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Revision of *Proterus* Raffray, 1897, with description of a new affiliated genus from Thailand (Coleoptera, Staphylinidae, Pselaphinae)

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The monobasic genus *Proterus*, type genus of Proterini, is revised. The type species *Proterus punctatus* Raffray is redescribed, and 7 new species from Sumatra and Java are described: *Proterus alexandrae* n. sp., *P. elenae* n. sp., *P. laureatus* n. sp., *P. lucilae* n. sp., *P. noai* n. sp., *P. observator* n. sp. and *P. pumilio* n. sp.. In addition *Exoterus lannaeus* n. gen. n. sp. is erected for a taxon from Thailand closely related to *Proterus*. All these taxa are illustrated and keyed. New potential synapomorphies supporting a more restricted concept for the tribe (i.e. Proterini sensu stricto) are also presented and briefly discussed.

Keywords: Coleoptera, Staphylinidae, Pselaphinae, Proterini, *Proterus*, *Exoterus*, taxonomy, Asia.

INTRODUCTION

Proterus Raffray, 1897, is a monobasic genus of Pselaphinae from Sumatra. It is the type genus of the tribe Proterini, which currently holds some 34 genera distributed in the Afrotropical, Oriental, Neotropical and Australian regions (Newton & Chandler 1989). As currently defined, Proterini genera are essentially Goniaceritae that possess elytra with a subhumeral fovea prolonged laterally by a longitudinal carina and sulcus, in combination with the first visible abdominal sternite being at least half as long as the second (Chandler 2001). However, the genera now placed in the Proterini appear to have not much more in common, and as it stands the tribe is most likely polyphyletic. In order to clarify this situation, it is first necessary to enhance our knowledge of *Proterus*, as well as to understand which key-characters would allow the delimitation of a genuinely monophyletic group of genera around *Proterus*.

Browsing the extensive and recent collections of Pselaphinae from the Oriental region housed in the Natural History Museum of Geneva, we recognized a large number of new forms of proterine-like Goniaceritae. Most of these are either difficult to accommodate into the known genera without significantly loosening their concept, or represent new genera. Progressing into a more detailed study of this material together with a critical reexamination of the types of Oriental genera of Proterini (so far most of them are monobasic, or contain only a couple of species), we noticed that *Imtempus* Reitter, 1882, *Mechanicus* Schaufuss, 1887, *Neodeuterus* Schaufuss, 1887, *Pareuplectops* Jeannel, 1957, *Phthartomicrus* Schaufuss, 1887,

Proterus Raffray, 1897, and *Exoterus* n. gen. uniquely share at least the following characters: 1) genal areas each with a marked and smooth depression allowing to accommodate the maxillary palpi, 2) posterior edge of female abdominal sternite 6 (Figs 8, 34) notched as in male, and 3) female abdominal sternite 7 modified as genital plate covering genital opening (Figs 9, 33) similar to that in male. These features are the presumed synapomorphies supporting our new concept for the core of the tribe (i.e. Proterini sensu stricto).

In the present study, we focused our attention on *Proterus*. We found representatives of this genus only in collections from Sumatra and Java. They appeared to belong to 7 new species, which are described and keyed below. A new genus and species from Thailand is also erected to accommodate what we hold as the nearest taxon to *Proterus* on the basis of their uniquely shared absence of a pair of metasternal longitudinal carinae with respect to the above mentioned genera. The study of the remaining Proterini and a phylogeny of the group are planned.

MATERIAL AND METHODS

The material (102 specimens) used in this study comes almost exclusively from sifted samples of vegetational debris in forests. The label data of the type of *P. punctatus* are reproduced literally between « », with additional information pertaining to labels, or localities between [], and | as a separator between each individual label. For new types and additional material label data are given in standard format, with major administrative units in English, name of collectors between (), and additional information from unpublished field trip reports between [].

Abbreviations of collections used in the present study are:

MHNG = Muséum d'histoire naturelle, Geneva, Switzerland

MNHN = Muséum National d'Histoire Naturelle, Paris, France

PCSK = Private collection of S. A. Kurbatov, Moscow, Russia

Measurements are defined as follows: body length is measured from anterior outline of head (i.e. apical margin of labrum) to apex of abdomen; head width (HW) = distance between outer outline of head just behind eyes; maximal head width (HWmax) = distance between outer outline of eyes; head length (HL) = distance between tip of frons to middle of occipital margin; pronotal length (PL) = medial distance between anterior and posterior margins of pronotum; pronotal width (PW) = maximal distance between lateral pronotal outlines; elytral length (EL) = elytral sutural length; elytral width (EW) = maximal width of the elytra taken together.

The abdominal tergites and sternites are numbered according to Chandler (2001) in Arabic (visible position) and Roman (morphological position) numerals. The abdominal segments are counted from tergite 1 (IV) and sternite 1 (III). The aedeagi and other body parts illustrated here were mounted in Canada balsam on acetate slides, and drawn using a drawing tube mounted on a compound microscope.

TAXONOMY

Key to species of Proterus and Exoterus

- 1 V-shaped vertexal sulcus extended posterior to tentorial foveae, where the two branches are joined in a median sulcus reaching posterior occipital margin; mesosternum with conspicuous median carina (*Proterus* Raffray) 2
- V-shaped vertexal sulcus not extended posterior to tentorial foveae; mesosternum lacking median carina *Exoterus lannaesus* n. gen. n. sp.
- 2 Sides of mesosternum impunctate 3
- Sides of mesosternum punctate 5
- 3 Interval between tentorial foveae slightly exceeding that between each fovea and posterior occipital margin. Males with eyes in lateral view reaching posterior edge of head; article 8 of antennae nearly as long as combined length of articles 5–7 *P. observator* n. sp.
- Interval between tentorial foveae not exceeding that between each fovea and posterior occipital margin. Males with eyes in lateral view not reaching posterior edge of head; article 8 of antennae much shorter than combined length of articles 5–7 4
- 4 Body 1.50–1.75 mm long; elytra with humeral fold indistinct; males with diameter of eyes in lateral view about 1.5 times that of temples; females with article 11 of antennae as long as combined length of articles 9–10 *P. pumilio* n. sp.
- Body 1.80–2.50 mm long; elytra with humeral fold distinct; males with diameter of eyes in lateral view subequal to that of temples; females with article 11 of antennae slightly shorter than combined length of articles 9–10 *P. alexandrae* n. sp.
- 5 Lateral outline of pronotum near lateral fovea with tooth 6
- Lateral outline of pronotum near lateral fovea without tooth 7
- 6 Body 2.20–2.85 mm long; each elytron about as wide as head with eyes *P. lucilae* n. sp.
- Body 1.70–1.95 mm long; each elytron distinctly wider than head with eyes *P. noai* n. sp.
- 7 Frons in dorsal view without medial tooth *P. laureatus* n. sp.
- Frons in dorsal view with inconspicuous medial tooth 8
- 8 Pronotal median sulcus narrowed anteriorly; elytra with humeral fold extended on more than half of elytral length; males with diameter of eyes in lateral view about 1.5 times larger than length of temples *P. elenae* n. sp.
- Pronotal median sulcus not narrowed anteriorly; elytra with humeral fold extended on one quarter of elytral length; males with diameter of eyes in lateral view less than 1.5 times larger than length of temples ... *P. punctatus* Raffray

