



Research article

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Comparative morphology of the endophallic structures of the genus *Laius* (Coleoptera, Melyridae), with the descriptions of three new species

Hiroyuki YOSHITOMI

Ehime University Museum, Bunkyo 3, Matsuyama, Ehime Pref. 790-8577, Japan.

E-mail: hymushi@agr.ehime-u.ac.jp (corresponding author)

[urn:lsid:zoobank.org/author:744FA6FC-2D84-41B7-8A6C-C1611CC68EE1](http://urn.lsid:zoobank.org/author:744FA6FC-2D84-41B7-8A6C-C1611CC68EE1)

Abstract. The endophallic structure of the genus *Laius* is studied and discussed based on the examination of 19 species from Asia to the Indian Ocean. The structure contains two primary sclerites (named gonoporal piece and ligula), a secondary sclerite on the basal part of the gonoporal piece (named additional sclerite) in some species, and a membranous basal area closely covered with many spines (named spinous area). Five species groups are recognized based on the morphology of the endophallic sclerites. The sympatric species have different body sizes and quite distinguishable endophallic sclerites (= different species group), while the allopatric species have overlapping body sizes and similar endophallic sclerites (= same species group). Three new species are described and six previously known species are redescribed with endophallic sclerites, and the descriptions of endophallic sclerites of the remaining ten species are added. The larva of *Laius rodriguesensis* sp. nov. is also described. The genus *Nossibeus* Evers, 1994 is synonymised with *Laius* Guérin-Méneville, 1830.

Keywords. Melyridae, taxonomy, distribution, endophallus, new species.

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Introduction

Male genitalia are considered one of the most important diagnostic traits in insect systematics (Simmons 2014), and this also applies to the order Coleoptera (e.g., Sharp & Muir 1912). Some groups in this order have developed endophallic structures (e.g., sclerites, projections, small denticles), and these characters provide important information both taxonomically and phylogenetically. The endophallic structures are mainly observed in relatively large body-sized beetle families (e.g., Carabidae, Cerambycidae, Chrysomelidae), because it is necessary to evert and inflate the endophallus to observe the structures (Sasakawa 2005; Yamasako & Ohbayashi 2011). Therefore, it is difficult to dissect and observe the endophallic structures in smaller-sized groups.

The melyrid genus *Laius* Guérin-Méneville, 1830 is represented by about 30 species from the Pacific Islands, Indian Ocean, Australia, and the eastern coast of Africa (see Appendix); however, numerous species have been erroneously included in this genus and will be transferred to other genera (Plonski

2013; Wittmer 1997). The genus has a well-developed endophallic structure consisting of many small spines and some large sclerites, and these characters have been observed through the aedeagus (Wittmer 1997; Yoshitomi 2008; also see Fig. 2B). However, the characters could not be well understood or described.

The main aim of this study is to inspect the validity of endophallic structures for the recognition of species in this genus. I firstly define the terminology of the endophallic structures of the genus *Laius* and secondly describe the endophallic sclerites of 19 species, including the descriptions of three new species and redescriptions of six poorly known species.

Materials and methods

General observations and dissections were made under a Leica MZ95 stereomicroscope. Microstructures of dissected parts were studied in pure glycerine under an Olympus BH-2 compound microscope. After observation, the dissected parts were mounted on the same card with the specimen. Photographs were taken under a Leica MZ95 using a microscopy camera system (Nikon DS-Fi1-L2), and combined with the automontage software Combine ZM (Alan Hadley, UK). Some structures were observed with an SEM (Hitachi S-225) after coating with gold.

The endophallus was extracted from the ventral part of the aedeagal apex using a pin and tweezers. If the endophallus could not be extracted from the aedeagal apex, endophallic sclerites were directly removed from the endophallus. After observation, the structures were preserved in pure glycerine.

The holotypes and paratypes are preserved in the Ehime University Museum, Matsuyama (EUMJ), Naturhistorisches Museum Wien (NMW), Natural History Museum Basel (NHMB) and Bishop Museum, Hawaii (BPBM).

Abbreviations

Morphological abbreviations used for measurements are as follows (also see Fig. 2):

- AL = aedeagal length
- EL = length of elytra in suture
- EW = maximum width of elytra
- GL = length of gonoporal piece
- HL = head length
- HW = head width across eyes
- L = length
- LL = length of ligula
- LW = width of ligula
- PL = length of pronotum in median line
- PW = maximum width of pronotum
- TL = total length (HL+PL+EL)
- W = width.

The average is given in parentheses after the range.

Results

Characteristics and terminology of endophallic structures

In the copulation position, only the endophallus of the male genitalia is engaged with the female structures (Fig. 1). Endophallic structures (Figs 1–2) consist of a membranous basal area (named spinous area),

two primary sclerites (named gonoporal piece and ligula), and a secondary sclerite in some species (named additional sclerite).

Spinous area (Figs 2A, 12D): membranous basal area, closely covered with many short spines (Fig. 12D), about $0.5 \times$ length of AL. The differences in this character between species cannot be observed, and the comparison and description of each species is not given in this study.

Gonoporal piece (Fig. 2C; *gp* in Figs 3–4): longest sclerite, about $0.6 \times$ length of AL, straight to rather curved, with pointed or rounded apex, closely covered with minute spines in basal portion of some species, projecting apically and straight from the apical portion of spinous area.

Ligula (Fig. 2D; *l* in Figs 3–4): straight to C-shaped curved sclerite, with pointed apex, shorter than gonoporal piece, projecting laterally from the apico-lateral portion of spinous area.

Additional sclerite (*as* in Figs 3–4): secondary sclerite situated in basal part of gonoporal piece, shorter than ligula, projecting laterally from the basal portion of gonoporal piece.

Taxonomy

Class Hexapoda Blainville, 1816
Order Coleoptera Linnaeus, 1758
Superfamily Cleroidea Latreille, 1802
Family Melyridae Leach, 1815
Subfamily Malachiinae Fleming, 1821

Genus *Laius* Guérin-Méneville, 1830

Laius Guérin-Méneville, 1830: 78 [Type species: *Laius cyaneus* Guérin-Méneville, 1830].

Megadeuterus Westwood, 1833: 678 [Type species: *Paussus flavicornis* Fabricius, 1801].

Rotamalachus Kôno, 1937 in Kôno & Esaki 1937: 121 [Type species: *Rotamalachus esakii* Kôno, 1937].

Nossibeus Evers, 1994: 173 [Type species: *Laius politus* Fairmaire, 1880]. syn. nov.

Remarks

The genus *Nossibeus* was erected for *Laius politus* Fairmaire, 1880 (Evers 1994). After observation of this species, including its endophallic structure, it was clear that this species cannot be recognised as another species of the genus *Laius*. In the present paper, *Nossibeus* Evers, 1994 is treated as a junior synonym of *Laius* Guérin-Méneville, 1830 (syn. nov.).

***Laius baliensis* sp. nov.**

[urn:lsid:zoobank.org:act:9D51A886-E14B-4DE6-96C3-410AF3CBC669](https://doi.org/10.3896/urn:lsid:zoobank.org:act:9D51A886-E14B-4DE6-96C3-410AF3CBC669)

Figs 1, 3A, 5A–B, 7A, 8A, 9A, 13A–B

Laius sp. – Yoshitomi 2008: 289.

Diagnosis

Body small, TL = 4.10–4.46 mm in male, 4.35–4.75 mm in female; male antennomere III oval, deeply concave in dorso-mesal portion, L/W = 0.95; aedeagal apex rounded; gonoporal piece straight and slender; ligula slightly curved; additional sclerite absent.

Etymology

After the type locality, Bali Island, Indonesia.

Type material

Holotype

♂ (EUMJ), “Nusa Dua, South Island 8°48’6.81”S 115°14’16.07”E, Bali, INDONESIA 8. VIII. 2010 H. Yoshitomi leg.”.

Paratypes

1 ♂, 6 ♀♀ (EUMJ), same data as for the holotype; 6 ♂♂, 10 ♀♀ (EUMJ, NMW, BPBM, NHMB), “Nusa Dua, North Island 8°47’52.72”S 105°14’9.31”E, Bali, INDONESIA 7-8. VIII. 2010 H. Yoshitomi

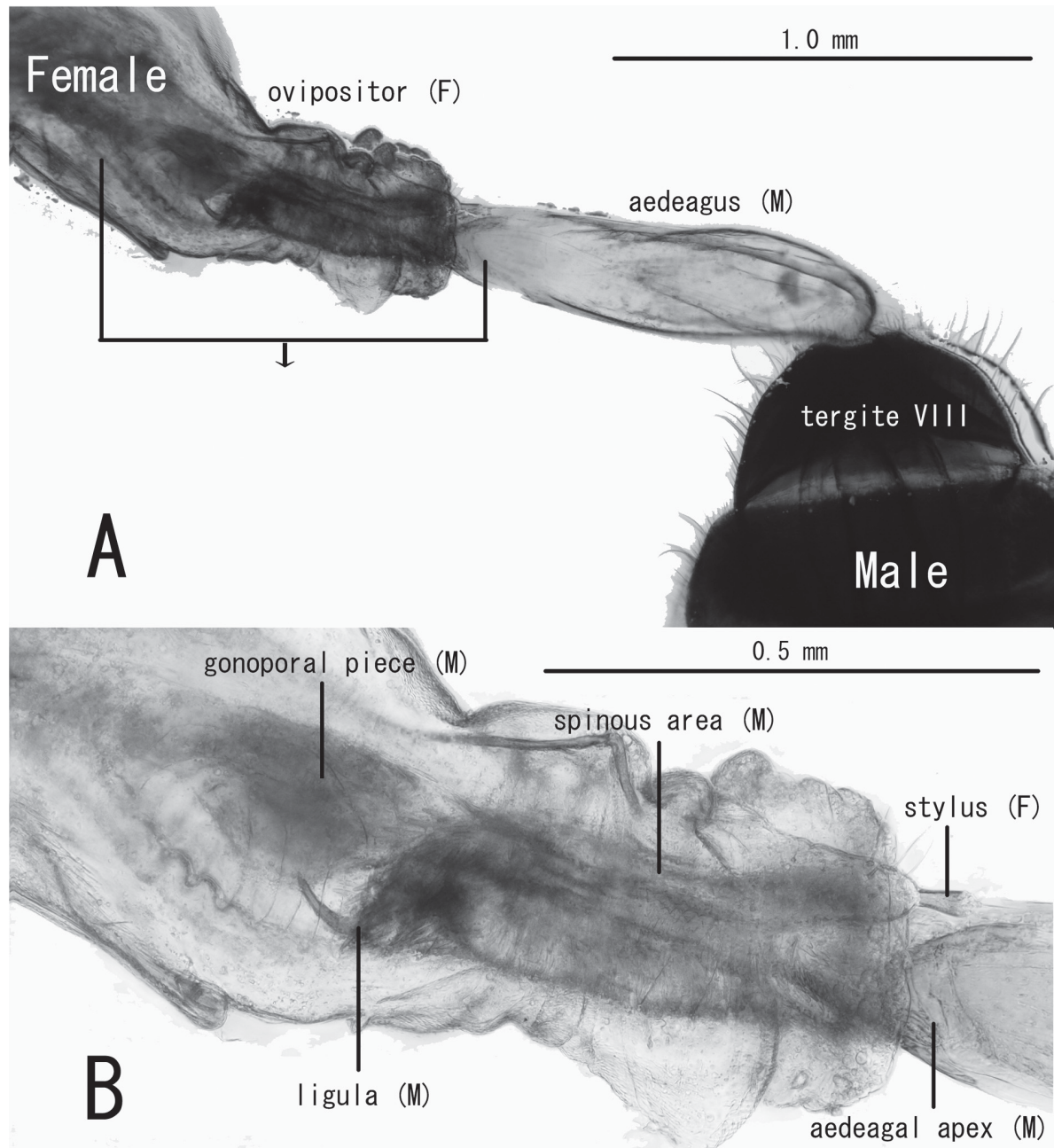


Fig. 1. Copulation of *Laius baliensis* sp. nov. **A.** Endophallus fully engaged with female structures in dorsal view. **B.** Endophallus fully engaged with female structures in dorsal view, close up. Abbreviations: M = male, F = female.

leg.”; 3 ♀♀ (EUMJ), “Nusa Dua, Bali Indonesia 5-I-2000 H. Yoshitomi leg.”; 2 ♀♀ (EUMJ), ditto but collector “M. Satō”; 1 ♀ (EUMJ), ditto but collector “N. Ohbayashi”.

Description

Male

Body oblong, shining, densely covered with short black setae. Coloration of body black with strong bluish luster on head, pronotum and elytra; labrum, maxillary palpomere III and tarsi brown; antennomeres I–III and maxillary palpomeres I–II yellowish-orange.

