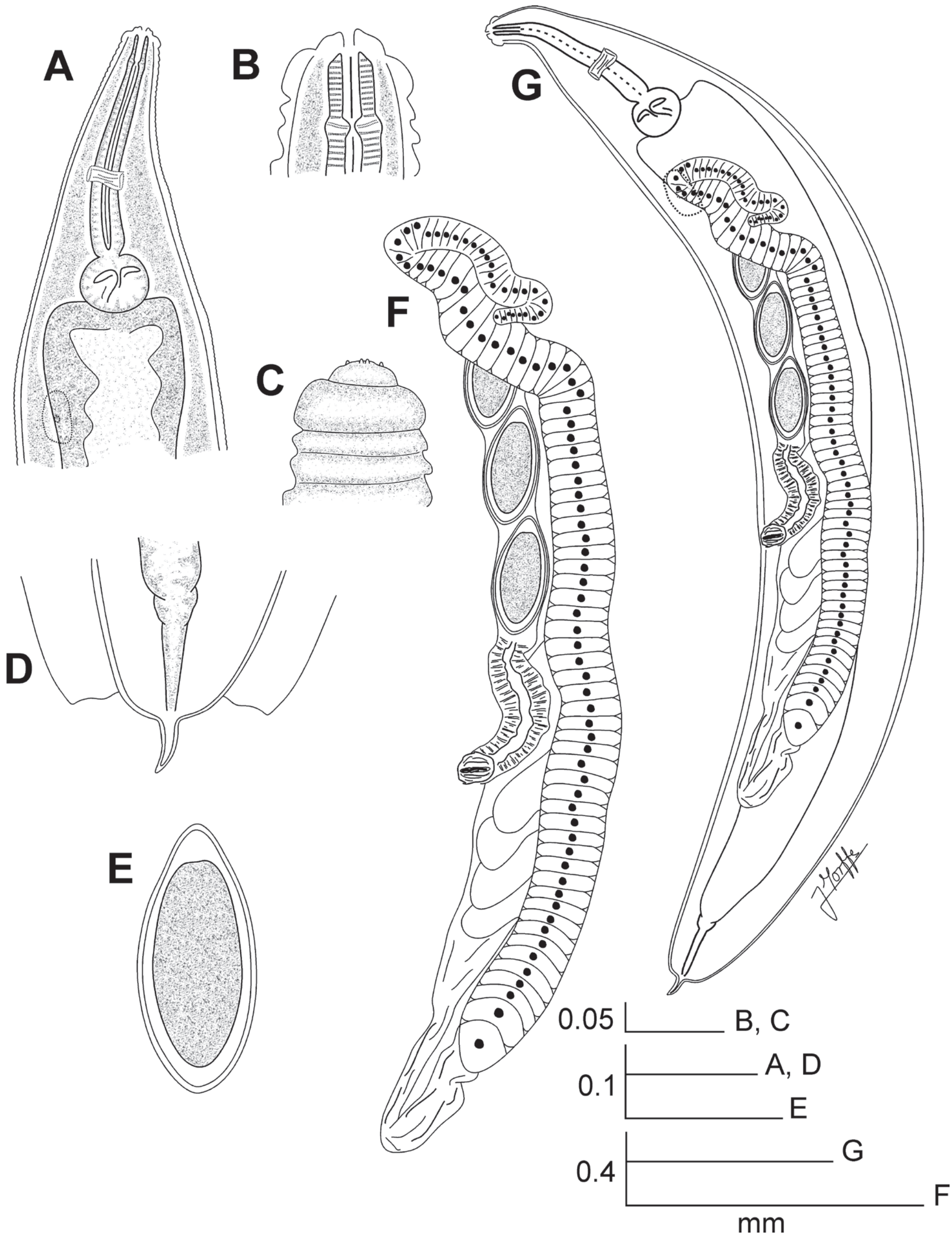

Figure 4. *Lubanema decraemerae* gen. n. sp. n. Female **A** Oesophageal region, ventrolateral view **B** Cephalic end, internal view **C** Cephalic end, external view **D** Tail, ventral view **E** Egg **F** Reproductive system, ventrolateral view. G. Entire nematode, ventrolateral view.

off from body by a single, deep groove. Amphids pore-like, laterally situated. Mouth trirradiate. First cephalic annule cone-like, slightly inflated, its margins convex, about two head-lengths long. Stoma long, about 1.5 first cephalic annule lengths long, surrounded by an oesophageal collar. Oesophagus consisting of a muscular, sub-cylindrical procorpus, its diameter little increased at its base. Isthmus as a constriction between the procorpus and the large, rounded, basal bulb. Valve plate well developed. Intestine simple, sub-rectilinear, its fore region very inflated. Rectum short. Anus sub-terminal. Nerve ring encircling procorpus at its posterior half (*ca.* 60% of its length). Excretory pore located at about the half of a body width behind the basal bulb. Vulva a median trasverse slit, displaced to the posterior half of body, lips less prominent. Vagina muscular, forwardly directed. Genital tract monodelphic-prodelphic. Ovary stout, reflexed at about one third of the body width behind the basal bulb. Oöcytes in a single row, about four times wider than long (*ca.* 8×2 μm). Eggs large, markedly ovoid, smooth-shelled. Male unknown.

Discussion. The Malagasian genus *Passalidophila* resembles *Lubanema* gen. n. by having both the body robust and fusiform, cervical cuticle unarmed and markedly annulated, a similar form of the cephalic end, the lateral alae extending from the level of the procorpus to the anus and the tail short (Van Waerebeke 1973). Differs by having a procorpus which diameter increases towards its joint with the isthmus. *Lubanema* gen. n. have a more cylindrical procorpus and the isthmus is absent. The tail of *Passalidophila* is subulate, instead of the current new genus, which presents a very short tail appendage arising from the rounded posterior end. In addition, the ovary of *Passalidophila* is slender *vs.* the robust ovary of *Lubanema* gen. n.

Other monogonant hystrignathid genera with smooth cervical cuticle are *Christiella* Travassos & Kloss, 1957; *Coronocephalus* Cordeira, 1981; *Glaber* Travassos & Kloss, 1958; *Longior* Travassos & Kloss, 1958; and *Vulcanonema* Travassos & Kloss, 1958. All of these taxa can be differentiated from *Lubanema* gen. n. by having a well developed tail, from attenuate to subulate. *Christiella* and *Longior* females have a comparatively slender body *vs.* the notably more robust and fusiform body of *Lubanema* gen. n. Also, both genera present cylindrical procorpus more elongate than in *Lubanema* gen. n.

Coronocephalus bears prominent, digitiform oral papillae, instead of the shorter, less developed papillae of *Lubanema* gen. n. In the latter genus the procorpus meets directly the basal bulb, while *Coronocephalus* present an isthmus. *Glaber* differs from *Lubanema* gen. n. by having the base of the procorpus clavate, instead of the sub-cylindrical procorpus present in the new genus.

Vulcanonema presents the cephalic end consisting of a narrow cephalic annule separated of the head by a conical region. In opposition, *Lubanema* gen. n. have the first cephalic annule just after the head. Also, the procorpus of *Vulcanonema* is sub-cylindrical, with a basal dilation, absent in the present new genus.

Lubanema gen. n. shows morphological affinities with the Australian genera *Anuronema* Clark, 1978 and *Sprentia* Clark, 1978 by having the cuticle unarmed and strongly annulated, reduction of the isthmus and the tail. Moreover, the lateral alae of *Anuronema* extends from the oesophageal region to almost the level of the anus, similar to *Lubanema* gen. n. The new genus differs from both by its genital tract monodelphic-prodelphic *vs.* didelphic-amphidelphic, procorpus sub-cylindrical *vs.* claviform and development of the lateral alae, which in *Lubanema* gen. n. are very wide and with

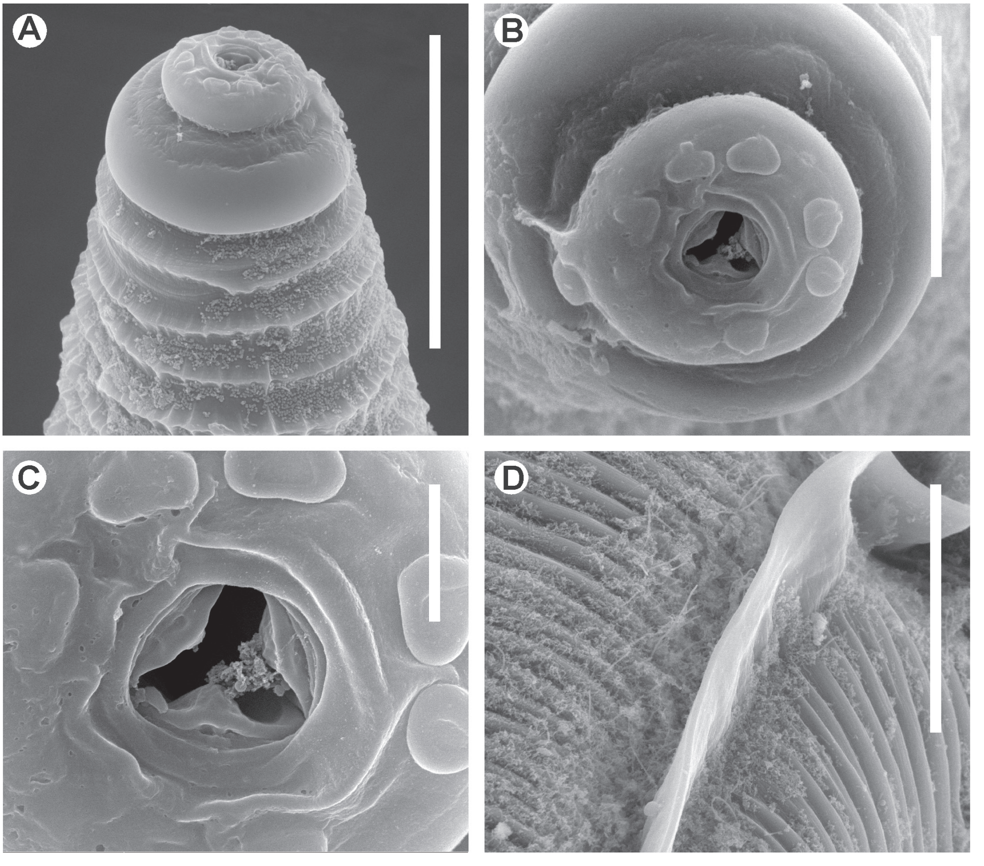

Figure 5. *Lubanema decraemerae* gen. n. sp. n. Female. SEM images **A** Cephalic end **B** Cephalic end, *en face* view **C** Mouth **D** Lateral ala, detail. Scale lines: A, D. 0.05 mm, B. 0.02 mm, C. 0.005 mm

lobes in the margins at their terminal ends. The procorpus is widely amalgamated with the basal bulb in *Anuronema* and *Sprentia*, whereas *Lubanema* gen. n. presents a well defined constriction separating both structures. *Anuronema* has a total reduction of the tail appendage (Clark 1978) not observed in *Lubanema* with a short, conical tail.

Carlosia Travassos & Kloss, 1957 also presents a reduction of the isthmus, a large, slightly inflated first cephalic annule and marked annule in the cervical region (Hunt 1982). It can be easily segregated from *Lubanema* gen. n. by having a didelphic-amphidelphic genital tract and the annule of the cervical cuticle retrorse, with posterior prolongations forming a double row of spines laterally situated.

Type host. *Didimus* sp. (Coleoptera: Passalidae).

Site. Hind gut, out of the caeca.

Type locality. Katale, Kivu region, Democratic Republic of Congo.

Etymology. Specific epithet dedicated to Prof. Dr. Wilfrieda Decraemer, from the Royal Belgian Institute of Natural Sciences. In appreciation for her help and support during the current research.

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We are grateful to Dr. Marc de Meyer, curator of the Entomological Collection of the Royal Museum of Central Africa, Tervuren, Belgium for his kind permission to access material deposited in this collection. To Dr. Wilfrieda Decraemer, Dr. Yves Samyn, Dr. Marie-Lucie Susini and Dr. Alain Drumont for their assistance during the visit of the senior author to the Royal Belgian Institute of Natural Sciences (RBINS), Brussels. To Julian Cillis (RBINS) for technical help with SEM. To Dr. Coralie Martin for permission to access the nematode collection of the Museum of Natural History, Paris. To MSc. Yamir Arias, MSc. Eduardo Furrazola and Lic. Susett González (Instituto de Ecología y Sistemática) for their help with the micrographs. To Dr. Pedro Reyes-Castillo (Instituto de Ecología, Veracruz, México) for his accurate identification of the hosts. Our thanks to Dr. Luis F. de Armas and Dr. Pedro Herrera (Instituto de Ecología y Sistemática) for their review of the manuscript and the English language, respectively. The visit to collections in Belgium and France to access the material and SEM techniques was supported by the Belgian Development Cooperation through the Belgian Focal Point of the Global Taxonomy Initiative (GTI), 2010 and 2012 calls.

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RESEARCH ARTICLE

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The genus *Brulleia* Szépligeti (Hymenoptera, Braconidae, Helconinae) from China, with descriptions of four new species

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Abstract

The species of the genus *Brulleia* Szépligeti, 1904 (Hymenoptera, Braconidae, Helconinae) from China are revised. Four new species, namely *B. fanjingensis* Yan and Chen, **sp. n.**, *B. longipalpis* Yan and Chen, **sp. n.**, *B. noncarinata* Yan and Chen, **sp. n.** and *B. punctata* Yan and Chen, **sp. n.** are described and illustrated. A key to the Chinese species of the genus *Brulleia* is included.

Keywords

Hymenoptera, Braconidae, Helconinae, *Brulleia*, new species, China

Introduction

The genus *Brulleia* Szépligeti, 1904 (Hymenoptera, Braconidae, Helconinae, Brulleiini) contains 18 valid species and is distributed in the eastern Palaearctic, Oriental and Australasian regions (van Achterberg 1983, 1993; Chen et al. 1993; Chou and Hsu 1998). The biology of this genus is largely unknown, but one species, *Brulleia obereae*

Chen and van Achterberg, 1993 is reported as parasitoid of larvae of *Oberea* sp. (Coleoptera, Cerambycidae) (Chen et al., 1993).

Ten species were already recorded from China (Chen et al. 1993; Chen et al. 1998, 2001; Chou and Hsu 1998). In the present paper additional four new species of this genus are described and illustrated from Guizhou, Tibet and Hebei, the western and northern parts of China: *B. fanjingensis* Yan and Chen, sp. n., *B. longipalpis* Yan and Chen, sp. n., *B. noncarinata* Yan and Chen, sp. n., and *B. punctata* Yan and Chen sp. n. They are described and illustrated in detail, and a key to all Chinese species of *Brulleia* is updated.

Material and methods

The terminology and measurements used follow van Achterberg (1983, 1988, 1993) and Chen et al. (1993). Additional sources for the description of sculpture and setation are Belokobylskij (1998). The following abbreviations are used for morphology: POL – postocellar line; OOL – ocular-ocellar line; OD – maximum diameter of lateral ocellus. Type specimens and other materials are deposited in the Parasitic Hymenoptera Collection of Zhejiang University, Hangzhou, China (ZJUH) and Shanghai Entomological Museum, Chinese Academy of Sciences, Shanghai, China (SEMS), respectively.

Descriptions and measurements were made under a stereomicroscope (Zeiss Stemi SV 6). All figures were made with a Leica DFC425 Camera attached to a stereomicroscope (Leica M205 A, Germany) and Leica Application Suite version 3.60 software.

Taxonomy

***Brulleia* Szépligeti, 1904**
http://species-id.net/wiki/Brulleia

Brulleia Szépligeti, 1904: 150; Shenefelt 1970: 190; van Achterberg 1983: 287; Chen et al. 1993: 378; Chou and Hsu 1998: 284.

Type species. *Brulleia melanocephala* Szépligeti, 1904.

Diagnosis. Mandibles evenly curved; maxillary and labial palpi with 2–6 and 2–3 segments, respectively; face densely reticulate-rugose; clypeus more or less convex or medially depressed; occipital carina arched medio-dorsally or reduced; vertex usually with longitudinal groove; frons weakly concave medially or nearly flat; length of hind tibia 1.6–2.0 times hind femur; second tergite smooth or sculptured basally; vein 1-SR of fore wing absent; vein 2A of hind wing absent.

Host. Larvae of *Oberea* sp. (Cerambycidae).

Distribution. China (Hebei, Zhejiang, Jiangxi, Sichuan, Fujian, Guangxi, Yunnan, Guizhou, Tibet); East Palaearctic, Oriental and Australasian regions.

Brulleia fanjingensis **Yan & Chen, sp. n.**
urn:lsid:zoobank.org:act:C1FEE184-259D-4DB6-92BB-2779E2CF7366
http://species-id.net/wiki/Brulleia_fanjingensis
Figs 1–10

Material examined. Holotype, ♂, China, Guizhou Prov., Fanjing Mountain Gokokuji Temple, 1000 m, 4.VIII.2001, Ma Yun, No. 200108606 (ZJUH).

Description. Body length 15.5 mm. Fore wing length 10.0 mm.

Head. Antennal segments 42; third segment 1.7 times longer than fourth segment; length of third, fourth and penultimate segments 5.3, 4.3 and 2.0 times their width, respectively. Maxillary palp 4-segmented; labial palp 3-segmented; length of maxillary palp 0.6 times height of head. Head in dorsal view 0.6 times as long as wide. Eye 1.4 times as long as temple in dorsal view. Length of malar space 0.7 times basal width of mandible, 0.4 times maximum width of eye. POL: OD: OOL=10: 8: 40. Temple densely punctate dorsally, coarsely rugose ventrally. Vertex densely punctate. Frons weakly concave, medially with coarsely transverse rugae, laterally with coarsely oblique striae. Face reticulate-punctate. Clypeus reticulate-punctate dorsally, with median notch on upper margin. Mandibles striated at basal 0.6. Labium with its apical margin convex medially.

Mesosoma. Almost twice as long as its height. Pronope spindle-shaped. Side of pronotum punctate, antero-medially and subdorsally crenulate, ventro-posteriorly rugose-punctate. Mesoscutum punctate, middle lobe with weak longitudinal groove medially. Notauli narrow and deep, crenulate, its posterior area with median carina. Scutellum rather flat and densely punctate, lateral carinae present at basal 0.5. Prepectal carina complete, weak, laterally obscure. Precoxal sulcus deep, coarsely crenulate. Metanotum with median carina. Propodeum coarsely rugose-reticulate, weakly rugose-punctate basolaterally.

Wings. Fore wing, r: 3-SR: SR1=15: 24: 85. 2-SR: 3-SR: r-m=25: 29: 30. 1-M: m-cu=74: 48. 1-CU1: 2-CU1=3: 28. r-m curved below, with remnant vein. Hind wing, marginal cell widened apically, its apical width 3.0 times minimum width of cell below vein R1. 1-M: 1r-m =21: 19. cu-a strongly inclivous.

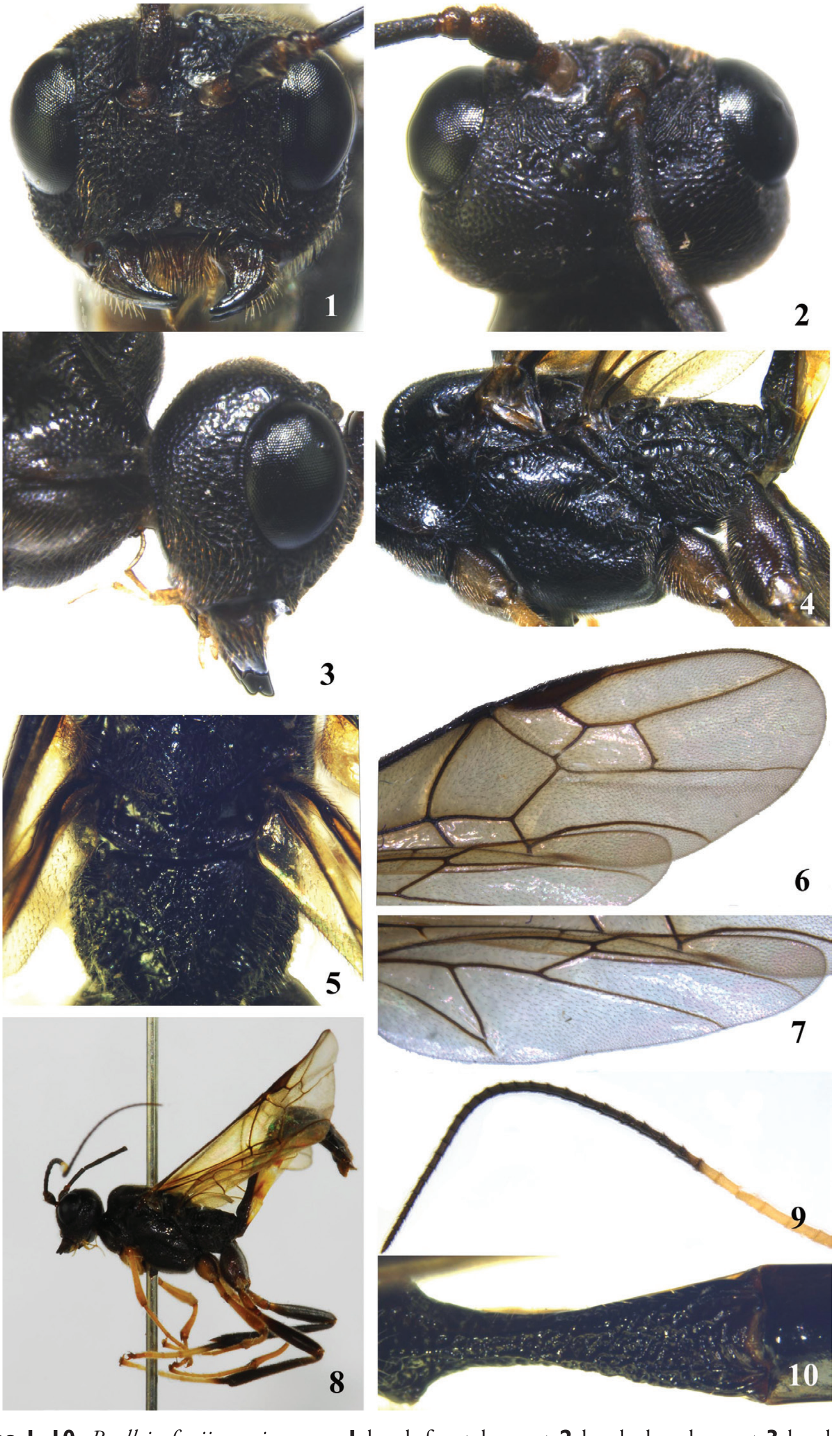
Legs. Length of hind femur, tibia and basitarsus 6.0, 11.8 and 9.8 times their width, respectively. Hind tibia 1.8 times as long as hind femur.

Metasoma. First tergite rather slender and widened posteriorly, coarsely rugose, but medio-apically smooth, dorsal carinae present in basal half. Length of first tergite 3.3 times its apical width. Second and following tergites smooth.

Colour. Body black. Antenna brown, but 10th-15th flagellomeres whitish yellow. Most of mandible reddish brown, apex of teeth black. Palpi yellow. Fore and middle legs, hind trochanters yellow, hind coxa and femur reddish brown, hind tibia dark brown, hind tarsus whitish yellow. Tegulae and pterostigma dark brown. Wing membrane yellowish brown with veins brown to dark brown.

Female. Unknown.

Diagnosis. This new species is similar to *B. flavibasalis* He and Chen, but differs in having the apical margin of labium convex medially (in latter truncate apically); side of



Figures 1–10. *Brulleia fanjingensis*, sp. n. **1** head, frontal aspect **2** head, dorsal aspect **3** head, lateral aspect **4** mesosoma, lateral aspect **5** propodeum, dorsal aspect; **6** fore wing **7** hind wing **8** habitus, lateral aspect **9** 10th-42th flagellomeres **10** first and basal second metasomal tergites, dorsal aspect.

pronotum punctate, antero-medially and subdorsally crenulate, and ventro-posteriorly rugose-punctate (in latter crenulate antero-medially and subdorsally, remainder rather smooth); scutellum densely punctate (in latter rather smooth) and most of the body black (in latter brownish yellow).

Distribution. China (Guizhou).

Etymology. It is named after the type locality of the species, Fanjing Mountain in Guizhou Province of China.

Brulleia longipalpis Yan & Chen, sp. n.

urn:lsid:zoobank.org:act:F1A04DF2-9445-4AF6-A3B4-0FEAD60D57CF
http://species-id.net/wiki/Brulleia_longipalpis
Figs 11–19

Material examined. Holotype, ♀, China, Tibet, Motuo, 1570 m, 21.V.1980, Jin Gentao and Wu Jianyi, No. 34201363 (SEMS).

Description. Body length (excluding ovipositor sheath) 16 mm. Fore wing length 13.5 mm.