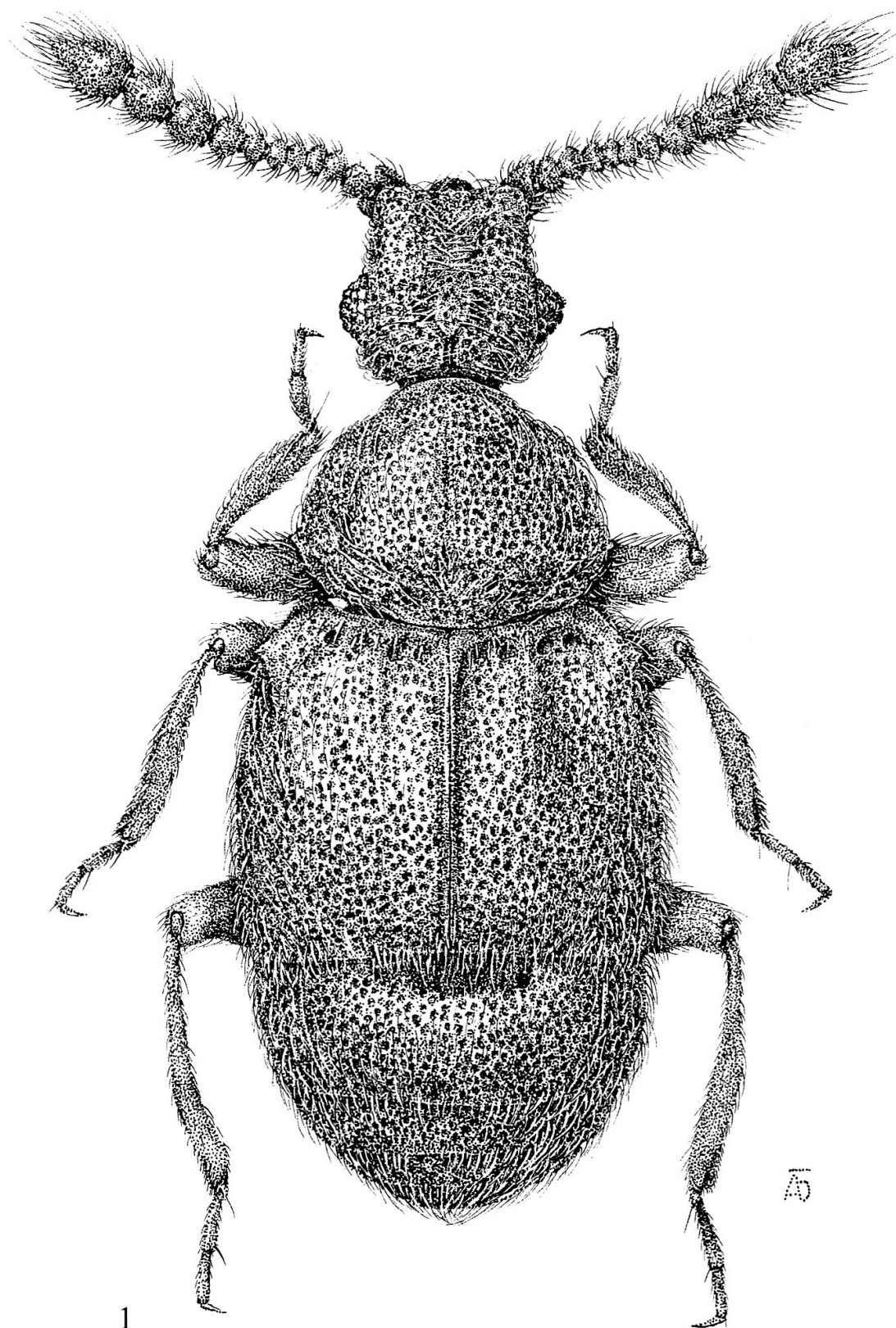


Fig. 1. Habitus of *Proterus lucilae* n. sp., male.

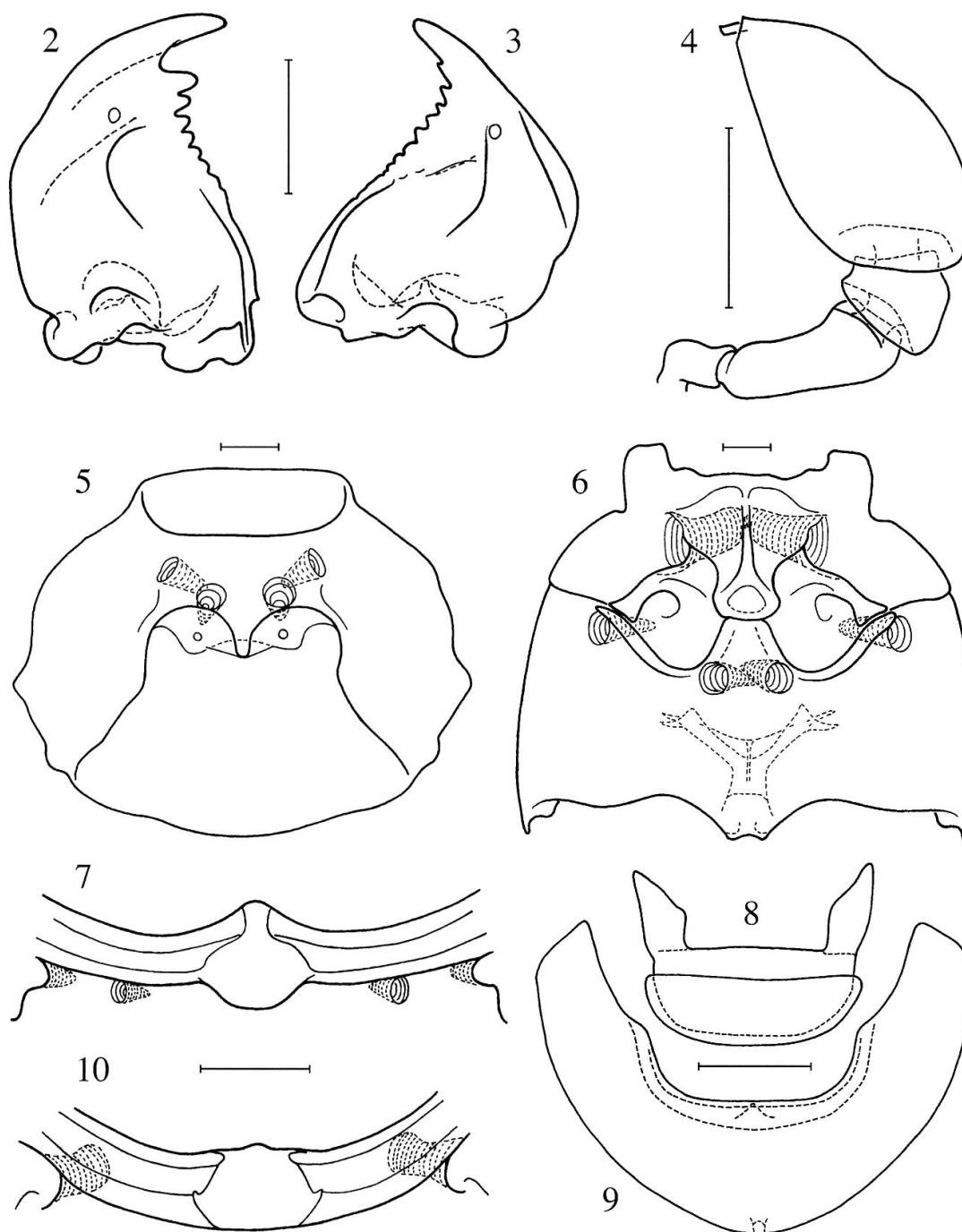
***Proterus* Raffray, 1897**

Proterus Raffray, 1897: 231; type species: *Proterus punctatus* Raffray (by monotypy).

Description. Body (Fig. 1) 1.5–3.0 mm long, uniformly brown, except paler maxillary palpi; entirely covered with dense punctation, except gular constriction and occasionally sides of mesosternum. Pubescence semi-recumbent, dense and fairly long, consisting of setae several times longer than distance between two neighboring punctures; medioapical pubescence of elytrae usually converging posteriorly. Head with pair of tentorial foveae connected anteriorly by confluent vertexal sulci (i.e. ‘V-shaped’ sulcus), the latter sulci connected also posteriorly to form median sulcus reaching posterior occipital margin. Vertex and frons distinctly depressed in middle with regards to their raised lateral sides. Antennal tubercles indistinct. Frons lacking postantennal notches. Mandibles as in Figs 2–3. Article 4 of maxillary palpi (Fig. 4) with group of setae (‘trichomes’ sensu Nomura 1991) on external side. Genal areas each with a marked and smooth depression allowing accommodation of maxillary palpi. Antenna consisting of 11 articles, rather short with at least articles 4–7 of funicle transverse; scape notched dorsally at base, revealing basal stalk of article 2; club composed of 3 or 4 articles, inconspicuous. Pronotum with median antebasal fovea and pair of lateral antebasal foveae, as well as 3 longitudinal sulci, but without carina behind median antebasal fovea; median sulcus sharper, extended from median antebasal fovea almost to anterior pronotal margin; lateral sulci shallower than median, extended anteriorly from lateral antebasal foveae, variable in length. Prosternum (Fig. 5) with pairs of lateral procoxal and anteroprosternal foveae; paranotal carinae absent; median carina absent. Elytra with 4 basal foveae, the external pair grouped in same depression; subhumeral fovea prolonged with marginal carina extended on entire elytral length. Mesosternum (Fig. 6) with pair of lateral foveae; median carina present, conspicuous. Mesocoxal cavities separated; pleural sulcus delimiting meso- and metasternum, sulcus distinctly ‘cariniform’. Metasternum (Fig. 6) with pair of lateral and lateral mesocoxal foveae; lacking a pair of longitudinal carinae. First three visible abdominal tergites fused to corresponding sternites; paratergal-tergal suture distinct only on tergite 1; junction between tergite 4 (VII) and sternite 5 (VII) carinate; tergite 1 conspicuously longer than any other, its basal median depression supporting laterally a pair of mediobasal foveae, basal carinae obsolete, or absent; tergites 2–3 lacking basal carinae; sternite 2 with 2 basolateral and occasionally 2 mediobasal foveae (Figs 7, 10); posterior edge of abdominal sternite 6 notched; sternite 7 modified as genital plate covering genital opening (its structure slightly different between male and female).

Male secondary sexual characters affecting the proportion of eyes (bigger), elytra (longer), and terminal articles of the antennae (bigger). Aedeagus with membranous median lobe and two asymmetrical parameres; the larger paramere (morphological left) is easily removed during dissection and usually possesses two setae grouped at its base on a digitiform tubercle (except in *P. elenae* and *P. observator*); the morphologically right paramere is very reduced in size.

