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Discovery of Eutheiini (Coleoptera: Staphylinidae: Scydmaeninae) in Australia, with implications for phylogeny and biogeography of *Paraneseuthia*

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Abstract. The scydmaenine tribe Eutheiini is recorded from Australia for the first time. *Paraneseuthia carltoni* sp. n. and *P. booloumba* sp. n. are described and illustrated, both from Queensland. In a parsimony-based phylogenetic analysis using adult morphological characters including genital features, the Australian species together with the Melanesian type species of *Paraneseuthia* Franz, *P. peckorum* Franz, were found to be more closely related to East Palearctic congeners than to most of the *Paraneseuthia* in the Sunda-Papuan area. The topology of the tree and biogeographic data suggest a Sundaland origin of this genus, with three major dispersal routes from a center located in present-day Sumatra: (i) north-eastern colonization of the Palearctic Far East, via a continental or island-arc route; (ii) south-eastern dispersal to East Australia; and (iii) eastern dispersal to Melanesia, possibly via the Quaternary Outer-Melanesian Arc. The important role of dispersal in the evolution of *Paraneseuthia* is supported by the presence of this genus on isolated volcanic islands, such as the southern Moluccas and Fiji, which were never connected to larger land masses.

INTRODUCTION

Paraneseuthia Franz, 1986 is one of the most enigmatic genera within the tribe Eutheiini. Originally not explicitly placed in any tribe (Franz, 1986), later treated as a member of the Cephenniini (Newton & Franz, 1998) and finally transferred to the Eutheiini (Jałoszyński & Hoshina, 2004), this genus initially was known only from Melanesia and the Russian Far East (Franz, 1986; Kurbatov, 1990, 1991). This disjunct distribution turned out to be a result of an inadequate study of Scydmaeninae and a general rareness of *Paraneseuthia*. More detailed recent work has resulted in transferring some previously misplaced Japanese species to this genus (Jałoszyński & Hoshina, 2004) and in descriptions of new species from Sumatra, Borneo, West Papua and East New Guinea (Jałoszyński, 2008a, 2009, 2010). Access to new material made it possible to describe the morphology of *Paraneseuthia* in detail and confirm that north-eastern species are truly congeneric with Sunda-Papuan taxa (Jałoszyński, 2010). The most unusual characters of this genus are the maxillary palpus composed of only three palpomeres and a relatively complicated aedeagus in some species. Also characteristic of *Paraneseuthia* are the relatively stout and strongly convex body, elytra more rounded than truncated and exposing only a part of the pygidium, rudimentary basal elytral foveae, very high (i.e., strongly projecting ventrad) keel on the mesoventrite and lack of an occipital constriction. Some of these characters, very unusual for the Eutheiini, are shared only with a single genus of this tribe, *Euthiconus* Reitter, 1881.

Recent studies yielded a number of specimens from islands located east of the Wallace's line, including the Moluku Archipelago and New Guinea (Jałoszyński, 2010). Unfortunately, most species from that area are known from females only and therefore undescribed. A survey of museum collections revealed two highly intriguing, relatively flat and elongate specimens of Eutheiini from Queensland, Australia. The tribe Eutheiini was previously known predominantly from the Palearctic and Nearctic regions, with only a few species reaching SE Asia, Melanesia and Mesoamerica (e.g., Franz & Löbl, 1990; Newton & Franz, 1998; O'Keefe, 1999; Jałoszyński, 2003). The discovery of this tribe on the Australian mainland significantly fills a gap in the general distribution of Eutheiini. Detailed examination revealed that both Australian specimens not only belong to *Paraneseuthia*, but also their aedeagi show surprising similarities, not with those of their Sunda-Papuan congeners, but rather the Palearctic Far Eastern species. This observation prompted the present study, in which results of a preliminary phylogenetic analysis of species of *Paraneseuthia* and biogeographic data are combined to propose a hypothesis concerning the evolution and dispersal routes of this unusual genus.

MATERIAL AND METHODS

Specimen handling, imaging and measurements

Specimens used in this study (Table 1) are deposited in the following collections: BM – Bishop Museum, Honolulu, Hawai; MHNG – Muséum d'Histoire Naturelle, Geneva, Switzerland; NHMW – Naturhistorisches Museum Wien, Vienna, Austria; PCPJ – private collection of the author, Wrocław, Poland; PCSK – private collection of Sergei Kurbatov, Moscow, Russia; SEMC – University of Kansas, Natural History Museum and Biodiversity Research Center (Snow Entomological Collections), USA; SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany.

Dry-mounted specimens were relaxed in warm water and dissected; details of the morphology of insects permanently mounted in Canada balsam were studied under light stereo-

TABLE 1. List of taxa examined and depositories of the specimens.