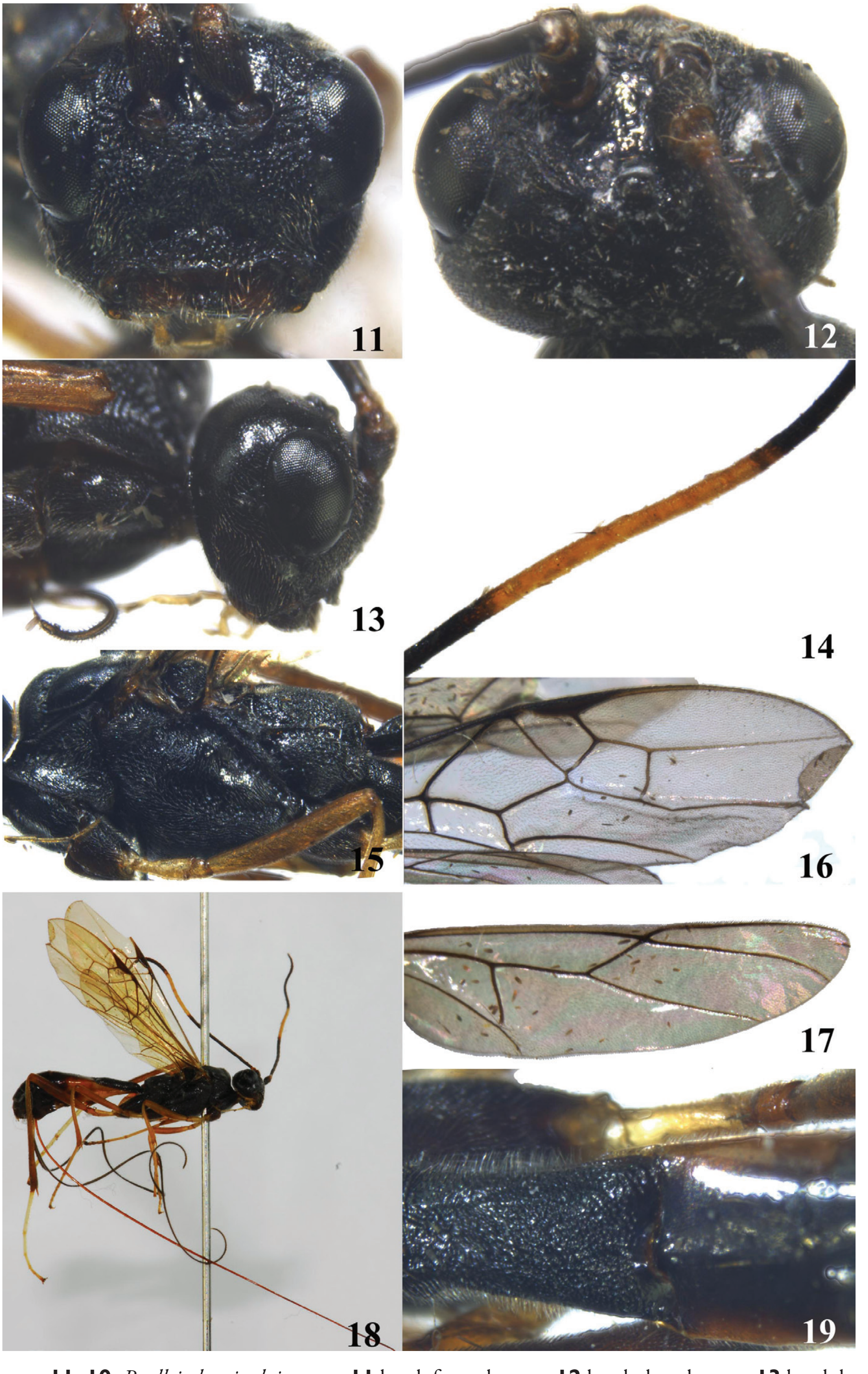
Head. Antennal segments 40; third segment 1.2 times longer than fourth segment; length of third, fourth and penultimate segments 5.0, 4.3 and 1.1 times their width, respectively. Maxillary palp 6-segmented; labial palp 3-segmented; length of maxillary palp 1.1 times height of head. Head in dorsal view 0.6 times as long as wide. Eye 1.1 times as long as temple in dorsal view. Length of malar space 0.9 times basal width of mandible, 0.4 times maximum width of eye. POL: OD: OOL=10: 10: 27. Vertex and temple densely punctate. Frons slightly concave, medially punctate with some rugae, obliquely rugose-punctate laterally. Face reticulate-punctate. Clypeus rugose-punctate, its apical margin slightly convex with median notch. Labium concave medially, apically with median notch.

Mesosoma. Length 1.8 times its height. Pronope deep, spindle-shaped. Side of pronotum punctate, antero-medially crenulate, subdorsally rugose-punctate, posteriorly reticulate-punctate. Notauli narrow and deep, crenulate. Scutellar sulcus with one carina and several lateral crenulae. Scutellum densely punctate, lateral carinae absent, with several striae posteriorly. Precoxal sulcus complete and wide, coarsely rugose-punctate. Metanotum with two short carinae. Propodeum coarsely reticulate, finely punctate basolaterally, coarsely rugose postero-laterally.

Wings. Fore wing, r: 3-SR: SR1=12: 20: 72. 2-SR: 3-SR: r-m=17: 20: 19. 1-M: m-cu=39: 30. 1-CU1: 2-CU1=5: 50. r-m curved slightly below, without remnant vein. Hind wing, marginal cell obviously widened apically, its apical width 3.0 times minimum width of cell below vein R1. 1-M: 1r-m=35: 22. cu-a inclivous.

Legs. Length of hind femur, tibia and basitarsus 6.0, 13.3 and 10.0 times their width, respectively. Hind tibia 1.8 times as long as hind femur.

Metasoma. First tergite reticulate-punctate, medio-posteriorly smooth, dorsal carinae distinct in basal 0.3. Length of first tergite twice its apical width. Ovipositor sheath



Figures 11–19. *Brulleia longipalpis*, sp. n. **11** head, frontal aspect **12** head, dorsal aspect **13** head, lateral aspect **14** 10th-17th flagellomeres **15** mesosoma, lateral aspect **16** fore wing **17** hind wing **18** habitus, lateral aspect **19** first and basal second metasomal tergites, dorsal aspect.

3.4 times as long as metasoma, 3.7 times as long as hind tibia, 5.0 times as long as mesosoma, and 2.3 times as long as fore wing.

Colour. Body black. Antenna dark brown but 10th-17th flagellomeres yellow. Palpi yellow. Tegulae, basal of mandible and labium reddish brown. Legs yellow to reddish yellow but coxae reddish brown, hind tarsus whitish yellow. Second tergite reddish yellow at two-thirds basolaterally. Ovipositor sheath dark brown. Wing membrane fumose with veins dark brown.

Male. Unknown.

Diagnosis. This new species is similar to *B. obereae* Chen and van Achterberg, but differs in having the maxillary palp longer, its length 1.1 times height of head (in latter 0.5 times); temple densely punctate (in latter sparsely and finely punctulate dorsally, and rugose ventrally) and first tergite mainly reticulate-punctate, but medio-posteriorly smooth (in latter basally transversely, medially irregularly and apically more or less longitudinally rugose).

Distribution. China (Tibet).

Etymology. It is named after its very long maxillary palp.

Brulleia noncarinata Yan & Chen, sp. n.

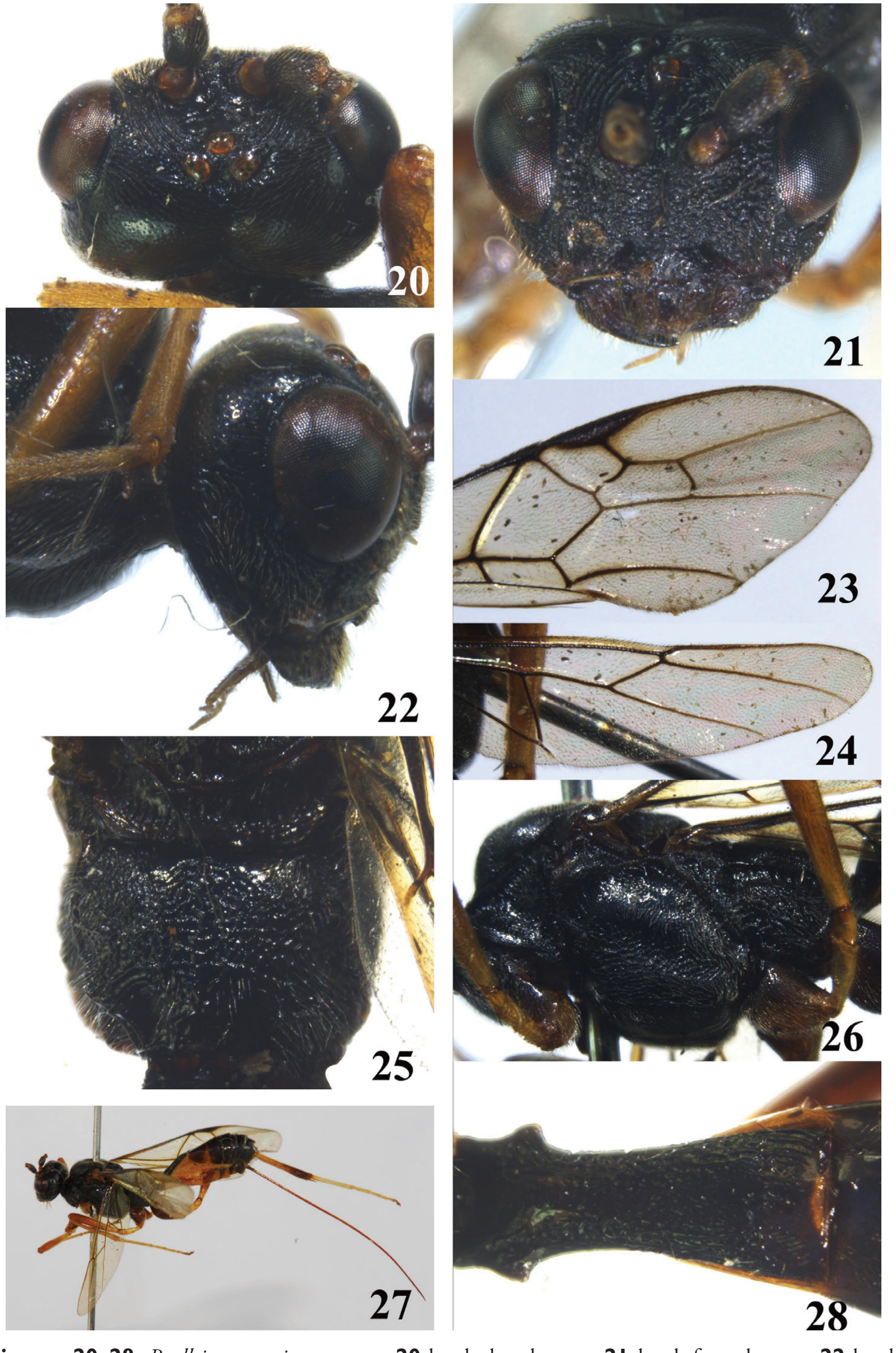
urn:lsid:zoobank.org:act:1D4A8931-D486-4789-90D8-9F8A348B158F
http://species-id.net/wiki/Brulleia_noncarinata
Figs 20–28

Material examined. Holotype, ♀, China, Tibet, Motuo, 1520 m, 8.VII.1980, Jin Gentao and Wu Jianyi, No. 34202321 (SEMS).

Description. Body length (excluding ovipositor sheath) 18.5 mm. Fore wing length 15.2 mm.

Head. Antennal flagellomeres missing. Maxillary palp 4-segmented; labial palp 3-segmented; length of maxillary palp 0.5 times height of head. Head in dorsal view 0.5 times as long as wide. Eye 1.4 times as long as temple in dorsal view. Length of malar space equal to basal width of mandible, 0.4 times maximum width of eye. POL: OD: OOL = 8: 12: 28. Vertex punctate. Temple punctate dorsally, densely rugose-reticulate ventrally. Frons concave, medially almost smooth with some rugae, laterally with slightly oblique striae. Face densely reticulate-punctate. Clypeus rugose-punctate, its apical margin convex and with median notch, ventrally with obscure transverse striae. Labium punctate, truncate apically, slightly concave medially.

Mesosoma. Length 1.7 times its height. Side of pronotum punctate, antero-medially, postero-medially and dorsally crenulate. Notauli narrow and shallow, crenulate. Mesoscutum densely punctate. Scutellum weakly convex, smooth medially, punctate laterally, with several striae posteriorly. Prepectal carina complete, weak, laterally obscure. Precoxal sulcus complete, anteriorly reticulate, rugose crenulate medially, posteriorly longitudinally punctato-striate, ventrally irregularly reticulate-punctate. Scutel-



Figures 20–28. *Brulleia noncarinata*, sp. n. **20** head, dorsal aspect **21** head, frontal aspect **22** head, lateral aspect **23** fore wing **24** hind wing **25** propodeum, dorsal aspect **26** mesosoma, lateral aspect **27** habitus, lateral aspect **28** first metasomal tergite, dorsal aspect.

lar sulcus with single carina. Metanotum with median carina. Propodeum coarsely rugose-reticulate, almost smooth basolaterally.

Wings. Fore wing, r: 3-SR: SR1=16: 27: 88. 2-SR: 3-SR: r-m=24: 27: 22. 1-M: m-cu=34: 23. 1-CU1: 2- CU1=7: 63. r-m curved slightly below, without remnant vein. Hind wing, marginal cell obviously widened apically, its apical width 2.5 times minimum width of cell below vein R1. 1-M: 1r-m=31: 20. cu-a inclivous.

Legs. Length of hind femur, tibia and basitarsus 5.8, 12.8 and 11 times their width, respectively. Hind tibia 1.7 times as long as hind femur.

Metasoma. First tergite widened posteriorly, densely punctate, postero-laterally longitudinally punctate-striate, postero-medially obscurely punctate, dorsal carinae absent. Length of first tergite 3.0 times its apical width. Second and following tergites smooth and shinny. Ovipositor sheath 1.9 times as long as metasoma, 2.1 times as long as hind tibia, 2.5 times as long as mesosoma, and 1.1 times as long as fore wing.

Colour. Body black. Malar space apically, base of mandible and labium dark red. Palps yellowish brown. Tegulae dark brown. Coxae, hind femur and apical one-fourth of hind tibia dark reddish brown; trochanters and tarsus whitish yellow; fore and middle femora, tibiae and basal three-fourthes of hind tibia yellowish brown. First-third metasomal sternites yellowish brown. Pterostigma and most of veins dark brown, wing membrane fumose.

Male. Unknown.

Diagnosis. This new species is similar to *B. flavibasalis* He and Chen, but differs in having the clypeus rugose-punctate, ventrally with obscure transverse striae, its apical margin convex and with median notch (in latter finely rugose, its apical margin slightly concave and without median notch); the dorsal carinae of first tergite absent (in latter present in basal half) and the most part of the body black (in latter brownish yellow).

Distribution. China (Tibet).

Etymology. From ""*non*" (Latin for "absent"), and "*carina*" (Latin for "carina"), because dorsal carinae of the first tergite absent.

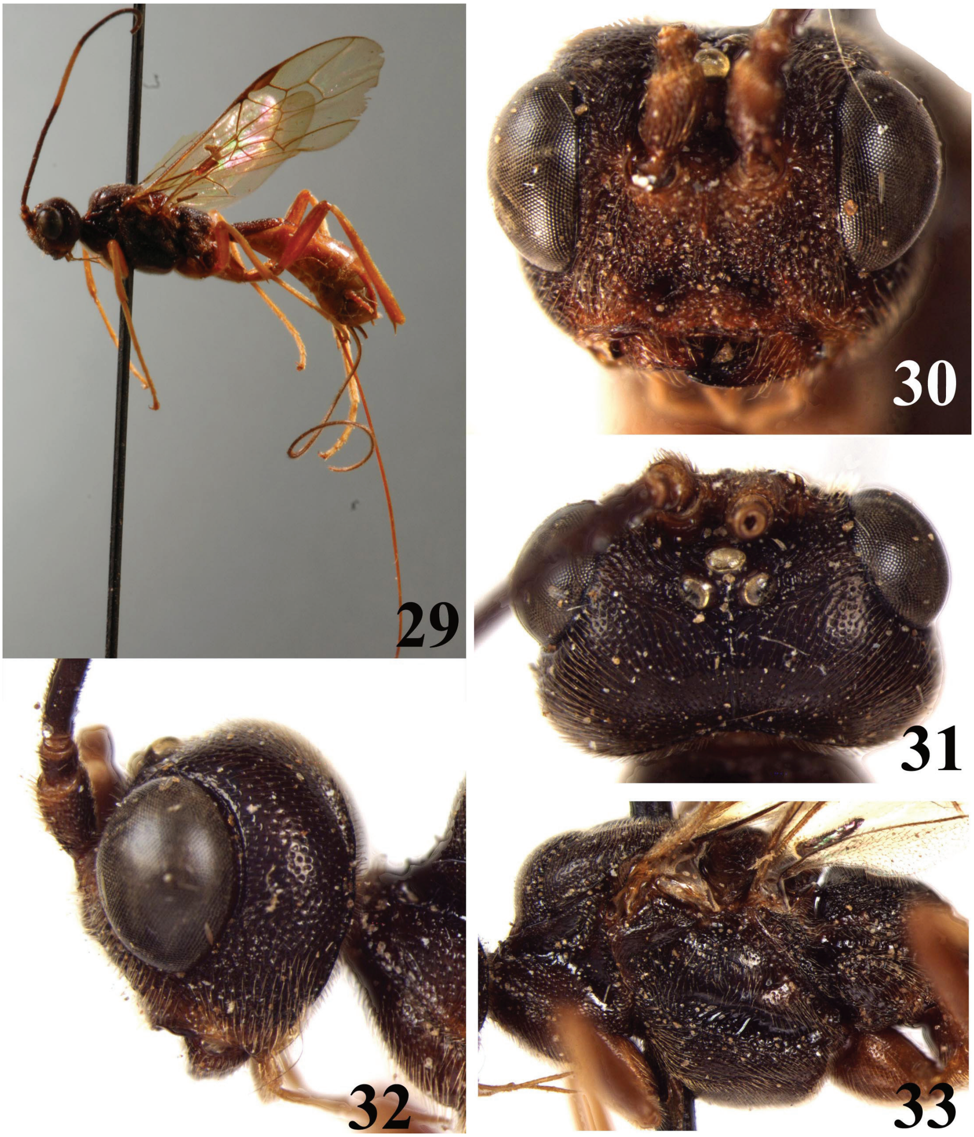
Brulleia punctata Yan & Chen, sp. n.

urn:lsid:zoobank.org:act:0582609A-F976-4115-AC2C-8A8A88C9F5E1
http://species-id.net/wiki/Brulleia_punctata
Figs 29–37

Material examined. Holotype, 1♀, China, Hebei, Chahar, Yangkiaping, 21.VII.1937, O. Piel, No. 201105603 (ZJUH). Paratype: 1♀, China, Hebei, Chahar, Yangkiaping, 21.VII.1937, O. Piel, No. 201105604 (ZJUH).

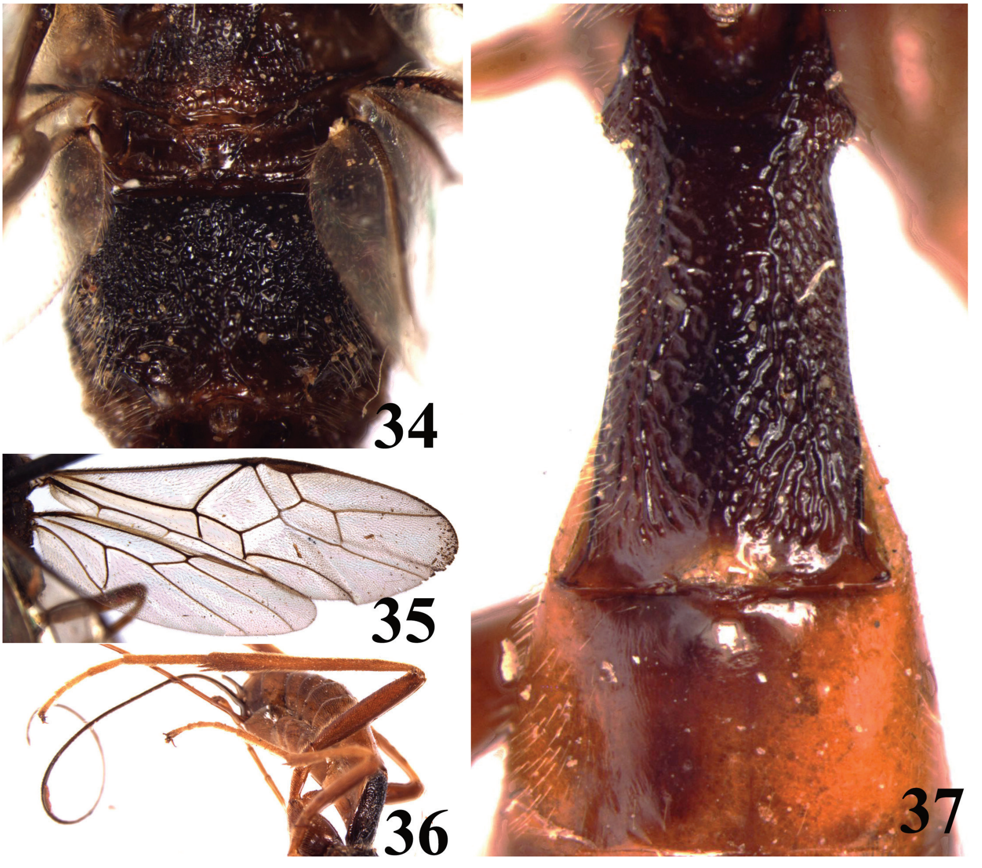
Description. Body length (excluding ovipositor sheath) 16.5 mm. Fore wing length 12.2 mm.

Head. Antennal segments more than 33 (apical segments missing); third segment 1.3 times longer than fourth segment; length of third and fourth segments 4.0 and 3.0 times their width, respectively. Maxillary palp 4-segmented; labial palp 3-segmented; length of maxillary palp 0.7 times height of head. Head in dorsal view 0.6 times as long as wide. Eye



Figures 29–33. *Brulleia punctata*, sp. n. **29** habitus, lateral aspect **30** head, frontal aspect **31** head, dorsal aspect **32** head, lateral aspect **33** mesosoma, lateral aspect.

1.3 times as long as temple in dorsal view. Length of malar space equal to basal width of mandible, 0.3 times maximum width of eye. POL: OD: OOL=9: 10: 24. Vertex densely punctate. Temple punctate dorsally, densely reticulate-punctate ventrally. Frons slightly concave, medially almost smooth with some rugae, laterally with oblique striae. Face densely rugose-reticulate, medially with a triangular promience near antennal sockets. Clypeus reticulate-punctate, apical margin with median notch, ventrally with transverse striae.



Figures 34–37. *Brulleia punctata*, sp. n. **34** propodeum, dorsal aspect **35** fore and hind wings **36** Hind leg, lateral aspect **37** first and second metasomal tergites, dorsal aspect.

Mesosoma. Length 1.6 times its height. Pronope deep, slit-shaped. Side of pronotum punctate, antero-medially, subdorsally and posteriorly crenulate, postero-medially almost smooth. Notauli narrow and deep, crenulate, its posterior area with median carina. Scutellum slightly convex and densely punctate, lateral carinae absent, with several striae posteriorly. Prepectal carina complete, weak, laterally obscure. Precoxal sulcus coarsely crenulate, anteriorly rugose-punctate. Metanotum without median carina. Propodeum coarsely rugose-reticulate.

Wings. Fore wing, r: 3-SR: SR1=17: 20: 60. 2-SR: 3-SR: r-m=15: 20: 21. 1-M: m-cu=40: 25. 1-CU1: 2-CU1=10: 51. r-m slightly curved below, without remnant vein. Hind wing, marginal cell widened apically, its apical width 2.5 times minimum width of cell below vein R1. 1-M: 1r-m=20: 14. cu-a inclivous, posteriorly slightly curved towards wing base.

Legs. Length of hind femur, tibia and basitarsus 6.4, 13.7 and 10.7 times their width, respectively. Hind tibia 1.8 times as long as hind femur.

Metasoma. First tergite robust and widened posteriorly, densely rugose, smooth apically, dorsal carinae obscure. Length of first tergite 1.8 times its apical width. Second and following tergites smooth and shinny. Ovipositor sheath twice as long as metasoma, 2.5 times as long as hind tibia, 2.7 times as long as mesosoma, and 1.3 times as long as fore wing.

Colour. Body dark reddish brown. Face, clypeus and mandible yellowish brown. Antennal scapus and pedicel yellowish brown, 8th-14th flagellomeres and palpi yellow. Tegula, metasoma (except first tergite) and legs reddish-brown. Ovipositor sheath dark brown. Pterostigma yellowish brown, veins dark brown to light brown, wing membrane faintly brown.

Variation. Body length (excluding ovipositor sheath) 12.8-16.5 mm, fore wing length 10.3–12.2 mm. First tergite dorsal carinae obscure or only visible basally.

Male. Unknown.

Diagnosis. This new species is similar to *B. flavibasalis* He and Chen, but differs in having the frons medially almost smooth with some rugae, laterally with oblique striae (in latter concave medially, with sparse, fine and obsolete punctures laterally); the length of maxillary palp 0.7 times height of head (in latter 0.5 times) and dorsal carinae of first tergite obscure or only visible basally (in latter present in basal half).

Remark. The tarsus of left hindleg of holotype missing. Most of the flagellomeres of paratype missing.

Distribution. China (Hebei).

Etymology. After dense punctation of scutellum.