Head slightly narrower than pronotum, densely punctate; vertex flat dorsally; eyes large, strongly prominent; HL/HW 0.73–0.82 (0.78). Antennae (Fig. 7A) stout; antennomere III (Fig. 8A) oval, deeply concave in dorso-mesal portion, L/W = 0.95; approximate ratio of each antennomeres (n = 1) as 8.0 : 1.0 : 6.0 : 2.2 : 2.0 : 1.8 : 1.8 : 1.8 : 2.0 : 1.8 : 2.8. Pronotum quadrate, widest near anterior margin, rounded and obscure in antero- and postero-lateral angles, punctate as in head; PW/PL 1.15–1.44 (1.26). Scutellum semicircular, covered with very fine punctures. Elytra oblong, subparallel-sided near base to apical 1/4; EL/EW 1.33–1.71 (1.50); EL/PL 2.50–2.89 (2.65); EW/PW 1.30–1.52 (1.41); TL/EW 2.33–2.93 (2.58). Legs relatively long and slender. Caudal margin of tergite VIII shallowly concave.

Aedeagus (Fig. 9A) about 1.12 mm, round at aedeagal apex. Gonoporal piece (Fig. 3A) straight, rather wide, 0.61 mm in GL; GL/AL 2.39. Ligula (Fig. 3A) short, curved in basal 1/3; LL 0.23 mm; LW 0.06 mm; LL/LW 3.73; GL/LL 2.68.

Female

Similar to male in general appearance; HL/HW 0.71–0.79 (0.76); PW/PL 1.20–1.36 (1.27); EL/EW 1.53–1.68 (1.59); EL/PL 2.65–2.93 (2.82); EW/PW 1.31–1.44 (1.39); TL/EW 2.60–2.82 (2.68). Antennae (Fig. 7A) stout; antennomere III short, L/W = 1.88; approximate ratio of each antennomeres (n = 1) as 8.8 : 1.0 : 4.2 : 2.4 : 2.2 : 2.2 : 2.0 : 1.8 : 2.0 : 2.0 : 3.0.

Measurements

Male (n = 7): TL 4.10–4.46 (4.27) mm; HL 0.80–0.90 (0.85) mm; HW 1.00–1.20 (1.10) mm; PW 1.08–1.30 (1.18) mm; PL 0.90–1.00 (0.94) mm; EL 2.40–2.60 (2.48) mm; EW 1.40–1.82 (1.67) mm. Female (n = 7): TL 4.35–4.75 (4.61) mm; HL 0.85–0.95 (0.90) mm; HW 1.15–1.25 (1.20) mm; PW 1.20–1.30 (1.24) mm; PL 0.90–1.00 (0.97) mm; EL 2.60–2.80 (2.73) mm; EW 1.60–1.80 (1.72) mm.

Distribution

Only known from the type locality, Indonesia (Bali Isl.).

Remarks

This species is similar to *Laius flavicornis* (Fabricius, 1801) and *L. sabangensis* Wittmer, 1985 in the shape of male antennomere III, and differs from them in the shape of endophallic sclerites and smaller body length.

Biological notes

This species was collected together with *Laius pankowi* Wittmer, 1999 and *L. satoi* Yoshitomi, 2008 at the same locality. Based on the data of Yoshitomi (2008) and the present study, *Laius baliensis* sp. nov. was collected in January and August, *L. pankowi* in January and December, and *L. satoi* in January, April, and August.

Laius andamanensis sp. nov.

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Figs 3B, 5C–D, 7B, 8B, 9B, 12

Diagnosis

Male antennomere III distinctly projecting laterally, shallowly concave in dorso-mesal portion, $L/W = 0.70$; aedeagal apex concave; gonoporal piece straight and slender; ligula long and slightly curved; additional sclerite absent.

Etymology

After the type locality, Andaman Islands, India.

Type material

Holotype

♂ (NHMB), “ANDAMAN Is.: Havelock I. env. of village No. 4, 11°59’N, 92°58’E, 22. iv-14. V. 1998, Karel & Simon Majer leg.”.

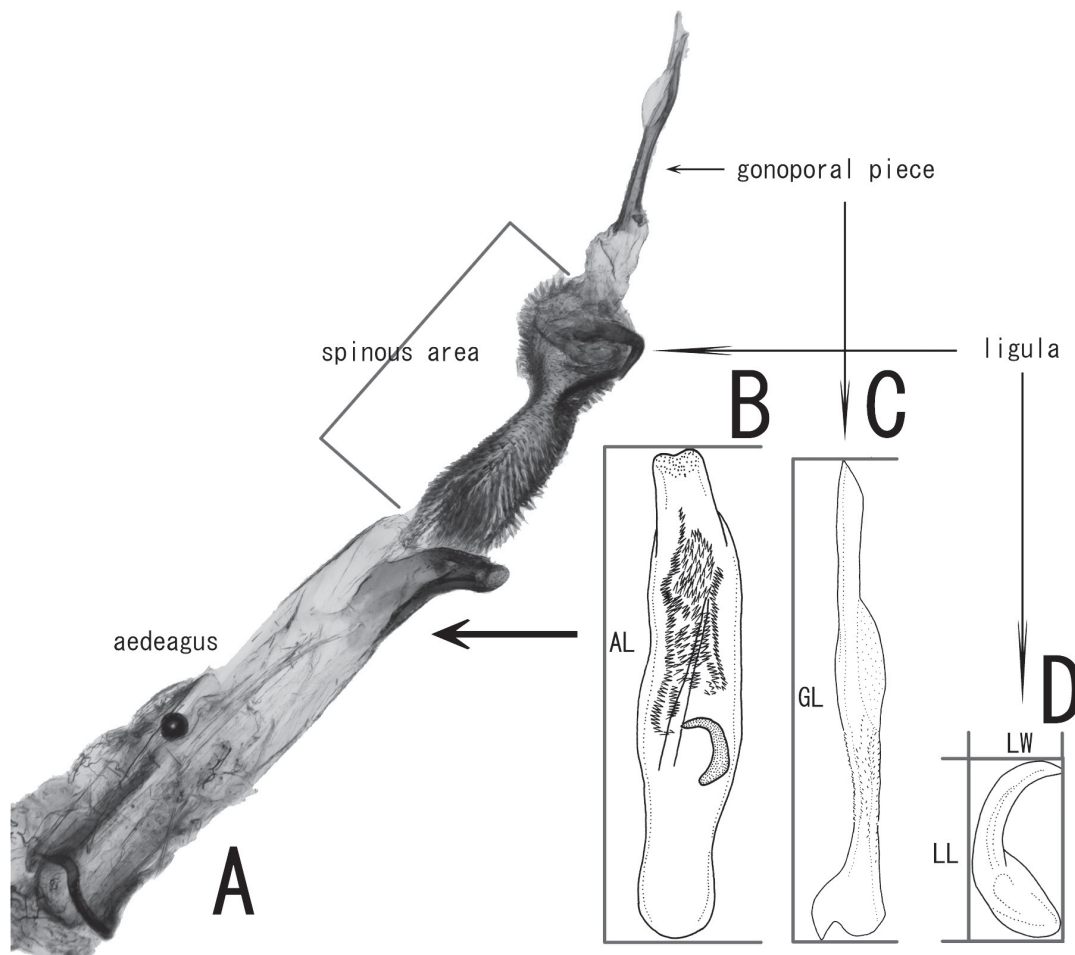


Fig. 2. Aedeagus of *Laius lutaensis* Yoshitomi & Lee, 2010, showing the terminology and abbreviations for measurement of endophallic structures. **A.** Aedeagus with extracted endophallus. **B.** Aedeagus with holding endophallus (from Yoshitomi & Lee 2010). **C.** Gonoporal piece. **D.** Ligula.

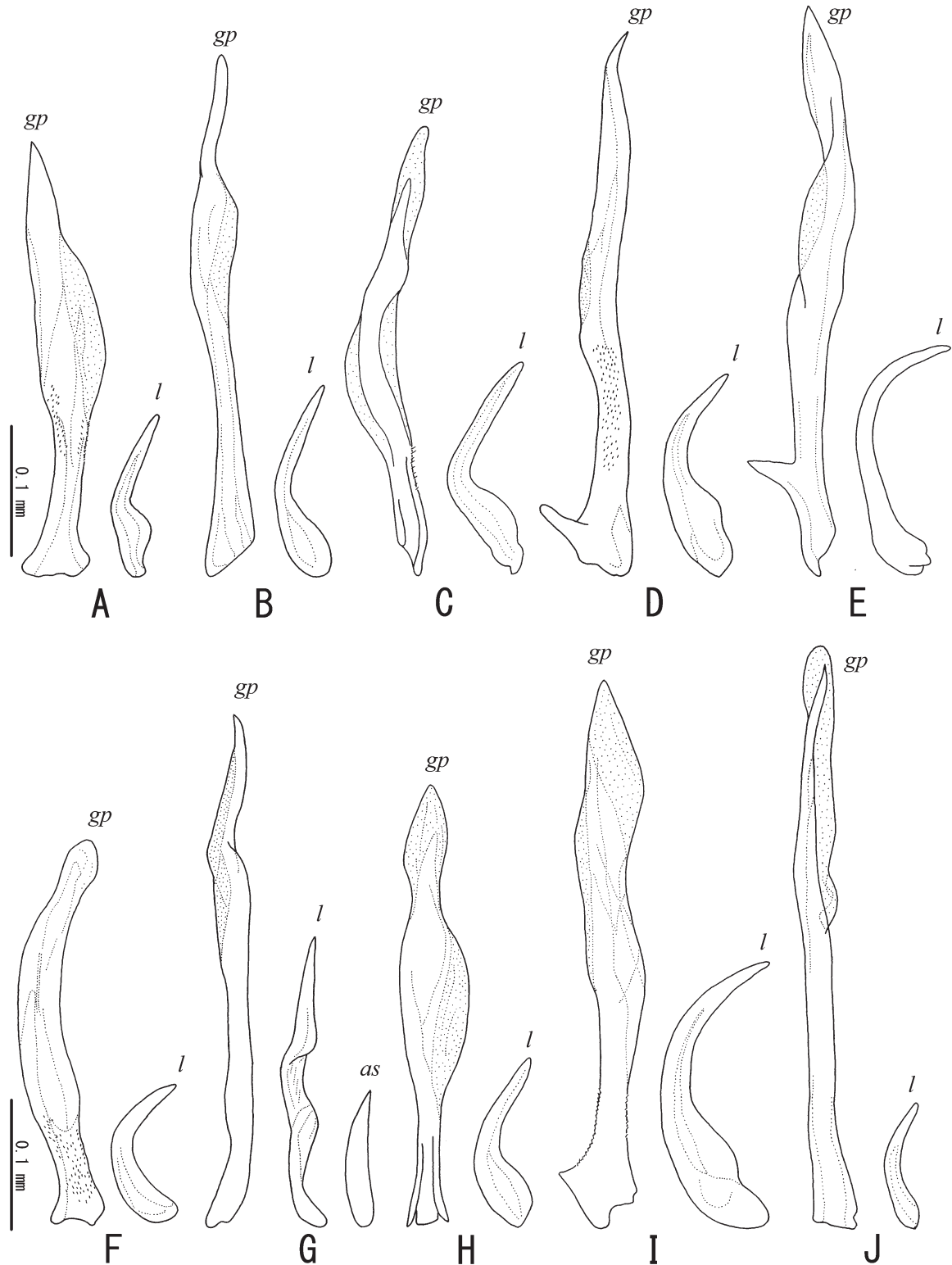


Fig. 3. Endophallic sclerites of *Laius* spp. **A.** *Laius baliensis* sp. nov. (paratype). **B.** *L. andamanensis* sp. nov. (paratype). **C.** *L. rodriguesensis* sp. nov. (paratype). **D.** *L. maai* Wittmer, 1973 (paratype). **E.** *L. marchei* Pic, 1922. **F.** *L. politus* Fairmaire, 1880. **G.** *L. sabangensis* Wittmer, 1985 (paratype). **H.** *L. sericatus* Champion, 1924. **I.** *L. submariniformis* Wittmer, 1985 (paratype). **J.** *L. asahinai* Nakane, 1955.



Fig. 4. Endophallic sclerites of *Laisus* spp. **A.** *Laisus etsukoae* Satô, Yoshitomi & Ohbayashi, 2006 (paratype). **B.** *L. flavicornis* (Fabricius, 1801). **C.** *L. keiichii* Satô, Yoshitomi & Ohbayashi, 2006 (paratype). **D.** *L. lutoensis* Yoshitomi & Lee, 2010 (paratype). **E.** *L. madli* Yoshitomi, 2010 (paratype). **F.** *L. miyamotoi* Nakane, 1955. **G.** *L. satoi* Yoshitomi, 2008. **H.** *L. taiwanus* Yoshitomi & Lee, 2010 (paratype). **I.** *L. pankowi* Wittmer, 1999.

Paratypes

22 ♂♂, 10 ♀♀ (NHMB, EUMJ), same data as for the holotype.

Description**Male**

Body oblong, shining, densely covered with short black setae. Coloration of body black with dully bluish luster on elytra; labrum, maxillary palpomere I, and tarsi brown; antennomeres I–III yellowish-orange.