Species	Origin	Depository
Eutheia scydmaenoides Stephens, 1830	Poland	PCPJ
Euthiconus conicicollis (Fairmaire et Laboulbène, 1855)	Poland	PCPJ
Paraneseuthia bicolor Jałoszyński, 2010	Indonesia: Sumatra	MHNG
Paraneseuthia booloumba sp. n.	Australia: Queensland	SEMC
Paraneseuthia carltoni sp. n.	Australia: Queensland	SEMC
Paraneseuthia devia Jałoszyński, 2008	Indonesia, West Papua	BM
Paraneseuthia guineana Jałoszyński, 2009	Indonesia, West Papua	SMNS
Paraneseuthia holzneri (Franz, 1976)	Japan: Honshu	NHMW
Paraneseuthia inexpectata Jałoszyński, 2006	Japan: Honshu	PCPJ
Paraneseuthia levigata Jałoszyński, 2010	Papua New Guinea: Madang	SEMC
Paraneseuthia paradoxa (K. Sawada, 1962)	Japan: Honshu	PCPJ
Paraneseuthia peckorum Franz, 1986	Fiji	NHMW
Paraneseuthia quadrifoveata Jałoszyński, 2010	E Malaysia: Sabah	MHNG
Paraneseuthia saga Kurbatov, 1991	Russia: Kunashir	PCSK
Paraneseuthia spinosa Jałoszyński, 2010	Indonesia: Sumatra	MHNG
Paraneseuthia trepida Kurbatov, 1990	Russia: Primorsky Krai	PCSK
Paraneseuthia sp. 1	Japan: Iriomote Is.	PCPJ
Paraneseuthia sp. 2	Papua New Guinea: Morobe	SEMC
Paraneseuthia sp. 3	Papua New Guinea: Morobe	SEMC
Paraneseuthia sp. 4	E Malaysia: Sabah	MHNG
Paraneseuthia sp. 5	Indonesia: Moluccas (Yamdena)	MHNG
Paraneseuthia sp. 6	Indonesia: Moluccas (Kai Besar)	MHNG
Paraneseuthia sp. 7	Indonesia: Moluccas (Kai Besar)	MHNG
Veraphis japonicus (K. Sawada, 1962)	Japan: Honshu	PCPJ

scopic and compound microscopes. Habitus images were taken using a Nikon Coolpix 4500 camera mounted on a Nikon Eclipse 1500 stereoscopic microscope; image stacks were processed using Combine ZP (Hadley, 2010). The measurements and abbreviations used in the text are as follows: body length (BL) is the sum of the lengths of the head, pronotum and elytra measured separately; length of head (LH) was measured from a hypothetical line joining posterior margins of eyes to anterior margin of the clypeus; width of head (HW) includes eyes; length of antennae (AnL) was measured in ventral view; length of pronotum (PL) was measured along midline; width of pronotum (PW) is its maximum width; length of elytra (EL) was measured along suture; width of elytra (EW) is its maximum width, combined; elytral index (EI) is length divided by combined width; length of aedeagus (AeL) was measured in ventral view, from the base of median lobe to apices of apical projections. All measurements are given in millimeters.

Terminology and palaeogeographic background

Terminology of morphological structures follows that of Jałoszyński (2010). Biogeographic terms and palaeogeographic data are based on Keast & Miller (1996), Hall & Holloway (1998) and Metcalfe et al. (2001). The term "Australian" is used strictly in its geographical sense, i.e. referring only to the Australian continent and not to the islands east of the Wallace's line, included in the Australian zoogeographic region.

Phylogenetic analysis

The cladistic analysis was focused on resolving relationships within *Paraneseuthia*. The ingroup taxa included all described species of the genus, except *P. vitilevui* Franz, 1986 from Fiji. As an outgroup three species of Eutheiini were selected, belonging to *Eutheia* Stephens, 1830, *Euthiconus* Reitter, 1881 and *Veraphis* Casey, 1897. These genera are partly sympatric with *Paraneseuthia* and it was possible to examine their morphology in detail. It was not possible to study the morphology (especially details of the mouthparts) of the three remaining genera of Eutheiini in detail – *Eutheimorphus* Franz & Löbl, 1990 and *Paeneutheia* Jałoszyński, 2003 (both from Borneo) are known from minute and fragile types only and the Italian endemic *Euthiopsis* Müller, 1925 is very rare and no specimens were available for dissection.