Key to the Chinese species of the genus *Brulleia* Szépligeti

1 Maxillary palp with 4 segments...**2**

– Maxillary palp with 5-6 segments **5**

2 Scutellum densely punctate..**3**

– Scutellum almost smooth, at most with some punctation laterally **4**

3 Middle mesoscutal lobe with weak longitudinal groove medially; scutellum rather flat and lateral carinae present at basal 0.5; metanotum with median carina; first tergite rather slender; length of first tergite 3.3 times its apical width; metasoma black. Guizhou............................... ***B. fanjingensis* sp. n.**

– Middle mesoscutal lobe normal, without longitudinal groove medially; scutellum slightly convex and lateral carinae absent; metanotum without median carina; first tergite robust; length of first tergite 1.8 times its apical width; metasoma (except first tergite) reddish brown. Hebei........***B. punctata* sp. n.**

4 Body brownish yellow; first tergite densely rugose, postero-medially polished, dorsal carinae present in basal half; clypeus finely rugose, its apical margin slightly concave and without median notch. Guangxi..........***B. flavibasalis* He & Chen**

– Body black; first tergite densely punctate, postero-laterally longitudinally punctato-striate, postero-medially obscurely punctate, dorsal carinae absent;

clypeus rugose-punctate, ventrally with obscure transverse striae, its apical margin convex and with median notch. Tibet............***B. noncarinata*** **sp. n.**

5 Body yellowish brown to reddish brown; vein 1-M of hind wing 0.8–1.5 times vein 1r-m; vein cu-a of hind wing comparatively less inclivous **6**

– Body black, only second tergite and its surrounding area dark reddish (or reddish-yellow basally); vein 1-M of hind wing 1.5–2.2 times vein 1r-m; vein cu-a of hind wing strongly inclivous **8**

6 Antenna black with yellowish white submedian band; pterostigma reddish yellow to yellowish brown. Fujian, Zhejiang............ ***B. rubida*** **Chen & He**

– Basal half of antenna reddish yellow or brownish yellow, apical half black; color of pterostigma variable **7**

7 First tergite densely rugose, transversely medially, and its dorsal carinae present extremely basally; second tergite rugulose basolaterally; temple smooth dorsally, with coarse punctures ventrally; wing membrane dark yellowish brown; vein 3–SR slightly longer than veins 2-SR or r-m; length of hind femur 5.8 times its width. Guangxi............................. ***B. lutea*** **He & Chen**

– First tergite smooth basally and apically, its basal 0.2-0.5 transversely rugose, remaining part irregularly rugose, dorsal carinae present at most of basal half; second tergite polished; temple punctulate dorsally, rugose-punctate ventrally; wing membrane yellowish brown; vein 3–SR slightly shorter than veins 2-SR or r-m; length of hind femur 8.6 times its width. Sichuan............ ***B. yangi*** **He & Chen**

8 Second tergite distinctly rugose medially, only apically and laterally smooth; length of first tergite 3.1–3.4 (♂) times its apical width **9**

– Second tergite almost smooth, at most obscurely rugose basally or rugose basolaterally; length of first tergite 1.9–2.9 (♂) and 2.1–2.6 (♀) times its apical width **10**

9 Length of maxillary palp 0.55 times height of head; vein cu-a of fore wing almost interstitial; apical width of marginal cell of hind wing about 1.8 times minimum width of cell below vein R1; vein 1-M of hind wing about 1.5 times vein 1r-m. Guizhou.............................***B. tenuipetiolata*** **Chen & He**

– Length of maxillary palp 0.7 times height of head; vein cu-a of fore wing obviously postfurcal; apical width of marginal cell of hind wing about 2.3 times minimum width of cell below vein R1; vein 1-M of hind wing about 2.2 times 1r-m. Yunnan...***B. chaoi*** **Chen & He**

10 Second tergite rugose basolaterally, remainder smooth; fourth segment of maxillary palp 1.8 times longer than fifth segment. Fujian...........................
....***B. auripes*** **Chen & He**

– Second tergite smooth, at most obscurely rugulose basally 11

11 Propodeum punctate basolaterally, subbasally finely rugulose; 2-SR: 3-SR: r-m=7: 7: 7. - Length of maxillary palp about 0.7 times height of head. Sichuan... ***B. subtilirugula*** **He & van Achterberg**

– Propodeum coarsely reticulate except its baso-lateral punctated area; 2-SR: 3-SR: r-m=7: 7–9: 7.7–8.5 .... **12**

12 Ovipositor sheath 2.3 times as long as fore wing; length of first tergite 2.0 (♀) times its apical width; propodeum coarsely reticulate, finely punctate basolaterally, coarsely rugose postero-laterally. Tibet..... ***B. longipalpis*** **sp. n.**

– Ovipositor sheath 1.4–1.5 times as long as fore wing; length of first tergite 2.1-2.6 (♀) times its apical width; propodeum coarsely reticulate or rugose-reticulate except its baso-lateral punctate area **13**

13 Frons smooth, medially with two submedial carinae, laterally with oblique striae; clypeus finely rugose; length of maxillary palp about 0.5 times height of head. Jiangxi .... ***B. obereae*** **Chen & van Achterberg**

– Frons rugose; clypeus reticulate-rugose, with small rather smooth triangular area medio-ventrallly; length of maxillary palp about 1.1 times height of head. Taiwan .... ***B. taiwanensis*** **Chou & Hsu**

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RESEARCH ARTICLE

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Molecular systematics of the genus *Troglophilus* (Rhaphidophoridae, Orthoptera) in Turkey: mitochondrial 16S rDNA evidences

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Abstract

This study focuses on the evolutionary relationships among Turkish species of the cave cricket genus *Troglophilus*. Fifteen populations were studied for sequence variation in a fragment (543 base pairs) of the mitochondrial DNA (mtDNA) 16S rDNA gene (16S) to reconstruct their phylogenetic relationships and biogeographic history. Genetic data retrieved three main clades and at least three divergent lineages that could not be attributed to any of the taxa known for the area. Molecular time estimates suggest that the diversification of the group took place between the Messinian and the Plio-Pleistocene.

Keywords

Troglophilus, Rhaphidophoridae, Orthoptera, 16S rDNA, mitochondrial DNA, molecular systematics, cave crickets

Introduction

Caves are traditionally considered as natural laboratories to understand evolutionary processes related to allopatric divergence because, similarly to remote oceanic islands, by their very nature greatly reduce or hamper gene flow among populations (Poulson and

White 1969; Sbordoni 1982; Barr and Holsinger 1985; Sbordoni et al. 1987; Venanzetti et al. 1993; Di Russo et al. 1998). Here we present a case study based on populations and species of the cave crickets genus *Troglophilus* from Turkish caves. This genus belongs to family Rhaphidophoridae, which has a worldwide distribution and typically includes wingless crickets with a clear preference for dump environments, including natural and artificial caves. In the Northern hemisphere these crickets are essentially confined to natural and artificial caves. Overall 10 subfamilies have been recognized to date (Rentz 1991; Di Russo and Sbordoni 1998; Gorochov 2001; Otte 2000; Eades et al. 2011).

In the peri-Mediterranean area the family is represented by two genera only (*Dolichopoda* and *Troglophilus*) with a fairly overlapping Eastern-Mediterranean distribution. *Dolichopoda* (49 described species) is by far more species-rich than *Troglophilus* (17 described species). Until now, seven species of *Dolichopoda* (*D. aranea* Bolivar, 1899, *D. pusilla* Bolivar, 1899*, D. euxina* Semenov, 1901*, D. sbordonii* Di Russo & Rampini, 2006*, D. lycia* (Galvagni, 2006), *D. noctivaga* Di Russo & Rampini, 2007, *D. sutini* Rampini & Taylan, 2012) and five species of *Troglophilus* (*T. escalerai* Bolivar, 1899*, T. gajaci* Us, 1974*, T. adamovici* Us, 1974, *T. bicakcii* Rampini & Di Russo, 2003, *T. tatyanae* Di Russo & Rampini, 2007) have been reported from Anatolian caves. As far as *Troglophilus* is concerned, the first species to be described from the area was *T. escalerai* (Jenidje-Kale cave) by Bolivar in 1889. After this early study, Us described *T. adamovici* (Isparta, Zindan cave) and *T. gajaci* (Mersin, Cennet cave) in 1974. About thirty years later Rampini and Di Russo (2003) identified the new taxon *T. bicakcii* (Derebucak, Bıçakçı Cave), while the description of *T. tatyanae* (Artvin, Kafkasor) was presented in Di Russo et al. (2007).

Of these two genera of cave crickets inhabiting the peri-Mediterranean area, *Dolichopoda* has received comparatively more scientific attention than *Troglophilus*. Both genera have been the object of a number of studies based on a variety of molecular markers. Nowadays for *Dolichopoda* we have a very detailed knowledge from the population level (with special emphasis on those species inhabiting the Italian peninsula) up to the phylogenetic relationships among the vast majority of taxa ascribed to the genus (Allegrucci et al. 2011 and references therein). Genetic studies conducted on *Troglophilus* have considered the Italian, Balkan, insular Greek and Anatolian species (Sbordoni et al. 1981; Cobolli et al. 1999; Ketmaier et al. 2000, 2004, 2010) but a well-resolved phylogeny of the genus is still awaited.

Cobolli et al. (1999) used allozymic markers to disentangle relationships among Anatolian species of *Troglophilus* from the Taurus Mountains between Isparta and Adana towns. The study revealed four distinct gene pools including the three species *T. adamovici*, *T. escalerai* and *T. gajaci* plus a genetically differentiated form that was later described as the new species *T. bicakcii* by Rampini and Di Russo (2003). That was a preliminary study; indeed only a limited number of populations were screened genetically and the markers employed (allozymes) notoriously reveal just a limited fraction of the total genetic variation. More recently, Kaya et al. (2012) presented a phylogeographic hypothesis for the Anatolian *Troglophilus*; the samplings in that and in the current study largely overlap but those authors did not include *T. escalerai* in their analyses. Markers differed between the studies; Kaya et al. (2012) sequenced fragments of the mitochondrial Cytochrome Oxidase I and II genes and the nuclear region spanning the Internal Transcribed Spacers 1 and 2. Anatolian representatives clustered in a monophyletic group of Miocene origin; divergence within the Anatolian clade occurred through the Plio-Pleistocene but earlier than the last four glacial periods of the late Pleistocene.

For this study, we explored 71 caves from the Black Sea, Aegean, Mediterranean and inland areas of Turkey and found and collected cave crickets belonging to the genus *Troglophilus* from 15 of them (Figure 1; Table 1). We included in the study all the five known Turkish species of *Troglophilus*, including *T. escalerai* that was not analyzed in Kaya et al. (2012). For some species we were able to collect multiple populations (Table 1). Samples were screened for sequence variation at the mitochondrial DNA (mtDNA) 16S rDNA gene (16S). The gene is known to be informative at the closely related species level in insects (Simon et al. 1994). The aims of this study are to reconstruct the evolutionary relationships among the Turkish *Troglophilus* species, to use genetic data to clarify the systematics of the group in the area and, ultimately, to identify the evolutionary trajectories it followed in the course of its diversification. The newly acquired data will be discussed in light of the results obtained by Cobolli et al. (1999) and Kaya et al. (2012). Patterns of relationships within *Troglophilus* will be finally compared to those presented in Allegrucci et al. (2011) for *Dolichopoda* for the same area to search for eventually overlapping patterns in two groups with similar ecologies.

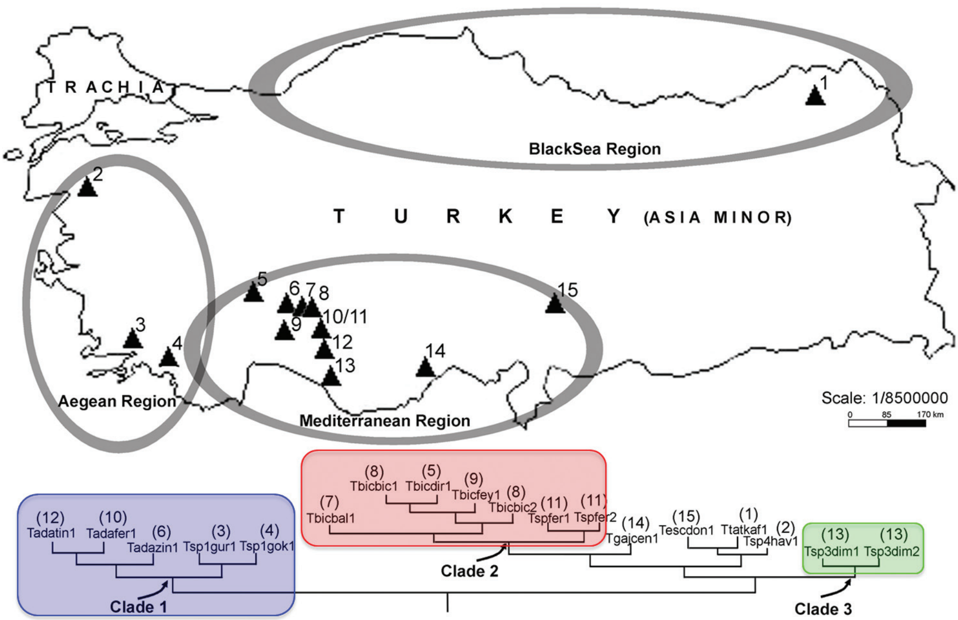

Figure 1. Geographic position of the fifteen caves were we sampled the *Troglophilus* populations analyzed in the study. Numbers correspond to those in Table 1. The lower half of the figure depicts the phylogeography of *Troglophilus* in Turkey (for details see Discussion); colors of clades match those in Figure 2.

Table 1. Species list and details of the sampling localities of Turkish *Troglophilus* populations and species. Numbers in the first column match those in Figure 1.

No	Species	Cave name	Locality	N (north)	E (east)	Date	Altitude (m a.s.l.)
Black Sea Region							
1	*T. tatyanae*	Epigian forest	Artvin, Kafkasor	41.098	41.475	29–30/06/2000	1300
Aegean Region							
2	*Troglophilus sp*.4	Havran cave	Balıkesir, Havran	39.34499	27.10.336	01/11/2008	115
3	*Troglophilus sp*.1	Gökçeler cave	Muğla, Milas	37.11378	27.45982	25/11/2008	120
4	*Troglophilus sp*.1	Güroluk cave	Muğla, Fethiye	36.47564	28.58646	26/06/2008	450
Mediterranean and Central Anatolia Region							
5	*T. adamovici*	Zindan cave	Isparta, Aksu	37.48424	31.05060	03/05/2009	1286
6	*T. bicakcii*	Direkliin cave	Konya, Beyşehir	37.35548	31.28549	02/07/2008	1209
7	*T. bicakcii*	Bıçakçı cave	Konya, Derebucak	37.23648	31.32166	23/08/2009	1372
8	*T. bicakcii*	Balatini cave	Konya, Derebucak	37.21706	31.35060	22/08/2009	1379
9	*T. bicakcii*	Feyzullah cave	Konya, Derebucak	37.15771	31.27314	22/08/2009	1508
10	*T. adamovici*	Ferzene cave	Konya, Seydişehir	37.22854	31.50071	24/08/2009	1390
11	*Troglophilus sp*.2	Ferzene cave	Konya, Seydişehir	37.22854	31.50071	24/08/2009	1390
12	*T. adamovici*	Tınaztepe cave	Konya, Seydişehir	37.14855	31.35692	24/08/2009	1461
13	*Troglophilus sp*.3	Dim cave	Antalya, Alanya	36.32405	32.06549	30/08/2009	232
14	*T. gajaci*	Cennet cave	Içel, Silifke	36.27120	34.06383	05/06/2009	135
15	*T. escalerai*	Döngel cave	Maraş, Narliseki	37.51557	36.38476	06/06/2009	647

Methods

Sampling and studying methods

Ten caves have been checked for each region in Turkey (Mediterranean, Central Anatolian, Aegean and Black Sea region) to collect cave crickets and fifteen sampled populations belonged to the genus *Troglophilus*; of these eleven were in the Mediterranean and Anatolian region, three in the Aegean region and one in the Black Sea region (Figure 1). All the known five Turkish species (*Troglophilus escalerai*, *T. gajaci*, *T. adamovici*, *T.*

bicakcii, *T. tatyanae*) and four new taxa/populations from Muğla, Alanya, Seydişehir and Balıkesir provinces (see Table 1, Figure 1) were included in this study. The latter four taxa are hereto considered as non-described species because it was not possible to attribute them on morphological grounds to any of the *Troglophilus* species known for the area. Specimens were collected between 2008 and 2009 by hands searching on walls and grounds of caves through the day. Morphological identification of specimens was performed using a stereomicroscope Leica MZ 12.5 equipped with a "camera lucida" and photo camera. Specimens were preserved in absolute ethyl alcohol at AUZM (Akdeniz University Zoology Museum, Antalya, Turkey).

DNA isolation, PCR (Polymerase Chain Reaction) and DNA sequencing

Genomic DNA was extracted from the hind femoral muscle using I-genomic CTB DNA Extraction Mini Kit (type G protocol for Insect, Cat. No 17341, Macrogen Inc.). A 532-535 base pair (bp) fragment of the mitochondrial 16S rDNA gene was amplified through the Polymerase Chain Reaction (PCR) from each individual samples. The primers used were ER232 (5'-CGCCTGTTTAACAAAAACAT-3') and ER233 (5'-CCGGTCTGAACTCAG ATGACTG-3') (Simon et al. 1994). PCR amplifications were performed with a Bio-Rad PTC0220 cycler (Macrogen Inc.) in a 50 µl reaction volume containing genomic DNA (50-100 ng), 25 mM dNTP, 10 µl Band Doctor (5x) 5 µl Buffer (10x), 2 µl (10 pmol/ µl) of each primer, 0.3 µl Ex-Taq (5U/ µl) and distiller water. The PCR conditions were as follows: 95 °C for 5 minutes, followed by 39 cycles of denaturation at 95 °C for 30 s, annealing of primers at 53 °C for 30 s, elongation at 72 °C for 1 min and one final extension step at 72 °C for 5 min. PCR products were purified using the QIAquick PCR Purification Kit (Qiagen); in some circumstances PCR products were excised from gel and purified with the QIAquick Gel Extraction Kit (Qiagen). Sequencing was carried out on an ABI 3730XL sequencer in both directions and with the same primer pair used for PCRs. Sequences data were edited and compiled using Codoncode Aligner (Codoncode Corporation MA, USA version 2.0.2).

Phylogenetic and divergence time analyses

Sequences were aligned in ClustalX (Thompson et al. 1997) with default parameters. Aligned sequences were analyzed phylogenetically by maximum parsimony (MP; heuristic searches, ACCTRAN character-state optimization, 100 random stepwise additions, TBR branch-swapping algorithm) (Farris 1970) and Bayesian methods (Rannala and Yang 1996; Mau and Newton 1997; Larget and Simon 1999; Mau et al. 1999; Huelsenbeck et al. 2000). MP analyses were performed using PAUP* 4.0b10 (Swofford 2003); Bayesian analysis was carried out using MRBAYES 3.1 (Ronquist and Huelsenbeck 2003). MP searches were run giving equal weight to all substitutions. We determined the best model of DNA substitutions fitting our data using

JMODELTEST (Posada 2008); the chosen model was then used for the Bayesian analyses allowing site-specific rate variation. MRBAYES was run for 2 million generations with a sampling frequency of 100 generations. We ran one cold and three heated Markov chains. From the 20000 trees found, we discarded the first 10% ("burn-in") in order to include only trees for which convergence of the Markov chain had been reached; the posterior probabilities were estimated only for those generations sampled after the burn-in. The remaining 18000 trees were used to construct a 50% majority rule consensus tree using PAUP* 4.0b10. The robustness of the MP hypotheses was tested by 1000 bootstrap replicates (Felsenstein 1985). In addition, we sequenced a single individual of *Dolichopoda geniculata* from Valmarino cave (Latium, Central Italy); the species belongs to the only other Rhaphidophoridae genus present in the Mediterranean area and was used as the outgroup for all phylogenetic searches. We calculated Maximum Likelihood (ML) genetic distances among the main lineages retrieved from the phylogenetic searches using the settings yielded by JMODELTEST.

Divergence times were calculated in a Bayesian MCMC framework by using Beast 1.4.6 (Drummond and Rambaut 2007). We adopted a model of uncorrelated but log-normally distributed rates of molecular evolution (Drummond et al. 2006). Neither fossil evidence nor geological events for the species analyzed here were available to calibrate our phylogeny. Consequently, we took advantage of the 16S substitution rate of 0.7% per lineage per million years estimated by Allegrucci et al. (2011) for the cave cricket genus *Dolichopoda* to date age of divergence among haplotypes. We used a Yule prior on rates of evolution because this more accurately resembles phylogenetic processes at the species level. We adopted the same GTR+ G model as in the ML and Bayesian searches. We ran five independent analyses of 50,000,000 generations each; the corresponding outputs were analyzed using Tracer 1.4, TreeAnnotator 1.4.6 and FigTree 1.0 (Drummond and Rambaut 2007). A Mantel test (Mantel 1967), considering all in-group taxa, was carried out to test for a possible correlation between genetic and geographic distances.

Results

Sequence variation

The 16S alignment consisted of 543 nucleotidic positions. Sequences were obtained for each individual and a total of 38 samples belonging to 15 populations were analyzed and 18 different haplotypes found. Sequences of these unique haplotypes have been deposited in GenBank under the Accession N. JX968473-JX968490. Table 2 shows the absolute frequency of these 18 haplotypes in the different populations included in the study. In the final alignment 123 sites were variable and 53 were parsimony informative. The transition/transversion (ti/tv) ratio ranged from 1.7 to 2.2. Ti values accounted for about 62% or 69% of all substitutions when the outgroup was alternatively included or excluded. Divergence in the 16S rDNA gene ranged from 1.1% to 13.1% at the ingroup level (16.1% with the outgroup included).

Table 2. *Troglophilus* species included in this study, the names of the sampling locations, their sample size per locality (*N*), number of haplotypes, the codes of the haplotypes as they appear in Figures 1 and 2.

Species	Population	Locality	N	Haplotype number	Haplotype code
Black Sea Region					
Troglophilus tatyanae	Kafkasor	Artvin	1	1	Ttat-kaf1
Aegean Region					
*Troglophilus sp.*1	Güroluk cave	Muğla, Fethiye	3	1	Tsp1-gur1
	Gökçeler cave	Muğla, Milas	1	1	Tsp1-gok1
*Troglophilus sp.*4	Havran Cave	Balıkesir, Havran	3	1	Tsp4-hav1
Mediterranean and Central Anatolia region					
T. escalerai	Döngel cave	K.Maraş, Döngel	3	1	Tesc-don1
T. gajaci	Cennet cave	İçel, Silifke	5	1	Tgaj-cen1
T. adamovici	Zindan cave	Isparta, Aksu	4	1	Tada-zin1
	Tınaztepe cave	Konya, Seydişehir	2	1	Tada-tin1
	Ferzene cave	Konya, Seydişehir	1	1	Tada-fer1
T. bicakcii	Bıçakçı cave	Konya, Derebucak	2	2	Tbic-bic1, Tbic-bic2
	Direkliin cave	Konya, Beyşehir	2	1	Tbic-dir1
	Feyzullah cave	Konya, Derebucak	2	1	Tbic-fey1
	Balatini cave	Konya, Derebucak	2	1	Tbic-bal1
*Troglophilus sp.*2	Ferzene cave	Konya, Seydişehir	2	2	Tsp2-fer1, Tsp2-fer2
*Troglophilus sp.*3	Dim Cave	Antalya, Alanya	5	2	Tsp3-dim1,Tsp3-dim2

Phylogenetic analyses and divergence times

Figure 2 shows the Bayesian phylogram based on the GTR + G (gamma distribution shape parameter a = 0.188) model chosen by JMODELTEST as the one best fitting our data and summarizes the results of the other phylogenetic methods employed in the study. Bayesian and MP searches were all largely congruent with one another. MP searches yielded three equally parsimonious trees with length (L) = 193 steps, homoplasy index (HI) = 0.249, consistency index (CI) = 0.751, retention index (RI) = 0.780. All analyses consistently recovered three well-supported clades, whose geographic distribution is shown in Figure 1.

Clade 1 includes *T. adamovici* and *Troglophilus sp.*1 populations, which are distributed in the Northern Mediterranean region (Isparta) through the western Taurus Mountain, Southern Central Anatolian regions with a Mediterranean climate and Southern Aegean region (Muğla, Fethiye, Milas). Clade 2 contains *T. bicakci* and *Troglophilus sp.*2 populations, which are distributed in the Southern Central Anatolian region through Kembos Polye and Konya, Seydişehir, Derebucak and Beyşehir Provinces. This clade overlaps with Clade 1 in the Seydişehir Province (Ferzene cave). Clade 3 comprises *Troglophilus sp.*3 population only and it is geographically restricted to the Antalya area (Alanya, Dim cave). The cave is located near the Dim River in the Southern Mediterranean Region.

Average GTR + G distance between Clade 1 and 2 is 0.063 ± 0.025, between Clade 2 and 3 is 0.058 ± 0.021 and between Clade 1 and 3 is 0.050 ± 0.005. Time estimates retrieved from the Bayesian MCMC analyses for the three main clades are illustrated in Figure 2. In all cases 95% credible intervals for node age estimates overlapped. The data did not conform to a clock-like behavior, the coefficient of variation being 0.87 (95% High Posterior Density, HPD: 0.393-1.435; ESS: 1214.24). Parent and daughter branches showed no co-variation, the mean covariance being -5.83^{-2} (HPD: -0.321-0.237; ESS: 7191.33). The 95% High Posterior Density spans zero; this implies that branches with fast and slow rates are next to each other in the phylogenetic tree. There is thus no evidence of autocorrelation of rates in the tree. Ages of Clades 1, 2, and 3 ranges between 5.8 and 2.3 million years; the lack of a clear calibration point resulted in a chronogram with relatively ample confidence intervals (Figure 2).

Results of the Mantel test (Mantel 1967), performed to explore a possible correlation between geographic and genetic distance in all studied taxa, suggested there was no correlation between genetic and geographic distances (r= -0.01, p value (two-tailed) = 0.881).

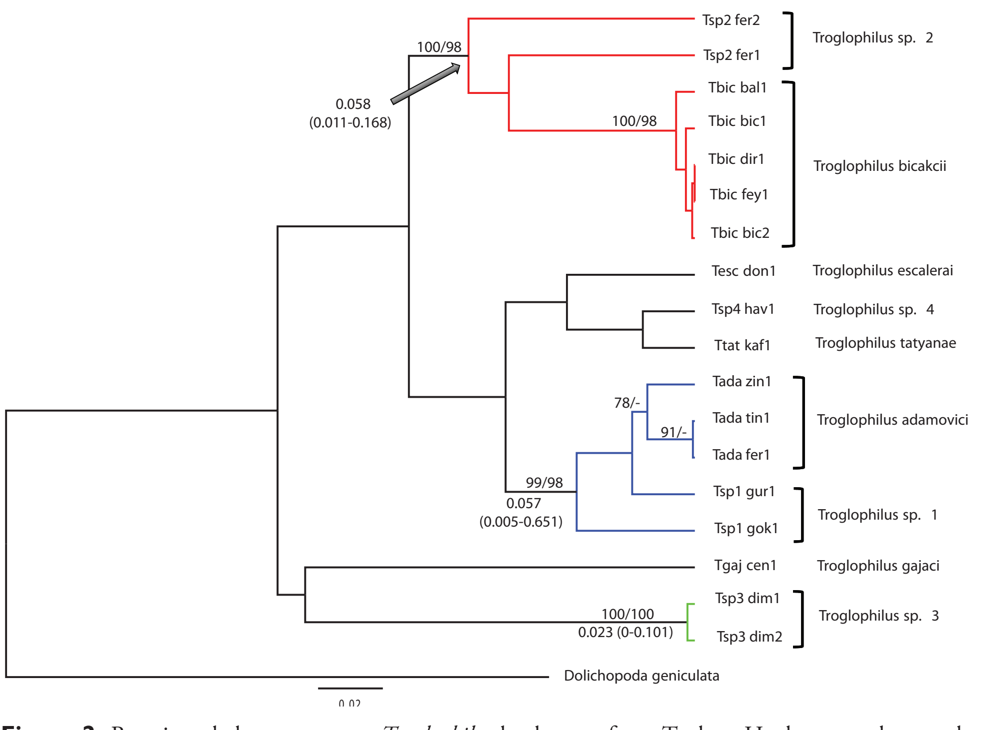

Figure 2. Bayesian phylogram among *Troglophilus* haplotypes from Turkey. Haplotype codes match those in Table 2. Numbers at nodes are statistical supports for the Bayesian and MP searches (first and second value, respectively); only values ≥ 75% are reported. The three supported clusters are described in the text are highlighted here in blue (clade 1), red (clade 2) and green (clade 3). Bold values are node ages (in Myr %) as obtained by the BEAST analyses; 95% HPD intervals are shown in parentheses.