Distribution and natural history. *Proterus* appears endemic to Sumatra (7 species) and Java (1 species). There the genus occurs in leaf litter and other decaying vegetational debris on soil in a wide range of forest habitats, predominantly in *Lithocarpus-Castanopsis* montane rain forests between 1400–2100 m (6 species), but occasionally also down to 500 m in secondary, or disturbed evergreen lowland



Figs 2–10: *Proterus lucilae* n. sp. (2–7), *P. observator* n. sp. (8–9) and *P. elenae* n. sp. (10); dorsal views of left (2) and right (3) mandibles, and right maxillary palpus (4); ventral views of prosternum (5), mesosternum and metasternum (6), abdominal sternite 1 and anterior portion of sternite 2 (7, 10), and female abdominal sternites 6 (8) and 7 (9). Scale bars = 0.1 mm.

forests (1 species), or up to 3300 m in Ericaceae scrubs (1 species). The genus is particularly diverse (6 species) in the highlands of the southern half of Sumatra (i.e. Barisan Range). At least four species inhabit the forested slopes of Mt. Kerinci (Jambi province), where they were collected in limited series of two to ten specimens representing consistently two species, or more.

Comments. The genus is very homogenous with regard to external morphology, and we have thus discriminated the species essentially by features of their aedeagus, in particular the shape of the larger paramere.

***Proterus alexandrae* n. sp.**

(Figs 11–12)

Holotype (♂, in MHNG): Indonesia, Sumatra, Jambi, Mt. Kerinci, 1750–1850 m, 11–12.xi.1989 (I. Löbl, D. Burckhardt & D. Agosti) #11 [sifting of vegetational debris in montane *Lithocarpus-Castanopsis* forest].

Paratypes (14): same data as holotype, 7 ♂♂ & 3 ♀♀ in MHNG & PCSK; same data but 3300 m, 12.xi.1989, #12a [sifting of vegetational debris in low Ericaceae scrubs] 1 ♂ in MHNG; same data but 1900 m, 13.xi.1989, #15a [sifting of vegetational debris in montane *Lithocarpus-Castanopsis* forest] 1 ♀ in MHNG; same data but 2100 m, 14.xi.1989, #16 [sifting of vegetational debris in transition upper montane *Lithocarpus-Castanopsis* to moss forest] 1 ♀ in MHNG; same data but W of Kersik Tua, 2160 m, 17–18.ii.2000 (P. Schwendinger) [sifting in ever-green hill forest] 1 ♀ in MHNG.

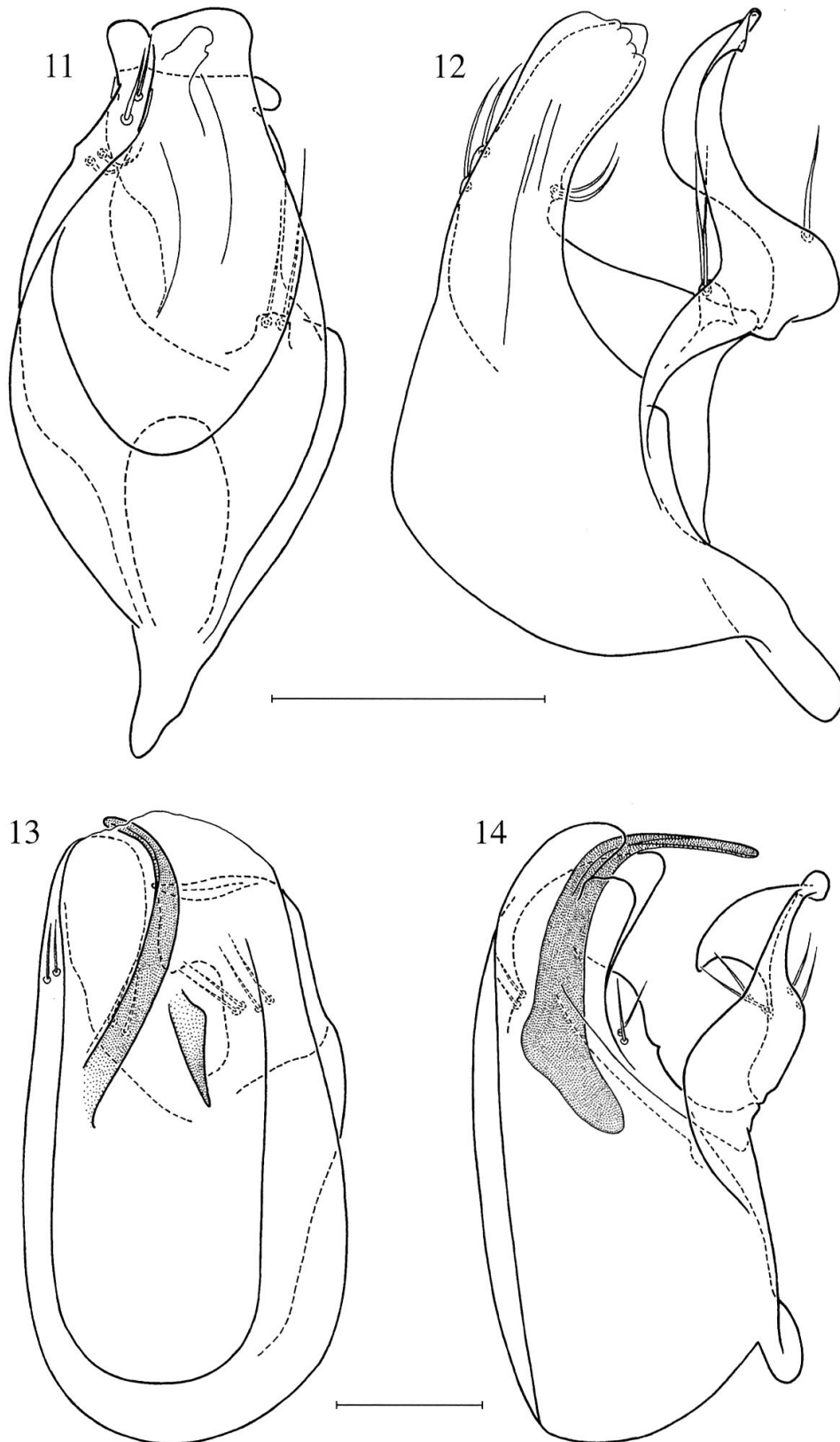
Additional material examined (1): Indonesia, Sumatra, Jambi, Mt. Kerinci, 3300 m, 12.xi.1989 (I. Löbl, D. Burckhardt & D. Agosti) #12a [sifting of vegetational debris in low Ericaceae scrubs] ♂ in MHNG.

Description. Body 1.80–2.50 mm long. Frons in dorsal view occasionally with inconspicuous medial tooth. Interval between tentorial foveae slightly narrower than that between each fovea and posterior occipital margin. Antennae with article 2 as wide as, or slightly wider than long; articles 3–7 transverse; article 3 slightly narrower than article 2; articles 4–6 about as wide as article 3, but slightly shorter; article 7 similar to article 6, but somewhat bigger. Pronotum 1.27–1.41 times as long as head and 1.17–1.32 times as wide as head with eyes; lateral outline near lateral fovea without tooth; median sulcus narrowed anteriorly, its middle portion about as wide as diameter of one pronotal puncture (female), or from one to more than two times as wide as diameter of one pronotal puncture (male). Elytra with humeral fold extended on one third of elytral length, occasionally slightly shorter. Sides of mesosternum impunctate.

Measurements: HL = 0.32–0.41 mm; HW = 0.33–0.41 mm; HWmax = 0.43–0.51 mm; PL = 0.45–0.54 mm; PW = 0.53–0.64 mm; EL = 0.61–0.84 mm; EW = 0.87–1.01 mm.

Male with eyes well-developed, rounded in dorsal view, with 35–40 facets; eyes in lateral view about as long as, or slightly longer than temples. Antenna with article 8 wider than article 7, transverse; article 9 similar to article 8, but slightly bigger; article 10 similar to article 9, but slightly bigger, article 11 as long as combined length of articles 9–10, or nearly. Aedeagus (Figs 11–12) 0.25–0.28 mm long; larger paramere with basal digitiform tubercle bearing two setae, its apical edge in dorsal view broadly rounded internally and forming a narrow projection externally.

Female with eyes angulate in dorsal view, with 5–7 facets; eyes in lateral view more than two times longer than temples. Antenna with article 8 similar to article 7; article 9 distinctly wider than article 8, transverse; article 10 similar to article 9, or slightly bigger; article 11 slightly shorter than combined length of articles 9–10.



Figs 11–14: *Proterus alexandrae* n. sp. (11–12) and *P. elenae* n. sp. (13–14); aedeagus in dorsal (11, 13) and lateral (12, 14) views. Scale bars = 0.1 mm.

Distribution. *Proterus alexandrae* is apparently restricted to Sumatra (Jambi province), where it was collected at elevations ranging from 1750–3300 m.

Comments. The specimen listed under ‘Additional material examined’ is unusually large (2.90 mm) and has one of the two setae usually located on the basal digitiform tubercle of the larger paramere apparently translocated. It is tentatively assigned to this species until further material will allow a better evaluation of the taxonomic significance of these features.

P. alexandrae, *P. observator* and *P. pumilio* are the only *Proterus* species with the sides of mesosternum impunctate. Among these, *P. alexandrae* and *P. pumilio* have in common the presence of a basal digitiform tubercle bearing two setae on their larger paramere, but they differ in body size and have diagnostic shapes of the larger paramere.

Etymology. The species is dedicated to Alexandra, the youngest daughter of S. Kurbatov.