Phylogenetic analysis was based on 40 parsimony-informative, non-additive adult morphological characters; inapplicable characters were assigned a gap value ("–") and treated equivalent to missing data ("?"). Data matrix was assembled in Nexus Data Editor for Windows v. 0.5.0 (Page, 2001); parsimony analysis was conducted in TNT (Goloboff et al., 2008) under equal weights using the implicit enumeration strategy; the analysis was rooted to *Eutheia*. The standard bootstrapping (1,000 replicates) was conducted also in TNT. Trees were displayed in TreeView (Page, 1996) and annotated in Corel Photo Paint. The data matrix is presented in Table 2.

List of adult morphological characters and character states used in phylogenetic analysis

1. Body shape: slender and flattened (0); moderately slender and moderately convex (1); stout and strongly convex (2).
2. Body length: large, distinctly more than 1 mm (0); small, 1 mm and less (1).
3. Vestiture on dorsum: short, dense and recumbent to suberect (0); long, sparse and erect (1).
4. Occipital constriction: present (0); absent (1).
5. Prostheca: absent (0); present (1).
6. Subapical mandibular tooth: with single apex (0); with double apex (1).
7. Maxillary palpomere I: broadens towards apex (0); subcylindrical (1).
8. Maxillary palpomere IV: subconical, gradually narrowing towards apex (0); very short, button-like (1); absent (2).
9. Antennomeres IX–XI: modified, with impressions or excavations (0); non-modified (1).
10. Basisternal part of prosternum: much longer than procoxal cavities (0); much shorter than procoxal cavities (1).

Table 2. Data matrix of adult morphological characters used in phylogenetic analysis. Inapplicable characters marked as "–", missing data as "?".

	1111111111222222222233333333334
	1234567890123456789012345678901234567890
Eutheia scydmaenoides	0000000000000000000000-000-000000000-00
Veraphis japonicus	00001100000020000000000-0001100000000-20
Euthiconus conicicollis	1011110111112101211001O-000011000000O---
Paraneseuthia paradoxa	1101001211111111110100-11000111100000-10
Paraneseuthia trepida	11010012111111111110100-1100010111011120
Paraneseuthia saga	11010012111111111110100-1100010111011020
Paraneseuthia holzneri	11010012111111111110100-11000111?01?-20
Paraneseuthia inexpectata	11010012111111111110100-1100010111011120
Paraneseuthia guineana	200100121111111111101011001110000010-20
Paraneseuthia quadrifoveata	1011001211111111111100111100010000000-20
Paraneseuthia levigata	20110012111111111111002-0100100100011020
Paraneseuthia spinosa	20110012111111111110110-0000100010110-10
Paraneseuthia devia	21010012111111111110102-0011100000010-20
Paraneseuthia bicolor	20110012111111111111100-0000101010110-10
Paraneseuthia carltoni	0111001211111111111000101110011100011021
Paraneseuthia booloumba	0111001211111111111000101110011100011021
Paraneseuthia peckorum	20110012111111111111000-1100011010110-10

11. Adcoxal part of prothoracic hypomeron: not projecting mesad (0); projecting mesad (1).
12. Mesothoracic anapleural clefts: strongly oblique in relation to the longitudinal body axis (0); nearly parallel to the longitudinal body axis or only slightly oblique (1).
13. Mesoventral process: very broad (ca. 3× as long as broad) (0); moderately broad (4–5× as long as broad) (1); narrow (7 or more times as long as broad) (2).
14. Mesothoracic pleural suture: outer part indiscernible (mesepimera and mesanepisterna partly fused) (0); entire (1).
15. Metaventrite: long and broadening caudally (0); short and nearly subquadrate (1).
16. Apex of elytron: truncated (0); rounded (1).
17. Basal elytral foveae: single and large (0); single, rudimentary (1); two (2).
18. Subcuticular sockets of basal elytral foveae: long, broad at base (0); very short, rudimentary (1).
19. Exposed abdominal tergites: two (pygidium and propygidium) (0); one (pygidium) (1).
20. Ante-basal pronotal impressions: shallow and diffused (0); deep and sharply delimited (1).
21. Protibiae in males: without median expansion (0); with an expansion on the internal margin near middle (1).
22. Protrochanters in males: non-modified (0); with distinctly angulate or projected distal part (1).
23. Dorsum of head of males: non-modified (0); with lateral pits (1); with lateral longitudinal grooves or impressions (2).
24. Lateral pits on dorsum of head of males: one pair (0); two pairs (1).
25. Aedeagus: strongly elongate (0); short, stout (1).
26. Basal part of median lobe of aedeagus: symmetrical (0); slightly asymmetrical (1).
27. Apical part of median lobe of aedeagus: symmetrical (0); distinctly asymmetrical (1).
28. Shape of ventral membranous area of aedeagus: circular (0); oval (1).
29. Location of ventral membranous area of aedeagus: distant from base of median lobe (0); close to base of median lobe (1).
30. Median part of ventral membranous area of aedeagus: not thickened and sclerotized similarly to surrounding areas (0); thickened and sclerotized more than surrounding areas (1).
31. Width of ventral membranous area of aedeagus: much wider than half width of basal capsule of median lobe (0); about half as wide as width of basal capsule of median lobe (1).
32. Subapical lateral lobes of aedeagus: absent (0); present (1).
33. Endophallus: without pair of elongate sclerites (0); with pair of elongate hook- or rod-like sclerites (1).
34. Median subapical part of apex of median lobe of aedeagus: without T-shaped or Y-shaped structure (0); with T-shaped or Y-shaped structure (1).
35. Setae on apex of median lobe of aedeagus: absent (0); present (1).
36. Apex of median lobe of aedeagus: straight, rounded or pointed (0); notched, emarginated or bifurcated (1).
37. Lateral apical projections on aedeagus: absent (0); present (1).
38. Shape of lateral apical projections on aedeagus: with narrow, pointed apices (0); with broadly rounded apices (1).
39. Length of parameres: long, reaching apex of median lobe (0); medium, not reaching apex of median lobe but their apices not very distant from it (1); short, apices distant from apex of median lobe (2).
40. Apices of parameres: not broadened (0); distinctly broadened (1).