Head narrower than pronotum, very densely punctate; vertex slightly convex dorsally; eyes relatively large, prominent; HL/HW 0.76–0.90 (0.81). Antennae (Fig. 7B) long; antennomere III (Fig. 8B) transversal trapezoidal, distinctly projecting laterally, shallowly concave in dorso-mesal portion, L/W = 0.70; approximate ratio of each antennomeres (n = 1) as 8.3 : 1.0 : 5.0 : 2.0 : 2.2 : 2.0 : 2.0 : 2.0 : 2.0 : 3.5. Pronotum quadrate, widest near anterior margin, rounded and obscure in antero- and postero-lateral angles, punctate as in head; PW/PL 1.18–1.33 (1.24). Scutellum semicircular, covered with fine punctures. Elytra oblong, widest at apical 1/4; sides gradually expanded postero-laterally; EL/EW 1.36–1.55 (1.45); EL/PL 2.52–2.88 (2.67); EW/PW 1.38–1.55 (1.48); TL/EW 2.30–2.56 (2.44). Legs relatively long and slender; fore tibia (Fig. 12A) enlarged, deeply excavate. Caudal margin of tergite VII shallowly concave.

Aedeagus (Fig. 9B) about 1.13 mm, concave at aedeagal apex (Fig. 12C). Gonoporal piece (Fig. 3B) straight, slender, 0.74 mm in GL; GL/AL 2.39. Ligula (Fig. 3B) relatively long, slightly curved; LL 0.27 mm; LW 0.11 mm; LL/LW 2.58; GL/LL 2.71.

Female

Similar to male in general appearance. HL/HW 0.75–0.80 (0.79); PW/PL 1.18–1.30 (1.23); EL/EW 1.36–1.48 (1.41); EL/PL 2.44–2.73 (2.60); EW/PW 1.45–1.58 (1.51); TL/EW 2.30–2.43 (2.36). Antennae (Fig. 7B) long; antennomere III (Fig. 12B) distinctly expanded laterally, shallowly concave in dorsal portion, L/W = 2.42; approximate ratio of each antennomeres (n = 1) as 8.0 : 1.0 : 4.4 : 2.2 : 2.4 : 2.2 : 2.2 : 2.0 : 2.0 : 3.6

Measurements

Male (n = 20): TL 5.52–6.33 (5.79) mm; HL 1.00–1.15 (1.05) mm; HW 1.22–1.38 (1.30) mm; PW 1.48–1.75 (1.61) mm; PL 1.20–1.48 (1.29) mm; EL 3.28–3.75 (3.45) mm; EW 2.18–2.70 (2.38) mm. Female (n = 6): TL 4.43–4.96 (4.67) mm; HL 0.75–0.85 (0.81) mm; HW 1.00–1.08 (1.03) mm; PW 1.20–1.42 (1.32) mm; PL 1.00–1.20 (1.07) mm; EL 2.60–3.00 (2.79) mm; EW 1.85–2.15 (1.98) mm.

Distribution

Only known from the type locality, India (Andaman Islands).

Remarks

This is distinct species in having transversal antennomere III of male.

***Laius rodriguesensis* sp. nov.**

[urn:lsid:zoobank.org:act:5ACC9D36-0154-4FE3-9D27-D5AAF61A9143](https://doi.org/10.21203/rs.3.rs-1011111/v1)

Figs 3C, 5E–F, 7C, 8C, 9C, 10, 11

Diagnosis

Male antennomere III transverse, deeply concave in dorso-mesal portion, L/W = 0.74; aedeagal apex rounded; gonoporal piece slightly curved; ligula strongly curved; additional sclerite absent; coloration of female antennomeres I–III black or dark brown.

Etymology

After the type locality, Rodrigues Island, Republic of Mauritius.

Type material

Holotype

♂ (NMW), “RODRIGUES Bucht zw. Trou d’Argent und Anse Bouteille intertidal zone 12.-13.4.11, leg. M. Madl”.

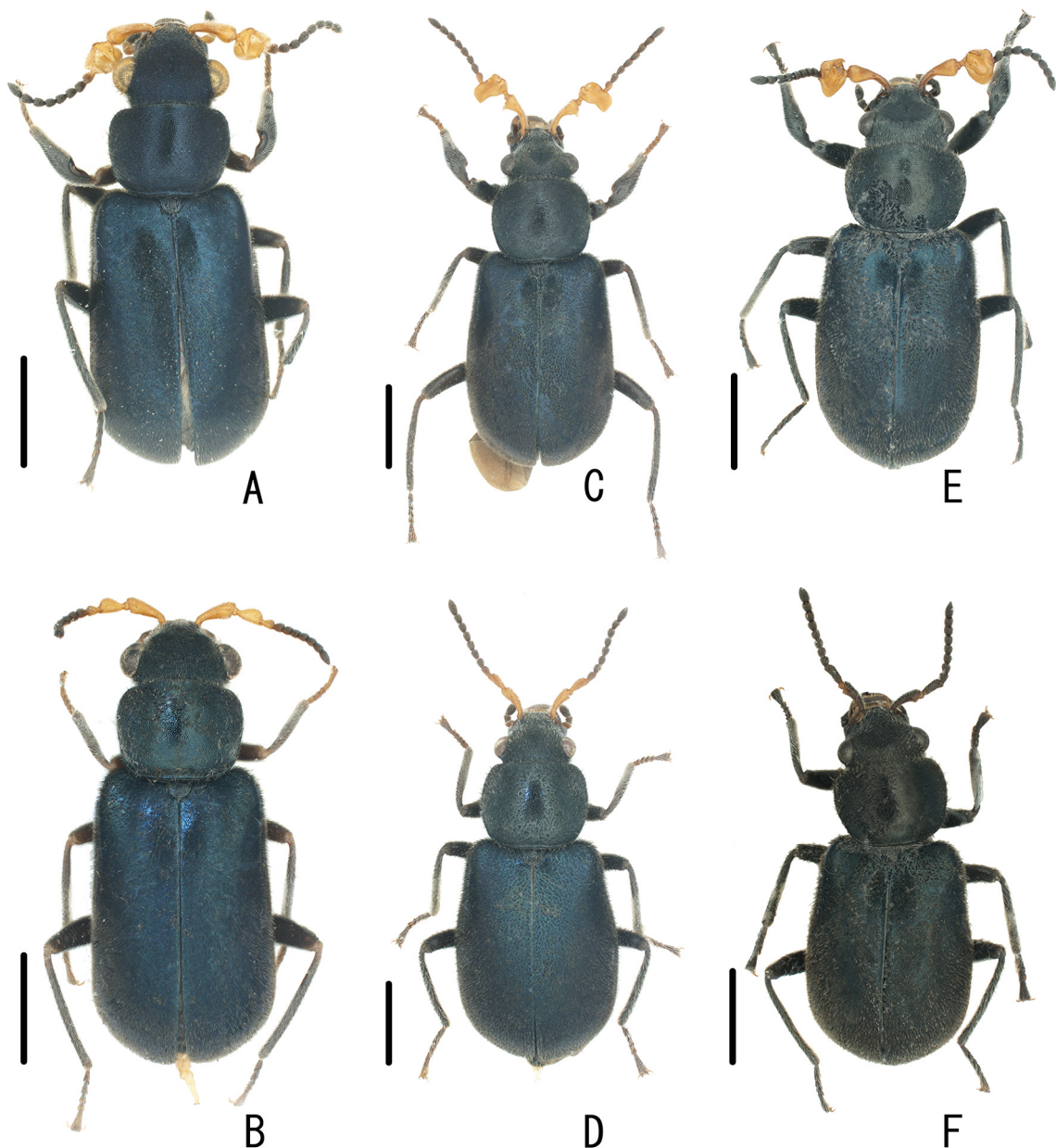


Fig. 5. Dorsal habitus of *Laius* spp. of ♂ (holotypes A, C, E) and ♀♀ (paratypes B, D, F). A–B. *Laius baliensis* sp. nov. C–D. *L. andamanensis* sp. nov. E–F. *L. rodriguesensis* sp. nov. Scale bars = 1.0 mm.

Paratypes

3 ♀♀ (NMW), same data as for the holotype; 1 ♀ (NMW), “MAURITIUS Rodrigues, Latanier Rivière Cascade Victoire 7.5.08. leg. M. Madl”; 2 ♀♀ (NMW), “MAURITIUS Rodrigues Anse Fumier 2.4.09, leg. M. Madl”; 4 ♂♂, 11 ♀♀ (NMW, EUMJ), ditto but “2.5.08”.

Description**Male**

Body oblong, shining, densely covered with short black setae. Coloration of body black with dully bluish luster on elytra; antennomeres I–III yellowish-orange, but anterior margin of antennomere I infuscate.

Head narrower than pronotum, very densely punctate; vertex slightly depressed dorsally; eyes relatively large, prominent; HL/HW 0.72–0.89 (0.78). Antennae (Fig. 7C) long; antennomere III (Fig. 8C) transverse, deeply concave in dorso-mesal portion, L/W = 0.74; approximate ratio of each antennomeres (n = 1) as 11.2 : 1.0 : 6.8 : 3.2 : 2.6 : 2.2 : 2.2 : 2.4 : 2.0 : 2.2 : 4.0. Pronotum quadrate, widest near anterior margin, rounded and obscure in antero- and postero-lateral angles; punctate as in head; PW/PL 1.33–1.49 (1.39). Scutellum semicircular, finely punctate. Elytra oblong, widest at apical 1/3; sides weakly expanded postero-laterally; EL/EW 1.31–1.50 (1.43); EL/PL 2.62–2.76 (2.69); EW/PW 1.31–1.42 (1.36); TL/EW 2.18–2.52 (2.42). Legs relatively long and slender. Caudal margin of tergite VII shallowly concave. Aedeagus (Fig. 9C) about 1.17 mm, round at aedeagal apex. Gonoporal piece (Fig. 3C) slightly curved, 0.63 mm in GL; GL/AL 1.81. Ligula (Fig. 3C) long, strongly curved in half; LL 0.30 mm; LW 0.11 mm; LL/LW 2.84; GL/LL 2.11.

Female

Similar to male in general appearance; bluish luster on elytra weak; coloration of antennomeres I–III black or dark brown; HL/HW 0.74–0.95 (0.84); PW/PL 1.32–1.42 (1.37); EL/EW 1.29–1.47 (1.39); EL/PL 2.47–2.86 (2.68); EW/PW 1.30–1.48 (1.41); TL/EW 2.25–2.47 (2.39). Antennae (Fig. 7C) long; antennomere III short, L/W = 2.16; approximate ratio of each antennomeres (n = 1) as 8.6 : 1.0 : 4.4 : 2.0 : 2.0 : 1.8 : 1.8 : 2.0 : 2.0 : 2.0 : 3.8.

Measurements

Male (n = 5): TL 5.50–5.75 (5.64) mm; HL 1.00–1.20 (1.08) mm; HW 1.30–1.45 (1.38) mm; PW 1.60–1.83 (1.72) mm; PL 1.20–1.30 (1.24) mm; EL 3.20–3.40 (3.32) mm; EW 2.20–2.60 (2.33) mm. Female (n = 10): TL 4.10–4.68 (4.41) mm; HL 0.80–1.00 (0.88) mm; HW 1.00–1.10 (1.05) mm; PW 1.20–1.38 (1.32) mm; PL 0.90–1.00 (0.96) mm; EL 2.35–2.80 (2.57) mm; EW 1.70–2.00 (1.85) mm.

Larvae

Coloration of head capsule and urogomphi dark brown; thoracic and abdominal segments and legs cream. Head capsule (Fig. 10B) suboblong, L/W = 1.3; four pairs of stemmata situated near antero-lateral corners. Antennae missing. Labrum (Fig. 11B) with a pair of long lateral and five pairs of short mesal setae in anterior portion; anterior margin of epipharynx bearing short stout setae. Maxillae (Fig. 11A) bearing long setae in antero-lateral portion. Mandibles (Fig. 11C) with two apical teeth; mola with two short teeth. Labium (Figs 10C, 11A) relatively wide, with 2-segmented palpi. Thorax weakly sclerotized, widest at posterior part of metathorax; pronotum with two pairs of longitudinal sclerotized bands in mesal portion, bearing short setae in lateral and mesal portions. Abdomen (Fig. 10A) weakly sclerotized, subparallel-sided, bearing short setae in lateral and postero-mesal portions. Urogomphi (Fig. 10D–F) subparallel-sided, closely covered with long setae, simply bifurcate in apical 1/2, upturned in apical portions, pointed at apices, with some very long hairy setae in apical parts. Legs relatively long.

Additional material examined

2 Larvae (NMW, in ethanol), “MAURITIUS Rodrigues Anse Fumier 10.05.2008, leg. M. Madl”.

Distribution

Only known from the type locality, Republic of Mauritius (Rodrigues Isl.).