Discussion

Molecular systematics

The genetic data confirmed the validity of the already described species, with conspecific populations firmly forming monophyletic clusters. On the other hand, four deeply genetically divergent lineages (*Troglophilus sp.*1, 2, 3 and 4) could not be attributed to any of the previously described species and could hence represent new taxa. The mean GTR + G genetic distance between the described *Troglophilus* species included in our study (Bolivar 1899; Us 1974; Rampini and Di Russo 2003; Di Russo et al. 2007) ranges from 0.028 to 0.065 ± 0.008. The four new taxa (*Troglophilus sp.*1, 2, 3 and 4) diverge from all the described species for a GTR + G distance range comprised between 0.023-0.132 ± 0.026. Hence, these four new lineages are genetically as divergent as the formally described species are, and in some cases even more.. In addition, they also show morphological differences in the shape of the ovipositor, which is one of the most important discriminating characters traditionally used for taxonomic purposes in *Troglophilus* (Taylan et al. 2011).

Cobolli et al. (1999), by using allozymes revealed four distinct gene pools among Anatolian species of *Troglophilus* from the Taurus Mountains between Isparta and Adana provinces. These corresponded to *T. adamovici*, *T. gajaci* and two lineages formally not described yet genetically differentiated. One of those lineages was later described as the new species *T. bicakcii* by Rampini and Di Russo (2003) (from the Balatini cave), while the second lineage is the *Troglophilus sp.*2 from the Ferzene cave included in the present study. *Troglophilus sp.*1, 3 and 4 were not reported in Cobolli et al. (1999). It is worth noting that *Troglophilus sp.*2 is syntopic with *T. adamovici* (Taylan et al. 2011).

Overall, we could distinguish three main clades; all received strong support in our phylogenetic analyses (Figures 1 and 2). Clade 1 includes *T. adamovici* and the new species *Troglophilus sp.*1 distributed in the Isparta, Konya and Izmir provinces. Clade 2 comprises *T. bicakcii* and the new species *Troglophilus sp.*2 (from Ferzene cave) both from the Konya province, while Clade 3 includes *Troglophilus sp.*3 population distributed in the Dim Cave in Antalya. The phylogenetic placement of *T. gajaci*, *T. escalerai*, *T. tatyanae*, and *Troglophilus sp.*4 could not be resolved by the data and remains controversial. Kaya et al. (2012), by using a combination of mitochondrial and nuclear genes, found good support for *T. gajaci* basal to a group of non-described forms, including a population corresponding to *Troglophilus sp.* 3 in our study. The placement of *T. tatyanae* is not resolved in either study, while Kaya et al. (2012) consistently retrieved a sister-species relationship for *T. adamovici* and *T. bicakcii*. Those authors did not analyze *T. escalerai*. It is evident that these discrepancies could be reconciled only by maximizing the overlap of both species and markers. Another point that shouldn't be overlooked is that a phylogenetic hypothesis for the whole genus *Troglophilus* is still missing. A study based on a multi-gene approach and aimed at producing such a hypothesis is in progress, which will likely shed light on the questions left open by this and previous studies.

Phylogeography

The Mantel test (Mantel 1967) shows that there is no correlation between genetic and geographic distances; hence genetic divergence is not function of the geographic distance separating the different caves. Considering the high level of genetic divergence found among our populations, we conclude that mitochondrial gene flow among these populations broke off completely sometimes in the past. This scenario is similar to what observed in subterranean diving beetles in isolated aquifers in Australia (Leijs et al. 2012), but, quite unexpectedly, it is different from that retrieved for the only other Mediterranean cave crickets (genus *Dolichopoda*). As a matter of fact, Allegrucci et al. (2005) and Taylan et al. (unpublished data) found strong evidence supporting isolation by distance pattern in *Dolichopoda*. The difference in the genetic structure between *Troglophilus* and *Dolichopoda* could be due to a higher tendency for the latter to maintain gene flow among caves. On the other hand, it shouldn't be overlooked that our sampling across Turkey is rather sparse and isolation by distance could fail to emerge from the data just because we missed too many intervening locations in our sampling. Finally, our study is based on a single marker with moderate evolving rates. On a more local scale, with a denser sampling and a multi-gene approach, isolation by distance was found in *Troglophilus cavicola* in Northern Italy (Ketmaier et al. 2004), suggesting that the result of the present study could be either sampling or marker-biased.

An additional point of interest of this study is the confirmation of the results of Cobolli et al. (1999) supporting the syntopic occurrence of two genetically divergent lineages in the Ferzene cave (*T. adamovici* and *Troglophilus sp.*2). This pattern suggests a secondary contact of these lineages after allopatric divergence, a phenomenon reported multiple times in cave dwelling-organisms (Sbordoni et al. 2000; Niemiller et al. 2008; Raşit et al. 2008). As a matter of fact, Cobolli et al. (1999) found nine allozymic loci fixed for alternative alleles with no heterozygotes in the large number of samples (147) used for that study. We could observe no sign of mitochondrial DNA introgression in the few samples we analyzed for the study. Based on previous allozymic data but keeping in mind our limitations in terms of sample size and markers, we would tentatively conclude that these two syntopically occurring lineages are reproductively isolated. It is evident that a multi-gene approach, based on both mitochondrial and nuclear fast evolving markers, is necessary to properly address the issue. It is nonetheless worth noting that the syntopic co-occurrence of closely related, non-intermixing lineages would imply a differential exploitation of resources to avoid competition. It is reasonable to hypothesize that these two divergent lineages have acquired (slightly) different ecological niches, a point that would be interesting to address with an *ad-hoc* designed study.

The estimated divergence times range from the Messinian to the Plio-Pleistocene (Figure 2). The oldest estimated divergence times are around 5.8 Ma (Messinian) and coincide with the last period of the uplifting the Anatolian Plateau, which arose 5-10 Ma as a consequence of the northward movement of the Arabian Plate (Qennell 1984; Steininger and Rögl 1984). The Messinian was a time of high rainfall and high sediment yields rates (Zeit Wet Phase, Griffin 1999). This phase, characterized by a humid climate, might have favored regional dispersal. The fact that our divergence times within Clades 1 and 2 are near the end of this wet phase suggests that the transition towards the drier Messinian climate was responsible for the splits. Cave crickets (and cave organisms in general) (Carchini et al. 1991; Taylan et al. 2011) cannot withstand epigean dry conditions; we envision a scenario where these crickets were forced to seek refuge in the subterranean environment during the Messinian and started diverging in allopatry. These estimates are in remarkable agreement with those obtained for the genus *Dolichopoda* in the Eastern Mediterranean area (Allegrucci et al. 2009).

The estimated divergence time for *Troglophilus sp.*3 is more recent (2.3 Ma), dating to the Plio-Pleistocene, which was characterized by alternating dry/cold and warm/humid phases. The climatic fluctuations during the Plio-Pleistocene likely led to ecological fragmentation with subsequent genetic isolation and speciation in the area. This hypothesis is also supported by the results from the *Dolichopoda* species, whose radiation also appears to have followed the climatic changes of the Plio-Pleistocene (Allegrucci et al. 2005, 2009).

Since the syntopic *T. adamovici* and *Troglophilus sp.*2 in the Ferzene cave do not interbreed, their secondary contact must have taken place after the diversification within Clades 1 and 2, certainly more recently than the Messinian. Even though we are not in the position to date when the secondary contact actually happened, we suspected that this was favored by one of the many warm and humid climatic phases of the Quaternary, which allegedly promoted epigean dispersal among lineages that had been previously confined to caves.

Our time estimates for the splitting events within the Anatolian representatives of *Troglophilus* are in agreement with those reported in Kaya et al. (2012). This concordance is even more remarkable considering the differences between the two studies in terms of sampled taxa, markers employed and (at least partially) phylogenetic relationships retrieved (see the molecular systematics section). Also those authors identified the climate changes of the Plio-Pleistocene as the cause that triggered divergence among Anatolian *Troglophilus*.

Finally, it should not be overlooked that this study is limited to the Turkish area and is based on a single mitochondrial marker. To place these results in a broader perspective and to understand in details the evolutionary trajectories followed by the genus, we need to expand our sampling by covering its whole distribution range and by combining multiple mitochondrial and nuclear loci. To these aims our ongoing research activity is currently devoted.

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Checklist of the ants (Hymenoptera, Formicidae) of the Solomon Islands and a new survey of Makira Island

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Abstract

The intent of this paper is to facilitate future research of the Solomon Islands ant fauna by providing the first comprehensively researched species inventory in over 75 years. The species list presented here includes the names of all ant species recorded from the islands that are available in the literature together with specimen records from several museum collections and new records from our 2008 Makira field expedition. All the names of described species presented are valid in accordance with the most recent Formicidae classification. In total, the checklist is composed of 237 species and subspecies (including 30 morphospecies) in 59 genera representing nine subfamilies. We report that the recent field expedition added 67 new species records to Makira and 28 new species records to the Solomon Islands. Our research recovered species occurrence records for 32 individual islands and five island groups. The five islands with the highest number of recorded species are: Makira (142 spp.), Guadalcanal (107 spp.), Malaita (70 spp.), Santa Isabel (68 spp.), and Rennell (66 spp.). Based on our results, we discuss the taxonomic composition of the archipelago's ant fauna, which islands are most in need of additional sampling, and the importance of establishing biodiversity baselines before environmental threats such as the invasive ant *Wasmannia auropunctata* cause irrevocable harm to the native biodiversity.

Keywords

Biogeography, checklist, Makira Island, Pacific Islands, Solomon Islands, species distributions, taxonomy, Formicidae

Introduction

The intent of this paper is to facilitate future research of the Solomon Island ant fauna and that of the larger Pacific Island region by providing the first comprehensively researched species list in over 75 years (Mann 1919; Wheeler 1935b). Reliable species lists are the foundation for biodiversity and biogeography research. This is especially true for archipelago systems such as the Solomons which serve as natural laboratories for studying the interface of geography, evolution and ecology (Diamond 1975; Diamond and Mayr 1976; Greenslade 1968; MacArthur and Wilson 1967; Mayr and Diamond 2001; Wilson 1959a; 1961). Accurate faunal lists at the archipelago level allow us to analyze biogeographic patterns at the regional scale, and faunal lists at the individual island level allow us to analyze more local scale patterns. These studies are crucial for the development of precise conservation plans that incorporate the distribution of endemic and rare taxa.

Faunal lists are also necessary for recognizing biodiversity blind spots and identifying which regions and islands are most in need of additional sampling. Increasing environmental threats such as deforestation, mining, agriculture and the spread of invasive species give urgency to surveying these poorly sampled regions. In order to assess how these threats affect native biodiversity, it is important to establish baseline inventories before local populations and endemic species are driven extinct.

Geography, geology and climate

The Solomon Islands is a nation in the Southwest Pacific that is composed of seven large islands, a dozen mid-sized islands and over a thousand smaller islands (Figure 1). These islands, which comprise a total land area of 27,556 km^2, are situated between the latitudes 5° and 13°S, and longitudes 155° and 169°E. The major central islands include the Shortlands, Choiseul, the New Georgias, Santa Isabel, the Russells, Guadalcanal, the Nggelas (Floridas), Malaita, Makira (San Cristóbal), and Olu Malau (Three Sisters). Rennell and Bellona are southern outlying islands situated along the northern margin of the Coral Sea Basin. Northern outlying islands include Sikaiana and the Ontong Java Atoll, which are on the southwestern edge of the Ontong Java Plateau. The eastern outlying islands of the Santa Cruz group are politically part of the Solomon Islands, but are geologically linked to the islands of Vanuatu (Kroenke and Rodda 1984).

The Solomons consist of a double chain of islands separating the Pacific Plate to the north from the Australian Plate to the south (Hall 2002). The islands are believed to have been formed entirely of oceanic origin, and there is no evidence that they were ever attached to continental systems or incorporated any terrains of continental origin (Kroenke and Rodda 1984). They are, in this sense, Darwinian Islands (Gillespie and Roderick 2002). According to several geologic models (Hall 2002) the Solomon Arc formed approximately 40 Ma as part of the Melanesian Arc system. It is unclear, however, when the islands emerged above sea level.

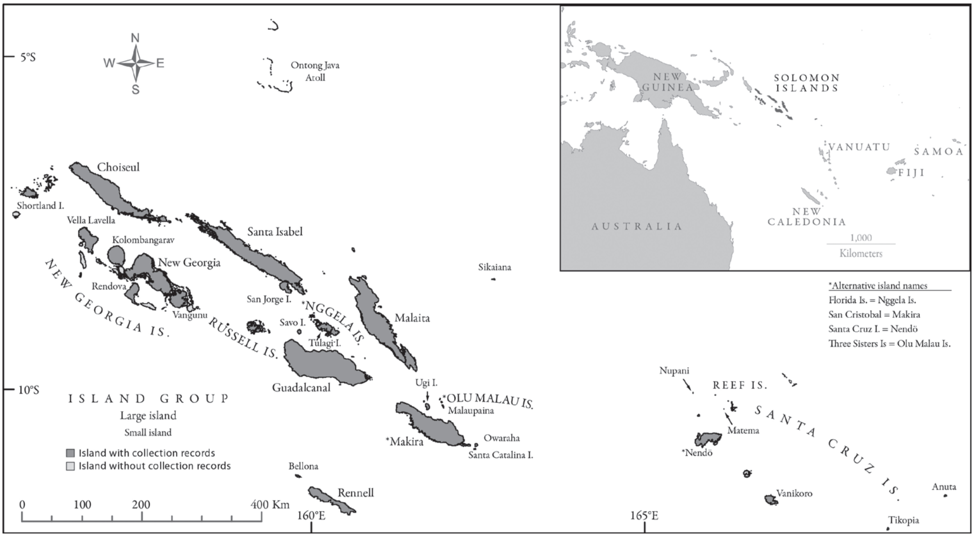

Figure 1. Map of the Solomon Islands. The map presents all islands and island groups for which ant species were recorded. Each island/island group from which ant species are known is labeled with the geographic name and filled darker grey. Islands for which no ant records appear in the literature are unlabeled and filled with lighter grey. Relevant historic island names from the colonial era are presented with their contemporary counterparts.

Bougainville, which lies to the west, belongs politically to Papua New Guinea but is geographically part of the Solomon Islands. The next closest neighbor nation is Vanuatu, which lies southeast of the main archipelago and nearly due south of the Santa Cruz Is.

The climate of the Solomon Islands is characterized as humid with a mean temperature of 27 °C (80 °F) and relatively few fluctuations of temperature or weather. The cooler and drier part of the year occurs from June through August, and the warmer and wetter season occurs from September through May. The annual rainfall is approximately 3050 mm (120 in).

History of ant collection and research in the Solomon Islands

The first ants described from the Solomon Islands were authored by Forel (1910) in a paper on Australian ants based on the collections of W.M. Froggatt and Rowland Turner. Froggatt visited the Solomon Islands to study the insects of the coconut palms, and collected at Tulagi I. and in the Russell Group. W.M. Mann (1919) provided the first and only comprehensive revision of the Solomon Island ant fauna. He spent six months on the archipelago from 19 May to 24 November 1916, and collected on the islands Guadalcanal, Makira, Malaita, Malaupaina, New Georgia, Nggela Sule, Owaraha, Rendova, Russell Is., Santa Cruz, Santa Isabel, Tulagi and Ugi. Mann reported the occurrence of 136 currently recognized species and subspecies, of which he described 68 from his own collections. In addition to a broad discussion of the archipelago's ant fauna, the treatise also includes keys to Melanesian species of *Anochetus*, *Crematogaster*, *Cryptopone*, *Eurhopalothrix*, *Leptogenys*, *Myrmecina*, *Triglyphothrix* (= *Tetramorium*), *Turneria*, and *Wheeleripone* (= *Gnamptogenys*). Additional relevant publications from Mann include descriptions of ant guests from Fiji and the Solomon Islands (Mann 1920), and accounts from his travels in the Solomon Islands (and elsewhere) in his book *Ant Hill Odyssey* (Mann 1948).

H. Viehmeyer (1924) described a new subspecies *Euponera* (*Mesoponera*) *melanaria* subsp. *manni* (= *Pachycondyla manni*) from Mann's collections at the Museum of Comparative Zoology (MCZ). H. Donisthorpe (1941) described *Nylanderia manni* from a worker that was on the same pin as several workers of *Camponotus loa* Mann, all of which were labeled as *Iridomyrmex myrmecodiae* Emery (= *Philidris myrmecodiae*). Donisthorpe attributed the close similarity of all three species to mimicry.

W.M. Wheeler's first contribution to the Solomon Island ant fauna was his description of *Opisthopsis manni* based on specimens collected by Mann from Malaupaina (Wheeler 1918). Wheeler (1934) later published on ants collected by Maurice Willows Jr. from the Santa Cruz and Danger Islands. He listed the names and collection records of 27 currently recognized taxa, including original descriptions for two species (*Nylanderia dichora*, *Stereomyrmex dispar*) and one subspecies (*Polyrhachis labella brunneipes*), along with the first published record of *Tapinoma melanocephalum* from the Solomons (Wetterer 2009). These records are combined with those of Forel and Mann in Wheeler (1935b).

William Brown treated many Solomon Island taxa in his revisions (Brown 1948; 1958a; b; 1960; 1975; 1976; 1978; 1988; 1995; Willey and Brown 1983). Gressitt (1958) reported on the pest behavior of *Iridomyrmex myrmecodiae* (= *Philidris myrmecodiae*) invading buildings in Malaita. According to Wilson (1962), the B.P. Bishop Museum, Honolulu, initiated a collecting program in the Solomons under the direction of Gressitt, and there is likely a considerable amount of ant material that remains unreported in the literature.

Research on economically important ants involved in coconut production was an active field in the Solomons from the 1930's through the 1960's (Leston 1973; Lever 1933; 1961; O'Conner 1949; 1950; Phillips 1940; 1956). E.S. Brown (1959) recorded over 60 species of ants (including five new country records) collected during his work among coconut plantations in Guadalcanal and Malaita.

Philip J.M. Greenslade has arguably collected more thoroughly across the Solomons than anyone since Mann. Greenslade published seven papers between 1964 and 1988 based on fieldwork he conducted in the Solomons (Greenslade 1964; 1971a; b; 1972; Greenslade and Greenslade 1970; 1971; 1977). The research focused primarily on the ecology of ants that are dominant in coconut plantations and are involved in the biological control of a coconut pest, *Amblypelta cocophaga* China and the premature nutfall of coconut fruit. In addition to providing valuable ecological information on the four most dominant ant species in these plantations (*Anoplolepis gracilipes* (Smith, F.), *Oecophylla smaragdina* Forel, *Pheidole megacephala* (Fabricius) and *Philidris cordata* (Smith, F.)), Greenslade also collected a broad diversity of less economically important ant species, mainly from Mt. Austen (Guadalcanal) and Kukum—the nearby Solomon Is. Department of Agriculture farm. These specimens, most of which were deposited at the ANIC, included many new species in addition to the first records of *Problomyrmex* (Taylor 1965) and *Colobostruma* (Bolton 2000) for the Solomon Islands. Interestingly, Greenslade's (1968) work on the avifauna of the Solomon Islands was the first to apply the taxon cycle model to birds.

E.O. Wilson included many species from the Solomon Islands during his revisionary work of the Melanesian ant fauna, including species currently in the genera *Amblyopone*, *Leptogenys*, *Platythyrea* and *Stigmatomma* (1958a); *Ponera*, *Cryptopone*, *Hypoponera*, *Pachycondyla* and *Rhytidoponera* (1958b); *Anochetus* and *Odontomachus* (1959c); and *Cerapachys* (1959d). Wilson & Taylor (1967) added several new species records for the Solomons, including *Ponera incerta* (Wheeler) and *Strumigenys karawajewi* Brown (as *S. dubia* (Brown)). Wilson and Hunt (1967) included records for the Solomons. In addition to these taxonomic studies, Wilson also included ants from the Solomons in his influential papers on the taxon cycle hypothesis (Wilson 1959a; 1961) and the theory of island biogeography (MacArthur and Wilson 1967).

Wilson's (1962) paper on the ants of Rennell and Bellona Islands examined specimens collected from three sources: a Danish Expedition (Wolff 1955); a British expedition (Bradley 1955), and a private collection made on Rennell and Bellona for several weeks during 1955, by Mr. E.S. Brown. Wilson recorded 25 species of ants in 17 genera from Rennell (including the first record of *Dilobocondyla* from the Solomons). He considered these to represent a large percentage of the actual ant diversity, but admitted that the lack of cryptobiotic ponerine and myrmicine species suggest that his list is incomplete. He concluded that the Rennell ant fauna is primarily composed of widespread Pacific natives that invaded the island relatively recently and are representative of 'Stage-I' species discussed in his taxon cycle hypothesis (Wilson 1959a; 1961).

Robert Taylor, in addition to describing *Problomyrmex salomonis* (Taylor 1965), also described *Eurhopalothrix greensladei* (Taylor 1968), and *Stigmatomma gnoma* (= *Amblyopone gnoma*) (Taylor 1979) from specimens collected by P.J.M. Greenslade on or near Mt. Austen. Rudolf Kohout's work on *Polyrhachis* added several new species records to the Solomons, introduced new synonyms and nomenclatural changes, and included the description of three new species (*P. greensladei*, *P. setosa*, *P. undulata*) endemic to the Solomons (Kohout 1990; 1998; 2006). Barry Bolton described *Polyrhachis nofra* (Bolton 1975), from the Solomons, provided the replacement name of *Tetramorium mutatum* Bolton for the junior secondary homonym *Triglyphothrix* (= *Tetramorium*) *pulchella* Mann (Bolton 1985), and added new records of dacetines in the Solomons (Bolton 2000). Bolton (1976) also described *Tetramorium vombis* from specimens Mann (1919) mistakenly identified as *T. obesa* André. Kugler described *Rogeria megastigmatica* from a Greenslade collection made on Guadalcanal (Kugler 1994). Lattke included the Solomon Islands in his biogeographic analysis of *Gnamptogenys* in Southeast Asia (Lattke 2003) and described two new species (*G. preciosa* and *G. solomonensis*) from there (Lattke 2004). Lucky & Sarnat (2008) included *Lordomyrma epinotalis* Mann in their phylogenetic and biogeographic analysis of the genus. Sarnat and Moreau (2011) included *Pheidole* species from the Solomons in their phylogenetic and biogeographic analysis of the Fijian *Pheidole* and selected congeners from across the Pacific.

Methods

Compilation of names

In order to compile a comprehensive and accurate inventory of ant species recorded from the Solomon Islands, we researched taxonomic names that were associated with the region in the literature. We reviewed the names of all taxa that were originally described from Solomons, reviewed specimen records from Antweb.org, reviewed the species list for the Solomon Islands presented on Antwiki <http://www.antwiki.org/Solomon_Islands>, searched the Formis database (Porter and Wojcik 2012) for all relevant literature containing the term 'Solomon', and reviewed relevant taxonomic and regional literature. We also reviewed a dataset of ca. 1,040 specimen records of identified ants collected in the Solomon Islands that are deposited at the ANIC (Australian National Insect Collection, Canberra). We used the Bolton (2012) catalog to determine the valid names of all the species on the list. The Bolton (2012) catalog does not recognize the synonymy of *Cryptopone* with *Pachycondyla*, as implicitly proposed by Mackay & Mackay (2010), and the name is retained here as valid.

Names were eliminated where we found evidence of misidentification or geographic inconsistencies such as geographic names erroneously considered as belonging to the Solomon Islands. We also reconciled situations in which different authors may have referred to the same species by different valid names. For example, there were instances in which we believe one author referred to a taxon using its specific name, and another author referred to the same taxon by its infraspecific name. In cases such as these, and in the absence of additional evidence, we use the infraspecific name. We also note which other names we interpret as referring to the same taxon, and which publications those names occur in.

In addition to the valid names, we also use morphospecies codes to refer to presumptive species that either we or previous authors were unable to determine. The morphospecies code is 'BP' (The administrative code for the Solomon Islands) followed and a unique two-digit number (e.g. '*Camponotus* sp. BP01').

Bougainville is considered to belong geographically but not politically to the Solomons. As such we do not include species recorded from Bougainville that have not also been reported from at least one of islands to its east.

Survey of Makira

In addition to basing the present study on the aforementioned published records, we also include records from our own recent survey of the Solomons. Three of the authors (E.P.E., E.M.S., J.F.) collected ants in the Solomons from 30 January to 9 February, 2008. Aside from a few collections made on Mt. Austen (Guadalcanal I.), the survey primarily focused on Makira Island (formerly San Cristóbal) where we trekked and collected from Kirakira on the coast to the interior village of Maraone, reaching a maximum elevation of 912 m. Survey methods included hand collection and litter sifting along standardized transects using Winkler extraction bags. All specimens were collected into and stored in 95% ethanol. Pinned specimens were identified using the available literature and compared to type and determined material at the United States National Museum of Natural History (USNM), Washington D.C., USA, and the Museum of Comparative Zoology (MCZC), Cambridge, Massachusetts, USA. These two collections are the primary depositories for Mann's type material and also include type material designated by W.L. Brown, W.M. Wheeler and E.O. Wilson. We include the species records from this survey with the literature records.

Island records

Occurrence data of ant species on individual islands and island groups were compiled from the relevant literature. More detailed data with literature references for each species-island occurrence is available from the authors upon request. A map of the Solomon Islands (Figure 1) is also presented in which the name of every island and island group from which ant species have been recorded is labeled. The constituent islands comprising the listed island groups are presented in Table 1. In addition to including all taxa from Appendixes 1 and 2, we also include taxa from the 2008 survey of Makira that remain undetermined but might belong to previously described species. Inclusion of these additional taxa may weakly bias the observed species richness of Makira towards a higher value, but exclusion of these taxa would cause an even greater bias towards a lower value.