***Proterus elenae* n. sp.**

(Figs 10, 13–14)

Holotype (♂, in MHNG): Indonesia, Sumatra, Jambi, Mt. Kerinci, 1750–1850 m, 11–12.xi.1989 (I. Löbl, D. Burckhardt & D. Agosti) #11 [sifting of vegetational debris in montane *Lithocarpus-Castanopsis* forest].

Paratypes (16): same data as holotype, 4 ♂♂ & 4 ♀♀ in MHNG & PCSK; same data but 1900 m, 13.xi.1989, #15a [sifting of vegetational debris in montane *Lithocarpus-Castanopsis* forest] 1 ♂ & 5 ♀♀ in MHNG; Jambi, W Mt. Tujuh Lake, 1400 m, 14.xi.1989 (I. Löbl, D. Burckhardt & D. Agosti) #17 [sifting of vegetational debris in montane *Lithocarpus-Castanopsis* forest] 1 ♂ & 1 ♀ in MHNG.

Description. Body 2.30–2.70 mm long. Frons in dorsal view with inconspicuous medial tooth. Interval between tentorial foveae slightly narrower than that between each fovea and posterior occipital margin. Antennae with article 2 as wide as, or only slightly wider than long (male), or distinctly transverse (female); articles 3–6 transverse, similar in width, somewhat narrower than article 2; articles 4–6 slightly shorter than article 3; article 7 similar to article 6, but somewhat bigger. Pronotum 1.38–1.51 times as long as head and 1.18–1.33 times as wide as head with eyes; lateral outline near lateral fovea without tooth; median sulcus narrowed anteriorly, about two times as wide as diameter of one pronotal puncture. Elytra with humeral fold extended on more than half of elytral length. Sides of mesosternum punctate.

Measurements: HL = 0.41–0.43 mm; HW = 0.41–0.50 mm; HWmax = 0.56–0.60 mm; PL = 0.57–0.65 mm; PW = 0.66–0.72 mm; EL = 0.70–0.87 mm; EW = 1.05–1.14 mm.

Male with eyes well-developed, rounded in dorsal view, with about 30–35 facets; eyes in lateral view about 1.5 times longer than temples. Antenna with article 8 slightly wider than long, longer than article 7; article 9 similar to article 8, but somewhat bigger; article 10 longer and about as wide as article 9; article 11 slightly shorter than combined length of articles 9–10. Aedeagus (Figs 13–14) 0.42–0.45 mm long; larger paramere lacking setose basal digitiform tubercle, its apical edge in dorsal view rounded internally and externally.

Female with eyes angulate in dorsal view, with about 10 facets; eyes in lateral view about 2 times shorter than temples. Antenna with articles 8–10 transverse; article 8 similar to article 7; article 9 slightly, or distinctly wider than article 8; article 10 similar to article 9, but somewhat bigger; article 11 about twice as long as combined length of articles 9–10.

Distribution. *Proterus elenae* is apparently restricted to Sumatra (Jambi province: Mt. Kerinci area), where it was collected at elevations ranging from 1400–1900 m.

Comments. *P. elenae* uniquely shares with *P. punctatus* the sides of mesosternum punctate, in combination with toothed pronotal lateral outlines and frontal apex. However *P. elenae* has much longer elytral humeral folds, and lacks a basal digitiform setiferous tubercle on its larger paramere.

Etymology. The species is dedicated to Elena, the eldest daughter of S. Kurbatov.

***Proterus laureatus* n. sp.**

(Figs 15–16)

Holotype (♂, in MHNG): Indonesia, Sumatra, Lampung, Road Krui – Liwa, 2 km SW of Kubuprahu, 480–540 m, 2.iii.2000 (P. Schwendinger) disturbed evergreen rain forest and secondary forest.

Paratypes (2): same data as holotype, 1 ♂ & 1 ♀ in MHNG.

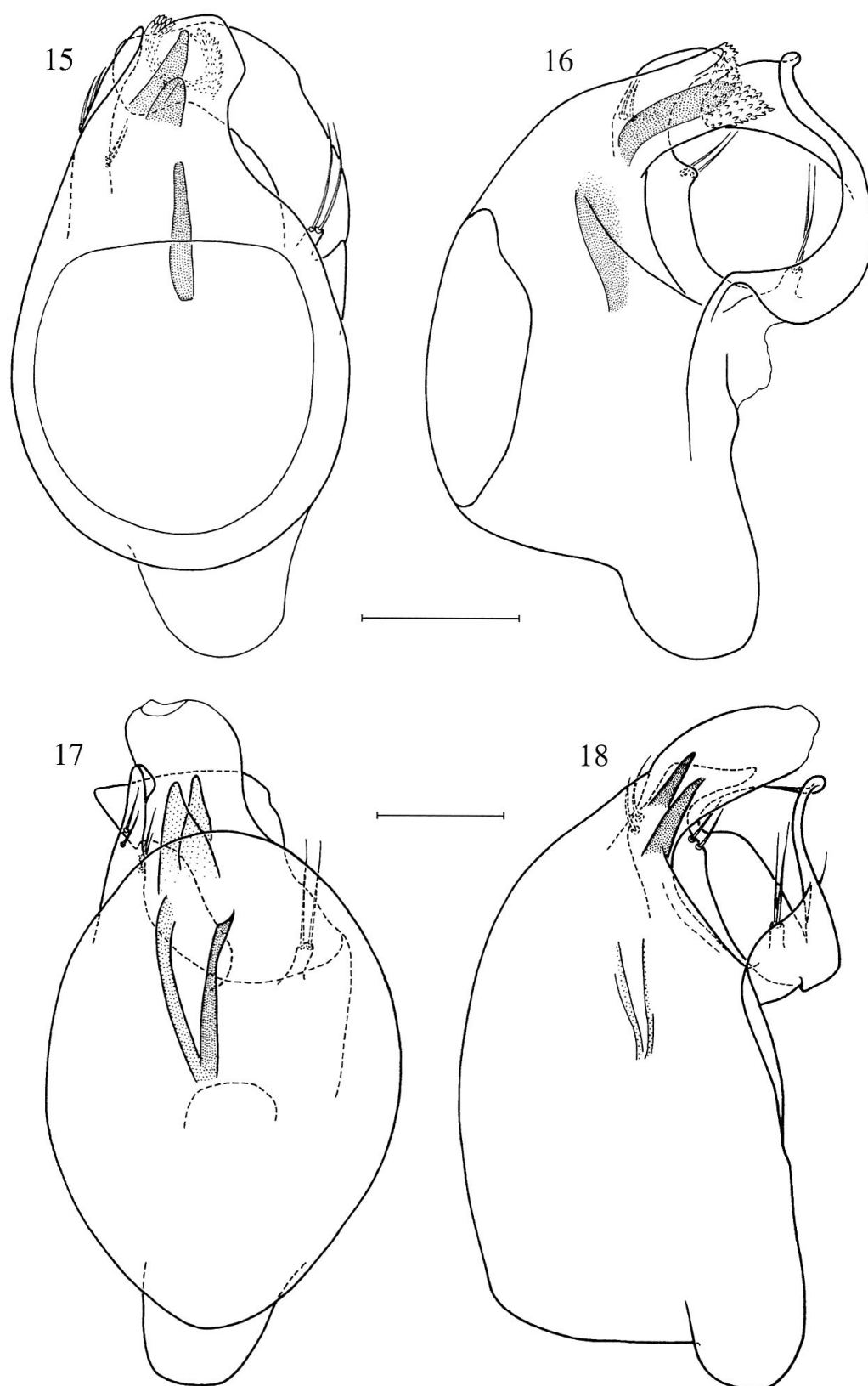
Description. Body 1.90–2.30 mm long. Frons in dorsal view lacking medial tooth. Interval between tentorial foveae slightly narrower than that between each fovea and posterior occipital margin. Antennae with articles 2–7 distinctly transverse; article 3 slightly narrower than article 2; articles 4–7 as wide as article 3, but shorter; article 7 as wide as article 6, or somewhat wider, about as wide as article 2. Pronotum 1.37–1.39 times as long as head and 1.17–1.27 times as wide as head with eyes; lateral outline near lateral fovea without tooth; median sulcus occasionally narrowed anteriorly, its width in middle portion variable from nearly one to more than two diameters of one pronotal puncture. Elytra with humeral fold extended on one quarter to one third of elytral length. Sides of mesosternum punctate.

Measurements: HL = 0.31–0.35 mm; HW = 0.32–0.35 mm; HWmax = 0.40–0.49 mm; PL = 0.44–0.48 mm; PW = 0.51–0.57 mm; EL = 0.50–0.68 mm; EW = 0.76–0.89 mm.

Male with eyes well-developed, rounded in dorsal view, with 30–35 facets; eyes in lateral view 1.5 times longer than temples. Antenna with article 8 similar to article 7; article 9 transverse, distinctly longer and larger than article 8; article 10 similar to article 9; article 11 as long, or somewhat shorter than combined length of articles 9 and 10. Aedeagus (Figs 15–16) 0.39–0.40 mm long; larger paramere with basal digitiform tubercle bearing two setae, its apical edge in dorsal view rounded internally and externally.