Remarks

This species is closely related to *Laius madli* Yoshitomi, 2010 known from Mauritius, but differs from the latter in the following characteristics: 1) ligula strongly curved in middle portion (rather weakly curved

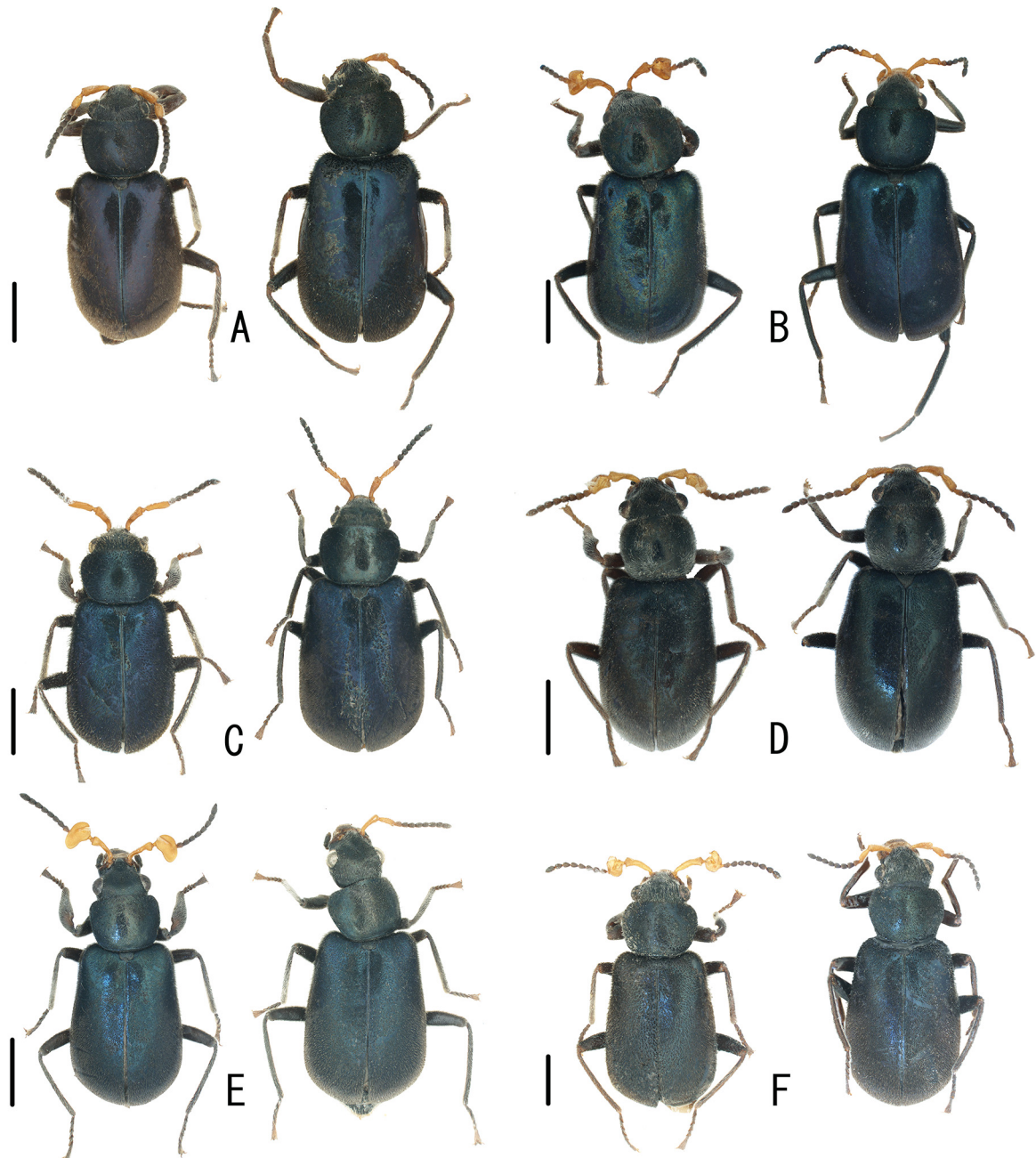


Fig. 6. Dorsal habitus of *Laius* spp. (left: ♂; right: ♀). **A.** *Laius maai* Wittmer, 1973 (paratype). **B.** *L. marchei* Pic, 1922. **C.** *L. politus* Fairmaire, 1880. **D.** *L. sabangensis* Wittmer, 1985 (paratype). **E.** *L. sericatus* Champion, 1924. **F.** *L. submariniformis* Wittmer, 1985 (paratype). Scale bars = 1.0 mm.

basally in *madli*); 2) male antennomere III projecting laterally, transverse, L/W = 0.7 (antennomere III slightly projecting laterally, L/W = 0.9 in *madli*).

The larvae of two Japanese species, *L. asahinai* Nakane, 1955 and *L. miyamotoi* Nakane, 1955, were described by Satô (1964) and Asano & Kojima (2009). The larva of *L. rodriguesensis* sp. nov. is similar to those of the aforementioned species, and differs from them in that the teeth of the mola are rather short, and that the head is narrower.

***Laius maai* Wittmer, 1973**
Figs 3D, 6A, 7D, 8D, 9D

Laius maai Wittmer, 1973: 336.

Type material

Paratypes 6 ♂♂, 2 ♀♀, (BPBM), “New Guinea: NE Sarmi, W Hollandia”, “20.-23.7.1959 T. C. Maa”.

Redescription

Male

HL/HW 0.82; PW/PL 1.36; EL/EW 1.51; EL/PL 2.95; EW/PW 1.43; TL/EW 2.46. Antennae (Fig. 7D) long; antennomere III (Fig. 8D) oblong, widened in basal 1/3, L/W = 2.08; approximate ratio of each antennomeres (n = 1) as 7.4 : 1.0 : 3.6 : 2.1 : 1.9 : 1.9 : 1.7 : 1.6 : 1.7 : 1.9 : 3.1. Caudal margin of tergite VII concave. Aedeagus (Fig. 9D) about 1.32 mm, concave at aedeagal apex. Gonoporal piece (Fig. 3D) straight, slender, with long and straight basal projection, 0.77 mm in GL; GL/AL 2.01. Ligula (Fig. 3D) relatively long, slightly curved; LL 0.29 mm; LW 0.09 mm; LL/LW 3.06; GL/LL 2.65.

Female

HL/HW 0.78–0.81 (0.80); PW/PL 1.31–1.37 (1.33); EL/EW 1.42–1.66 (1.50); EL/PL 2.70–2.96 (2.83); EW/PW 1.35–1.46 (1.41); TL/EW 2.39–2.67 (2.48). Antennae (Fig. 7D) long; antennomere III short, L/W = 1.88; approximate ratio of each antennomeres (n = 1) as 11.3 : 1.0 : 5.3 : 2.8 : 3.0 : 3.0 : 3.0 : 2.5 : 2.8 : 2.5 : 4.5.

Measurements

Male (n = 1): TL 5.05 mm; HL 0.90 mm; HW 1.10 mm; PW 1.43 mm; PL 1.05 mm; EL 3.10 mm; EW 2.05 mm. Female (n = 4): TL 4.50–4.68 (4.58) mm; HL 0.80–0.85 (0.82) mm; HW 1.00–1.05 (1.03) mm; PW 1.30–1.33 (1.31) mm; PL 0.95–1.00 (0.98) mm; EL 2.70–2.90 (2.78) mm; EW 1.75–1.90 (1.85) mm.

Distribution

New Guinea.

***Laius marchei* Pic, 1922**
Figs 3E, 6B, 7E, 8E, 9E

Laius marchei Pic, 1922: 158.

Rotamalachus esakii Kôno, 1937 in Kôno & Esaki 1937: 121. Synonymised by Nakane (1955).

Laius marchei – Wittmer 1958: 72 [redescription]. — Satô *et al.* 2006: 344.

Material examined

56 ♂♂, 14 ♀♀ (EUMJ), “(MARIANA Is.) Teteto Beach Rota I. 22. Jan. 1980 M. Tomokuni”; 1 ♀ (EUMJ), “Is. Rota mariana VIII. 8. 1940 D. Matsusita”, “*Laius marchei* Pic det. W. Wittmer”; 1 ♂

(EUMJ), “(Rota Tatchio) South Sea Islands of Nippon: 8-VIII. 1940 Coll. Dengo Matsusita”; 2 ♂♂, 1 ♀ (BPBM), “Tumon Bay, Guam 24 June 1969”, “A. A. LaPlante Collection BISHOP Museum Acc. #1977.84”.

Redescription

Male

HL/HW 0.71–0.93 (0.79); PW/PL 1.21–1.36 (1.28); EL/EW 1.28–1.48 (1.42); EL/PL 2.42–2.86 (2.68); EW/PW 1.41–1.58 (1.48); TL/EW 2.25–2.44 (2.36). Antennae (Fig. 7E) long; antennomere I long and curved laterally, with small projection in lateral margin; antennomere III (Fig. 8E) trapezoidal, deeply concave in dorso-mesal portion, L/W = 0.76; approximate ratio of each antennomeres (n = 1) as 11.8 : 1.0 : 7.0 : 2.6 : 2.0 : 2.2 : 2.2 : 2.4 : 2.4 : 2.4 : 3.8. Caudal margin of tergite VII concave. Aedeagus

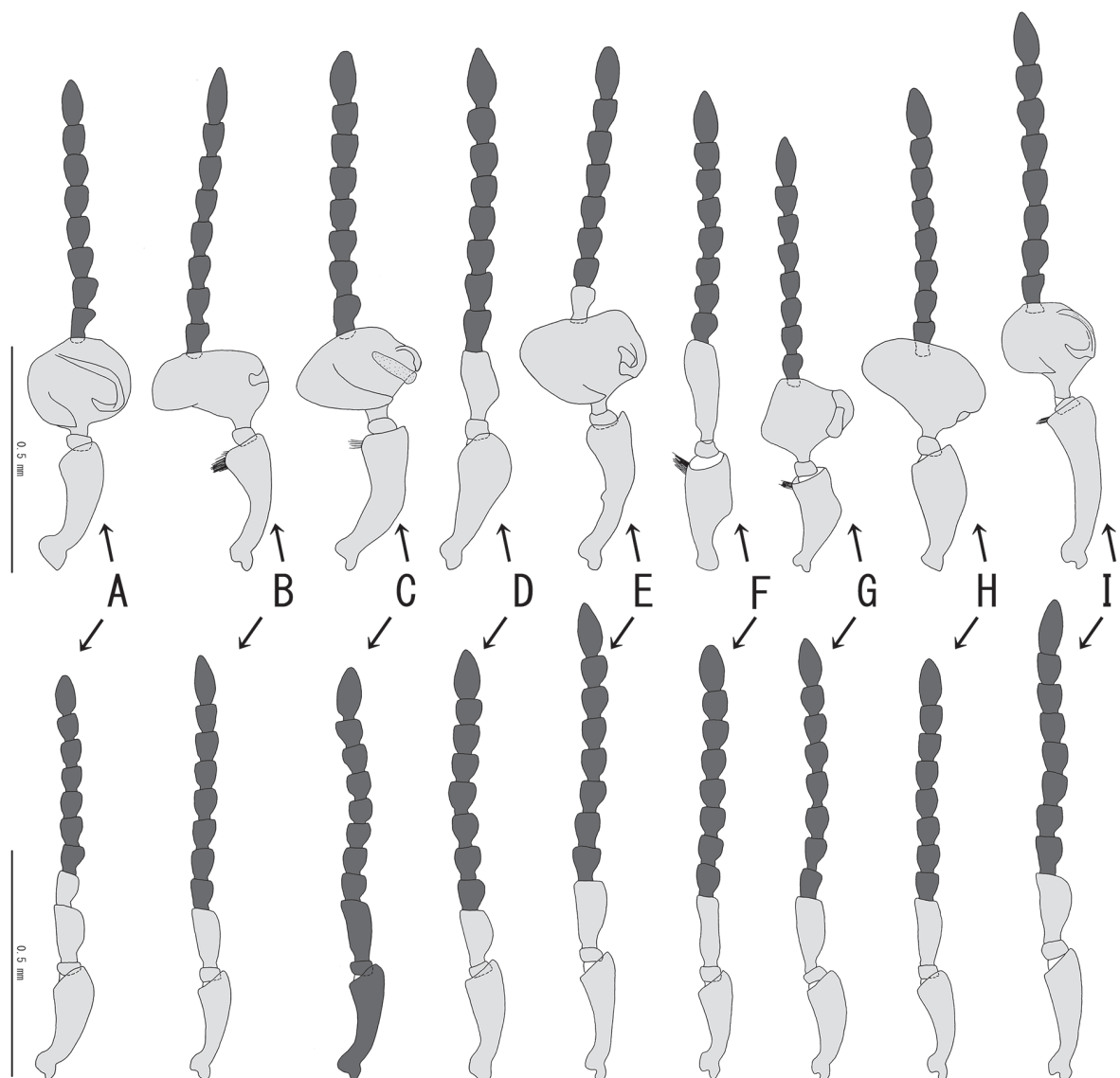


Fig. 7. Left antennae of *Laius* spp. (above: male; below: female). **A.** *Laius baliensis* sp. nov. (paratype). **B.** *L. andamanensis* sp. nov. (paratype). **C.** *L. rodriguesensis* sp. nov. (paratype). **D.** *L. maai* Wittmer, 1973 (paratype). **E.** *L. marchei* Pic, 1922. **F.** *L. politus* Fairmaire, 1880. **G.** *L. sabangensis* Wittmer, 1985 (paratype). **H.** *L. sericatus* Champion, 1924. **I.** *L. submariniformis* Wittmer, 1985 (paratype).

(Fig. 9E) about 1.28 mm, concave at aedeagal apex. Gonoporal piece (Fig. 3E) straight, slender, with long and straight basal projection, 0.80 mm in GL; GL/AL 1.91. Ligula (Fig. 3E) long and slender, strongly curved in apical half; LL 0.33 mm; LW 0.17 mm; LL/LW 2.81; GL/LL 2.44.