Sampling analysis

We used our data compilation to estimate in a general sense how undersampled the Solomon Islands are for ants. First, we compared the species richness of individual islands in the Solomons with counts of the Fijian islands, which were the target of recent intensive sampling and taxonomic analysis (Sarnat and Economo 2012). We also compared the species richness of Makira from records before and after our 2008 survey.

Table 1. Island groups and their constituent islands.

Island Group	Islands
Santa Cruz Is.	Anuta, Nendö (Santa Cruz), Nupani, Reef Is., Tikopia, Vanikoro
Olu Malau Is. (Three Sisters)	Malaupaina
Nggela Is. (Florida Is.)	Nggela Sule (Florida), Tulagi
New Georgia Is.	Kolombangarav, New Georgia, Rendova, Vangunu, Vella Lavella
Reef Is.	Matema

Table 2. Number of presumptive native species from Appendix 1 for each genus (arranged from greatest to least). Diverse genera with well-established subgenera are nested under the genus name and the species number of each is presented in parentheses.

Genus (Subgenus)	Native spp.	%Total
Polyrhachis	30	14
P. (*Myrma*)	(7)	–
P. (*Cyrtomyrma*)	(5)	–
P. (*Chariomyrma*)	(4)	–
P. (*Hedomyrma*)	(4)	–
P. (*Myrmhopla*)	(3)	–
P. (*Myrmatopa*)	(2)	–
P. (*Myrmothrinax*)	(1)	–
P. (*Hirtomyrma*)	(1)	–
Pheidole	15	7
Camponotus	14	7
C. (*Colobopsis*)	(5)	–
Tetramorium	11	5
Vollenhovia	11	5
Pachycondyla	9	4
Strumigenys	9	4
Crematogaster	7	3
C. (*Crematogaster*)	(5)	–
C. (*Orthocrema*)	(2)	–
Gnamptogenys	6	3
Cryptopone	5	2
Hypoponera	5	2
Myrmecina	5	2
Nylanderia	5	2
Ponera	5	2
Acropyga	4	2
Cerapachys	4	2
Eurhopalothrix	4	2
Leptogenys	4	2
Myopias	4	2
Odontomachus	4	2
Anochetus	3	1
Rogeria	3	1
Adelomyrmex	2	1
Arnoldius	2	1
Cardiocondyla	2	1
Carebara	2	1
Colobostruma	2	1
Iridomyrmex	2	1
Podomyrma	2	1
Prionopelta	2	1
Pristomyrmex	2	1
Proceratium	2	1
Rhytidoponera	2	1

Genus (Subgenus)	Native spp.	%Total
Solenopsis	2	1
Stigmatomma	2	1
Turneria	2	1
Amblyopone	1	<1
Anonychomyrma	1	<1
Discothyrea	1	<1
Lordomyrma	1	<1
Monomorium	1	<1
Myopopone	1	<1
Oecophylla	1	<1
Opisthopsis	1	<1
Paraparatrechina	1	<1
Philidris	1	<1
Platythyrea	1	<1
Probolomyrmex	1	<1
Stereomyrmex	1	<1
Tapinoma	1	<1
Tetraponera	1	<1

Results

Ant records from the Solomon Islands

We present a list of nine subfamilies, 60 genera and 215 valid ant species and subspecies for the Solomon Islands based on our review of the literature and our recent collections from Makira (Appendix 1). We also present a list of 23 presumptively undescribed species that have also been recorded from the Solomons (Appendix 2). The generic composition and diversity of the Solomons is presented in Table 1. In total, our research suggests that the Solomon Islands support at least 237 unique ant taxa. The full species list with associated images and specimen data is available on Antweb.org <http://www.antweb.org/solomons.jsp>.

We excluded the following taxa from the list as they were reported from Bougainville but not from within the political boundaries of the Solomon Islands: *Cryptopone crassicornis* (Emery), *Polyrhachis aurea* (Mayr), *Polyrhachis obliqua* Stitz, and *Polyrhachis salomo* subsp. *hiram* Forel.

The following taxa were reported from the Solomon Islands, but are not believed to occur there either because the records were based on misidentified material or erroneous interpretation of locality data.

Camponotus pallens (Le Guillou, 1842): 316. Type locality: Tonga, Vavao. The website Antwiki.org, accessed 5 October 2012, listed this species under its Solomon Island webpage. The list was generated by extracting all species for which the Solomon Is. were listed as the type locality from the Bolton Catalog (Bolton et al. 2006). Although there are several Vavao islands in the Pacific (including in the Solomon

Is.) the original description lists the type locality as *Vavao* (*íles des Amis*), which suggests Tonga (often referred to in older literature as the 'Friendly Islands') is the more likely country. Moreover, the species does not appear in any of the reviewed literature as occurring in the Solomons.

Camponotus reticulatus Roger, 1863: 139. Type locality: Sri Lanka. The first record of *C. reticulatus* Roger appeared in Wilson (1962). Wilson explicitly applied *C. reticulatus* Roger to the Solomons material that Wheeler (1934) referred to as *C. reticulatus* subsp. *bedoti* Emery. In following the current classification (Bolton 2012), we accept *C. bedoti* Emery as a valid species, and apply that name to all the material from the Solomons referred to as *C. reticulatus* Roger. The decision to do so is somewhat arbitrary given the current state of taxonomy for Indo-Australian *Camponotus*, but we believe that both names refer to the same species in the Solomons.

Hypoponera pallidula (Emery, 1900): 320. Type locality: New Guinea. Mann (1919) reported this species as occurring in the Solomon Is., but Wilson (1958b) believed Mann's specimens belonged to *Ponera sororcula* (= *Hypoponera sororcula*) Wilson.

Leptogenys laeviceps (Smith, 1857): 69. Type locality: Borneo. Mann (1919) reported this species as occurring in the Solomon Islands, but Wilson (1958a) considered Mann's specimens to be a mixed series, part of which belong to *Leptogenys diminuta* Smith, F. and the other part to *Leptogenys oresbia* Wilson.

Odontomachus haematodus (Linnaeus, 1758): 582. Type locality: "America meridionali." It is presumed that specimens referred to as *O. haematodus* by Mann (1919), Wheeler (1934; 1935a) and E. S. Brown (1959) prior to Wilson's (1959b) revision belong instead to *O. simillimus* Smith, F.

Odontomachus insularis Guérin-Méneville, 1844: 423. Type locality: Cuba. Forel (1910) reported this species as occurring in the Solomon Is., but it is more likely that this was a misidentification and that the specimens he examined belong to *Odontomachus simillimus* Smith, F. *Odontomachus insularis* is not known from the Old World and was not included in Wilson (1959c).

Pheidole punctulata Mayr, 1866: 899. Type locality: South Africa. Forel (1910) reported this species as occurring in the Solomon Is., but it is more likely that the specimens he examined belong to the cosmopolitan tramp *Pheidole megacephala*.

Philidris cordata (Smith, F. 1859): 137. Type locality: Indonesia, Aru I. In his introduction, Greenslade (1972) treated *Iridomyrmex cordatus* (= *Philidris cordata*) Smith, F. as the senior synonym of *I. cordatus* var. *myrmecodiae* (= *P. myrmecodiae*) Emery. However, *P. myrmecodiae* has been accepted as a valid species since 1903

(Bolton 2012; Shattuck 1994). The correct name for the Solomons material would require comparison against type material for both taxa. In the meantime, our decision to use *P. myrmecodiae* rather than *P. cordata* reflects our belief that (1) insofar as the Solomon Is. are concerned, the use of both names refer to the same species; and (2) there is no taxonomic evidence proposed by Greenslade that Mann's (1919) use of *P. myrmecodiae* was misapplied.

Tetramorium obesum André, 1887: 294. Type locality: India. Mann (1919) misidentified a series of specimens as belonging to *T. obesa* André that Bolton (1976) subsequently described as *Tetramorium vombis*. We assume here that the specimens referred to as *T. obesum* by Taylor (1976) are also *T. vombis*.

Makira Island Survey

We collected a total of 67 described species and 30 presumptive species that are either undescribed or that we were unable to determine. Based on comparisons with type material, previously determined material and literature review, we suspect approximately 15 of the presumptive species are new to science. These taxa are included in Appendix 2. The survey added 67 new species records to Makira of taxa included in Appendixes 1 and 2, bringing the total number of species known from the island to 142. The survey also added 28 new species records to the Solomon Islands. Of these, six are previously described species (including three introduced species), and the remainder of species are included in Appendix 2.

Island records and sampling analysis

Our research recovered species occurrence records for 32 individual islands and five island groups out of the approximately 75 named small to large individual islands and approximately 12 named island groups. These occurrence records are presented in Appendix 3. The 261 taxon names include the 215 described species and subspecies from Appendix 1, the 22 presumptive undescribed species from Appendix 2, and 24 additional morphospecies that likely represent a mixture of previously described species and undescribed species. This latter group is restricted to specimens collected during the 2008 Makira survey. The five islands with the highest number of species records, listed from greatest to least, are: Makira (142 spp.), Guadalcanal (107 spp.), Malaita (71 spp.), Santa Isabel (68 spp.), and Rennell (66 spp.). Fourteen individual islands have occurrence records for between 11–38 species. Thirteen individual islands have occurrence records for between 1–8 species.

The ten most widely distributed species, with the number of islands each is reported from, are: *Odontomachus simillimus* (27), *Anoplolepis gracilipes* (18), *Camponotus bedoti* (17), *Nylanderia vaga* (15), *Anochetus graeffei* (13), *Eurhopalothrix procera* (13), *Myopopone castanea* (13), *Oecophylla smaragdina subnitida* (13), *Pachycondyla stigma* (13), *Philidris myrmecodiae* (13). One hundred seven of the species and morphospecies included in Appendix 3 are only reported from single islands.

Discussion

In total, our research suggests that the Solomon Islands support at least 237 unique ant species and subspecies. The poor sampling of many islands–some of which are quite large–and the unexamined material at the ANIC suggests that the true number is likely much greater. For example, our eight days of intensive hand collection and Winkler extractions on Makira added 67 new species records to the island (including all morphospecies) and 28 new records to the archipelago. Prior to the survey, Makira Island's 75 species records were the second highest of the entire archipelago. Choiseul Island by comparison is approximately equal in area to Makira and closer to New Guinea, but the ant fauna of the island is virtually unknown with only eleven species recorded in the literature. There are approximately as many species known from the islands of Santa Isabel and Malaita as there are from Rennell, despite the substantially larger area of the former islands and their closer proximity to other large islands within the archipelago. The difference is that although no ant specialists have thoroughly sampled Rennell, general entomologists have collected there and the ant specimens of those surveys were the subject of several faunistic reviews (Taylor 1976; Wilson 1962). Besides Makira and Rennell Islands, the only island that has been moderately sampled–thanks to the works of Mann and Greenslade–is Guadalcanal.

Compared to Fijian islands of similar size, known species richness is generally much lower for individual islands within the Solomons, despite the fact that Fiji is much more isolated in the Pacific (Figure 2). This is likely due to relative sampling intensity of the two areas. Fiji has recently received intensive sampling efforts (Sarnat and Economo 2012), while richness differences among the Solomon Islands are still driven in large part by which islands were visited by W.M. Mann in 1916. For example, the 38 recorded species reported from the small island of Ugi (42 km^2), where Mann resided and collected for several weeks, is a richness comparable with a similar-sized Fijian island. Several large islands not visited by Mann have almost no records (e.g. Choiseul 2,966 km^2, 11 spp.; Kolombangara 704 km^2, 17 spp.). Our modest survey of Makira, where we spent approximately one week of collecting time, increased known richness from 75 to 142 species. There is no doubt that such modest collecting efforts elsewhere in the archipelago would yield similar increases.

The species list compiled from our research suggests several interesting taxonomic patterns. For example, species richness across the 51 native ant genera of the Solomons appears uneven. The 30 *Polyrhachis* species represent 14% of the total native species. The nine most diverse genera (*Polyrhachis*, *Pheidole*, *Camponotus*, *Tetramorium*, *Vollenhovia*, *Pachycondyla*, *Strumigenys*, *Crematogaster*, and *Gnamptogenys*) collectively contain over half of the total native species, while fifteen genera are represented by a single native species.

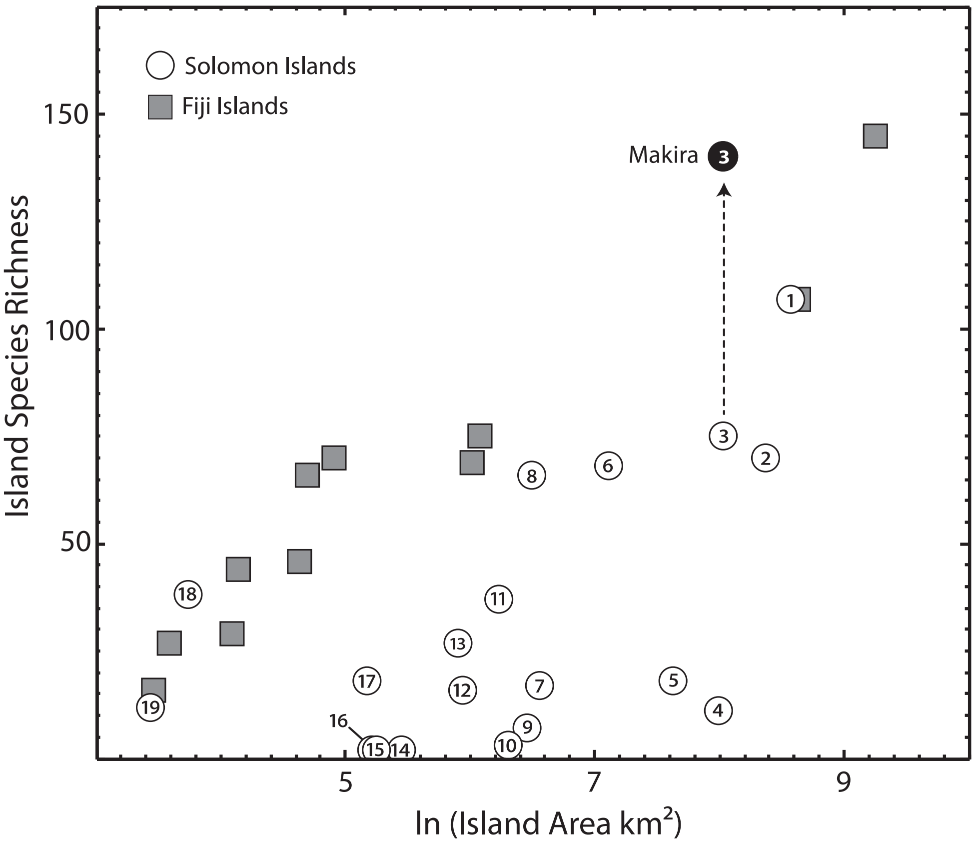

Figure 2. The relationship between islands area and known species richness. The figure presents individual islands in the Solomon (circles) and Fijian (squares) archipelagos, illustrating the undersampling of most Solomon Islands relative to the better collected Fiji Islands. For Makira, we present known species richness before (open circle) and after (filled circle) our recent collecting expedition. Numbers: **1** Guadalcanal **2** Malaita **3** Makira **4** Choiseul **5** New Georgia **6**Santa Isabel **7** Kolombangara **8** Rennell **9** Vella Lavella **10** Vangunu **11** Nendö (Santa Cruz) **12** Rendova **13** Nggela Sule **14** Shortland **15** Vanikoro **16** San Jorge **17** Russell Is. **18** Ugi **19** Savo.

Why is *Polyrhachis* so strongly represented in the Solomons? These results are likely biased to some extent by idiosyncratic collecting and taxonomic study. Besides the work of Mann, and to a lesser extent Greenslade, most of the collections from the Solomons have been made by more generalist collectors, which tend to take larger, more conspicuous ants that forage on and nest in vegetation–all of which are characteristic of *Polyrhachis*. Furthermore, Rudolf Kohout, who has access to the considerable collection of Solomons material at the ANIC, has devoted much of his taxonomic efforts towards revising the *Polyrhachis* of the Indo-Australian region (Kohout 1990; 1998; 2006; 2012). Despite these apparent biases, it is somewhat remarkable that with a single exception, the eight distinct *Polyrhachis* lineages that colonized the Solomons (as inferred from their subgeneric classifications) were unable to colonize, or at least persist in the more eastern Pacific islands. That single exception, *Polyrhachis rotumana* Wilson & Taylor, is known from the island of Rotuma which belongs politically to Fiji but is quite isolated from the Fijian archipelago and shares more geological and biological affinity with the islands of Polynesia.

Pachycondyla (9 native spp.), *Crematogaster* (7 native spp.) and *Gnamptogenys* (6 native spp.) are also among the most diverse ant genera in the Solomon Islands, but are either absent from or poorly represented in more easterly archipelagos. Fiji, for example, supports a single native *Gnamptogenys* species (*Gnamptogenys aterrima* Mann), and does not support any native *Pachycondyla* or *Crematogaster* species (Sarnat and Economo 2012). The Solomons are the known eastern limit for many ant genera. Out of the 51 genera native to the Solomons, the following 19 are not known to occur in the Pacific in or east of the Fijian archipelago: *Anonychomyrma*, *Arnoldius*, *Cardiocondyla*, *Colobostruma*, *Crematogaster*, *Cryptopone*, *Myopias*, *Myopopone*, *Myrmecina*, *Oecophylla*, *Opisthopsis*, *Pachycondyla*, *Podomyrma*, *Polyrhachis*, *Probolomyrmex*, *Rhytidoponera*, *Stereomyrmex*, *Tetraponera*, *Turneria.*

While additional sampling may prove otherwise, the current analysis of the Solomons ant fauna does not appear to support the type of *in situ* single-lineage radiations that characterize much of the Fijian ant fauna to the east. Parallels to the dramatic radiations of the *Pheidole roosevelti* group (Economo and Sarnat 2012; Sarnat 2008), *Lordomyrma* (Lucky and Sarnat 2008; Sarnat 2006), and the *Camponotus dentatus* group (Sarnat and Economo 2012) are largely unknown from the Solomons. It is likely that the Solomons ant fauna is derived more from relatively frequent colonization events from nearby New Guinea than from sweepstakes colonists that diversified into largely unoccupied ecological niches as occurred in the more isolated Fijian archipelago. Unlike New Guinea and Fiji, the Solomons do not support any endemic ant genera.

The importance of establishing baseline faunal inventories for the entire Solomon Island archipelago and its constituent islands is especially important when considering the growing environmental impacts resource extraction, plantation agriculture and invasive species are having on native biodiversity. Perhaps the greatest threat to native ant species in the Solomons is the spread of the Little Fire Ant (Fasi 2009). The introduction of *W. auropunctata* into the Solomon Islands is believed to have occurred around 1974, possibly with the arrival of coconut nurseries (Fabres and Brown 1978; Ikin 1984; Wetterer 1997). Foucaud et al. (2010) determined that a single clonal queen genotype is shared between the Melanesian populations of *W. auropunctata* from the Solomons, Vanuatu, Papua New Guinea and Australia, and suggested that the population spread by means of traditional exchange of plants and goods among Melanesian people. Although there have been reports of the ant's effect on vertebrates in the Solomons, such as blinding dogs and attacking hatchlings of the ground-nesting Melanesian Scrubfowl (*Megapodius eremita* Hartlaub) (Wetterer 1997), and also its effect on food crops and subsistence agriculture (Fasi 2009), there have yet to be any studies examining the effect of *W. auropunctata* on native ant diversity in the Solomons. The potential for spread of *W. auropunctata* across the entire archipelago is high (Fasi 2009), and it is likely a matter of years before all the major islands are infested.

We hope the research presented here will help facilitate more study of the neglected Solomon Island ant fauna and aid conservation efforts before *Wasmannia* and other environmental threats cause irrevocable harm.

Acknowledgments

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Appendix I

List of valid species recorded from the Solomon Islands arranged by subfamily, genus and species. (*) Species known to be introduced to the Solomons from outside the Pacific region. 'Year' refers to the first year the species was reported from the Solomon Islands. References are arranged in chronological order. Footnotes appended to reference codes indicate that the author misidentified the species or associated it with a different valid name. Reference codes: (1) Forel 1910; (2) Wheeler 1918; (3) Mann 1919; (4) Wheeler 1933; (5) Wheeler 1934; (8) Wheeler 1935a; (9) Chapman and Capco 1951; (10) Wilson 1957; (11) Brown 1958a; (12) Brown Jr. 1958b; (13) Wilson 1958a; (14) Wilson 1958b; (15) Brown 1959a; (16) Brown 1959b; (17) Wilson 1959a; (18) Wilson 1962; (19) Wilson 1959b; (20) Wilson 1959c; (21) Brown Jr. 1960; (22) Brown and Kempf 1960; (23) Taylor 1965; (24) Ettershank 1966; (25) Taylor 1967; (26) Wilson and Taylor 1967; (28) Taylor 1968; (29) Greenslade and Greenslade 1970; (30) Greenslade 1971b; (31) Bolton 1975; (32) Brown Jr. 1975; (33) Brown Jr. 1976; (34) Taylor 1976; (35) Bolton 1977; (36) Greenslade and Greenslade 1977; (37) Brown Jr. 1978; (38) Taylor 1979; (39) Willey and Brown 1983; (40) Ikin 1984; (41) Bolton 1987; (42) Shattuck 1990; (43) Taylor 1991a; (44) Taylor 1991b; (45) Kugler 1994; (46) Brown Jr. 1995; (47) Lin and Wu 1996; (48) Bolton 2000; (49) Ward 2001; (50) Baroni Urbani and De Andrade 2003; (51) Seifert 2003; (52) Wang 2003; (53) LaPolla 2004; (54) Lattke 2004; (55) Kohout 2006; (56) Bolton 2007; (58) Lucky and Sarnat 2008; (59) Seifert 2008; (60) Shattuck 2008; (61) Hosoishi and Ogata 2008; (62) LaPolla 2009; (63) Sorger and Zettel 2009; (64) Kohout 2012; (65) Shattuck and Slipinska 2012; (66) Shattuck et al. 2012; (67) Brown Jr. 1975; (68) Greenslade 1972; (69) Bolton 1985; (70) Forel 1912; (71) Viehmeyer 1924; (72) Donisthorpe 1941; (73) Wetterer 2009; (74) Kohout 1990; (75) Wetterer 1997; (76) Fasi 2009; (77) Foucaud et al. 2010; (78) Fisher and Smith 2008; (79) Collections of Economo and Sarnat 2008; (80) British Natural History Museum, London (Antweb.org records); (81) Australian National Insect Collection, Canberra; (82) Taylor 1980.

Taxon	Author	Year	Reference
Amblyoponinae			
Amblyopone australis	Erichson, 1842: 261	1919	3, 8, 9, 13, 17, 38, 81
Myopopone castanea	(Smith, F. 1860): 105	1919	3, 8, 9, 13, 17, 21, 81
Prionopelta majuscula	Emery, 1897b: 595	2008	60, 81
Prionopelta opaca	Emery, 1897b: 596	1976	34, 60, 79, 81
Stigmatomma celata	(Mann, 1919): 279	1919	3, 8, 13, 17, 21, 34, 38, 81
Stigmatomma gnoma	Taylor, 1979: 829	1978	38, 81
Cerapachyinae			
Cerapachys inconspicuus	Emery, 1901: 153	1919	3, 8, 9, 18, 20, 34
Cerapachys pawa	Mann, 1919: 277	1919	3, 8, 20, 32
Cerapachys terricola	Mann, 1919: 277	1919	3, 8, 32, 79
Dolichoderinae			
Anonychomyrma dimorpha	(Viehmeyer, 1912): 7	1919	3, 8, 9, 79
Arnoldius pusillus	(Mayr, 1876): 83	1959	15
Iridomyrmex anceps	(Roger, 1863a): 164	1919	3, 6, 8, 15, 36, 81
Iridomyrmex pallidus	Forel, 1901: 22	1963	81
Iridomyrmex rufoniger	(Lowne, 1865): 279	1919	3, 8
*Ochetellus glaber**	(Mayr, 1862): 705	2009	79
Philidris myrmecodiae	(Emery, 1887): 249	1919	3, 6, 8, 15, 16, 29[1], 30[1], 68[1], 34[1], 36[1], 79
Tapinoma (Micromyrma) indicum timidum	Santschi, 1928	1959	15
*Tapinoma melanocephalum**	(Fabricius, 1793): 353	1934	6, 8, 15, 18, 34, 36, 73, 81
Tapinoma minutum	Mayr, 1862: 703	1967	26
*Technomyrmex albipes**	(Smith, F. 1861): 38	1910	1, 3, 8, 15, 18, 34, 36, 56, 79, 81
Technomyrmex vitiensis	Mann, 1921: 473	2008	79
Turneria dahlii	Forel, 1901: 17	1959	18, 34, 42, 81
Turneria pacifica	Mann, 1919: 361	1919	3, 42, 81
Ectatomminae			
Gnamptogenys albiclava	(Mann, 1919): 283	1919	3, 8, 11, 17, 54
Gnamptogenys crenaticeps	(Mann, 1919): 285	1919	3, 8, 11, 17, 54, 79
Gnamptogenys lucida	(Mann, 1919): 285	1919	3, 8, 11, 17, 54
Gnamptogenys malaensis	(Mann, 1919): 281	1919	3, 8, 11, 17, 54, 79
Gnamptogenys preciosa	Lattke, 2004: 66	2004	54, 81
Gnamptogenys solomonensis	Lattke, 2004: 66	2004	54, 81
Rhytidoponera araneoides	(Le Guillou, 1842): 317	1910	1, 3, 14, 17, 79, 81
Rhytidoponera chalybaea	Emery, 1901b: 51	1959	15
Formicinae			
Acropyga acutiventris	Roger, 1862: 243	1919	3, 8, 53, 79, 81
Acropyga lauta	Mann, 1919: 365	1919	3, 8, 53, 79, 81
Acropyga oceanica	Emery, 1900: 333	2008	79
Acropyga pallida	(Donisthorpe, 1938): 598	1965	81
*Anoplolepis gracilipes**	Smith, F. 1857: 55	1919	3, 6, 8, 15, 15, 18, 29, 30, 68, 34, 36, 81
*Brachymyrmex obscurior**	Forel, 1893: 345	1976	34, 79
Camponotus (Myrmamblys) bedoti	Emery, 1893: 196	1919	3, 6, 8, 15, 18[2], 34[2], 36[2]

[1] Referred to as *Philidris cordata* (Smith, F.).