Female with eyes angulate in dorsal view, with 10 facets; eyes in lateral view almost 2 times shorter than temples. Antenna with articles 8–11 resembling those in male, but article 11 distinctly shorter than combined length of articles 9 and 10.

Distribution. *P. laureatus* is known only from its type locality in southern Sumatra (Lampung province), where it was collected at 450–580 m. It is the only modern material of the genus collected below 1200 m.



Figs 15–18: *Proterus laureatus* n. sp. (15–16) and *P. lucilae* n. sp. (17–18); aedeagus in dorsal (15, 17) and lateral (16, 18) views. Scale bars = 0.1 mm.

Comments. *P. laureatus* is the only member of the genus possessing the sides of the metasternum punctate, in combination with lateral outlines of pronotum and apex of frons lacking teeth. The 'laurel crown-like' armature of minute teeth on its aedeagal internal sac is diagnostic.

Etymology. The name '*laureatus*' refers to the presence of the above mentioned 'laurel crown-like' aedeagal armature.

***Proterus lucilae* n. sp.**

(Figs 1–7, 17–18)

Holotype (♂, in MHNG): Indonesia, Sumatra, Jambi, Mt. Kerinci, 1750–1850 m, 11–12.xi.1989 (I. Löbl, D. Burckhardt & D. Agosti) #11 [sifting of vegetational debris in montane *Lithocarpus-Castanopsis* forest].

Paratypes (29): same data as holotype, 13 ♂♂ & 5 ♀♀ in MHNG & PCSK; same data, but 2100 m, 14.xi.1989, #16 [sifting of vegetational debris in transition upper montane *Lithocarpus-Castanopsis* to moss forest] 1 ♂ in MHNG; same data but W of Kersik Tua, 2160 m, 17–18.ii.2000 (P. Schwendinger) [sifting in] evergreen hill forest, 1 ♂ and 1 ♀ in MHNG; Jambi, km 8 road Sungaipanuh to Tapan, 1200 m, 9.xi.1989 (I. Löbl, D. Burckhardt & D. Agosti) #8 [sifting of vegetational debris of trees and bamboos in ravine] 1 ♂ & 3 ♀♀ in MHNG; Jambi, W Mt. Tujuh Lake, 1400 m, 14.xi.1989 (I. Löbl, D. Burckhardt & D. Agosti) #17 [sifting of vegetational debris in montane *Lithocarpus-Castanopsis* forest] 2 ♂♂ & 2 ♀♀ in MHNG & PCSK.

Description. Body (Fig. 1) 2.20–2.85 mm long. Frons in dorsal view with medial tooth, or not. Interval between tentorial foveae slightly narrower than that between each fovea and posterior occipital margin. Antennae with article 2 only slightly wider than long, slightly wider than article 3; articles 3–7 distinctly transverse; article 4 as wide as article 3; articles 5–7 gradually widening to article 7, article 7 as wide as article 2. Pronotum 1.28–1.41 times as long as head and 1.23–1.39 times as wide as head with eyes; lateral outline near lateral fovea with tooth, the latter occasionally blunt; median pronotal sulcus occasionally slightly narrowed anteriorly, its middle portion half as wide as, or slightly wider than diameter of one pronotal puncture. Elytra with humeral fold absent, or extended on less than one quarter of elytral length. Sides of mesosternum punctate.

Measurements: HL = 0.40–0.48 mm; HW = 0.40–0.49 mm; HWmax = 0.50–0.60 mm; PL = 0.54–0.62 mm; PW = 0.67–0.81 mm; EL = 0.65–0.82 mm; EW = 0.98–1.17 mm.

Male with eyes well-developed, rounded in dorsal view, with about 25–30 facets; eyes in lateral view about as long as, or somewhat longer than temples. Antenna with article 8 somewhat wider than long, wider and slightly longer than article 7; articles 9 and 10 longer and somewhat larger than article 8, distinctly transverse; article 11 slightly shorter than combined length of articles 9 and 10. Aedeagus (Figs 17–18) 0.49–0.53 mm long; larger paramere with basal digitiform tubercle bearing two setae, its apical edge in dorsal view straight internally, rounded externally.

Female with eyes angulate in dorsal view, with 10 facets; eyes in lateral view almost 2 times shorter than temples. Antenna with article 8 as wide as article 7; articles 9 and 10 similar, distinctly wider than article 8, more transverse than in male; article 11 about as long as combined length of articles 9 and 10.

Distribution. The species is known only from Sumatra (Jambi province: Mt. Kerinci area), where it has been collected at elevations ranging from 1200 to 2160 m.

Comments. Among *Proterus*, only *P. lucilae* and *P. noai* possess the sides of mesosternum punctate, in combination with toothed lateral outlines of pronotum. Their aedeagal features are diagnostic.

Etymology. The species is dedicated to Lucile, the daughter of G. Cuccodoro.

***Proterus noai* n. sp.**

(Figs 19–20)

Holotype (♂, in MHNG): Indonesia, Sumatra, N Sumatra, 7 km North of Bras-tagi, 1500 m, 2.xii.1989 (I. Löbl, D. Burckhardt & D. Agosti) #28a [sifting of vegetational debris in montane *Lithocarpus-Castanopsis* forest].

Paratypes (10): same data as holotype, 1 ♂ & 9 ♀♀ in MHNG & PCSK.

Description. Body 1.70–1.95 mm long. Frons in dorsal view without medial tooth. Interval between tentorial foveae slightly narrower than that between each fovea and posterior occipital margin. Antennae with article 2 only slightly wider than long, wider than article 3; article 3 wider than long; articles 4–7 about as wide as article 3, but shorter, distinctly transverse; article 7 occasionally somewhat longer than article 6; article 8 similar to article 7. Pronotum 1.56–1.67 times as long as head and 1.51–1.59 times as wide as head with eyes; lateral outline near lateral fovea with tooth; median sulcus not narrowed anteriorly, as wide as, or slightly wider than diameter of one pronotal puncture. Elytra with humeral fold extended on one quarter of elytral length. Sides of mesosternum punctate.

Measurements: HL = 0.29–0.33 mm; HW = 0.34–0.39 mm; HWmax = 0.39–0.43 mm; PL = 0.46–0.53 mm; PW = 0.60–0.67 mm; EL = 0.58–0.74 mm; EW = 0.88–1.05 mm.

Male with eyes well-developed, rounded in dorsal view, with about 20–25 facets; eyes in lateral view about as long as temples. Antenna with article 9 transverse, distinctly longer and wider than article 8; article 10 somewhat wider and as long as, or somewhat longer than article 9; article 11 slightly shorter than combined length of articles 9–10. Aedeagus (Figs 19–20) 0.33 mm long; larger paramere with basal digitiform tubercle bearing two setae, its apical edge in dorsal view rounded externally and forming a narrow projection internally.

Female with eyes angulate in dorsal view, with 7–10 facets; eyes in lateral view about 1.5 times shorter than temples. Antenna with article 9 distinctly wider and somewhat longer than article 8, transverse; article 10 similar to article 9, but slightly bigger; article 11 somewhat shorter than combined length of articles 9–10.

Distribution. *P. noai* is the only species recorded from northern Sumatra (North Sumatra province), where it was collected at 1500 m.

Comments. *Proterus noai* may be easily distinguished from other congeners by its narrow head. See discussions under *P. lucilae* and *P. pumilio*.

Etymology. The species is dedicated to Noa, the son of G. Cuccodoro.



Figs 19–22: *Proterus noai* n. sp.: aedeagus in dorsal (19) and lateral (20) views; *P. observator* n. sp.: aedeagus in dorsal (21, with both parameres) and lateral (22, larger paramere broken while reorienting the aedeagus figured separately on the right) views. Scale bars = 0.1 mm.

***Proterus observator* n. sp.**

(Figs 8–9, 21–22)

Holotype (♂, in MHNG): Indonesia, Java, W Java, Cibodas, 50 km E Bogor, 1400 m, 3–6.xi.1989 (I. Löbl, D. Burckhardt & D. Agosti) #2a [sifting of vegetational debris in montane *Lithocarpus-Castanopsis* forest].

Paratype (1): same data as holotype, 1 ♀ in MHNG.

Description. Body 2.10–2.15 mm long. Frons in dorsal view without medial tooth. Interval between tentorial foveae slightly exceeding that between each fovea and posterior occipital margin. Antennae with article 2 as wide as long (male), or transverse (female); articles 3–6 about as wide as article 2, or somewhat narrower; article 3 slightly wider than long, or distinctly transverse; articles 4–6 similar, transverse; article 7 similar to article 6 (male), or somewhat wider (female). Pronotum 1.47–1.56 times as long as head and 1.12–1.13 times as wide as head with eyes; lateral outline near lateral fovea with indistinct, blunt tooth; median sulcus distinctly narrowed anteriorly, its middle portion about as wide as, or slightly wider than diameter of one pronotal puncture. Elytra with humeral fold extended on half of elytral length, or nearly so. Sides of mesosternum impunctate.

Measurements: HL = 0.32–0.36 mm; HW = 0.36–0.42 mm; HWmax = 0.51–0.53 mm; PL = 0.50–0.53 mm; PW = 0.57–0.60 mm; EL = 0.60 (female) – 0.78 (male) mm; EW = 0.89 (female) – 0.99 (male) mm.