RESULTS

Descriptions

Paraneseuthia carltoni sp. n.

(Figs 1, 3, 4)

Diagnosis

Aedeagus in ventral view with left apical projection bearing a sub-basal sub-triangular tooth and right projection broadly rounded at apex.

Description (male)

Body (Fig. 1). Small (BL 0.85), slender and flattened, light brown, glossy, with yellowish vestiture.

Head. Head capsule broadest across large and strongly convex compound eyes; HL 0.13, HW 0.18; vertex and frons confluent and weakly convex, frons between eyes with pair of small and shallow pits; supra-antennal tubercles barely marked; entire dorsum of head appears impunctate at magnification 125× and sparsely covered with long, erect setae. Antennae with distinctly delimited club composed of antennomeres IX–XI, AnL 0.30, antennomeres I–II enlarged, each much longer than broad, III–VI each slightly longer than broad, VII–VIII slightly transverse, IX–X strongly transverse, XI broader than X and about as long as IX–X together.

Pronotum. In dorsal view sub-quadrate with all margins broadly rounded, barely marked front angles and distinct but blunt hind angles; PL 0.23, PW 0.25; base on each side with obtuse L-shaped shallow impression; disc covered with very sparse, shallow and small, inconspicuous punctures and sparse, long sub-erect setae.

Elytra. Oval, more convex than pronotum, broadest in middle; EL 0.50, EW 0.34, EI 1.48; punctures on elytral disc slightly more distinct than those on pronotum, fine and sparse; setae slightly denser and less erect than those on pronotum. Hind wings fully developed.

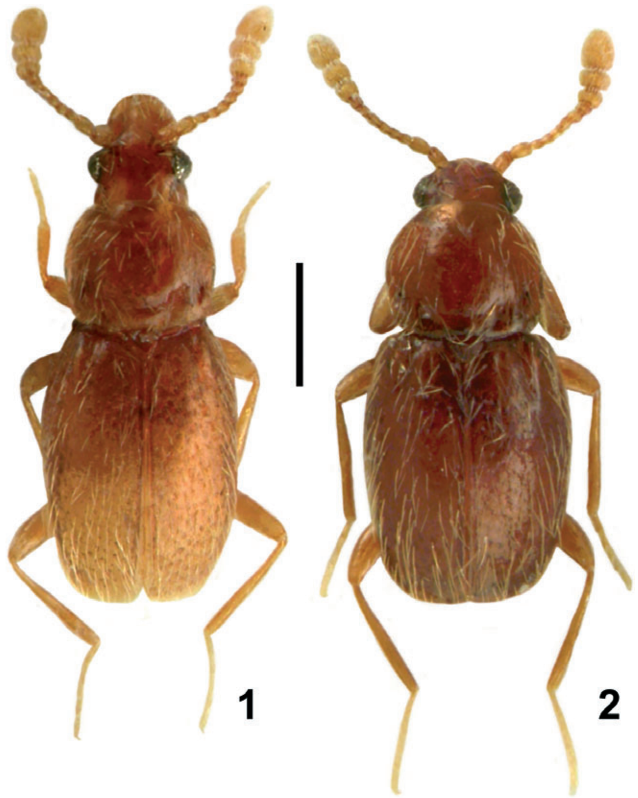
Legs. Without modifications and tibiae nearly straight.