Female

HL/HW 0.72–0.87 (0.80); PW/PL 1.13–1.32 (1.24); EL/EW 1.43–1.55 (1.46); EL/PL 2.64–2.96 (2.82); EW/PW 1.52–1.67 (1.57); TL/EW 2.34–2.45 (2.38). Antennae (Fig. 7E) long; antennomere III short, L/W = 2.25; approximate ratio of each antennomeres (n = 1) as 9.4 : 1.0 : 5.0 : 2.4 : 2.8 : 2.4 : 2.4 : 2.4 : 2.4 : 2.4 : 4.0.

Measurements

Male (n = 15): TL 4.90–6.75 (5.36) mm; HL 0.80–1.40 (0.94) mm; HW 1.10–1.50 (1.19) mm; PW 1.35–1.90 (1.53) mm; PL 1.10–1.50 (1.20) mm; EL 2.90–3.85 (3.21) mm; EW 2.10–3.00 (2.27) mm. Female (n = 6): TL 5.15–5.73 (5.37) mm; HL 0.85–1.00 (0.92) mm; HW 1.10–1.25 (1.15) mm; PW 1.35–1.50 (1.44) mm; PL 1.10–1.30 (1.17) mm; EL 3.15–3.43 (3.28) mm; EW 2.20–2.40 (2.25) mm.

Distribution

Mariana Isls. (Rota, Guam).

Remarks

This is the first record of this species from Guam, Mariana Islands.

Laius politus Fairmaire, 1880

Figs 3F, 6C, 7F, 8F, 9F

Laius politus Fairmaire, 1880: 246.

Nossibeus politus – Evers 1994: 173 [see page 3].

Material examined

18 ♂♂, 40 ♀♀ (NHMB, EUMJ), “MADAGASCAR Katsepy (Majunga) 24-31. xii. 1977 P. Pacholátko leg”.

Redescription

Male

HL/HW 0.69–0.94 (0.80); PW/PL 1.33–1.57 (1.43); EL/EW 1.39–1.52 (1.46); EL/PL 2.82–3.40 (3.05); EW/PW 1.37–1.59 (1.46); TL/EW 2.24–2.51 (2.36). Antennae (Fig. 7F) long; antennomere I stout; antennomere III (Fig. 8F) elongate, widened in apical portion, L/W = 3.08; approximate ratio of each antennomeres (n = 1) as 8.4 : 1.0 : 7.4 : 2.2 : 2.0 : 2.0 : 2.2 : 2.0 : 2.2 : 2.0 : 3.8. Caudal margin of tergite VII shallowly concave. Aedeagus about 1.18 mm, round at aedeagal apex. Gonoporal piece (Fig. 3F) curved, rather wide, 0.54 mm in GL; GL/AL 2.45. Ligula (Fig. 3F) short, evenly curved; LL 0.19 mm; LW 0.09 mm; LL/LW 2.13; GL/LL 2.88.

Female

HL/HW 0.64–0.90 (0.79); PW/PL 1.38–1.47 (1.42); EL/EW 1.30–1.55 (1.44); EL/PL 2.80–3.10 (2.96); EW/PW 1.37–1.54 (1.45); TL/EW 2.17–2.50 (2.35). Antennae (Fig. 7F) long; antennomere III long and slender, L/W = 3.1; approximate ratio of each antennomeres (n = 1) as 8.0 : 1.0 : 5.2 : 2.4 : 2.0 : 2.2 : 2.0 : 2.2 : 2.2 : 2.2 : 3.4.

Measurements

Male (n = 17): TL 5.15–5.92 (5.55) mm; HL 0.90–1.13 (1.00) mm; HW 1.18–1.33 (1.25) mm; PW 1.50–1.75 (1.61) mm; PL 1.00–1.20 (1.13) mm; EL 3.10–3.62 (3.42) mm; EW 2.15–2.60 (2.35) mm.
Female (n = 10): TL 4.05–5.00 (4.48) mm; HL 0.70–0.90 (0.81) mm; HW 0.93–1.10 (1.02) mm; PW 1.18–1.38 (1.32) mm; PL 0.85–1.00 (0.93) mm; EL 2.50–3.10 (2.75) mm; EW 1.62–2.00 (1.92) mm.

Distribution

Madagascar.

Laius sabangensis Wittmer, 1985

Figs 3G, 6D, 7G, 8G, 9G

Laius sabangensis Wittmer, 1985: 386.

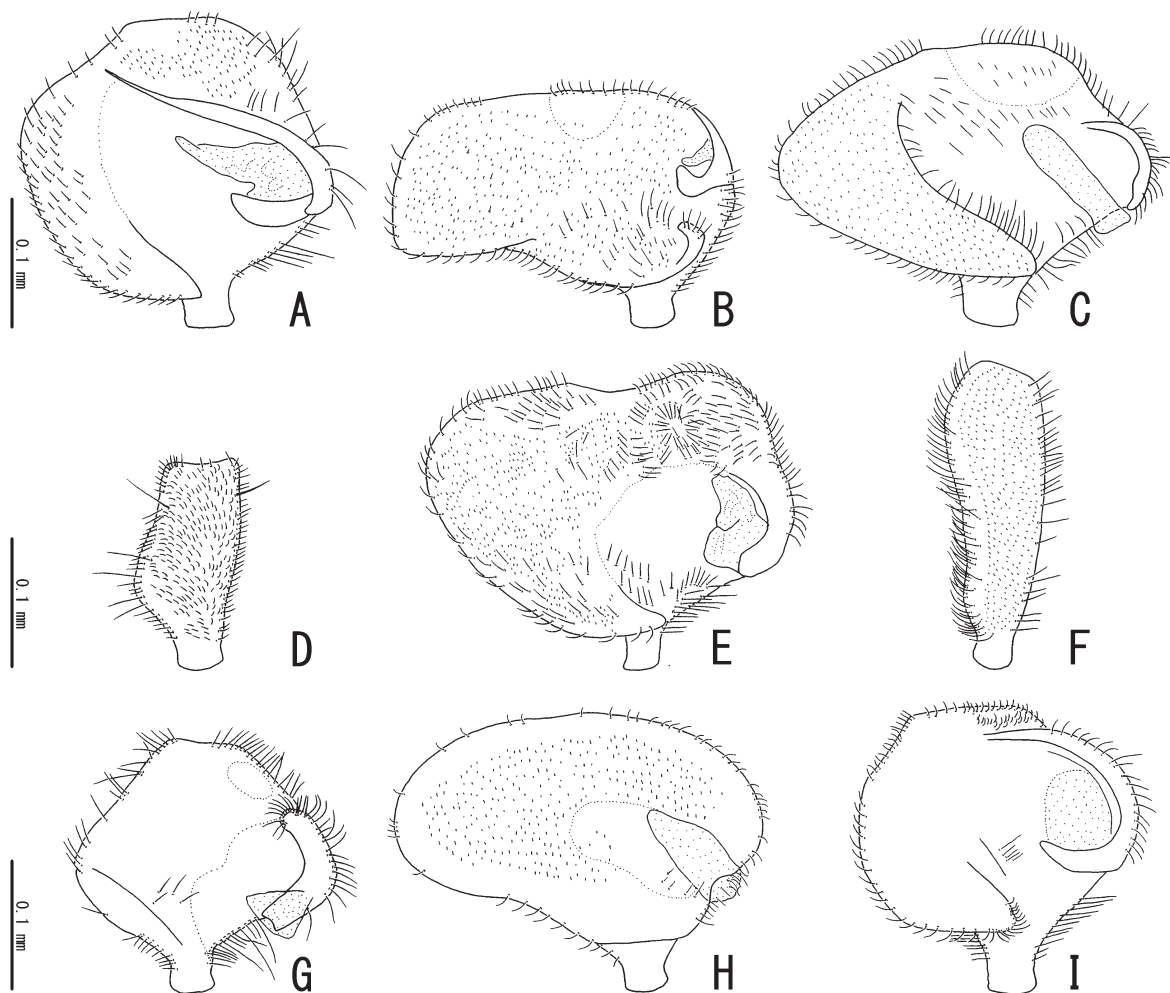


Fig. 8. Male antennomere III of *Laius* spp. **A.** *Laius baliensis* sp. nov. (paratype). **B.** *L. andamanensis* sp. nov. (paratype). **C.** *L. rodriguesensis* sp. nov. (paratype). **D.** *L. maai* Wittmer, 1973 (paratype). **E.** *L. marcheii* Pic, 1922. **F.** *L. politus* Fairmaire, 1880. **G.** *L. sabangensis* Wittmer, 1985 (paratype). **H.** *L. sericatus* Champion, 1924. **I.** *L. submariniformis* Wittmer, 1985 (paratype).

Material examined

Holotype, ♂ (EUMJ), “PHILIPPINES Sabang, N. of Mt. St. Paul, Palawan Julu, 11-13, 1977 M. Sato leg.”; 2 ♀♀ paratypes, 9 ♂♂, 6 ♀♀ (EUMJ), same data as for the holotype.

Redescription

Male

HL/HW 0.84–0.91 (0.88); PW/PL 1.10–1.22 (1.16); EL/EW 1.38–1.50 (1.43); EL/PL 2.53–2.67 (2.59); EW/PW 1.50–1.62 (1.56); TL/EW 2.37–2.60 (2.48). Antennae (Fig. 7G) stout and short; antennomere I stout; antennomere III (Fig. 8G) trapezoidal, deeply concave in dorso-mesal portion, L/W = 0.86; approximate ratio of each antennomeres (n = 1) as 6.6 : 1.0 : 6.0 : 2.4 : 2.0 : 2.2 : 2.0 : 2.2 : 2.0 : 2.2 : 3.6. Caudal margin of tergite VII straight. Aedeagus (Fig. 9G) about 0.94 mm, concave at aedeagal apex. Gonoporal piece (Fig. 3G) straight, slender, 0.72 mm in GL; GL/AL 1.87. Ligula (Fig. 3G) long and winding; LL 0.41 mm; LW 0.06 mm; LL/LW 7.30; GL/LL 1.77. Additional sclerite (Fig. 3G) present, 0.10 mm.

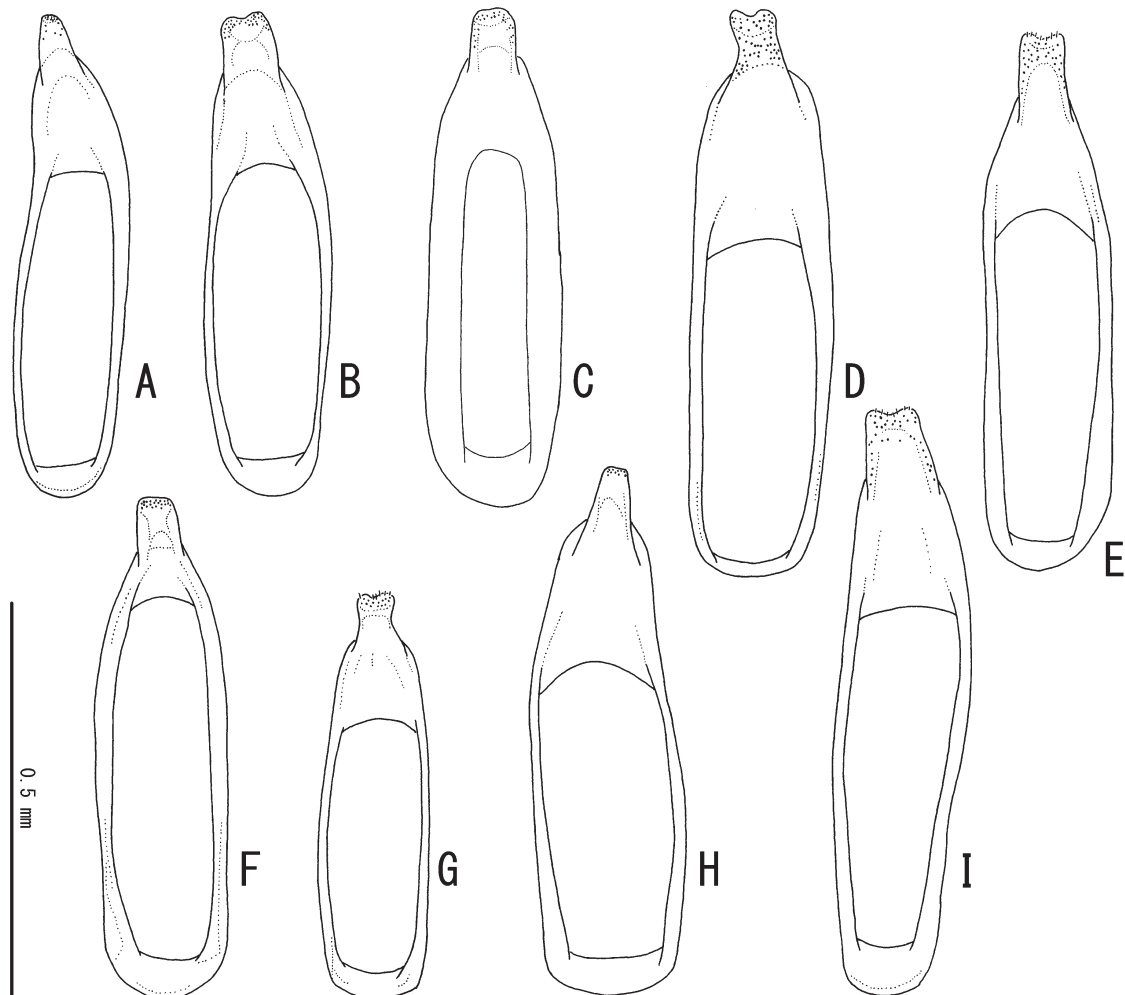


Fig. 9. Aedeagi of *Laius* spp. **A.** *Laius baliensis* sp. nov. (paratype). **B.** *L. andamanensis* sp. nov. (paratype). **C.** *L. rodriguesensis* sp. nov. (paratype). **D.** *L. maai* Wittmer, 1973 (paratype). **E.** *L. marchei* Pic, 1922. **F.** *L. politus* Fairmaire, 1880. **G.** *L. sabangensis* Wittmer, 1985 (paratype). **H.** *L. sericatus* Champion, 1924. **I.** *L. submariniformis* Wittmer, 1985 (paratype).