[2] Referred to as *Camponotus reticulatus* Roger.

Taxon	Author	Year	Reference
Camponotus chloroticus	Emery, 1897b: 574	1959	15
Camponotus elysii	Mann, 1919: 372	1919	3, 8
Camponotus guppyi	Mann, 1919: 370	1919	3, 8
Camponotus loa	Mann, 1919: 373	1919	3, 8
Camponotus loa belli	Mann, 1919: 375	1919	3, 8
Camponotus novaehollandiae	Mayr, 1870: 939	1919	3
*Nylanderia bourbonica**	(Forel, 1886): 210	1959	15, 34, 36, 81
Nylanderia braueri glabrior	(Forel, 1902): 490	1954	81
Nylanderia dichroa	Wheeler 1934: 181	1934	6, 8, 81
Nylanderia manni	Donisthorpe, 1941: 41	1941	72, 15, 36
Nylanderia obscura bismarckensis	(Forel, 1901): 26	1919	3, 6, 8
Nylanderia stigmatica	Mann, 1919: 367	1919	3, 8, 62, 79, 81
*Nylanderia vaga**	(Forel, 1901): 26	1934	6, 8, 18, 26, 34, 36, 79, 81
*Nylanderia vividula**	(Nylander, 1846): 900	1919	3, 15, 79
Oecophylla smaragdina subnitida	Emery 1892: 565	1910	1, 3, 6, 8, 15[3], 16[3], 29[3], 30[3], 68[3], 36[3], 79[3], 81[3]
Opisthopsis manni	Wheeler, W.M. 1918: 361	1918	2, 3, 8, 15
Paraparatrechina minutula	(Forel, 1901): 25	1919	3, 8, 15, 34, 79, 81
*Paratrechina longicornis**	(Latreille, 1802): 113	1919	3, 8, 15, 34, 79, 81
*Plagiolepis alluaudi**	Emery, 1894: 71	1959	15
Polyrhachis (*Myrma*) *andromache*	Roger, 1863b: 8	1959	3[4], 18, 34[5], 79
Polyrhachis (*Hedomyrma*) *annae*	Mann, 1919: 377	1919	3, 6, 8, 15, 18, 34
Polyrhachis (*Chariomyrma*) *arcuata acutinota*	Forel, 1901: 31	1934	6
Polyrhachis (*Hedomyrma*) *campbelli*	Mann, 1919: 376	1919	3, 8, 79
Polyrhachis (*Myrmothrinax*) *dahlii*	Forel, 1901: 30	1919	3, 8, 9, 64
Polyrhachis (*Cyrtomyrma*) *emeryana*	Mann, 1919: 390	1919	3, 8, 55
Polyrhachis (*Cyrtomyrma*) *fulakora*	Mann, 1919: 389	1919	3, 8, 15, 55
Polyrhachis (*Hedomyrma*) *geminata*	Mann, 1919: 376	1919	3, 8, 79
Polyrhachis greensladei	Kohout, 1990: 503	1990	74
Polyrhachis (*Myrma*) *ithona*	Smith, F., 1860: 99	1934	6, 8
Polyrhachis (*Cyrtomyrma*) *johnsoni*	Mann, 1919: 390	1919	3, 8, 55
Polyrhachis (*Chariomyrma*) *kaipi*	Mann, 1919: 382	1919	3, 6, 8, 79
Polyrhachis (*Myrma*) *labella brunneipes*	Wheeler, 1934	1934	6, 8
Polyrhachis (*Myrma*) *litigiosa*	Emery, 1897b: 581	1919	3, 8, 79
Polyrhachis (*Myrma*) *malaensis*	Mann, 1919: 386	1919	3, 8
Polyrhachis nofra	Bolton, 1975: 9	1975	31
Polyrhachis (*Myrmatopa*) *osae*	Mann, 1919: 384	1919	3, 6, 8, 9, 15
Polyrhachis pacifica	Kohout, 2006: 140	2006	55
Polyrhachis (*Chariomyrma*) *rere*	Mann, 1919: 381	1919	3, 6, 8, 15
Polyrhachis (*Myrmhopla*) *saevissima argentea*	Mayr, 1862: 82	1919	3, 8, 9
Polyrhachis (*Myrma*) *salomo*	Forel, 1910: 87	1910	1, 3, 8, 15
Polyrhachis (*Hedomyrma*) *santschii*	Mann, 1919: 375	1919	3, 8
Polyrhachis setosa	Kohout, 2006: 141	2006	55

[3] Referred to as *Oecophylla smaragdina* (Fabricius).
[4] The material referred to by the unavailable name *Polyrhachis* (*Myrma*) relucens subsp. *andromache* var. *nesiotis* Mann is provisionally assigned to *P. andromache* Roger.
[5] Referred to as *Polyrhachis relucens* (Latreille).

Taxon	Author	Year	Reference
Polyrhachis (*Myrma*) *similis*	Viehmeyer, 1912: 8	1919	3, 8
Polyrhachis (*Cyrtomyrma*) *ugiensis*	Mann, 1919: 389	1919	3, 8, 55, 79
Polyrhachis (*Myrmatopa*) *ulysses*	Forel, 1910: 91	1910	1, 3, 8
Polyrhachis (*Cyrtomyrma*) *undulata*	Kohout, 2006: 142	2006	55, 79
Polyrhachis (*Myrmhopla*) *wheeleri*	Mann, 1919: 387	1919	3, 8, 9
Myrmicinae			
*Cardiocondyla kagutsuchi**	Terayama, 1999: 100	2009	79
Cardiocondyla nivalis	Mann, 1919: 317	1919	3, 8, 34, 36
Cardiocondyla nuda	(Mayr, 1866): 508	1959	15, 34, 36, 51, 59
Carebara atoma	(Emery, 1900): 328	1919	3, 8, 34, 36, 79
Carebara viehmeyeri	(Mann, 1919): 331	1919	3, 8, 79
Colobostruma foliacea	Emery, 1897a: 573	2000	48, 81
Crematogaster (*Crematogaster*) *abrupta*	Mann, 1919: 320	1935	8, 15, 61
Crematogaster (*Crematogaster*) *elysii*	Mann, 1919: 319	1935	8, 3, 61
Crematogaster (*Crematogaster*) *foxi*	Mann, 1919: 321	1935	8, 3, 61
Crematogaster (*Crematogaster*) *nesiotis*	Mann, 1919: 322	1935	8, 3, 61
Crematogaster (*Crematogaster*) *obnigra*	Mann, 1919: 323	1919	3, 15, 61
Crematogaster (*Orthocrema*) *scita*	Forel, 1902: 409	1959	15
Crematogaster (*Orthocrema*) *wheeleri*	Mann, 1919: 318	1935	8, 3, 61
Eurhopalothrix brevicornis	(Emery, 1897a): 572	1977	36, 80, 28, 82
Eurhopalothrix greensladei	Taylor, 1968: 342	1968	28, 82
Eurhopalothrix isabellae	(Mann, 1919): 357	1919	3, 8, 22, 80, 28, 82
Eurhopalothrix procera	(Emery, 1897a): 572	1919	3, 8, 22, 28, 79, 81, 82
Lordomyrma epinotalis	(Mann, 1919): 343	1919	3, 8, 34, 58, 79
Monomorium australicum	Forel, 1907:20	1919	3, 8, 15, 34, 36
*Monomorium destructor**	(Jerdon, 1851): 105	1959	18, 34
*Monomorium floricola**	(Jerdon, 1851): 107	1959	15, 34, 36, 41, 79, 81
*Monomorium pharaonis**	(Linnaeus, 1758): 580	1919	3, 8, 15, 34, 41, 81
Myrmecina modesta	Mann, 1919: 335	1919	3, 8, 34[6]
Myrmecina modesta subarmata	Mann, 1919: 337	1919	3, 8
Myrmecina transversa	Emery, 1897a: 582	2008	79
Pheidole belli	Mann, 1919: 306	1919	3, 8
Pheidole erato	Mann, 1919: 307	1919	3, 8
Pheidole fuscula	Emery, 1900: 325	1919	3, 8
Pheidole isis	Mann, 1919: 311	1919	3, 8
Pheidole isis taki	Mann, 1919: 314	1919	3, 8, 79
*Pheidole megacephala**	(Fabricius, 1793): 361	1910	1[7], 6, 8, 15, 26, 30, 34, 81
Pheidole mendanai	Mann, 1919: 311	1919	3, 8
Pheidole nindi	Mann, 1919: 314	1919	3, 8, 34, 36, 79
Pheidole oceanica	Mayr, 1866: 510	1919	3, 8, 15, 18, 34, 36, 79
Pheidole philemon	Forel, 1910: 44	1910	1, 3, 8, 15, 79
Pheidole sexspinosa	Mayr, 1870: 977	1919	3, 8, 34, 36, 79
Pheidole sexspinosa fuscescens	Emery, 1900: 323	1919	3, 8, 18
Pheidole umbonata	Mayr, 1870: 978	1919	3, 8, 15, 18, 34, 36
Podomyrma basalis salomo	Mann, 1919: 333	1919	3, 8

[6] Referred to as *Myrmecina ?modesta*.

[7] Referred to as *Pheidole punctulata* Mayr.

Taxon	Author	Year	Reference
Podomyrma basalis woodfordi	Mann, 1919: 334	1919	3, 8
Pristomyrmex levigatus	Emery, 1897a: 583	1919	3, 52, 79
Pristomyrmex obesus	Mann, 1919: 339	1919	3, 8, 80, 52
Rogeria megastigmatica	Kugler, C. 1994: 35	1994	45, 79
Rogeria stigmatica	Emery, 1897: 589	1919	3, 8, 34, 45
Romblonella elysii	(Mann, 1919): 346	1919	3, 8, 44
*Solenopsis geminata**	(Fabricius, 1804): 423	1977	36
Solenopsis papuana	Emery, 1900: 330	1919	3, 79
Solenopsis pawaensis	Mann, 1919: 329	1919	3, 79
Stereomyrmex dispar	(Wheeler, W.M. 1934): 175	1934	6, 18, 34, 44
Strumigenys chyzeri	Emery, 1897a: 576	1919	3, 48, 79
Strumigenys decollata	Mann, 1919: 353	1919	3, 8, 12, 48
*Strumigenys emmae**	Emery, 1890: 70	1976	34, 36, 48, 81
Strumigenys eurycera	Emery, 1897a: 581	2000	48, 81
Strumigenys frivaldszkyi	Emery, 1897: 580	1976	34, 48, 79
*Strumigenys godeffroyi**	Mayr, 1866: 516	1919	3, 15, 34, 36, 47, 48, 79
Strumigenys karawajewi	(Brown, 1948): 44	1976	34, 46, 48, 79, 81
*Strumigenys membranifera**	(Emery, 1869): 24	2000	48, 36, 81
Strumigenys mocsaryi	(Emery, 1897a): 580	2000	48
*Strumigenys rogeri**	Emery, 1890: 68	2000	48
Strumigenys szalayi	Emery, 1897: 578	2000	48, 79
Strumigenys undras	Bolton, 2000: 752	2000	48
Strumigenys yaleopleura	Brown, 1988: 41	2000	48
Tetramorium antennatum	(Mann, 1919): 350	1919	3
Tetramorium aspersum	(Smith, F. 1865): 72	1919	3, 6, 8, 35, 79
*Tetramorium bicarinatum**	(Nylander, 1846): 1061	1919	3[8], 6[8], 8[8], 15[8], 34[8], 35, 36
Tetramorium carinatum	(Smith, F. 1859): 148	1919	3, 8
Tetramorium insolens	(Smith, F., 1861)	1934	6, 8, 18, 34, 35
*Tetramorium lanuginosum**	Mayr, 1870: 976	1935	8, 69
Tetramorium mayri	(Mann, 1919: 351)	1919	3, 8, 79
Tetramorium melanogyna	Mann, 1919: 345	1919	3, 8, 79
Tetramorium mutatum	Bolton, 1985: 247	1919	3, 8, 69
Tetramorium pacificum	Mayr, 1870: 976	1934	6, 8, 18, 34, 35
Tetramorium salomo	Mann, 1919: 344	1935	8, 35, 79
*Tetramorium simillimum**	(Smith, F. 1851): 118	1959	15, 34, 35, 36, 79
Tetramorium tonganum	Mayr, 1870: 976	1919	3, 8, 15, 18, 34, 35
Tetramorium vombis	Bolton, 1976: 358	1985	3[9], 34[9], 69
Vollenhovia dentata	Mann, 1919: 325	1919	3, 8, 24, 79
Vollenhovia dentata marginata	Mann, 1919: 327	1919	3, 8, 24
Vollenhovia elysii	Mann, 1919: 327	1919	3, 8, 24
Vollenhovia foveaceps	Mann, 1919: 328	1919	3, 8, 24
Vollenhovia loboii	Mann, 1919: 324	1919	3, 8, 24
Vollenhovia oblonga	(Smith, F. 1861): 46	1959	18, 34, 43
Vollenhovia oblonga pedestris	(Smith, F. 1860): 107	1919	3, 8, 15, 79
Vollenhovia subtilis	Emery, 1887: 454	1919	3, 8
*Wasmannia auropunctata**	(Roger, 1863a): 183	1984	40, 75, 76, 77, 79

[8] Misidentified as *Tetramorium guineense* (Bernard).
[9] Misidentified as *Tetramorium obesum* André.

Taxon	Author	Year	Reference
Ponerinae			
Anochetus cato	Forel, 1901: 6	1919	3, 8, 17, 19, 79, 81
Anochetus graeffei	Mayr, 1870: 961	1919	3, 8, 15, 17, 19, 34, 36, 65, 79, 81
Anochetus isolatus	Mann, 1919: 302	1919	3, 8, 17, 19, 34, 37, 65, 79, 81
Cryptopone butteli	Forel, 1913: 9	1965	81
Cryptopone crassicornis	(Emery, 1897): 533	1965	81
Cryptopone fusciceps	(Emery, 1900): 321	1919	3, 4, 8, 14, 17, 81
Cryptopone testacea	(Emery, 1893): cclxxv	1919	3, 4, 8, 14, 17, 32, 81
Hypoponera biroi	(Emery, 1900): 7	1959	17, 34
Hypoponera confinis	(Roger, 1860): 284	1959	17
Hypoponera pallidula	(Emery, 1900): 320	1919	3, 8, 9
Hypoponera papuana	(Emery, 1900): 319	1919	3, 8, 79
Hypoponera pruinosa	(Emery, 1900): 319	1919	3, 8, 9, 14, 17, 34, 79
*Hypoponera punctatissima**	(Roger, 1859): 246	1976	34, 79
*Hypoponera ragusai**	(Forel, 1899): 28	1919	3, 8, 14, 17, 36
Hypoponera sororcula	(Wilson, 1958a): 338	1958	14, 17
Leptogenys diminuta	(Smith, F. 1857): 69	1919	3, 8, 17, 79
Leptogenys foreli	Mann, 1919: 297	1919	3, 8, 13, 17, 18[10], 34[10]
Leptogenys oresbia	Wilson, 1958b: 131	1958	3[11], 13, 17
Leptogenys truncata	Mann, 1919: 26	1919	3, 17
Odontomachus malignus	Smith, F. 1859: 144	1919	3, 17, 18[12], 19, 33, 34[12], 63, 81
Odontomachus rufithorax	Emery, 1911: 534	1919	3, 17, 19, 33, 81
Odontomachus saevissimus	(Smith, F. 1858)	1959	15, 33, 81
Odontomachus simillimus	(Smith, F. 1858): 80	1910	1[13], 3[14], 6[14], 8[14], 15[14], 17, 18, 19, 26, 34, 36, 79, 81
Pachycondyla acuta	Emery, 1900	1958	14, 17
Pachycondyla aequalis	(Mann, 1919): 289	1919	3, 8, 14, 17, 79
Pachycondyla croceicornis	(Emery, 1900): 315	1919	3, 14, 17, 36, 79
Pachycondyla darwinii	(Forel, 1893): 460	1959	17
Pachycondyla exarata	Emery, 1901b: 156	1919	3, 8
Pachycondyla manni	(Viehmeyer, 1924): 228	1924	71, 14, 17
Pachycondyla melancholica	Smith, F. 1865: 71	1919	3
Pachycondyla papuana	(Viehmeyer, 1914): 608	1919	3, 9
Pachycondyla sheldoni	(Mann, 1919): 292	1919	3, 8, 14, 17
*Pachycondyla stigma**	(Fabricius, 1804): 400	1919	3, 8, 9, 15, 17, 18, 34, 79
Platythyrea parallela	(Smith, F., 1859): 143	1919	3, 9, 17
Ponera clavicornis	Emery, 1900: 317	1919	3, 8, 10, 25, 34[15], 81
Ponera incerta	(Wheeler, W.M. 1933): 18	1959	17, 25, 81
Ponera swezeyi	(Wheeler, W.M. 1933): 16	2009	79

[10] Referred to as *Leptogenys ?foreli*.

[11] Specimens from Malaita referred to by Mann (1919) as *Leptogenys (Lobopelta) diminuta* var. *laeviceps* Smith, F. (Wilson 1958a).

[12] Referred to as *Odontomachus ?malignus*.

[13] Misidentified as *Odontomachus insularis* Guérin-Méneville.

[14] Misidentified as *Odontomachus haematodus* (Linnaeus).

[15] Referred to as *Ponera ?clavicornis*.

Taxon	Author	Year	Reference
Ponera szaboi	Wilson, 1957: 371	1976	34
Ponera tenuis	(Emery, 1900): 321	1965	81
Proceratiinae			
Discothyrea clavicornis	Emery, 1897b: 593	1919	3, 8, 9, 17, 81
Probolomyrmex salomonis	Taylor, 1965: 358	1965	23, 66, 81
Proceratium austronesicum	De Andrade, in Baroni Urbani & De Andrade, 2003: 313	2003	50, 81
Proceratium papuanum	Emery, 1897b: 592	2003	50, 81
Pseudomyrmecinae			
Tetraponera laeviceps	(Smith, F. 1859): 145	1919	3, 8, 49

Appendix 2

Presumed undescribed species recorded from the Solomon Islands arranged by species name. The 'Year' column refers to the year the species was first recorded from the Solomon Islands. Reference codes are the same as those used in Appendix 11.

Taxon	Notes	Year	Reference
Adelomyrmex sp. BP02	nr. *hirsutus*	2008	79
Adelomyrmex sp. BP03	as "*Adelomyrmex* (*Arctomyrmex*) sp."	1976	34
Arnoldius sp. BP01	as "nr. *flavus*"	1959	15
Camponotus sp. BP02	nr. *guppyi*	2008	79
Camponotus sp. BP05	nr. *elysii*	2008	79
Camponotus sp. BP06	as "*Camponotus* (*Colobopsis*) sp. A"	1976	34
Camponotus sp. BP07	as "*Camponotus* (*Colobopsis*) sp. B"	1976	34
Camponotus sp. BP08	as "*Camponotus* (*Colobopsis*) sp. C"	1976	34
Camponotus sp. BP09	as "*Camponotus* (*Colobopsis*) spp. (2)"	1959	18,34
Camponotus sp. BP10	as "*Camponotus* (*Colobopsis*) spp. (2)"	1959	18,34
Cerapachys sp. BP01	as "*Cerapachys*? (*Syscia*) sp. 1"	1959	18,34
Colobostruma sp. BP01	nr. *foliacea*	2008	79
Cryptopone sp. BP01	nr. *testacea*	2008	79
Myopias sp. BP01		2008	79
Myopias sp. BP02		2008	79
Myopias sp. BP03		2008	79
Myopias sp. BP04	as "*Myopias* cf. *tenuis*"	1983	39
Myrmecina sp. BP01		2008	79
Myrmecina sp. BP03		2008	79
Pheidole sp. BP02		2008	79
Pheidole sp. BP12	nr. *mendanai*	2008	79
Pheidole sp. BP13	as "*Pheidole* (*Pheidolacanthinus*) sp."	1976	34
Platythyrea sp. BP01	as "*Platythyrea* sp."	1976	34
Polyrhachis sp. BP01	*Polyrhachis (Myrmhopla)* nr. *bismarckensis*	2008	79
Polyrhachis sp. BP03	as "*Polyrhachis* (*Chariomyrma*) sp."	1976	34
Rogeria sp. BP01	nr. *stigmatica*	2008	79
Strumigenys sp. BP05	nr. *mocsaryi*	2008	79
Vollenhovia sp. BP01	nr. *elysii*	2008	79
Vollenhovia sp. BP02	nr. *loboii*	2008	79
Vollenhovia sp. BP03	as "*Vollenhovia* sp."	1976	34

Appendix 3

Occurrence records of individual islands and island groups from which ant species have been recorded arranged by species name and island/island group name. The valid names refer to those presented in Appendix 1. Infraspecific names are abbreviated from trinomials to binomials composed of the genus and infraspecific name (e.g. *Nylanderia obscura bismarckensis* (Forel) is presented as "*N. bismarckensis*"). Asterisks (*) are appended to morphospecies presumed to be undescribed species (Appendix 2). Morphospecies that we were unable to determine but might represent previously described species are also presented. Individual island names appear in regular type and island group names appear in uppercase bold type. Island groups and their constituent islands from which ants have been recorded are presented in Table 1. The penultimate column 'Solomon Is.' includes species records for which no individual island or island group was associated (Brown 1960; 1975; 1976; 1995; Chapman and Capco 1951; Ettershank 1966; Forel 1893; Lin and Wu 1996; Shattuck et al. 2012; Wilson 1959a). The 'Total' column sums the number of islands from which each species is recorded, but does not include records from the aforementioned 'Solomon Is.' column.

Taxon	*Anuta*	*Bellona*	*Choiseul*	*Guadalcanal*	*Kolombangara*	*Makira*	*Malaita*	*Malaupaina*	*Matema*	*Mbanika*	*New Georgia*	***NEW GEORGIA IS.***	***NGGELA IS.***	*Nggela Sule*	*Nupani*	***OLU MALAU IS.***	*Ontong Java Is.*	*Owaraha*	***REEF IS.***	*Rendova*	*Rennell*	*Russell Is.*	*San Jorge*	*Santa Catalina*	*Santa Cruz*	***SANTA CRUZ IS.***	*Santa Isabel*	*Savo*	*Shortland*	*Sikaiana*	*Tikopia*	*Tulagi*	*Ugi*	*Vangunu*	*Vanikoro*	*Vella Lavella*	*SOLOMON IS.*	***Total***
Acropyga																																						
A. acutiventris				x		x	x					x								x							x						x					7
A. lauta				x	x	x	x					x	x														x											7
A. oceanica						x																																1
A. pallida					x																																	1
Adelomyrmex																																						
A. sp. BP02*						x																																1
A. sp. BP03*		x																			x																	2
Amblyopone																																						
A. australis				x			x					x																									x	3
Anochetus																																						
A. cato						x	x	x				x	x	x		x				x							x					x	x				x	11
A. graeffei		x		x		x	x				x	x	x	x							x				x	x	x					x					x	13
A. isolatus			x	x		x		x								x					x				x	x											x	8
Anonychomyrma																																						
A. dimorpha						x	x																				x										x	3
Anoplolepis																																						
A. *gracilipes*		x	x	x	x	x	x		x			x	x		x				x		x	x		x	x	x	x	x										18
Arnoldius																																						
A. sp. BP01				x																																		1
A. pusillus				x																																		1
Brachymyrmex																																						0
B. *obscurior*		x				x															x																	3
Camponotus																																						
C. bedoti	x	x		x			x				x	x	x	x	x			x		x	x	x		x	x	x						x						17

Taxon	Anuta	Bellona	Choiseul	Guadalcanal	Kolombangara	Makira	Malaita	Malaupaina	Matema	Mbanika	New Georgia	**NEW GEORGIA IS.**	**NGGELA IS.**	Nggela Sule	Nupani	**OLU MALAU IS.**	Ontong Java Is.	Owaraha	**REEF IS.**	Rendova	Rennell	Russell Is.	San Jorge	Santa Catalina	Santa Cruz	**SANTA CRUZ IS.**	Santa Isabel	Savo	Shortland	Sikaiana	Tikopia	Tulagi	Ugi	Vangunu	Vanikoro	Vella Lavella	SOLOMON IS.	**Total**
C. chloroticus				x														x																				2
C. elysii						x		x								x																						3
C. guppyi							x																															1
C. loa						x	x	x					x			x		x							x	x						x	x					10
C. loa belli													x	x																								2
C. novaehollandiae						x																			x	x	x											4
C. sp. BP01						x																																1
C. sp. BP02*						x																																1
C. sp. BP04						x																																1
C. sp. BP05*						x																																1
C. sp. BP06*																					x																	1
C. sp. BP07*																					x																	1
C. sp. BP08*		x																			x																	2
C. sp. BP09*																					x																	1
C. sp. BP10*																					x																	1
Cardiocondyla																																						
C. kagutsuchi						x																																1
C. nivalis				x		x				x		x								x	x							x								x		8
C. nuda				x			x														x			x			x											5
Carebara																																						
C. atoma		x		x		x															x						x											5
C. viehmeyeri						x																																1
Cerapachys																																						
C. inconspicuus																					x						x										x	2
C. pawa																																	x				x	1

Taxon	Anuta	Bellona	Choiseul	Guadalcanal	Kolombangara	Makira	Malaita	Malaupaina	Matema	Mbanika	New Georgia	**NEW GEORGIA IS.**	**NGGELA IS.**	Nggela Sule	Nupani	**OLU MALAU IS.**	Ontong Java Is.	Owaraha	**REEF IS.**	Rendova	Rennell	Russell Is.	San Jorge	Santa Catalina	Santa Cruz	**SANTA CRUZ IS.**	Santa Isabel	Savo	Shortland	Sikaiana	Tikopia	Tulagi	Ugi	Vangunu	Vanikoro	Vella Lavella	SOLOMON IS.	**Total**
C. terricola						x							x	x		x											x					x					x	6
C. sp. BP01*																					x																	1
Colobostruma																																						
C. foliacea			x	x								x								x		x					x											6
C. sp. BP01*						x																																1
Crematogaster																																						
C. abrupta				x				x								x																						3
C. elysii								x								x																						2
C. foxi						x																																1
C. nesiotis																						x																1
C. obnigra				x																		x																2
C. scita				x																																		1
C. wheeleri							x																															1
Cryptopone																																						
C. butteli				x																																		1
C. crassicornis				x																																		1
C. fusciceps				x		x	x					x															x										x	5
C. testacea		x		x	x	x						x									x						x						x				x	8
C. sp. BP01*						x																																1
Dilobocondyla																																						
D. sp. BP01																					x																	1
Discothyrea																																						
D. clavicornis				x		x	x													x		x	x				x		x								x	8
Eurhopalothrix																																						
E. brevicornis				x								x	x	x													x									x		5