Aedeagus (Figs 3, 4**).** Median lobe stout, with slightly asymmetrical basal part and strongly asymmetrical apical projections: in ventral view left projection strongly recurved and with large, sub-triangular tooth near base, right projection with broadly rounded apex; AeL 0.20.

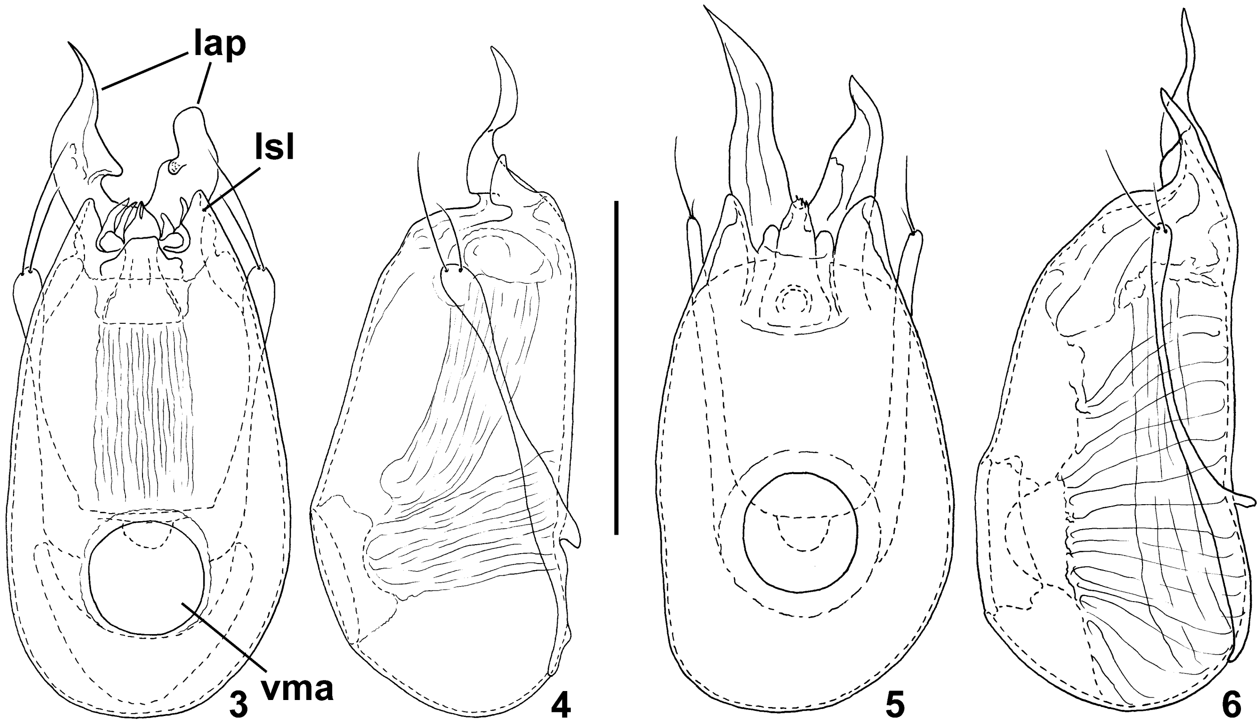
Type material. Holotype (male): Australia, Queensland, 20 km NW Maleny, Booloumba Creek, 150 m, 26.–29.iii.1993, C. Carlton, at black light (SEMC).

Etymology. The name of this species is dedicated to Christopher Carlton (Louisiana State Arthropod Museum), who collected both species described in this paper.

Distribution. Australia, Queensland.



Figs 1–2. Dorsal habitus of Australian *Paraneseuthia*. 1 – *Paraneseuthia carltoni* sp. n., holotype male; 2 – *Paraneseuthia booloumba* sp. n., holotype male. Scale bar: 0.2 mm.



Figs 3–6. Aedeagi of Australian *Paraneseuthia* from ventral (3, 5) and lateral (4, 6) view. 3, 4 – *Paraneseuthia carltoni* sp. n.; 5, 6 – *Paraneseuthia booloumba* sp. n. Abbreviations: lap – lateral apical projection; lsl – lateral subapical lobe; vma – ventral membranous area. Scale bar: 0.1 mm.

Fig. 7. Two most parsimonious trees (L = 78; CI = 0.60; RI = 0.75) obtained from implicit enumeration analysis of a data matrix of unweighted and unordered adult morphological characters (A, B) and a strict consensus tree (C). Numbers beneath branches represent mapped synapomorphies, standard bootstrap (1,000 replicates) support values are shown above branches (values < 50 not shown).

Paraneseuthia booloumba sp. n.