Male with eyes particularly well-developed, rounded in dorsal view, with about 30 large facets; eyes in lateral view reaching posterior edge of head, thus lacking temples. Antenna with article 8 about as wide as article 7, elongate, subcylindrical, nearly as long as combined length of articles 5–7; articles 9–10 subcylindrical, slightly longer and somewhat wider than article 8; article 11 elongate, longer and slightly wider than article 10. Aedeagus (Figs 21–22) 0.25 mm long; larger paramere with basal digitiform tubercle obsolete, bearing only one seta, its apical edge in dorsal view rounded externally and forming a broad projection internally.

Female with eyes angulate in dorsal view, with 4–5 facets; eyes in lateral view nearly 2 times shorter than temples. Antenna with article 8 as wide and slightly longer than article 7, transverse; article 9 slightly longer and distinctly wider than article 8, transverse; article 10 similar to article 9, but somewhat bigger; article 11 somewhat wider than article 10 and slightly shorter than combined length of articles 9–10.

Distribution. *P. observator* is the only member of the genus found outside of Sumatra. It is apparently restricted to Java (West Java province), where it was collected at 1400 m.

Comments. This species is easily distinguished from other congeners by the shortened interval between each tentorial fovea and the posterior occipital margin, and also by the antennae and eyes markedly well-developed in the male. Its larger paramere possessing an obsolete basal digitiform tubercle bearing only one seta is diagnostic. *Proterus observator* has also the areas in the middle of the frons and along the pronotal median sulcus notably more depressed than the other members of the genus.

Etymology. The specific epithet refers to the particularly well-developed antennae and eyes in the male of this species.

***Proterus pumilio* n. sp.**

(Figs 23–24)

Holotype (♂, in MHNG): Indonesia, Sumatra, Jambi, W Mt. Tujuh Lake, 1400 m, 14.xi.1989 (I. Löbl, D. Burckhardt & D. Agosti) #17 [sifting of vegetational debris in montane *Lithocarpus-Castanopsis* forest].

Paratypes (3): same data as holotype, 2 ♂♂ & 1 ♀ in MHNG.

Description. Body 1.50–1.75 mm long. Frons in dorsal view with inconspicuous medial tooth. Interval between tentorial foveae equal to, or slightly narrower than that between each fovea and posterior occipital margin. Antennae with article 2 only slightly wider than long, or distinctly transverse, wider than article 3; articles 3–7 transverse; articles 4–6 as wide as article 3, but shorter; article 7 similar to article 6, but somewhat bigger. Pronotum 1.27–1.50 times as long as head and 1.14–1.35 times as wide as head with eyes; lateral outline near lateral fovea without tooth; median sulcus not narrowed anteriorly, except occasionally near its apex, in middle portion 1.5–2.0 times as wide as diameter of one pronotal puncture. Elytra with humeral fold indistinct, extended on nearly one third of elytral length. Sides of mesosternum impunctate.

Measurements: HL = 0.26–0.28 mm; HW = 0.26–0.30 mm; HWmax = 0.35–0.39 mm; PL = 0.33–0.42 mm; PW = 0.40–0.47 mm; EL = 0.45–0.61 mm; EW = 0.67–0.79 mm.

Male with eyes well-developed, rounded in dorsal view, with about 30–35 facets; eyes in lateral view about 1.5 times longer than temples. Antenna with articles 8–10 transverse; article 8 wider and slightly longer than article 7; article 9 similar to article 8, but slightly bigger; article 10 similar to article 9, but slightly bigger; article 11 as long as combined length of articles 9–10. Aedeagus (Figs 23–24) 0.20–0.23 mm long; larger paramere with basal digitiform tubercle bearing two setae, its apical edge in dorsal view slightly sinuate internally and forming a narrow projection externally.

Female with eyes angulate in dorsal view, with 6–7 facets; eyes in lateral view more than 2 times shorter than temples. Antenna with articles 8–10 transverse; article 8 somewhat narrower than article 7; article 9 similar to article 8, but bigger; article 10 similar to article 9, but bigger; article 11 as long as combined length of articles 9–10.

Distribution. This species is known only from Sumatra (Jambi province: Mt. Kerinci area), where it was collected at 1400 m.

Comments. *P. pumilio* is the smallest species of the genus. The only other species measuring occasionally 1.75 mm or less, is *P. noai*, which has the sides of mesosternum punctate. See discussion under *P. alexandrae*.

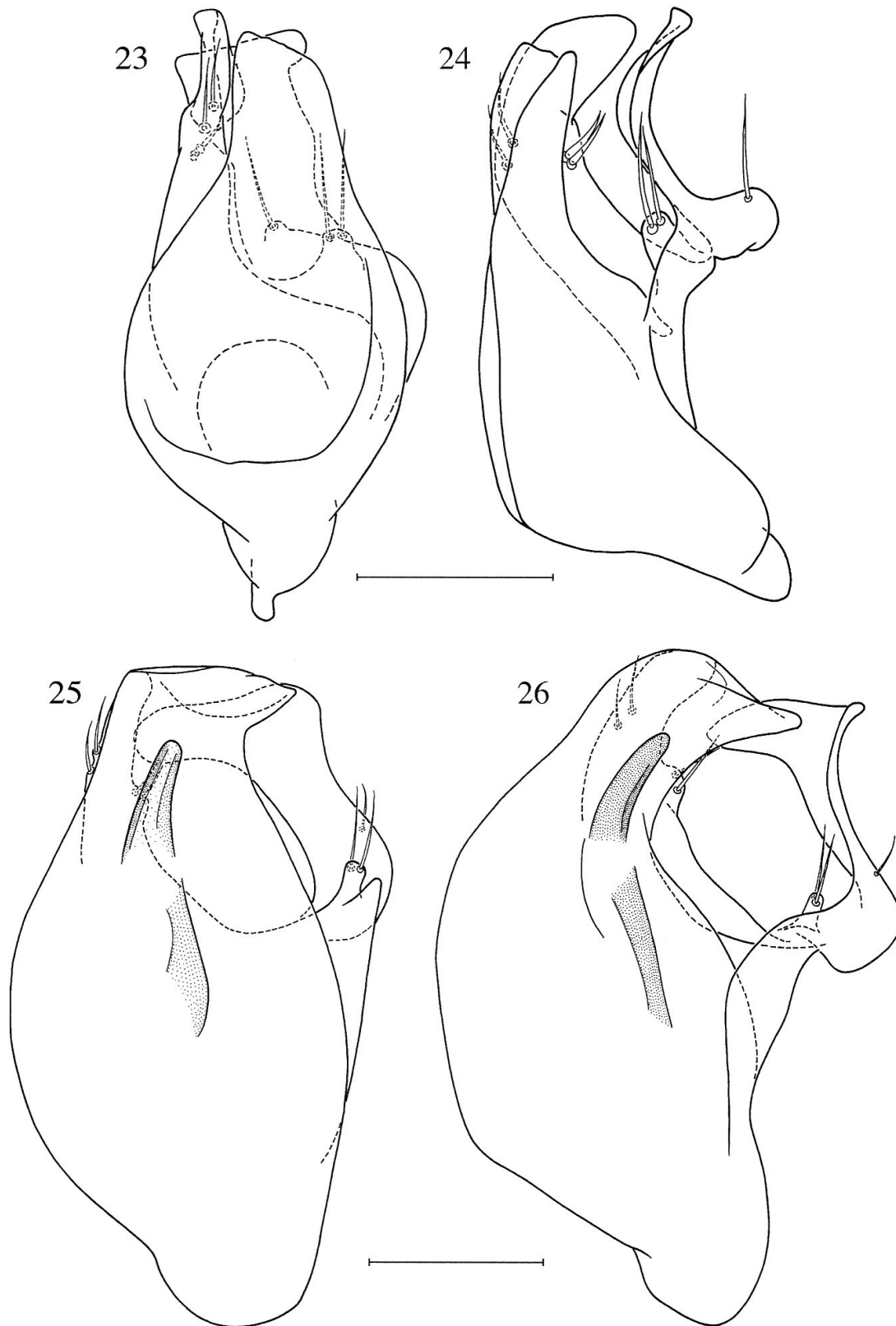
Etymology. The specific epithet refers to the small body size of this species.

***Proterus punctatus* Raffray, 1897**

(Figs 25–26)

Proterus punctatus Raffray, 1897: 231.

Type material examined (lectotype ♂, by present designation, in MNHN): «Sumatra [handwritten on white rectangular label] [Palembang] | Muséum Paris, 1917 / col. A. Raffray [typewritten on white rectangular label] | Type [typewritten on red rectangular label] | *P. punctatus* [handwritten] / A. Raffray det. [typewritten on white rectangular label] | Lectotype / *Proterus punctatus* Raffray / det. Cuccodoro & / Kurbatov 2006' [typewritten on red rectangular label]».



Figs 23–26: *Proterus pumilio* n. sp. (23–24) and *P. punctatus* Raffray (25–26); aedeagus in dorsal (23, 25) and lateral (24, 26) views; Scale bars = 0.1 mm.