Taxon	Anuta	Bellona	Choiseul	Guadalcanal	Kolombangara	Makira	Malaita	Malaupaina	Matema	Mbanika	New Georgia	**NEW GEORGIA IS.**	**NGGELA IS.**	Nggela Sule	Nupani	**OLU MALAU IS.**	Ontong Java Is.	Owaraha	**REEF IS.**	Rendova	Rennell	Russell Is.	San Jorge	Santa Catalina	Santa Cruz	**SANTA CRUZ IS.**	Santa Isabel	Savo	Shortland	Sikaiana	Tikopia	Tulagi	Ugi	Vangunu	Vanikoro	Vella Lavella	SOLOMON IS.	**Total**
E. greensladei				x																																		1
E. isabellae				x								x															x									x		4
E. procera				x		x	x	x				x	x	x		x				x					x	x	x	x				x						14
Gnamptogenys																																						
G. albiclava				x																							x										x	2
G. crenaticeps						x																					x										x	2
G. lucida							x																														x	1
G. malaensis					x	x	x				x	x										x												x		x	x	8
G. preciosa				x																																		1
G. solomonensis				x	x							x																										3
G. sp. BP03						x																																1
Hypoponera																																						
H. biroi																					x																x	1
H. confinis																																					x	0
H. pallidula							x																				x										x	2
H. papuana						x		x								x											x						x				x	5
H. pruinosa		x				x	x	x					x	x		x					x						x					x	x				x	11
H. punctatissima						x															x																	2
H. ragusai				x		x																															x	2
H. sororcula																																					x	0
H. sp. BP01						x																																1
H. sp. BP06						x																																1
H. sp. BP07						x																																1
H. sp. BP08						x																																1
Iridomyrmex																																						

Taxon	*Anuta*	*Bellona*	*Choiseul*	*Guadalcanal*	*Kolombangara*	*Makira*	*Malaita*	*Malaupaina*	*Matema*	*Mbanika*	*New Georgia*	***NEW GEORGIA IS.***	***NGGELA IS.***	*Nggela Sule*	*Nupani*	***OLU MALAU IS.***	*Ontong Java Is.*	*Owaraha*	***REEF IS.***	*Rendova*	*Rennell*	*Russell Is.*	*San Jorge*	*Santa Catalina*	*Santa Cruz*	***SANTA CRUZ IS.***	*Santa Isabel*	*Savo*	*Shortland*	*Sikaiana*	*Tikopia*	*Tulagi*	*Ugi*	*Vangunu*	*Vanikoro*	*Vella Lavella*	*SOLOMON IS.*	***Total***
I. anceps				x	x		x		x		x	x					x		x			x					x	x										11
I. pallidus				x																																		1
I. rufoniger							x																															1
Leptogenys																																						
L. diminuta						x		x								x																	x				x	4
L. foreli							x	x								x					x																x	4
L. oresbia								x																													x	1
L. truncata																									x	x											x	2
Lordomyrma																																						
L. epinotalis						x	x			x			x								x						x						x					7
Monomorium																																						
M. australicum		x		x		x															x												x					5
M. destructor																					x																	1
M. floricola		x		x		x					x	x	x								x											x						8
M. pharaonis				x			x									x					x												x					5
Myopias																																						
M. sp. BP01*						x																																1
M. sp. BP02*						x																																1
M. sp. BP03*						x																																1
M. sp. BP04*				x		x																																2
Myopopone																																						
M. castanea				x	x	x	x				x	x	x	x											x	x	x					x			x		x	13
Myrmecina																																						
M. modesta						x		x								x					x				x	x	x						x					8
M. subarmata							x																															1

Taxon	Anuta	Bellona	Choiseul	Guadalcanal	Kolombangara	Makira	Malaita	Malaupaina	Matema	Mbanika	New Georgia	**NEW GEORGIA IS.**	**NGGELA IS.**	Nggela Sule	Nupani	**OLU MALAU IS.**	Ontong Java Is.	Owaraha	**REEF IS.**	Rendova	Rennell	Russell Is.	San Jorge	Santa Catalina	Santa Cruz	**SANTA CRUZ IS.**	Santa Isabel	Savo	Shortland	Sikaiana	Tikopia	Tulagi	Ugi	Vangunu	Vanikoro	Vella Lavella	SOLOMON IS.	**Total**
Myrmecina																																					
M. transversa						x																															1
M. sp. BP01*						x																															1
M. sp. BP03*						x																															1
Nylanderia																																					
N. bourbonica		x		x																	x																3
N. braueri glabrior				x		x															x							x									4
N. dichroa			x	x	x	x	x					x	x							x								x									9
N. manni				x																																	1
N. bismarckensis						x															x						x										3
N. stigmatica				x	x	x	x	x								x																	x				7
N. vaga	x	x		x	x	x			x						x				x		x			x		x	x	x		x			x				15
N. vividula				x		x																											x				3
Ochetellus																																					
O. glaber						x																															1
Odontomachus																																					
O. malignus				x			x														x				x	x	x									x	6
O. rufithorax			x										x	x													x									x	4
O. saevissimus				x	x																															x	2
O. simillimus	x	x	x	x	x	x	x	x	x			x	x	x	x	x	x		x		x	x			x	x	x	x			x	x	x	x	x		x	27
Oecophylla																																					
O. subnitida				x		x	x	x					x	x		x		x				x					x	x				x	x				13
Opisthopsis																																					0
O. manni				x		x	x	x								x						x															6
Pachycondyla																																					

Taxon	*Anuta*	*Bellona*	*Choiseul*	*Guadalcanal*	*Kolombangara*	*Makira*	*Malaita*	*Malaupaina*	*Matema*	*Mbanika*	*New Georgia*	***NEW GEORGIA IS.***	***NGGELA IS.***	*Nggela Sule*	*Nupani*	***OLU MALAU IS.***	*Ontong Java Is.*	*Owaraha*	***REEF IS.***	*Rendova*	*Rennell*	*Russell Is.*	*San Jorge*	*Santa Catalina*	*Santa Cruz*	***SANTA CRUZ IS.***	*Santa Isabel*	*Savo*	*Shortland*	*Sikaiana*	*Tikopia*	*Tulagi*	*Ugi*	*Vangunu*	*Vanikoro*	*Vella Lavella*	*SOLOMON IS.*	***Total***
P. acuta																x																					x	1
P. aequalis						x	x						x	x																							x	4
P. croceicornis				x		x																					x										x	3
P. darwinii																																					x	0
P. exarata													x														x					x						3
P. manni						x																					x										x	2
P. melancholica																									x													1
P. papuana						x																					x										x	2
P. sheldoni						x																															x	1
P. stigma				x		x	x				x	x	x	x							x				x	x	x					x	x				x	13
P. sp. BP01						x																																1
Paraparatrechina																																						
P. minutula		x		x		x															x						x						x					6
Paratrechina																																						
P. longicornis		x	x	x		x	x					x						x			x				x	x												10
Pheidole																																						
P. belli							x																															1
P. erato																											x											1
P. fuscula																											x											1
P. isis																											x											1
P. taki						x																																1
P. megacephala	x			x			x		x								x		x		x					x											x	8
P. mendanai																											x											1
P. nindi				x		x															x												x					4
P. oceanica		x		x		x	x	x								x					x				x	x	x						x					11

Taxon	*Anuta*	*Bellona*	*Choiseul*	*Guadalcanal*	*Kolombangara*	*Makira*	*Malaita*	*Malaupaina*	*Matema*	*Mbanika*	*New Georgia*	***NEW GEORGIA IS.***	***NGGELA IS.***	*Nggela Sule*	*Nupani*	***OLU MALAU IS.***	*Ontong Java Is.*	*Owaraha*	***REEF IS.***	*Rendova*	*Rennell*	*Russell Is.*	*San Jorge*	*Santa Catalina*	*Santa Cruz*	***SANTA CRUZ IS.***	*Santa Isabel*	*Savo*	*Shortland*	*Sikaiana*	*Tikopia*	*Tulagi*	*Ugi*	*Vangunu*	*Vanikoro*	*Vella Lavella*	*SOLOMON IS.*	***Total***
P. philemon				x		x	x	x								x									x	x											x	7
P. sexspinosa		x		x		x	x						x								x				x	x	x					x						10
P. fuscescens													x	x																								2
P. umbonata		x		x		x	x														x												x					6
P. sp. BP02*						x																																1
P. sp. BP09						x																																1
P. sp. BP10						x																																1
P. sp. BP11						x																																1
P. sp. BP12*						x																																1
P. sp. BP13*																					x																	1
Philidris																																						
P. myrmecodiae		x		x		x	x						x	x		x		x			x				x	x	x						x					13
Plagiolepis																																						
P. alluaudi				x																																		1
Platythyrea																																						
P. parallela																									x	x											x	2
P. sp. BP01*																					x																	1
Podomyrma																																						
P. salomo							x						x	x																		x						4
P. woodfordi								x								x																						2
Polyrhachis																																						
P. andromache						x																																1
P. annae		x		x		x		x	x							x			x		x				x	x												10
P. acutinota				x																																		1
P. argentea							x						x	x																							x	3

Taxon	*Anuta*	*Bellona*	*Choiseul*	*Guadalcanal*	*Kolombangara*	*Makira*	*Malaita*	*Malaupaina*	*Matema*	*Mbanika*	*New Georgia*	***NEW GEORGIA IS.***	***NGGELA IS.***	*Nggela Sule*	*Nupani*	***OLU MALAU IS.***	*Ontong Java Is.*	*Owaraha*	***REEF IS.***	*Rendova*	*Rennell*	*Russell Is.*	*San Jorge*	*Santa Catalina*	*Santa Cruz*	***SANTA CRUZ IS.***	*Santa Isabel*	*Savo*	*Shortland*	*Sikaiana*	*Tikopia*	*Tulagi*	*Ugi*	*Vangunu*	*Vanikoro*	*Vella Lavella*	*SOLOMON IS.*	***Total***
P. brunneipes		x					x																															1
P. campbelli						x																x																2
P. dahlii				x		x	x	x					x	x		x																x					x	8
P. emeryana							x																															1
P. fulakora				x																							x											2
P. geminata						x							x	x																								3
P. greensladei				x																								x										2
P. ithona									x										x																			2
P. johnsoni								x				x				x				x																		4
P. kaipi	x					x	x																			x												4
P. litigiosa						x																					x											2
P. malaensis							x																															1
P. nofra						x																																1
P. osae				x		x																											x				x	3
P. pacifica				x																																		1
P. rere	x			x																						x												3
P. salomo				x			x															x															x	3
P. santschii													x	x																								2
P. setosa				x																																		1
P. similis						x					x	x	x	x								x					x					x	x					9
P. ugiensis						x										x																	x					3
P. ulysses													x	x																		x					x	3
P. undulata				x		x																																2
P. wheeleri							x																				x											2
P. sp. BP01						x																																1

Taxon	Anuta	Bellona	Choiseul	Guadalcanal	Kolombangara	Makira	Malaita	Malaupaina	Materna	Mbanika	New Georgia	**NEW GEORGIA IS.**	**NGGELA IS.**	Nggela Sule	Nupani	**OLU MALAU IS.**	Ontong Java Is.	Owaraha	**REEF IS.**	Rendova	Rennell	Russell Is.	San Jorge	Santa Catalina	Santa Cruz	**SANTA CRUZ IS.**	Santa Isabel	Savo	Shortland	Sikaiana	Tikopia	Tulagi	Ugi	Vangunu	Vanikoro	Vella Lavella	SOLOMON IS.	**Total**
P. sp. BP03																					x																	1
P. sp. BP04						x																																1
Ponera																																						
P. clavicornis			x	x		x	x					x	x	x					x	x	x						x	x										12
P. incerta				x		x						x	x												x	x	x										x	7
P. swezeyi						x																																1
P. szaboi		x																			x																	2
P. tenuis				x																																		1
P. sp. BP01						x																																1
P. sp. BP02						x																																1
Prionopelta																																						
P. majuscula		x		x	x																																	3
P. opaca		x		x	x	x					x	x	x								x							x	x							x		11
Pristomyrmex																																						
P. levigatus						x																			x	x												3
P. obesus				x		x	x	x			x	x				x									x	x	x											10
Probolomyrmex																																						
P. salomonis				x		x																															x	2
Proceratium																																						
P. austronesicum						x																																1
P. papuanum																			x			x			x	x												4
Rhytidoponera																																						
R. araneoides				x		x	x					x	x	x						x							x					x	x				x	10
R. chalybaea				x																																		1
Rogeria																																						

Taxon	*Anuta*	*Bellona*	*Choiseul*	*Guadalcanal*	*Kolombangara*	*Makira*	*Malaita*	*Malaupaina*	*Matema*	*Mbanika*	*New Georgia*	***NEW GEORGIA IS.***	***NGGELA IS.***	*Nggela Sule*	*Nupani*	***OLU MALAU IS.***	*Ontong Java Is.*	*Owaraha*	***REEF IS.***	*Rendova*	*Rennell*	*Russell Is.*	*San Jorge*	*Santa Catalina*	*Santa Cruz*	***SANTA CRUZ IS.***	*Santa Isabel*	*Savo*	*Shortland*	*Sikaiana*	*Tikopia*	*Tulagi*	*Ugi*	*Vangunu*	*Vanikoro*	*Vella Lavella*	*SOLOMON IS.*	***Total***
R. megastigmatica				x		x																																2
R. stigmatica		x																			x						x						x					4
R. sp. BP01*						x																																1
Romblonella																																						
R. elysii								x					x	x		x		x																				5
Solenopsis																																						
S. geminata				x																																		1
S. papuana						x																																1
S. pawaensis						x																					x						x					3
Stereomyrmex																																						
S. dispar		x																																				1
Stigmatomma																																						
S. celata				x		x	x				x	x	x	x							x						x					x					x	10
S. gnoma				x																																		1
Strumigenys																																						
S. chyzeri				x	x	x	x				x	x															x						x			x		9
S. decollata																											x											1
S. emmae		x		x							x	x								x	x																	6
S. eurycera				x							x	x	x							x																		5
S. frivaldszkyi						x															x																	2
S. godeffroyi				x		x	x	x								x					x	x			x	x	x						x				x	11
S. karawajewi		x		x		x													x							x											x	5
S. membranifera				x		x																			x	x												4
S. mocsaryi				x								x	x																							x		4
S. rogeri				x																																		1

Taxon	*Anuta*	*Bellona*	*Choiseul*	*Guadalcanal*	*Kolombangara*	*Makira*	*Malaita*	*Malaupaina*	*Matema*	*Mbanika*	*New Georgia*	***NEW GEORGIA IS.***	***NGGELA IS.***	*Nggela Sule*	*Nupani*	***OLU MALAU IS.***	*Ontong Java Is.*	*Owaraha*	***REEF IS.***	*Rendova*	*Rennell*	*Russell Is.*	*San Jorge*	*Santa Catalina*	*Santa Cruz*	***SANTA CRUZ IS.***	*Santa Isabel*	*Savo*	*Shortland*	*Sikaiana*	*Tikopia*	*Tulagi*	*Ugi*	*Vangunu*	*Vanikoro*	*Vella Lavella*	*SOLOMON IS.*	***Total***
S. szalayi				x		x					x	x								x																		5
S. undras				x																																		1
S. yaleopleura			x								x	x															x							x				5
S. sp. BP05						x																																1
S. sp. BP06						x																																1
Tapinoma																																						
T. melanocephalum	x		x	x		x	x						x								x	x				x												9
T. minutum																																					x	0
T. timidum				x																																		1
Technomyrmex																																						
T. albipes			x	x	x	x	x				x	x	x							x	x						x						x				x	12
T. vitiensis				x		x																																2
T. sp. BP01						x																																1
Tetramorium																																						
T. antennatum																									x	x												2
T. aspersum						x	x				x	x										x	x				x											7
T. bicarinatum	x			x			x									x					x				x	x												7
T. carinatum						x	x	x					x	x		x						x					x					x						9
T. insolens		x				x	x	x								x																	x					6
T. lanuginosum																					x												x					2
T. mayri						x																																1
T. melanogyna						x		x								x																	x					4
T. mutatum							x																															1
T. pacificum		x																			x																	2
T. salomo				x		x	x																															3

Taxon	*Anuta*	*Bellona*	*Choiseul*	*Guadalcanal*	*Kolombangara*	*Makira*	*Malaita*	*Malaupaina*	*Matema*	*Mbanika*	*New Georgia*	***NEW GEORGIA IS.***	***NGGELA IS.***	*Nggela Sule*	*Nupani*	***OLU MALAU IS.***	*Ontong Java Is.*	*Owaraha*	***REEF IS.***	*Rendova*	*Rennell*	*Russell Is.*	*San Jorge*	*Santa Catalina*	*Santa Cruz*	***SANTA CRUZ IS.***	*Santa Isabel*	*Savo*	*Shortland*	*Sikaiana*	*Tikopia*	*Tulagi*	*Ugi*	*Vangunu*	*Vanikoro*	*Vella Lavella*	*SOLOMON IS.*	***Total***
T. simillimum				x		x											x				x																	4
T. tonganum				x		x						x								x	x																	5
T. vombis																																	x					1
Tetraponera																																						
T. laeviceps				x									x														x											3
Turneria																																						
T. dahlii		x		x			x														x																	4
T. pacifica						x																			x	x												3
Vollenhovia																																						
V. dentata						x																											x				x	2
V. marginata							x																										x				x	2
V. elysii								x								x																					x	2
V. foveaceps																											x										x	1
V. loboii							x																														x	1
V. oblonga						x	x														x				x	x	x											6
V. pedestris				x		x	x											x							x	x	x											7
V. subtilis						x	x																															2
V. sp. BP01*						x																																1
V. sp. BP02*						x																																1
V. sp. BP03*																					x																	1
Wasmannia																																						
W. auropunctata						x																																1
Total	8	32	11	107	17	142	71	29	7	2	18	40	43	28	4	35	4	8	10	16	66	18	2	4	32	37	68	12	2	1	1	21	38	3	2	7	60	217

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A new species of *Aeneator* Finlay, 1926 (Mollusca, Gastropoda, Buccinidae) from northern Chile, with comments on the genus and a key to the Chilean species

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Abstract
A new species of the genus *Aeneator* Finlay, 1926 is described from off the coast of Caldera (27°S), northern Chile. *Aeneator martae* sp. n. has a small, broad, stout, angulated shell with more prominent axial ribs and a more obviously keeled periphery than all previously named Chilean species. Comparisons are provided with all other South American named species of *Aeneator*.

Keywords
New taxa, East Pacific, deep water

Introduction

The genus *Aeneator* Finlay, 1926 comprises a group of deep-water gastropods of moderate size, distributed in the South Pacific Ocean around New Zealand (Powell 1979, Beu 1979) and Chile (Rehder 1971, McLean and Andrade 1982, Fraussen and Sellanes 2008). Almost all the species have offshore distributions, and they are common on the sea floor (Dawson 1965, Powell 1979, Beu and Maxwell 1990). Their elongate fusiform shells have rounded whorls with a subsutural concavity, a lip with a broad shallow sinus below the suture, and a sculpture of strong axial ribs overridden by spiral cords (McLean and Andrade 1982).

In the southeastern Pacific the genus encompasses five extant species: *Aeneator castillai* McLean & Andrade, 1982, *Aeneator fontainei* (d'Orbigny, 1839), *Aeneator (Ellicea) loisae* Rehder, 1971, *Aeneator portentosus* Fraussen & Sellanes, 2008 and *Aeneator prognaviter* Fraussen & Sellanes, 2008. The distribution of these species ranges from Bahía Independencia (14°S), in the south of Peru to Canal Moraleda 45°22'S, southern Chile (Osorio et al. 2006). Their bathymetric range is from 10 m depth for *A. fontainei* collected at Mejillones Bay, in the north of Chile (Guzmán et al. 1998, Laudien et al. 2007) to 800 m depth for *A. portentosus*, collected off Iquique (Fraussen and Sellanes 2008). Most of the species have been recovered in the trawls of the local shrimp industry (McLean and Andrade 1982, Rehder 1971, Párraga 2012, Queirolo et al. 2011), and very little is known of their population biology, ecology and conservation status.

The present work describes a new species of *Aeneator* from northern Chile based on shell morphological features. Criteria were shell shape, number of primary spiral cords, development of secondary spirals, and axial sculpture. An identification key, based on shell characters, is given for all the extant Chilean *Aeneator* species.

Material and methods

Material examined: *Aeneator martae* sp. n. types, Chile, Region of Atacama, Caldera, holotype MZUC 37890, paratype 1 MZUC 37891, paratype 2 MZUC 37892, paratype 3 MG 200105.

Examination was made of shell only specimens; all measurements were made with vernier callipers (± 0.1 mm). For the measure of length of aperture and angle of the spire, the methodology of Dépraz et al. (2009) and Chiu et al. (2002) was used.

Abbreviations: KF; Private collection of Mr Koen Fraussen, Aarschot, Belgium, MG: private collection of the author, section marine Gastropoda, MZUC; Museo de Zoología de la Universidad de Concepción, Concepción, Chile, RC Coll; private collection of Mr Ricardo Catalán, Servicio Nacional de Pesca, Chile.

Results

Systematics

Class: Gastropoda Cuvier, 1797
Order: Neogastropoda Wenz, 1938
Superfamily: Buccinoidea Rafinesque, 1815
Family: Buccinidae Rafinesque, 1815

Genus: *Aeneator* Finlay, 1926:414

Type species. *Verconella marshalli* Murdoch 1924 (by original designation), Pleistocene and recent, New Zealand.

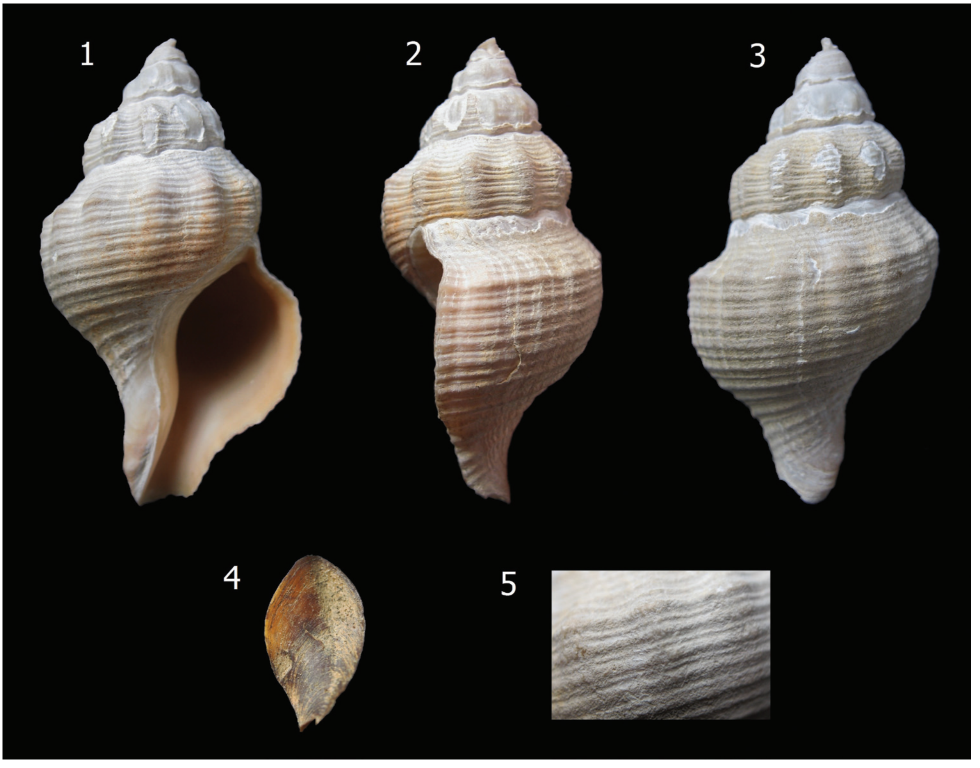
***Aeneator martae* sp. n.**
urn:lsid:zoobank.org:act:73AC9156-214E-4941-BFF6-0F94F8E17381
http://species-id.net/wiki/Aeneator_martae
Figs 1–14, 18, Tables 1, 2, 3

Type material. Holotype (MZUC 37890), 47.9 mm. Chile, off Caldera (27°04'S, 70°50'W), 550–600 m depth, live collected on shrimp trawl nets, January 2001, S. Castillo leg. Paratype 1 (MZUC 37891), length 44.0 mm. Paratype 2 (MZUC 37892), 41.7 mm, Paratype 3 (MG 200105), length 40.2 mm. All the paratypes with same locality as the holotype.

Distribution. Known only from the type locality; Chile, Region de Atacama, Caldera (27°04'S, 70°50'W), 550–600 m depth.

Diagnosis. A small species of *Aeneator*, height up to 47.9 mm, shell stout, inside of aperture pale orange, exterior sculptured by well-defined axial ribs, spiral cords, and a conspicuous stepped shoulder.

Description. Shell small for genus (height up to 47.9 mm, Table 1), thick, solid, fusiform, chalky white to pale brownish, inside of aperture pale orange. Shape broad, angulate, length of aperture and canal more than half length of shell, width/height ratio 0.53



Figures 1–5. *Aeneator martae* sp. n. shell, Holotype 47.9 mm, Chile, Off Caldera, 27°04'S, 70°50'W. 550–600 m. MZUC 37890.

Table 1. *Aeneator martae* sp. n. measurements of specimens. (%) means percentage compared to the total length of the shell.