(Figs 2, 5, 6)

Diagnosis

Aedeagus in ventral view with left apical projection devoid of subbasal tooth and right projection with pointed apex.

Description (male)

Body (Fig. 2) externally differs from that of *P. carltoni* only in proportions; BL 0.85, HL 0.13, HW 0.19, AnL 0.33, PL 0.23, PW 0.28, EL 0.50, EW 0.35, EI 1.43.

Aedeagus (Figs 5, 6). Median lobe stout, with slightly asymmetrical basal part and strongly asymmetrical apical projections: in ventral view left projection slightly recurved and without sub-basal tooth, right projection with pointed apex; AeL 0.20.

Type material. Holotype (male): Australia, Queensland, 20 km NW Maleny, Booloumba Creek, 150 m, 26.–29.iii.1993, C. Carlton, at black light (SEMC).

Etymology. Locotypical; this species is named after the Booloumba Creek.

Distribution. Australia, Queensland.

Bionomics of Australian *Paraneseuthia*

According to the collector (Carlton, pers. comm.) both new species were collected at UV light in an open riparian area with the invasive *Lantana* (Verbenaceae) growing abundantly along the sides of the creek. The area near the collecting site was mainly riparian rainforest with large trees and a closed canopy, palms at midcanopy and a lush understory of shrubs and vines; nearby forests range from wet sclerophyll to small patches of rainforest. There is very little information on where hitherto described Sunda-Papuan species were collected, so this is by far the most detailed information on the biotope of hot-climate *Paraneseuthia*. Nothing is known about the microhabitat preferences of the subtropical group, while the temperate north-eastern species have been usually collected from rotten deciduous wood, in some cases hollow