Description. Body 2.00 mm long. Frons in dorsal view with inconspicuous medial tooth. Interval between tentorial foveae slightly narrower than that between each fovea and posterior occipital margin. Antennae with article 2 only slightly wider than long, somewhat wider than article 3; articles 3–7 similar, distinctly transverse. Pronotum 1.40 times as long as head and 1.25 times as wide as head with eyes; lateral outline near lateral fovea without tooth; median sulcus not narrowed anteriorly, as wide as, or slightly wider than diameter of one pronotal puncture. Elytra with humeral fold extended on one quarter of elytral length. Sides of mesosternum punctate.

Measurements: HL = 0.32 mm; HW = 0.35 mm; HWmax = 0.46 mm; PL = 0.46 mm; PW = 0.58 mm; EL = 0.70 mm; EW = 0.93 mm.

Male with eyes well-developed, rounded in dorsal view, with about 30 facets; eyes in lateral view nearly 1.5 times longer than temples. Antenna with article 8 similar to article 7, but slightly bigger; article 9 transverse, somewhat longer and wider than article 8; article 10 somewhat longer and about as wide as article 9; article 11 somewhat shorter than combined length of articles 9–10. Aedeagus (Figs 25–26) 0.385 mm long; larger paramere with basal digitiform tubercle bearing two setae, its apical edge in dorsal view rounded internally and externally.

Female unknown.

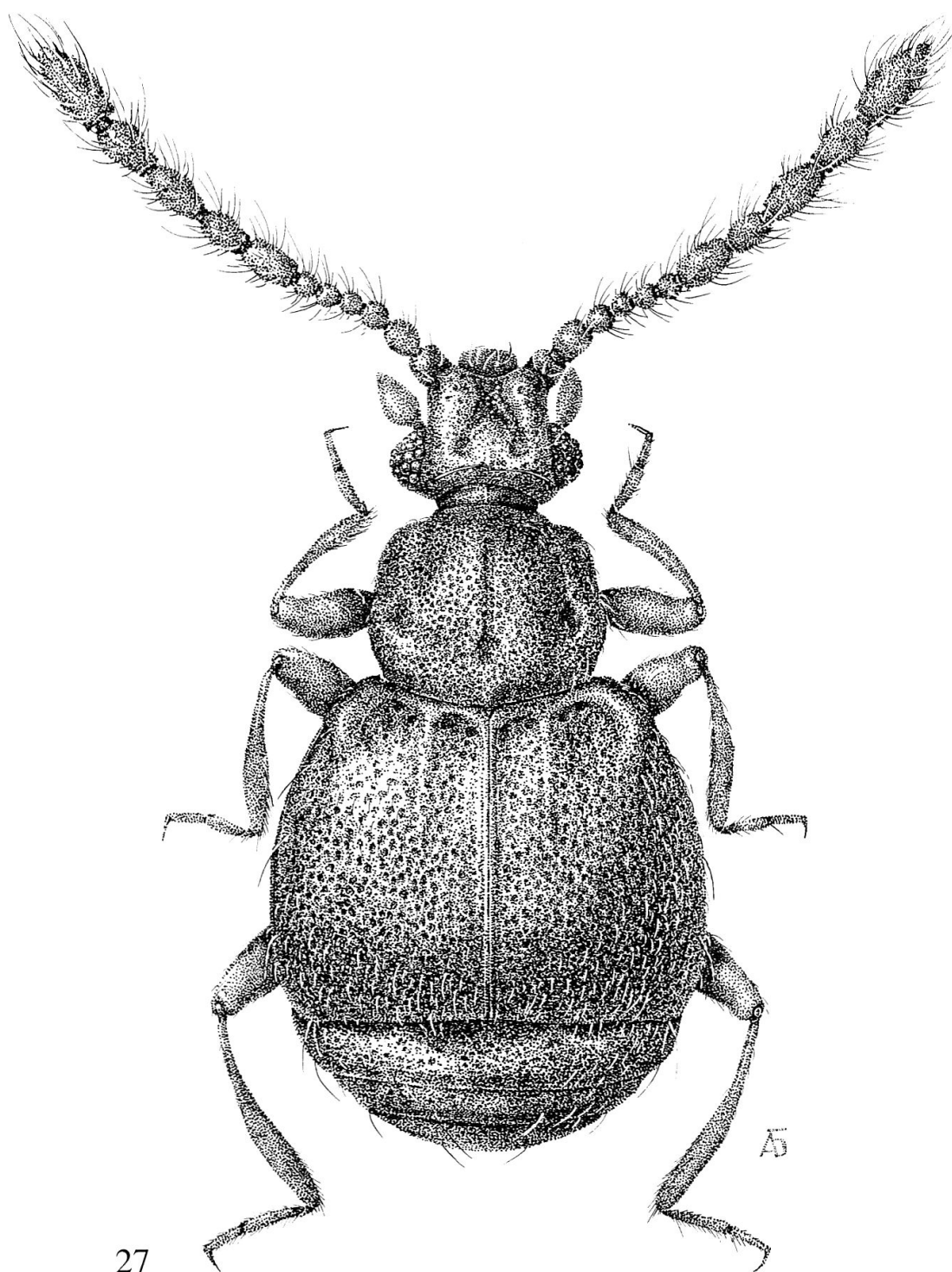
Distribution. The species is known only from the ancient type material labelled as from ‘Sumatra’, and quoted in the original description as from ‘Palembang’, which is the capital of the actual province of South Sumatra.

Comments. Raffray (1897) described *P. punctatus* on the basis of four specimens quoted as from ‘Palembang (Sumatra)’ and of ‘same very doubtful sex’. With regard to the diversity of the genus in the Barisan Range (6 species) and in the interest of stability of nomenclature, we designate here the single male type examined as lectotype.

***Exoterus* n. gen.**

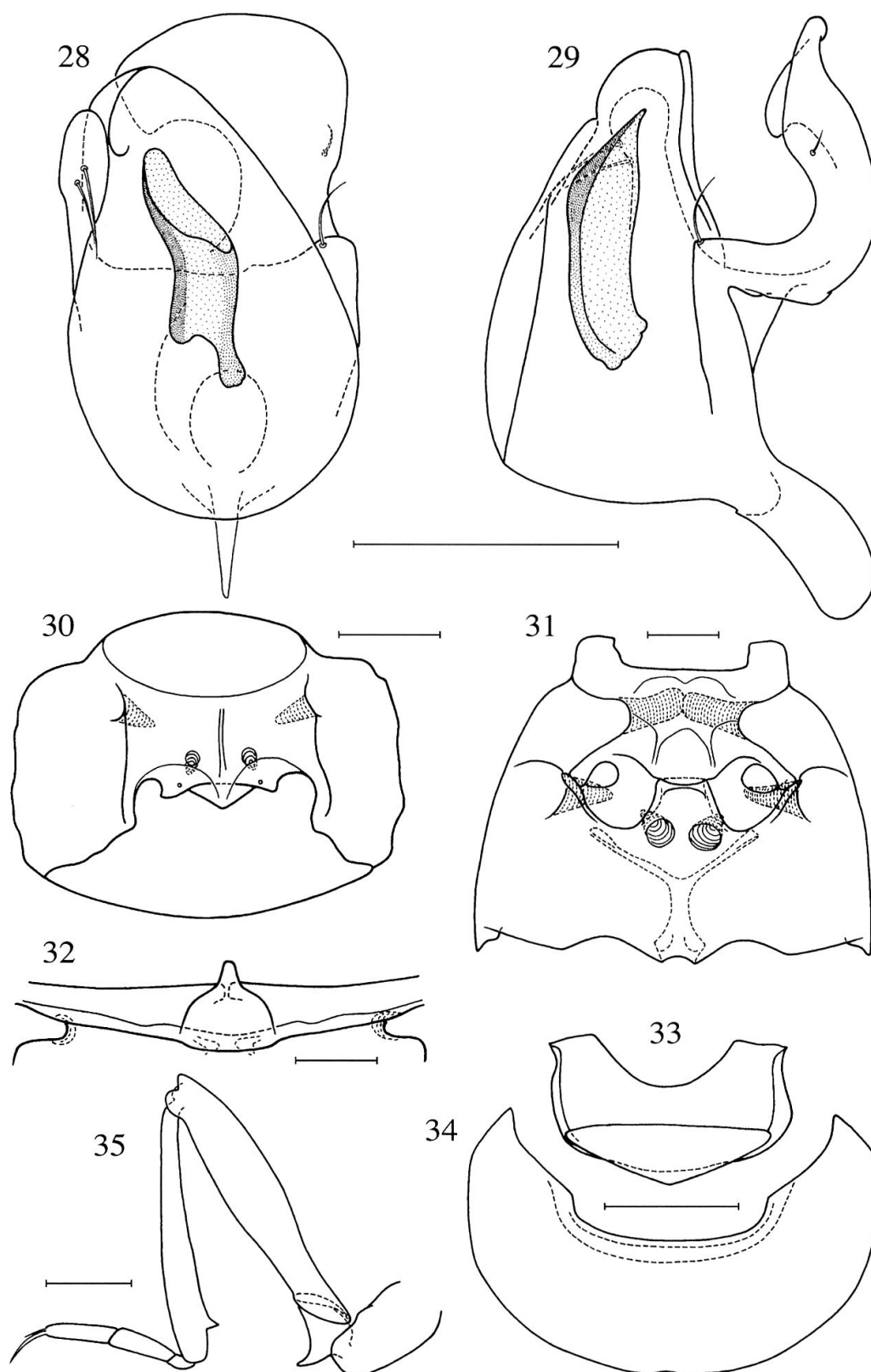
Type species: *Exoterus lannaesus* n. sp.; gender: masculine.