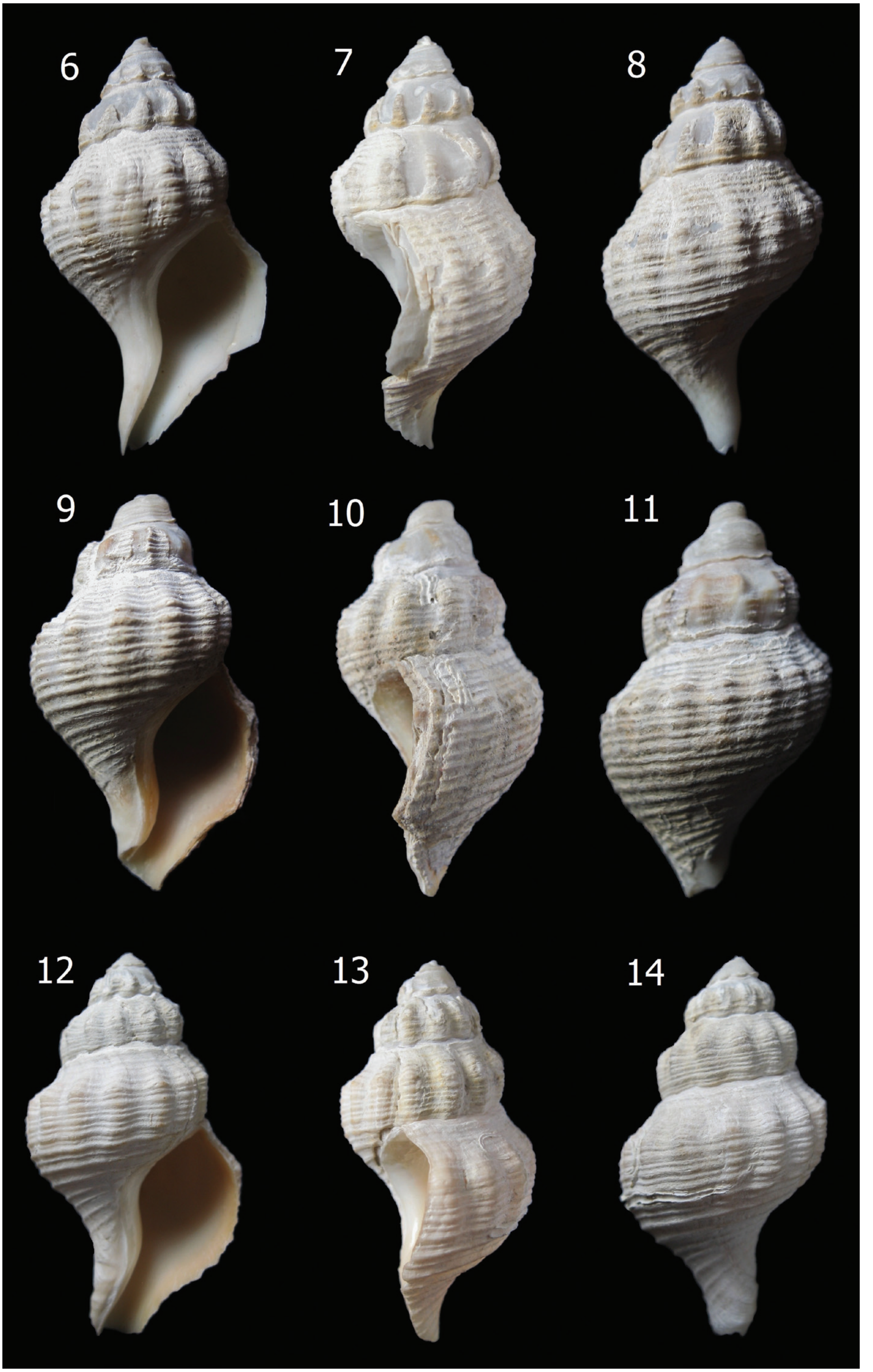
	Maximum length (mm)	Maximum width (mm)	Length of aperture	Width/Length
Holotype	47.9	25.6	26.8 (56 %)	0.53
Paratype 1	44.0	23.6	27.9 (57 %)	0.54
Paratype 2	41.7	23.4	23.0 (57 %)	0.56
Paratype 3	40.2	22.1	22.6 (56 %)	0.55
Average	43.4	23.6	25.1 (56 %)	0.54

to 0.56, whorls convex apart from slightly concave sutural ramp, suture shallow but impressed. Spire angle 63° to 68°. Protoconch and upper teleoconch whorls missing, remaining whorls about 4.5, last 3 with sculpture intact with 7–9 primary spiral cords, interspaces each occupied by one narrow, well defined secondary cord. Last whorl with 16–18 spiral cords, more prominent at periphery of shell than elsewhere, forming a distinct keel. Spire whorls with 24–28 pronounced axial ribs, interspaces deep, each almost equal to a rib in width. Last whorl with 14–15 such ribs. Ribs more pronounced towards the anterior end of shell. Aperture ovate. Parietal and columellar area well-defined, glazed; outer lip thin, slightly crenulated, without lirae or teeth. Siphonal canal short, open, directed slightly to left. Operculum large, thin, dark brown, elongate, nucleus terminal, tip sharp.

Etymology. Named in honour of Mrs Marta Araya, Caldera, Chile, who presented the specimens to the author.

Remarks. In Chile the genus *Aeneator* encompasses five extant species: *A. castillai*, found from Coquimbo (29°55'S) to Punta Peñablanca (33°22'S) in 200–450 m (McLean and Andrade 1982), *A. fontainei*, the most common species, with records from Bahía Independencia (14°S) in the south of Peru (McLean and Andrade 1982) to Estero Elefantes, 46°05'S (Osorio et al. 2006) and with a bathymetric range of 10 m near Mejillones (Guzmán et al. 1998, Laudien et al. 2007) to 421 m for a specimen collected off Coquimbo (Figs 27–30), *A. (Ellicea) loisae*, distributed from Caldera (27°04'S), for material examined in this work (Figs 27–30), to Canal Moraleda (45°22'S), in the fjords area (Osorio et al. 2006) with a bathymetric range of 200 m (McLean & Andrade 1982) to 465 m, *A. portentosus* reported only form the original locality off Iquique (21°19'S) in 605 m and off Coquimbo at 800 m and *A. prognaviter*, distributed off Antofagasta (22°51'S) in 318 m (Fraussen and Sellanes 2008) and in 748 m off Iquique for material examined in this work (Fig. 37). Data on the localities of Chilean species of *Aeneator* is provided in Table 3.

In size, the shell of *Aeneator martae* sp. n. is similar to *A. prognaviter* (Figs 20, 37, 38) and *A. portentosus* (Figs 35, 36). However, the former of these two can be clearly differentiated from the new species by its wider and shorter siphonal canal, less numerous and more curved axial ribs and a thinner, snow white shell (Fraussen and Sellanes 2008). From *A. portentosus* the new species differs by having a much wider, thicker shell with a shorter spire, a more elongate aperture, dominant axial sculpture and less rounded whorls. Moreover *A. portentosus* exhibit a very distinctively sculptured peri-



Figures 6–14. *Aeneator martae* sp. n. shells. **6–8** Paratype 1 (MZUC 37891), 44.0 mm height **9–11** Paratype 2 (MZUC 37892), 41.7 mm height **12–14** Paratype 3 (MG 200105), 40.2 mm height.

Table 2. Synthesis of characters of the Chilean species of *Aeneator* Finlay, 1926 based on Rehder (1971), McLean and Andrade (1982), Fraussen and Sellanes (2008) and material examined in this work.

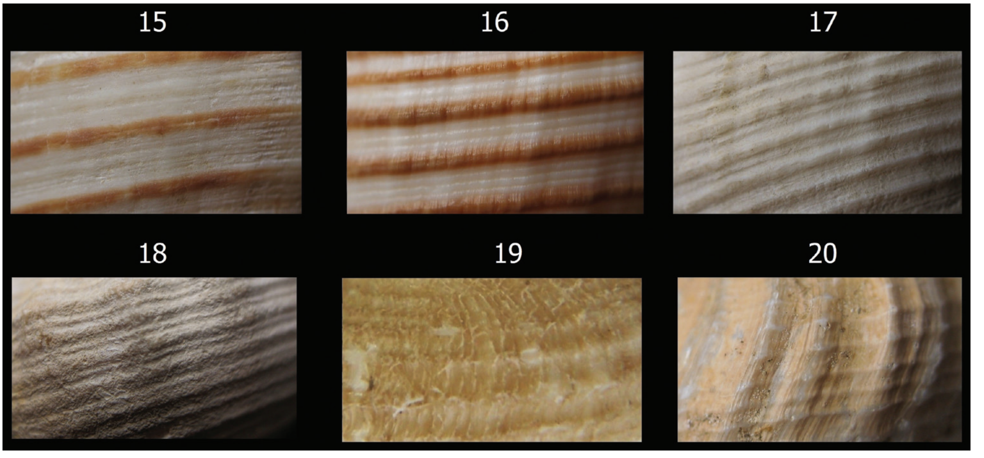
	Aeneator castillai	***Aeneator fontainei***	***Aeneator loisae***	***Aeneator portentosus***	***Aeneator prognaviter***	***Aeneator martae* sp. n.**
Length	85.7	85.8	104	45.5	32.2	47.9
Width / Length	0.50–0.51	0.48–0.54	0.43–0.48	0.49–0.59	0.55 – 0.60	0.54–0.56
Aperture length/ total length	0.55–0.63	0.55–0.56	0.54 – 0.56	0.43–0.52	0.49 – 0.53	0.55–0.56
Spire angle	50°	51°–57°	44°–46°	44°–51°	60°	63°–68°
Axial ribs on last whorl	16, absent in subsutural area	12–15	Faint, absent	Faint, absent	22, bent	14–15, straight
Spiral cords in last whorl	12 – 15 brown primary, 1–3 secondary in each interspace	12–15 brown primary, 3–5 secondary in each interspace	9–10 primary, many secondary	20	20–24	16–18 primary, 7–9 secondary
Siphonal canal	short, twisted	medium to long, straight	long	short, broad, slightly bent	short, broad	short, slightly curved to left
Aperture	ovate	ovate	elongate ovate	round	oval	oval
Shell color	brown	white - yellowish	white	snow white	snow white	white, pale brownish
Distribution	29°55'S to 39.1°S	14°13'S to 46°S	27°04'S to 53.7°S	21.19°S and 29.95°S	21°19'S and 22°51'S	27°04'S

Table 3. Table of localities of Chilean species of *Aeneator* Finlay, 1926 based on Rehder (1971), McLean and Andrade (1982), Fraussen and Sellanes (2008), and material examined in this work.

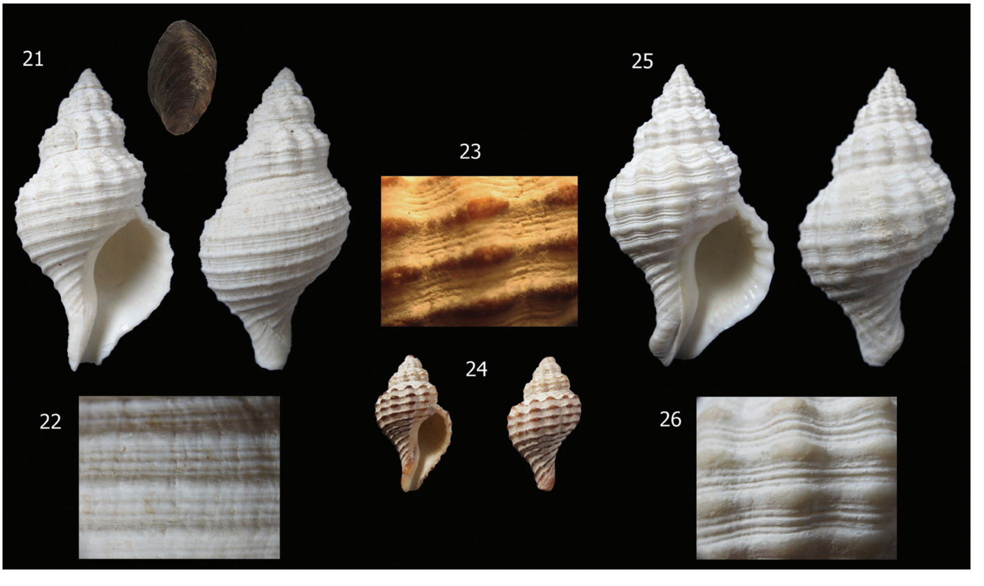
Species	Latitude	Longitude	Depth (m)
A. castillai	29°55'S to 33°22'S	71°53'W to 71°20'W	200–450
A. fontainei	14°14'S to 46°05'S	76°11'W to 73°41'W	10–421
A. loisae	27°04'S to 45°22'S	73°21'W to 70°50'W	200–465
A. martae	27°04'S	70°50'W	550–600
A. portentosus	21°19'S to 29°55'S	71°20'W to 70°09'W	800
A. prognaviter	21°19'S to 22°51'S	70°24'W to 70°09'W	600–748

ostracum (Fig. 19), with low axial ridges, very different from all the other Chilean *Aeneator* species. A periostracum is absent in the examined specimens of *A. martae* sp. n.

Aeneator castillai (Figs 33, 34), and *A. fontainei* (Figs 21–26) differ markedly from the new species by their much larger shells, reaching up to 85.8 mm, more fusiform shells, with a much less stepped or indistinct shoulder, lower and fewer axial ribs,

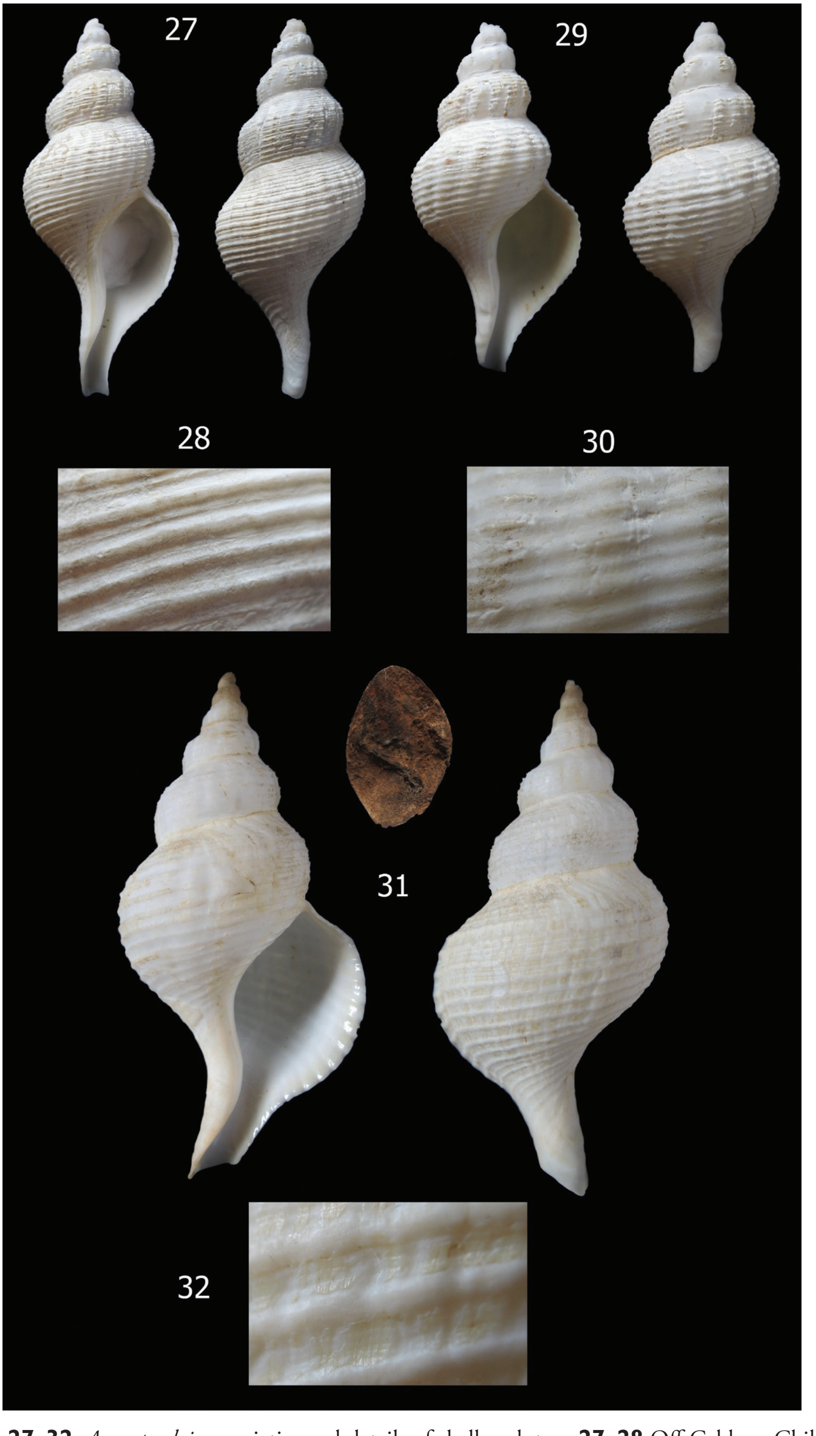


Figures 15–20. Details of shell sculpture of Chilean *Aeneator* species. **15** *A. castillai* (RC Coll.), 85.7 mm **16** *A. fontainei* (RC Coll.), 48.0 mm **17** *A. loisae* (MG 200003), 78 mm **18** *A. martae* sp. n. paraype 3 (MG 200105), 40.2 mm **19** *A. portentosus*, Paratype KF-0338, 45.5 mm **20** *A. prognaviter* (MG 200124), 33,0 mm.



Figures 21–26. *Aeneator fontainei* varieties and details of shell sculpture. **21–22** Off Coquimbo, Chile, trawled 421 m (RC Coll), 58 mm **23–24** Washed ashore, Calderilla beach, Caldera, Chile (MG 200011), 28.5 mm **25–26** Dredged 20 m depth off Loreto beach, Caldera, Chile (MG 200012), 52.8 mm.

brown primary spiral cords (Figs 15, 16) and lip lirated within. The spiral sculpture is quite different; *A. fontainei* has 13 to 16 dark brown major cords, with interspaces filled with five secondary cords separated by fine grooves or by secondary and tertiary cords. *Aeneator castillai* has brown primary cords with 3 to 5 fine secondary cords fill-



Figures 27–32. *Aeneator loisae* varieties and details of shell sculpture **27–28** Off Caldera, Chile, 450–500 m depth (MG 200003), 78 mm **29–30** Off Caldera, Chile, 420 m depth (MG 200007) 71.9 mm **31–32** Off Coquimbo, Chile, 400 m depth (RC Coll.), 104 mm

ing the interspaces and exhibits a longer, twisted, siphonal canal. In contrast *A. martae* sp. n. lacks any brown coloration, shows a sculpture of alternated single major and minor spiral cords defined mostly in the posterior part of the whorls, and has a conspicuous stepped shoulder, forming a keel at the periphery.

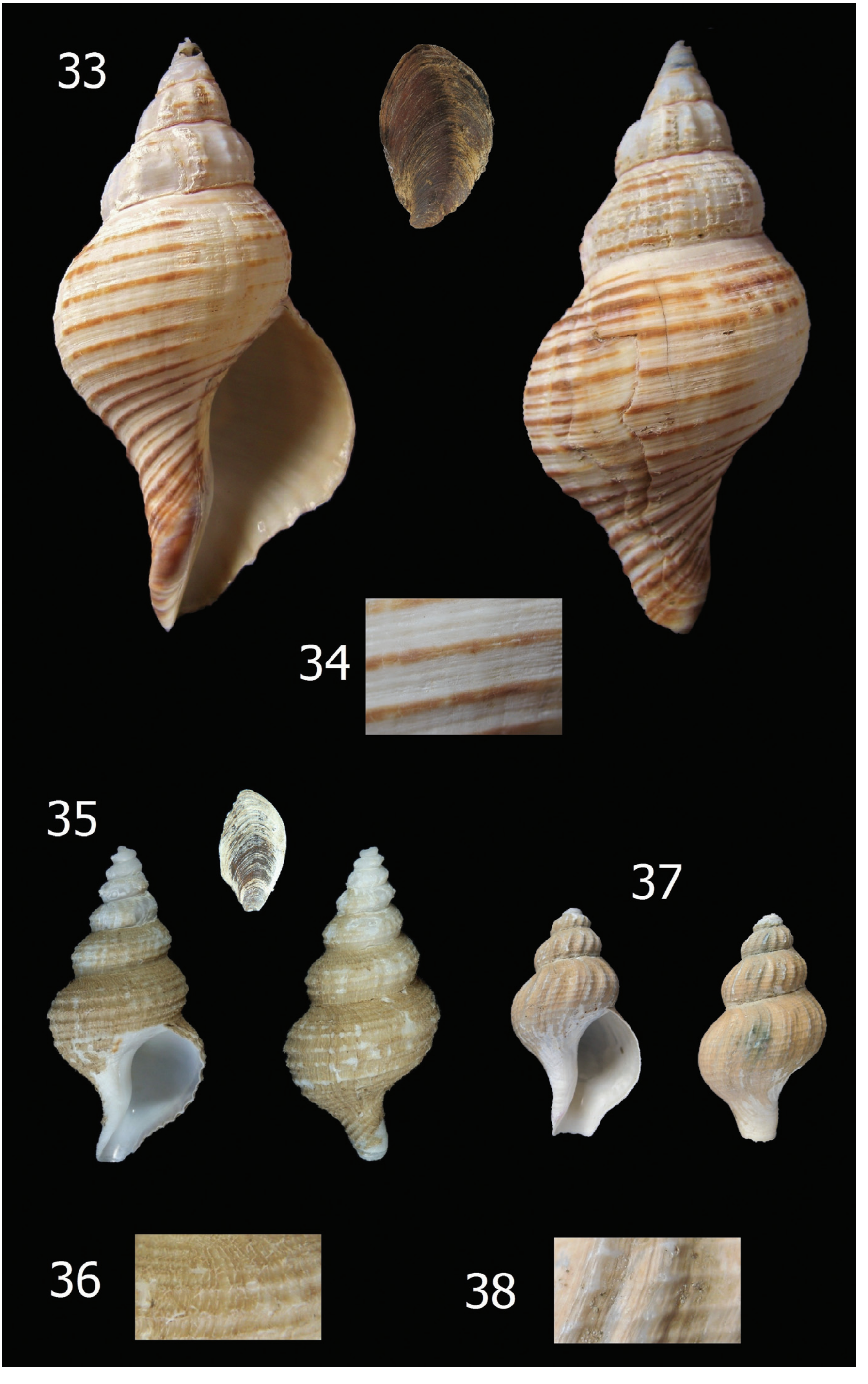
Aeneator loisae (Figs 27–32) differs from the new species in having a larger, up to 104 mm, white to snow white shell (different from the white to light brown shell of *A. martae* sp. n.), more inflated last whorl, with a much longer siphonal canal, a higher number of primary and secondary spiral cords, more prominent spiral sculpture, and fewer, more tenuous, axial ribs.

The new species is tentatively assigned, given the generic uncertainties within the Chilean species, to the genus *Aeneator* Finlay 1926, typified by the species *A. marshalli marshalli* (Murdoch, 1924) recorded from Castlecliff (as fossils) and, as a recent species (= *A. marshalli separabilis* Dell, 1956), from Wanganui and Ohope beach, Whakatane, New Zealand. Similar to the type species, *A. martae* sp. n. has a fusiform shell with moderately tall spire, shallow sinus in outer lip and a spiral sculpture of cords crossed by axial costae (Beu and Maxwell 1990). The new species differs from *A. marshalli* in its smaller shell, shorter anterior canal, the absence of nodules along the columellar lip, less inflated whorls and by the presence of a distinct keel at the periphery. From the genus *Austrofusus* Kobelt, 1879, with the type species *Austrofusus glans* (Röding, 1798), the new species differs in the smaller size, its thicker shell, more prominent sculpture, the more prominent ridges over the periphery, and the pale orange colour of the aperture, which is white in *A. glans* (Beu & Marshall 2010). Comparative characters in the Chilean species of *Aeneator* are compared in table 2.

In a recent revision of the fossil fauna of Mejillones, north of Chile (Nielsen 2012), the species *Aeneator loisae* was synonymized with the fossil species *Fusus steinmanni* Möricke, 1896 into *Austrofusus*. However, this was based partly on the incorrect conclusion by Beu and Marshall (2010) that *A. fontainei* is the type species of *Austrofusus*; this was later corrected by Beu and Marshall (2011). On morphological grounds, the author concurs with McLean and Andrade (1982) and considers that *Aeneator (Ellicea) loisae* does belong to the genus *Aeneator* and the sub-genus *Ellicea* Finlay in Marwick, 1928. However the generic placement of the species *A. fontainei*, *A. castillai,* and possibly the new species described here, should be further investigated or even be ascribed to a new genus.

Further study of radular characters, comparative anatomy and DNA will improve the taxonomic placement of the Chilean species. Fossil studies would also give a general insight into the development of the genus and their relationships with the South Pacific related fauna, especially those from New Zealand and adjacent waters.

Comparative material examined: *A. castillai*, Chile, Region of Coquimbo, Coquimbo, 2 specimens RC Coll. *A fontainei*, Chile, Region of Atacama, Caldera, 3 specimens MG 200011–200013, 5 specimens RC Coll. *A loisae*, Chile, Region of Atacama, Chile, 4 specimens MG 200003–200006, 1 specimen RC Coll, *A prognaviter*, 2 specimens MG 200124–200125, *A portentosus*, 1 specimen (examined from images), KF-0338.



Figures 33–38. *Aeneator* species and details of shell sculpture. **33–34** *A. castillai*, off Coquimbo, Chile, 380 m depth (RC Coll.), 85.7 mm **35–36** *A. portentosus*, Paratype KF-0338, 45.5 mm **37–38** *A. prognaviter*, off Iquique, Chile, 748 m depth (MG 200124), 33,0 mm.

Key for the identification of fully-grown Chilean species of *Aeneator* based on shell characters

1	Aperture ovate-elongate **2**
–	Aperture rounded, shell pagodoid, periostracum sculptured .... ***A. portentosus* Fraussen & Sellanes, 2008**
2(1)	Siphonal canal short **3**
–	Siphonal canal long, outer lip reflexed, shell elongated .... ***A. loisae* Rehder, 1971**
3(2)	Spiral cords brown **5**
–	Spiral cords white, axial ribs thick, shell length up to 49 mm **4**
4(3)	Siphonal canal broad, axial ribs strongly curved .... ***A. prognaviter* Fraussen & Sellanes, 2008**
–	Shell with a distinct keel, aperture almost subquadrate .... ***A. martae* sp. n.**
5(3)	Axial ribs on subsutural area .... ***A. fontanei* (d'Orbigny, 1841)**
–	Sculpture absent on subsutural area, siphonal canal twisted .... ***A. castillai* MacLean & Andrade, 1982**

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