Female

HL/HW 0.79–0.86 (0.81); PW/PL 1.16–1.21 (1.17); EL/EW 1.42–1.47 (1.45); EL/PL 2.61–2.78 (2.70); EW/PW 1.57–1.62 (1.59); TL/EW 2.36–2.47 (2.42). Antennae (Fig. 7G) short; antennomere III short, L/W = 2.5; approximate ratio of each antennomeres (n = 1) as 8.0 : 1.0 : 5.4 : 2.0 : 2.2 : 2.4 : 2.6 : 2.2 : 2.2 : 3.4.

Measurements

Male (n = 4): TL 4.03–4.73 (4.23) mm; HL 0.80–0.98 (0.85) mm; HW 0.90–1.08 (0.97) mm; PW 1.02–1.20 (1.09) mm; PL 0.88–1.05 (0.94) mm; EL 2.35–2.70 (2.44) mm; EW 1.57–1.90 (1.71) mm. Female (n = 4): TL 4.18–4.30 (4.23) mm; HL 0.75–0.80 (0.76) mm; HW 0.92–0.95 (0.94) mm; PW 1.05–1.15 (1.10) mm; PL 0.90–0.95 (0.94) mm; EL 2.48–2.60 (2.53) mm; EW 1.70–1.82 (1.75) mm.

Distribution

Philippines (Palawan).

Laius sericatus Champion, 1924 Figs 3H, 6E, 7H, 8H, 9H

Laius sericatus Champion, 1924: 301.

Material examined

2 ♂♂ (NMW), “SEYCHELLES: Mahé Anse aux Coubes 23.03.2011 leg. M. Madl”; 1 ♂, 1 ♀ (NMW), ditto but “21.03.2011”; 3 ♂♂, 2 ♀♀ (1 ♀ in ethanol; NMW, EUMJ), “SEYCHELLES: Mahé Petite Police intertidal 28.10.2010, leg. M. Madl”.

Redescription

Male

HL/HW 0.74–0.75 (0.75); PW/PL 1.27–1.31 (1.29); EL/EW 1.40–1.52 (1.47); EL/PL 2.90–3.04 (2.95); EW/PW 1.54–1.58 (1.56); TL/EW 2.27–2.42 (2.37). Antennae (Fig. 7H) long; antennomere I stout; antennomere III (Fig. 8H) transverse, shallowly and narrowly concave in dorsal portion, L/W = 0.72; approximate ratio of each antennomere (n = 1) as 6.6 : 1.0 : 4.7 : 1.7 : 1.7 : 1.6 : 1.6 : 1.6 : 1.6 : 2.6. Caudal margin of tergite VII concave. Aedeagus (Fig. 9H) about 1.22 mm, round at aedeagal apex. Gonoporal piece (Fig. 3H) straight, wide, 0.62 mm in GL; GL/AL 2.11. Ligula (Fig. 3H) short, slightly curved; LL 0.24 mm; LW 0.09 mm; LL/LW 2.69; GL/LL 2.58.

Female

HL/HW 0.77–0.92 (0.85); PW/PL 1.27–1.29 (1.28); EL/EW 1.41–3.53 (2.47); EL/PL 2.73–2.89 (2.81); EW/PW 0.61–1.59 (1.10); TL/EW 2.37–5.82 (4.10). Antennae (Fig. 7H) long; antennomere III relatively long, L/W = 2.73; approximate ratio of each antennomeres (n = 1) as 8.0 : 1.0 : 4.8 : 2.0 : 2.0 : 2.0 : 2.0 : 2.0 : 2.0 : 3.4.

Measurements

Male (n = 3): TL 5.20–5.55 (5.43) mm; HL 0.90–0.95 (0.92) mm; HW 1.20–1.28 (1.23) mm; PW 1.40–1.55 (1.47) mm; PL 1.10–1.18 (1.14) mm; EL 3.20–3.50 (3.37) mm; EW 2.15–2.45 (2.30) mm. Female (n = 2): TL 4.62–4.95 (4.79) mm; HL 0.85–0.92 (0.89) mm; HW 1.00–1.10 (1.05) mm; PW 1.23–1.40 (1.32) mm; PL 0.95–1.10 (1.03) mm; EL 2.75–3.00 (2.88) mm; EW 0.85–1.95 (1.40) mm.

Distribution

Seychelles (Mahé, Félicité Isls.).

Laius submariniformis Wittmer, 1985

Figs 3I, 6F, 7I, 8I, 9I

Laius submariniformis Wittmer, 1985: 385.

Material examined

2 ♂♂, 6 ♀♀ (EUMJ), “Damai, Sarawak 17. IX. 1990 Ken Itô leg.”; 5 ♂♂, 29 ♀♀ (including 10 paratypes; EUMJ), “PHILIPPINES Sabang, N. of Mt. St. Paul, Palawan July, 11-13, 1977 M. Sato leg.”; 5 ♂♂, 4 ♀♀ (BPBM), “PHILIPPINES (S.) Cagayan Sulu I. Feb. 27. 1957”, “Yoshio Kondo collector”.

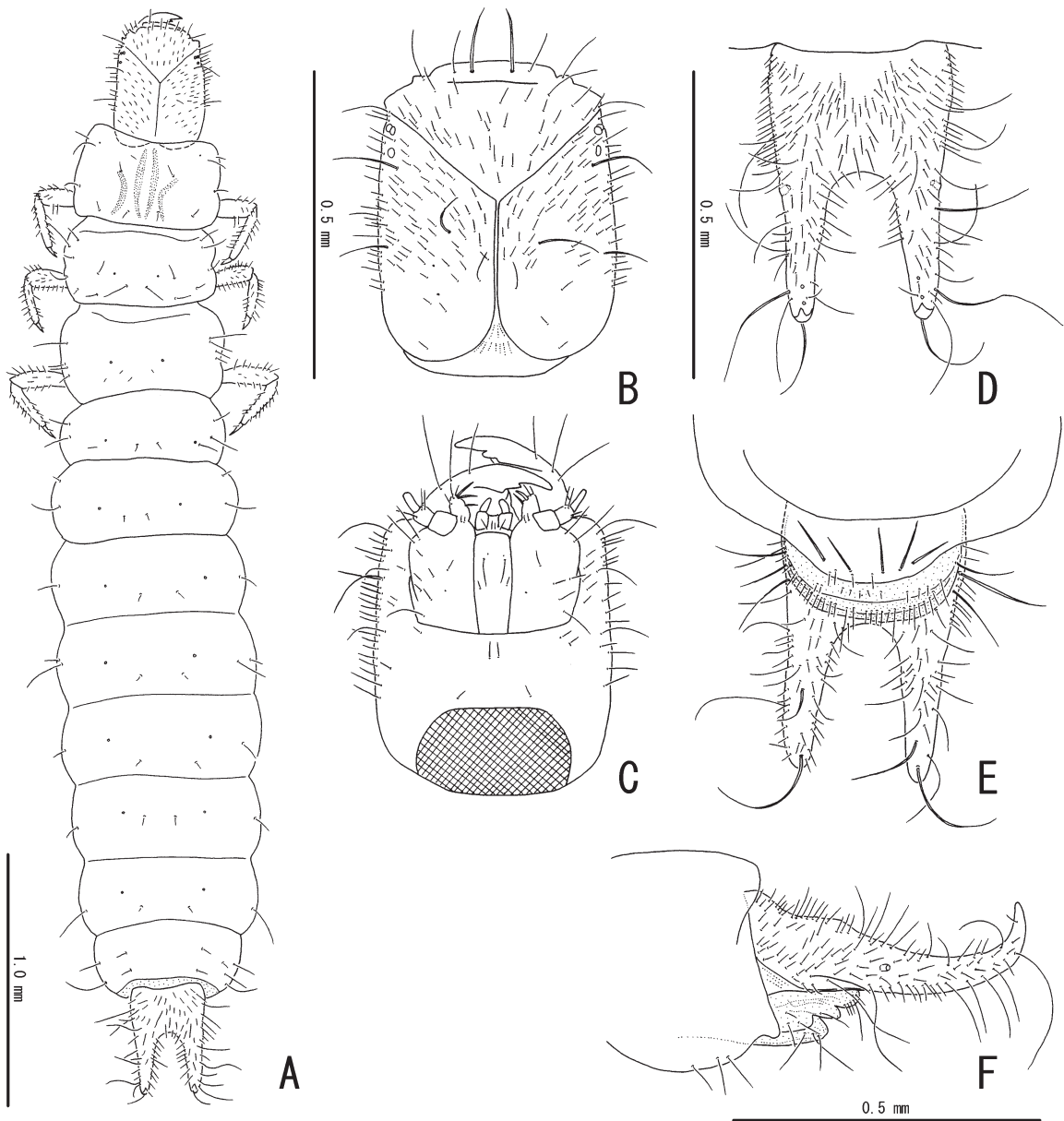


Fig. 10. Larva of *Laius rodriguesensis* sp. nov. **A.** Dorsal habitus. **B.** Head in dorsal view. **C.** Head in ventral view. **D.** Abdominal segment IX in dorsal view. **E.** Abdominal segment IX in ventral view. **F.** Abdominal segment IX in lateral view.

Redescription

Male

HL/HW 0.75–0.86 (0.80); PW/PL 1.27–1.37 (1.32); EL/EW 1.38–1.50 (1.42); EL/PL 2.64–2.94 (2.79); EW/PW 1.43–1.56 (1.48); TL/EW 2.25–2.49 (2.37). Antennae (Fig. 7I) long; antennomere I long and slightly curved laterally; antennomere III (Fig. 8I) oval, deeply concave in dorso-mesal portion, L/W = 0.88; approximate ratio of each antennomeres (n = 1) as 15.0 : 1.0 : 9.0 : 3.3 : 3.3 : 3.0 : 3.3 : 3.3 : 3.3 : 5.0. Caudal margin of tergite VII deeply concave. Aedeagus (Fig. 9I) about 1.37 mm, concave at aedeagal apex. Gonoporal piece (Fig. 3I) straight, rather wide, with very short basal projection, 0.77 mm in GL; GL/AL 1.51. Ligula (Fig. 3I) long, evenly curved; LL 0.37 mm; LW 0.14 mm; LL/LW 2.58; GL/LL 2.06.

Female

HL/HW 0.67–0.85 (0.76); PW/PL 1.32–1.45 (1.36); EL/EW 1.33–1.52 (1.39); EL/PL 2.64–2.91 (2.75); EW/PW 1.31–1.59 (1.46); TL/EW 2.15–2.48 (2.31). Antennae (Fig. 7I) long; antennomere III short, L/W = 2.14; approximate ratio of each antennomeres (n = 1) as 8.0 : 1.0 : 4.2 : 2.3 : 2.0 : 2.0 : 2.0 : 1.8 : 1.8 : 1.8 : 3.3.

Measurements

Male (n = 4): TL 4.90–6.33 (5.60) mm; HL 0.88–1.20 (1.02) mm; HW 1.05–1.52 (1.29) mm; PW 1.40–1.82 (1.60) mm; PL 1.02–1.40 (1.21) mm; EL 3.00–3.78 (3.37) mm; EW 2.00–2.70 (2.37) mm. Female (n = 5): TL 4.95–5.65 (5.30) mm; HL 0.80–1.10 (0.95) mm; HW 1.20–1.32 (1.24) mm; PW 1.45–1.68 (1.58) mm; PL 1.10–1.25 (1.16) mm; EL 3.05–3.30 (3.19) mm; EW 2.10–2.40 (2.30) mm.

Distribution

Philippines (Palawan, Sulu Isls.), Malaysia (Sarawak).

Remarks

This is the first record of this species from Sulu Island and Borneo.

Laius asahinai Nakane, 1955

Figs 3J, 13D

Material examined

JAPAN: 1 ♀ (EUMJ), “Oshima, Okada, Shinkai, Nodahama, 31. V. 2013, H. Kamezawa leg.”; 1 ♀ (EUMJ), “[IZ60] Ookubohama, Miyakejima, Izu Isls., N34 07.272 E139 30.930, ca 152 m, 29. VI. 2013, H. Yoshitomi leg.”; 1 ♂, 9 ♀♀ (EUMJ), “[IZ58] Sabigahama, Miyake-jima, Izu Isls., N34 04.241 E139 28.837, ca 151 m, 28-30. VI. 2013, H. Yoshitomi leg.”; 1 ♀ (EUMJ), “Shimo-Koshiki Is. Kagoshima, Japan 25-26. V. 2013 N. Ohbayashi leg.”; 2 ♂♂, 3 ♀♀ (EUMJ), “Hachijo Is. Mitsune 20. V. 2001 Y. Kawabata”. Others see Yoshitomi & Lee (2010).