Description. Body (Fig. 27) 1.5–3.0 mm long, uniformly pale brown, except paler maxillary palpi; entirely covered with dense punctation, except gular constriction and sides of mesosternum. Pubescence dense and short, consisting of setae only slightly longer than distance between two neighboring punctures, with some curved, long, erect setae; medioapical pubescence of elytra not converging posteriorly. Head with pair of tentorial foveae connected anteriorly by ‘V-shaped’ sulcus, the latter not extended behind tentorial foveae. Vertex and frons distinctly depressed in middle with regards to their raised lateral sides. Antennal tubercles indistinct. Frons lacking postantennal notches. Mandibles similar to Figs 2–3. Article 4 of maxillary palpi similar to Fig. 4, with group of setae on external side. Genal areas each with a marked and smooth depression allowing accommodation of the maxillary palpi. Antenna consisting of 11 articles, with at least articles 4–6 of funicle transverse; scape notched dorsally at base, revealing basal stalk of article 2; club composed of 3 or 5 articles. Pronotum with median antebasal fovea and pair of lateral antebasal foveae, as well as median sulcus and small median carina behind antebasal fovea; median sulcus sharp, extended from median antebasal fovea almost to anterior pronotal margin; area anterior to lateral antebasal foveae depressed, lacking true later-



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Fig. 27. Habitus of *Exoterus lannaeus* n. gen. n. sp., male.



Figs 28–35: *Exoterus lannaeus* n. gen. n. sp.; aedeagus in dorsal (28) and lateral (29) views; ventral views of prosternum (30), mesosternum and metasternum (31), abdominal sternite 1 and anterior portion of sternite 2 (32), and female abdominal sternites 6 (34) and 7 (33); right anterior leg of male (35). Scale bars = 0.1 mm.

al sulci. Prosternum (Fig. 30) with pairs of lateral procoxal and anteroprosternal foveae; paranotal carinae absent; median carina present, very fine. Elytra with 4 basal foveae, the external pair grouped in same depression; subhumeral fovea prolonged with marginal carina extended on entire elytral length. Mesosternum (Fig. 31) with pair of lateral foveae; median carina absent. Mesocoxal cavities separated; pleural sulcus delimiting meso- and metasternum, sulcus distinctly 'cariniform'. Metasternum (Fig. 31) with pairs of lateral and lateral mesocoxal foveae; lacking pair of longitudinal carinae. First three visible abdominal tergites fused to corresponding sternites; paratergal-tergal suture distinct only on tergite 1; junction between tergite 4 and sternite 5 carinate; tergite 1 conspicuously longer than any other, its basal median depression supporting laterally angulate margins that project posteriorly, with pair of mediobasal foveae; tergites 2–3 lacking basal carinae; sternite 2 with 2 basolateral and 2 mediobasal foveae, the latter very reduced (Fig. 32); posterior edge of abdominal sternite 6 notched (Fig. 34); sternite 7 (Fig. 33) modified as genital plate covering genital opening (its structure slightly different between male and female).

Male secondary sexual characters affecting occasionally the size of eyes (bigger), terminal articles of the antennae (bigger and longer), and elytra (longer), as well as the shape of protrochanters, protibiae, and mesotibiae. Aedeagus with membranous median lobe and two asymmetrical parameres; larger paramere (morphologically left) lacking a basal digitiform setiferous tubercle.

Distribution and natural history. *Exoterus* is so far monotypic and apparently restricted to Thailand, where it was found in leaf litter and other decaying vegetational debris in forests at elevations ranging from 950–2500 m.

Comments. Among the genera of Proterini sensu stricto, *Proterus* and *Exoterus* uniquely share the notable absence of a pair of metasternal longitudinal carinae. They also possess very similar aedeagi. *Exoterus* differs mainly from *Proterus* by the 'V-shaped' vertexal sulcus not extended behind the tentorial foveae, by the presence of a small median carina behind the pronotal antebasal fovea and of a very fine prosternal median carina, and by the absence of a mesosternal median carina and of pronotal lateral sulci. With respect to *Proterus*, males exhibit sexual dimorphism on the legs and a much more elongate antennal club. The occurrence of two forms of conspecific males is also unknown in *Proterus*.

Etymology. Contraction of 'exo-' and 'Proterus' suggesting that *Exoterus* resembles *Proterus* but occurs elsewhere.

Exoterus lannaesus n. sp.

(Figs 27–35)

Holotype (♂, in MHNG): Thailand, Chiang Mai Prov., Chomthong Distr., Doi Inthanon, 2500 m, vi.1987 (P. Schwendinger) Barber funnel.

Paratypes (15): same data as holotype, 1 ♂ & 1 ♀ in MHNG & PCSK; same data, but 9.ii.1986, sifting, 1 ♂ in MHNG; same data, but 1780 m, 3.vi.1987, 1 ♂ in MHNG; same data, but 2300 m, 23.v.1987, 2 ♀ ♀ in MHNG & PCSK; same data, but 29.viii.1990, 1 ♂ & 2 ♀ ♀ in MHNG; same data, but 1650 m, 7.xi.1985 (D. Burckhardt & I. Löbl) [sifting of vegetational debris in forest on steep slope] 1 ♂ & 1 ♀ in MHNG; same data, but 1000 m, 8.xi.1985, 1 ♀ in PCSK; same data, but 2450 m, 9.xi.1985, #19 [sifting dead leaves at forest's edge on steep slope] 1 ♂ & 2 ♀ ♀ in MHNG.

Additional material examined (2): Thailand, Chiang Mai Prov., Chomthong Distr., Doi Inthanon, 2500 m, 9.xi.1985 (D. Burckhardt & I. Löbl) [sifting of dead leaves, rotting branches and mosses in very wet forest in ravine] 1 ♂ with unmodified antennae in MHNG; Tak Prov., Doi Musoe, 950 m, 18.ix.1990 (P. Schwendinger) 1 ♀ in MHNG.

Description. Body (Fig. 27) 1.20–1.25 mm long. Frons with anterior edge gradually deflected toward clypeus, lacking medial tooth in dorsal view. Interval between tentorial foveae slightly exceeding that between each fovea and posterior occipital margin. Antennae with article 2 as long as wide, or slightly longer than wide, distinctly wider than article 3; article 3 longer than wide; article 4 as wide as article 3, but shorter, transverse; articles 5–6 similar to, or somewhat bigger than article 4. Pronotum 1.32–1.56 times as long as head and 1.16–1.36 times as wide as head with eyes; lateral outline near lateral fovea without tooth; median sulcus straight, about as wide as diameter of one pronotal puncture. Elytra with humeral fold indistinct. Sides of mesosternum impunctate.

Measurements: HL = 0.18–0.22 mm; HW = 0.20–0.26 mm; HWmax = 0.28–0.32 mm; PL = 0.28–0.29 mm; PW = 0.36–0.40 mm; EL = 0.42–0.52 mm; EW = 0.58–0.63 mm.

Male with eyes well-developed, rounded in dorsal view, with about 20–25 facets; eyes in lateral view at least 3 times longer than temples. Antenna with articles 7–11 elongate, forming a long and distinct club about 1.5 times as long as the rest of antenna; article 7 slightly wider and two times longer than article 6; article 8 about as wide as article 7, but somewhat shorter; article 9 slightly wider and longer than article 7; article 10 as long and slightly larger than 9; article 11 shorter than combined length of articles 9–10. Protochanter (Fig. 35) with internal edge forming a spine. Protibia (Fig. 35) with internal oblique spine near apex. Mesotibia with minute internal denticle near apex. Aedeagus (Figs 28–29) 0.17–0.20 mm long; larger paramere lacking distinct basal digitiform setiferous tubercle; smaller paramere (morphological right) bearing two setae oriented toward its base.

Female with eyes angulate in dorsal view, with 5–7 facets; eyes in lateral view slightly shorter than temples. Antenna with articles 7–8 similar to articles 4–5, but slightly bigger; article 9 transverse, distinctly longer and slightly wider than article 8; article 10 wider and somewhat longer than article 9; article 11 as long as, or slightly longer than combined length of articles 9–10.

Distribution. *E. lannaeus* has been found only on the forested slopes of Doi Inthanon and Doi Musoe (Chiang Mai and Tak provinces, respectively) in north-western Thailand, where it was collected in series never exceeding 3 specimens. Most specimens (72 %) were found at elevations ranging from 2300–2500 m.

Comments. A single male from Doi Inthanon (2500 m, 9.xi.1985) exhibits eyes, antennae and elytra as those in females. It is identical to the other males with respect to the features on aedeagus and mesotibiae, but possesses much more developed protibial spines and the tip of the protochanteral spines are ventrally recurved. We place this male as conspecific with the others, and think that it represents a second male form (which is not exceptional within Pselaphinae), but in the absence of additional similar males we prefer not to include it in the type material. Considering the situation observed in *Proterus*, where females are often difficult to identify to the species level with confidence, we have also removed the single female from Doi Musoe from the type material.

Etymology. The specific epithet is derived from the ancient kingdom of Lanna, of which Chiang Mai was the capital.

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