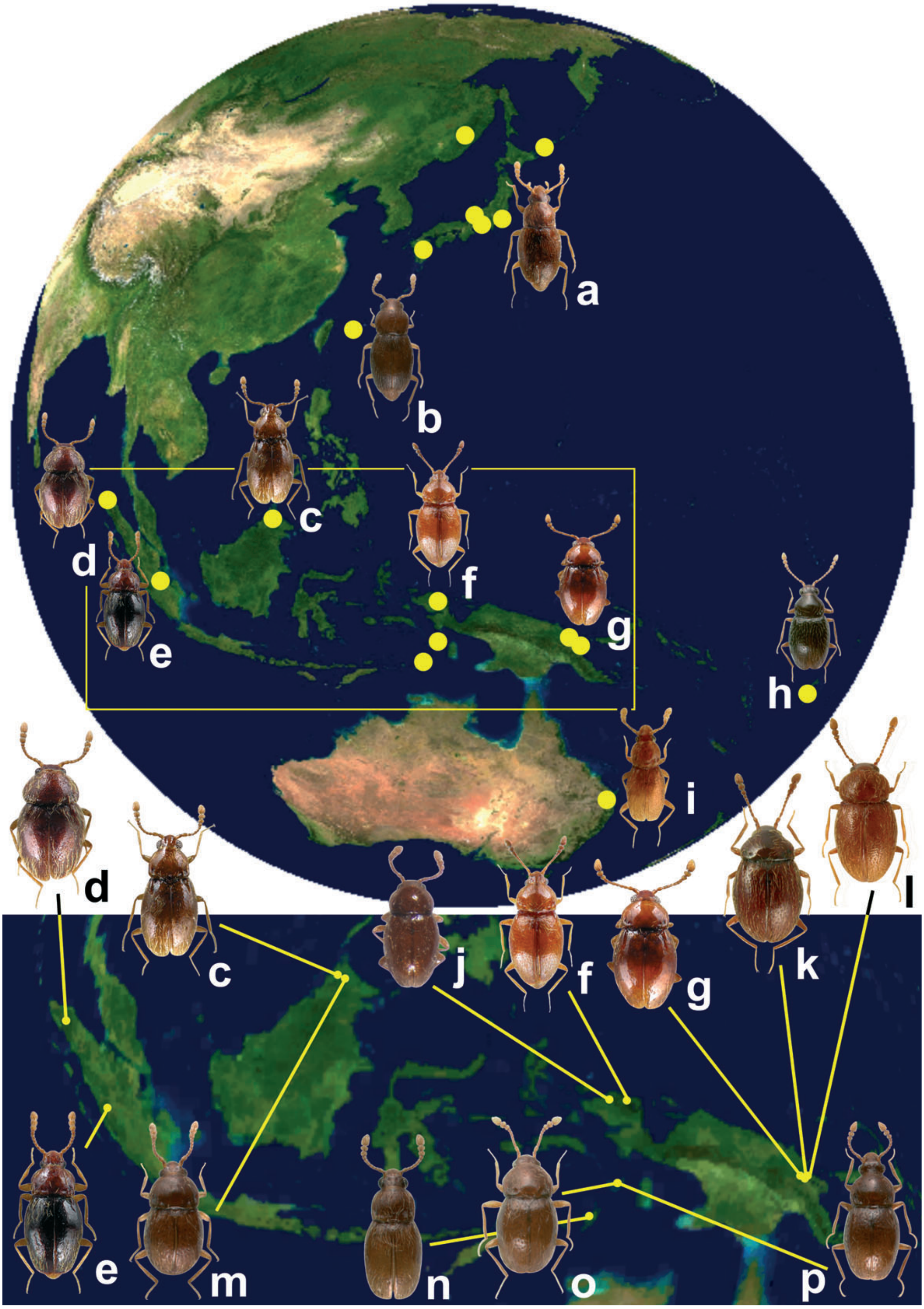


Fig. 8. World distribution of *Paraneseuthia* (area in yellow frame magnified in bottom panel), with examples of the diversity in habitus: a – *Paraneseuthia inexpectata*, Honshu; b – *Paraneseuthia* sp. 1, Iriomote Is.; c – *P. quadrifoveata*, Sabah; d – *P. spinosa*, Sumatra; e – *P. bicolor*, Sumatra; f – *P. guineana*, West Papua; g – *P. levigata*, East New Guinea; h – *P. peckorum*, Fiji; i – *P. carltoni* sp. n., Queensland; j – *P. devia*, West Papua; k – *Paraneseuthia* sp. 2, East New Guinea; l – *Paraneseuthia* sp. 3, East New Guinea; m – *Paraneseuthia* sp. 4, Sabah; n – *Paraneseuthia* sp. 5, Yamdena Is.; o – *Paraneseuthia* sp. 6, Kai Besar Is.; p – *Paraneseuthia* sp. 7, Kai Besar Is.