Description of endophallic sclerites

Gonoporal piece (Fig. 3J) straight, slender, 0.81 mm in GL; GL/AL 3.96. Ligula (Fig. 3J) short, slightly curved; LL 0.17 mm; LW 0.04 mm; LL/LW 3.88; GL/LL 4.71.

Distribution

Japan (Honshu, Izu Isls. [Oshima, Miyake-jima, Hachijo-jima], Shikoku, Kyushu, Shimo-koshiki-jima, Yakushima).

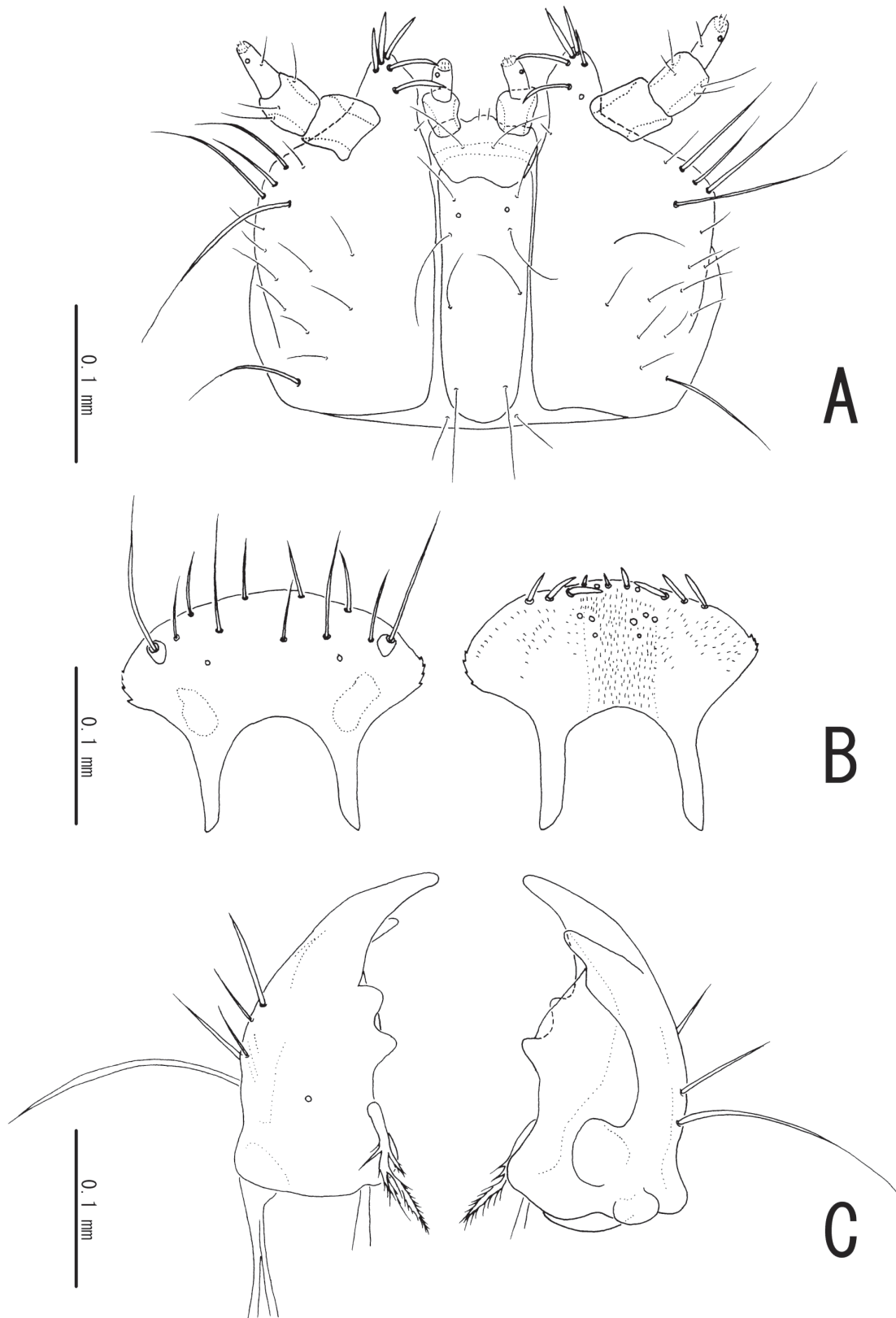


Fig. 11. Larva of *Laius rodriguezensis* sp. nov. **A.** Maxillae and labium in ventral view. **B.** Labrum in dorsal (left) and ventral (right) views. **C.** Mandible in dorsal (left) and ventral (right) views.

Remarks

This is the first record of this species from Oshima, Miyake-jima, and Shimo-koshiki-jima. This species is distributed in the northernmost area in the genus, and widely spread. The local variation of the endophallic sclerites was not observed in this study, but the specimens in the Izu Isls. have somewhat darker elytral coloration.

Laius etsukoae Satô, Yoshitomi & Ohbayashi, 2006

Fig. 4A

Material examined

Same as in Satô *et al.* (2006).

Description of endophallic sclerites

Gonoporal piece (Fig. 4A) straight, slender, 0.59 mm in GL; GL/AL 2.49. Ligula (Fig. 4A) short, distinctly curved in apical portion; LL 0.24 mm; LW 0.10 mm; LL/LW 2.39; GL/LL 2.49. Additional sclerite (Fig. 4A) present, 0.05 mm.

Laius flavicornis (Fabricius, 1801)

Fig. 4B

Material examined

Same as in Yoshitomi (2008).

Description of endophallic sclerites

Gonoporal piece (Fig. 4B) straight, slender, with short and curved basal projection, 0.74 mm in GL; GL/AL 2.14. Ligula (Fig. 4B) short, strongly curved in half; LL 0.26 mm; LW 0.12 mm; LL/LW 2.14; GL/LL 2.85.

Laius keiichii Satô, Yoshitomi & Ohbayashi, 2006

Fig. 4C

Material examined

Same as in Satô *et al.* (2006).

Description of endophallic sclerites

Gonoporal piece (Fig. 4C) straight, slender, 0.54 mm in GL; GL/AL 1.48. Ligula (Fig. 4C) long and slender, evenly and strongly curved; LL 0.31 mm; LW 0.16 mm; LL/LW 1.90; GL/LL 1.76. Additional sclerite (Fig. 4C) present. 0.04 mm.

Laius lutaoensis Yoshitomi & Lee, 2010

Figs 2, 4D

Material examined

3 ♂♂, 7 ♀♀ (EUMJ), “Taitung, TAIWAN Is. Ludao 4-6. IV. 2012 N. OHBAYASHI leg.”. Other material studied is already mentioned in Yoshitomi & Lee (2010).

Description of endophallic sclerites

Gonoporal piece (Fig. 4D) straight, slender, 0.64 mm in GL; GL/AL 2.09. Ligula (Fig. 4D) short, strongly curved in half; LL 0.23 mm; LW 0.12 mm; LL/LW 2.00; GL/LL 2.74.

Laius madli Yoshitomi, 2010

Fig. 4E

Material examined

Same as in Yoshitomi (2010).

Description of endophallic sclerites

Gonoporal piece (Fig. 4E) curved, rather wide, 0.63 mm in GL; GL/AL 2.10. Ligula (Fig. 4E) relatively short, curved in basal portion; LL 0.28 mm; LW 0.09 mm; LL/LW 2.94; GL/LL 2.26.

Laius miyamotoi Nakane, 1955

Fig. 4F

Material examined

Same as in Yoshitomi & Lee (2010).

Description of endophallic sclerites

Gonoporal piece (Fig. 4F) straight, slender, 0.72 mm in GL; GL/AL 4.13. Ligula (Fig. 4F) short, strongly curved in half; LL 0.15 mm; LW 0.08 mm; LL/LW 1.80; GL/LL 4.81.

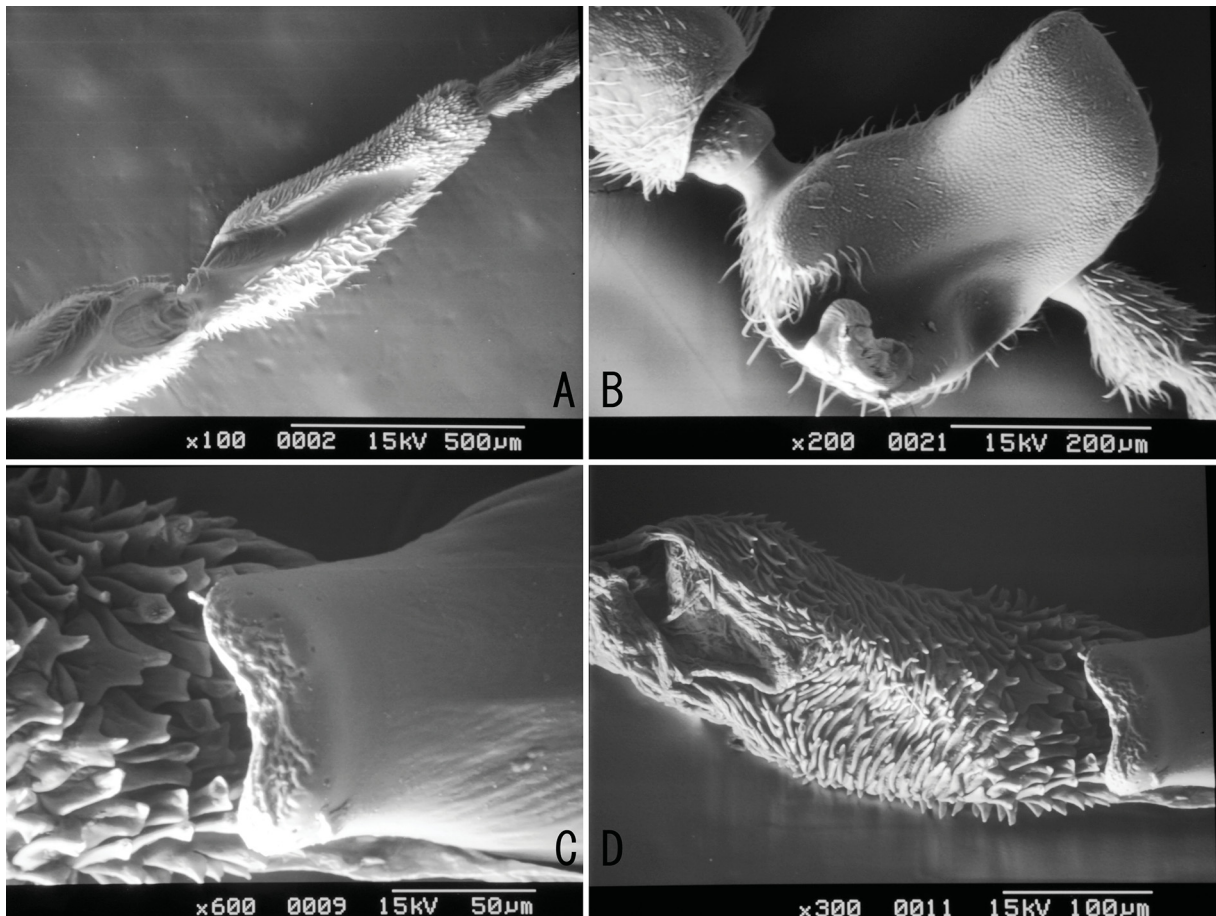


Fig. 12. *Laius andamanensis* sp. nov., ♂, paratype. A. Inner part of fore leg, showing enlarged femur and tibia. B. Antennomere III. C. Aedeagal apex. D. Spinous area (SEM photographs).

Laius pankowi Wittmer, 1999

Fig. 4I

Material examined

Same as in Yoshitomi (2008).

Description of endophallic sclerites

Gonoporal piece (Fig. 4I) curved, wide, 1.04 mm in GL; GL/AL 0.85. Ligula (Fig. 4I) long and straight, with reticulate and rounded apex; LL 0.77 mm; LW 0.09 mm; LL/LW 8.18; GL/LL 1.35.

Laius satoi Yoshitomi, 2008

Figs 4G, 13C

Material examined

2 ♂♂, 12 ♀♀ (EUMJ), “Nosa Dua, North Island 8°47’52.72”S 105°14’9.31”E, Bali, INDONESIA 7-8. VIII. 2010 H. Yoshitomi leg.”; 1 ♀ (EUMJ), “Nosa Dua, South Island 8°48’6.81”S 115°14’16.07”E, Bali, INDONESIA 8. VIII. 2010 H. Yoshitomi leg.”. Other material studied is already mentioned in Yoshitomi (2008).

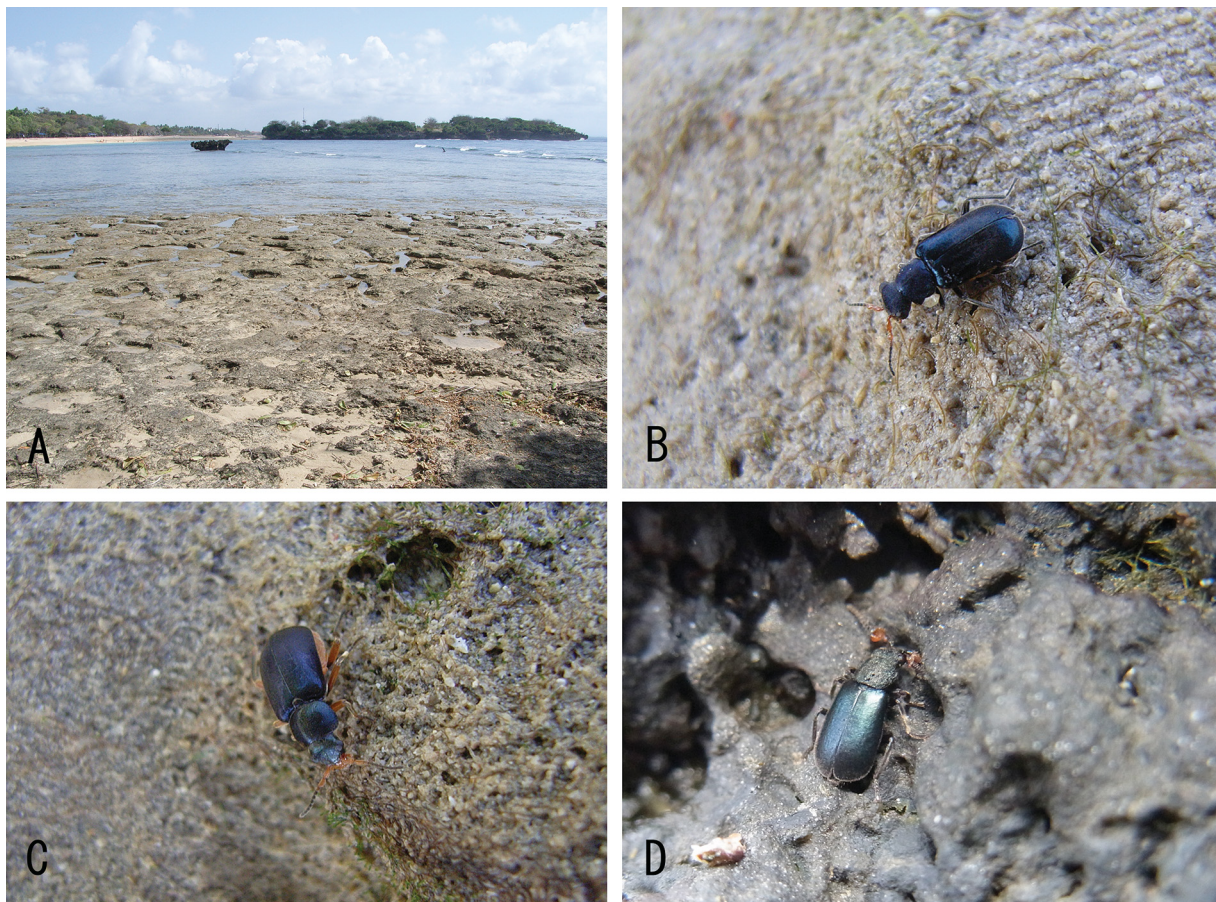


Fig. 13. Habitat and habits of *Laius* spp. **A.** Type locality (Nusa Dua, Bali, Indonesia) of *Laius baliensis* sp. nov. and *L. satoi* Yoshitomi, 2008, three *Laius* species living sympatrically. **B.** *L. baliensis* sp. nov., female. **C.** *L. satoi*, male. **D.** *L. asahinai* Nakane, 1955 (at Miyake-jima). Photographs by HY.

Description of endophallic sclerites

Gonoporal piece (Fig. 4G) straight, slender, 0.94 mm in GL; GL/AL 1.25. Ligula (Fig. 4G) long, slightly curved apical portion; LL 0.49 mm; LW 0.07 mm; LL/LW 7.33; GL/LL 1.92.

Laius taiwanus Yoshitomi & Lee, 2010

Fig. 4H

Material examined

1 ♂ (EUMJ), “Taitung, TAIWAN Is. Ludaο 4-6. IV. 2012 N. OHBAYASHI leg.”. Other material studied is already mentioned in Yoshitomi & Lee (2010).

Description of endophallic sclerites

Gonoporal piece (Fig. 4H) curved, rather wide, 0.67 mm in GL; GL/AL 1.68. Ligula (Fig. 4H) long, slightly curved; LL 0.38 mm; LW 0.08 mm; LL/LW 4.60; GL/LL 1.74. Additional sclerite (Fig. 4H) present, 0.09 mm.

Remarks

Yoshitomi & Lee (2010) pointed out that this species has local variations between the populations from mainland Taiwan, Lutaο and Lanyu Isls. in body size and elytral luster. For the present study, I examined the endophallic structures of these populations, and it became clear that they certainly belong to the same species because of the highly similar features of the endophallic structures.

Discussion

The endophallic structure of the genus *Laius*

The results in this paper show that the endophallic structures of the genus *Laius* are important taxonomically. For close and precise examination of the endophallic sclerites, it is necessary to remove the sclerites from the aedeagus directly or extract them from the ventral part of the aedeagal apex.

Based on the constructions of endophallic sclerites in 19 species, the genus is subdivided into the following five species groups:

- Group 1 (*sericatus*, *etsukoae*, *keiichii*, *taiwanus*, *sabangensis*): additional sclerite present.
- Group 2 (*maai*, *marchei*, *submariniformis*, *flavicornis*): gonoporal piece with basal projection.
- Group 3 (*baliensis* sp. nov., *andamanensis* sp. nov., *rodriguesensis* sp. nov., *politus*, *sericatus*, *asahinai*, *lutaοensis*, *miyamotoi*, *madli*): ligula short, curved.
- Group 4 (*satoi*): ligula long and straight; gonoporal piece long.
- Group 5 (*pankowi*): ligula long, straight, microcuticulate in apical portion.

Distribution

The species of *Laius* inhabit rocky seashores (Fig. 13A), and 1–3 species are distributed in the same place. Table 1 shows the distribution pattern in five areas (Japan, Taiwan, Palawan Isl., Palau, and Bali Isl.). Two species in Taiwan (Lutaο Isl.) and the Philippines (Palawan Isl.), and three in Indonesia (Bali Isl.) are sympatric, and have different body sizes and endophallic structures (= different species group) in each area. On the other hand, two species in Japan and Palau are allopatric (or parapatric), their body sizes overlap and the endophallic structures are also similar to each other (= same species group) in each area.

All members of *Laius* have developed hind wings and are capable of flying, and in fact they often fly in the field. In addition, they are able to stay submerged in seawater for up to 30 hours (Hashimoto

Table 1. Distribution of *Laius* spp. in five areas.

Distribution		Pattern	Species	Species group	Measurement in male (mm)				Reference
	Locality				TL	AL	GL	LL	
Japan	Honshu to Yakushima	allopatric	<i>asahinai</i>	3	3.95–4.65 (4.27)	1.19	0.81	0.17	Yoshitomi & Lee 2010
	Ryukyu Isls.		<i>miyamotoi</i>	3	3.50–4.20 (3.88)	1.17	0.72	0.15	Yoshitomi & Lee 2010
Taiwan	Lutao Isl.	sympatric	<i>taiwanus</i>	1	3.90–4.88 (4.18)	1.03	0.67	0.38	Yoshitomi & Lee 2010
			<i>lutaensis</i>	3	4.80–5.45 (5.18)	1.31	0.64	0.23	Yoshitomi & Lee 2010
Philippines	Palawan	sympatric	<i>submariniformis</i>	2	4.90–6.33 (5.60)	1.37	0.77	0.37	present study
			<i>sabangensis</i>	1	4.03–4.73 (4.23)	0.94	0.72	0.41	present study
Palau	Merir, Sonsorol Isls.	allopatric	<i>etsukoae</i>	1	3.4–4.5	1.00	0.59	0.24	Satô <i>et al.</i> 2006
	Peleliu Isl.		<i>keiichii</i>	1	3.8	1.19	0.54	0.31	Satô <i>et al.</i> 2006
Indonesia	Bali Isl.	sympatric	<i>satoi</i>	4	5.7	1.53	0.94	0.49	Yoshitomi 2008
			<i>pankowi</i>	5	6.13–6.55 (6.34)	1.58	1.04	0.77	Yoshitomi 2008
			<i>baliensis</i>	3	4.10–4.46 (4.27)	1.12	0.61	0.23	present study

1970). Therefore it is supposed that the distribution of each species is widely spread through flight and tidal currents. However, most of the species show narrow distributions (see Appendix). The genus *Aegialites* Mannerheim, 1853 (Coleoptera, Salpingidae, Aegialitinae) also lives in rocky seashores, and the distribution of each of its species is generally restricted as the ones of the species of the genus *Laius* (see Doyen 1976; Zerche 2004). However, *Aegialites* is flightless with degenerated hind wings, and its distribution is limited in the Northern Pacific (latitude *c.* 30–60°N; Northern Japan, Kuril Isls., to North America). The speciation and distribution pattern of *Laius* provide interesting zoogeographical and evolutionary themes.

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Appendix. Updated list of the true *Laius* species of the world. * *Laius heterocerus* Boisduval, 1835 was treated as a junior synonym of this species, and recorded from New Guinea, India, Key Isls., Karoline, New Caledonia (Evers 1994). ** This species has also been recorded from Larat, Key Isls., Borneo, Lundu, Sarawak, and China (Evers 1994); however, these records were probably based on the misidentification of another species.

<i>Laius alleni</i> Lea, 1909.....	Australia (Queensland) [after Evers 1994]
<i>Laius ambonensis</i> Wittmer, 1996.....	Indonesia (Ambon Isl.) [after Plonski 2013]
<i>Laius andamanensis</i> Yoshitomi sp. nov.....	India (Andaman Islands)
<i>Laius asahinai</i> Nakane, 1955.....	Japan (Honshu to Yakushima)
<i>Laius baliensis</i> Yoshitomi sp. nov.....	Indonesia (Bali Isl.)
<i>Laius cyaneus</i> Guérin-Ménéville, 1830*	India, New Guinea [after Evers 1994]
<i>Laius cyanoxanthus</i> Bourgeois, 1897	New Hebrides (Mallicolo) [after Evers 1994]
<i>Laius etsukoae</i> Satô, Yoshitomi & Ohbayashi, 2006	Palau (Merir, Sonsorol Isls.)
<i>Laius flavicornis</i> (Fabricius, 1801)**	Indonesia (Java Isl.)
<i>Laius impressus</i> Wittmer, 1985.....	Philippines (Mindanao Isl.) [after Evers 1994]
<i>Laius keiichii</i> Satô, Yoshitomi & Ohbayashi, 2006	Palau (Peleliu Isl.)
<i>Laius lutaoensis</i> Yoshitomi & Lee, 2010	Taiwan
<i>Laius miyamotoi</i> Nakane, 1955.....	Japan (Ryukyu Isls.)
<i>Laius maai</i> Wittmer, 1973.....	New Guinea
<i>Laius madli</i> Yoshitomi, 2010.....	Republic of Mauritius (Mauritius Isl.)
<i>Laius marchei</i> Pic, 1922.....	Mariana (Rota, Guam Isls.)
<i>Laius miles</i> Bourgeois, 1905.....	Ceylon [after Evers 1994]
<i>Laius mindanaonus</i> Wittmer, 1985	Philippines (Mindanao Isl.)
<i>Laius obscurus</i> (Pic, 1908)	Kenya [after Evers 1994]
<i>Laius pankowi</i> Wittmer, 1999	Indonesia (Bali Isl.)
<i>Laius politus</i> Fairmaire, 1880	Madagascar
<i>Laius purpureipennis</i> Lea, 1916	Australia [after Evers 1994]
<i>Laius riedeli</i> Evers, 1994	Malaysia (Sarawak)
<i>Laius rodriguesensis</i> Yoshitomi sp. nov.	Republic of Mauritius (Rodrigues Isl.)
<i>Laius rufipes</i> Montrouzier, 1860.....	New Caledonia [after Evers 1994]
<i>Laius sabangensis</i> Wittmer, 1985	Philippines (Palawan Isl.)
<i>Laius satoi</i> Yoshitomi, 2008	Indonesia (Bali Isl.)
<i>Laius sericatus</i> Champion, 1923.....	Seychelles (Mahé, Félicité Isls.)
<i>Laius submarinus</i> Champion, 1921	Philippines (Mindanao Isl.), New Guinea
<i>Laius submariniformis</i> Wittmer, 1985	Philippines (Palawan Isl.)
<i>Laius taiwanus</i> Yoshitomi & Lee, 2010.....	Taiwan (including Lutao Isls.)
<i>Laius tibialis</i> Gahan, 1900	Christmas Isl.
<i>Laius velutinus</i> Gerstaecker, 1873	Zanzibar Coast [after Champion 1921]
<i>Laius wallecei</i> Pic, 1937	Malaysia (Borneo)

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