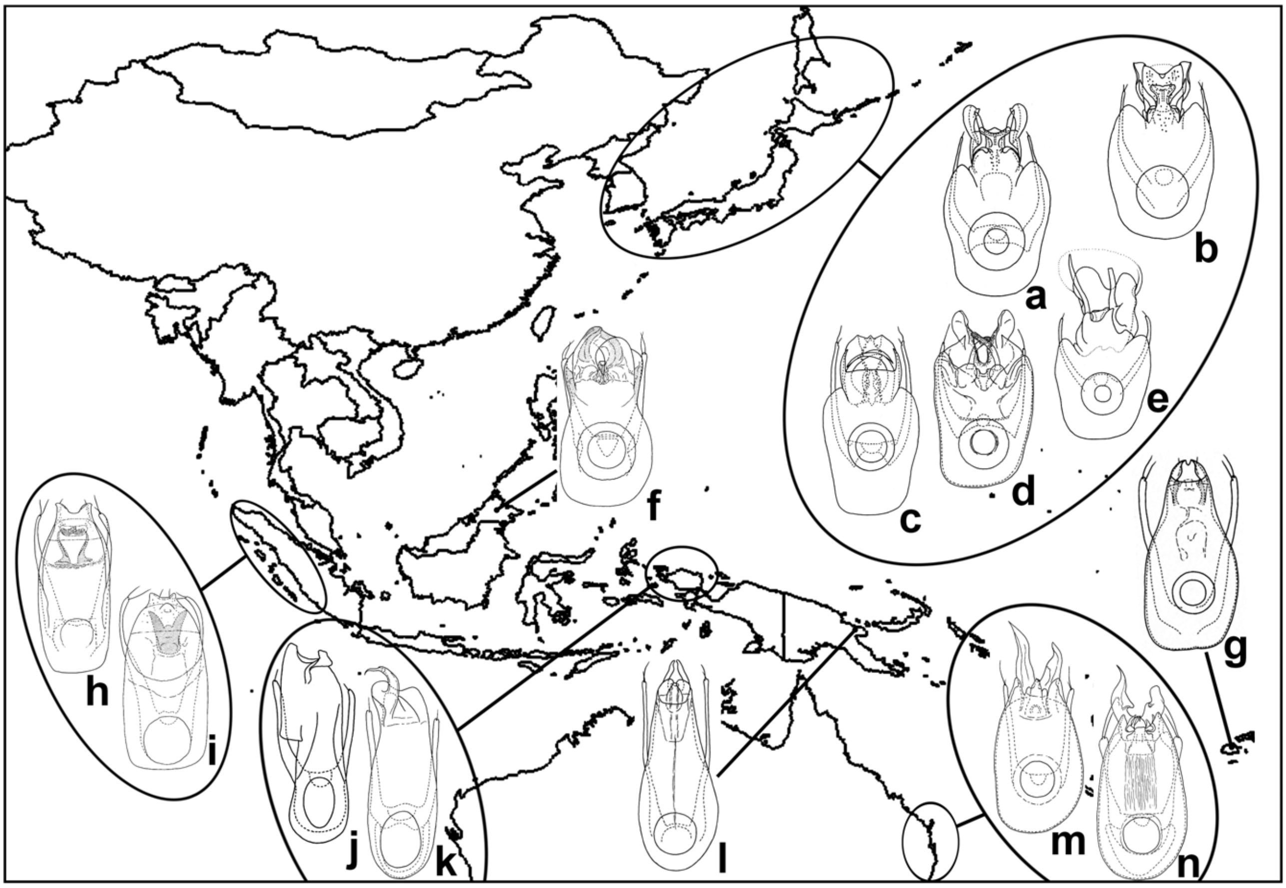


Fig. 9. World distribution of *Paraneseuthia* and diversity of aedeagi: a – *Paraneseuthia trepida*, Primorsky Krai; b – *P. saga*, Kunashir; c – *P. paradoxa*, Honshu and Kyushu; d – *P. inexpectata*, Honshu; e – *P. holzneri*, Honshu; f – *P. quadrifoveata*, Sabah; g – *P. peckorum*, Fiji; h – *P. bicolor*, Sumatra; i – *P. spinosa*, Sumatra; j – *P. devia*, West Papua; k – *P. guineana*, West Papua; l – *P. levigata*, East New Guinea; m – *P. booloumba* sp. n., Australia; n – *Paraneseuthia carltoni* sp. n., Australia.

trees (see Jałoszyński, 2006, 2010). Other aspects of the biology of *Paraneseuthia* remain unknown.

Phylogeny

The implicit enumeration run of TNT resulted in two equally parsimonious trees (L = 78, CI = 0.60, RI = 0.75) (Fig. 7A, B). Although mostly resolved, the strict consensus tree (Fig. 7C) has generally low support values for most of the recovered branches. Species of the Sunda-Papuan branch (*P. bicolor*, *P. spinosa*, *P. devia* and *P. guineana*) share non-modified protibiae of males (character #21(0)) and a symmetrical base of the aedeagus (#26(0)); this lineage was recovered as a sister to all other *Paraneseuthia* – a branch comprising all East Palearctic, Australo-Melanesian and two Sunda-Papuan species (*P levigata* and *P. quadrifoveata*), the base of the aedeagus of which is also asymmetrical (#26(1)). The clade composed of the north-eastern group + Australian species, characterized by a very small body size (#2(1)), shallow and diffused ante-basal pronotal impressions (#20(0)) and the presence of subapical lateral projections on the median lobe of aedeagus (#32(1)), was recovered as sister to Bornean *P. quadrifoveata*, Papuan *P. levigata* and Melanesian *P. peckorum*. The Australian species, which share a flattened and strongly elongate body (#1(0)), the dorsum of the head of males with lateral pits (#23), aedeagus with an asymmetrical apex (#27(1)) and parameres with broadened apices (#40(1)), were placed on the tree as a sister group to the north-eastern branch (composed of Russian Far Eastern and Japanese *Paraneseuthia*). The north-eastern lineage is characterized by the short and dense vestiture (#3(0)), modified protibiae in males (#21(1)) and an endophallus bearing a pair of elongate sclerites (#33(1)).

Links between morphology and biogeography

Fifteen described and several undescribed species of *Paraneseuthia* are distributed from the sub-siberian and temperate zones of the Palearctic Far East in the north, through the Sunda Islands, New Guinea, eastern Australia and Fiji in the south (Fig. 8). The north-eastern group associated with a cool climate inhabits Primorsky Krai, Kunashir Is., Honshu and Kyushu and is extremely uniform in its external morphology and structures associated with the aedeagi. These species are very difficult to identify on the basis of their external morphology, and their aedeagi (Fig. 9) are stout, with a slightly asymmetrical base of the median lobe. The apical part of the latter is sharply delimited and relatively complicated, and the endophallus is provided with a pair of elongate sclerites, partly protruding from the apex of the aedeagus even in the resting position (detailed illustrations can be found in

Jałoszyński & Hoshina, 2004 and Jałoszyński, 2006). This is a more complicated structure than that recorded for all remaining congeners. In contrast, species of the hot and moist environment of Sumatra, Borneo and New Guinea show a distinctly broader range of morphological variation, including much more diversified aedeagi which differ from the copulatory organs of the northern *Paraneseutheia*. This geographic group (Fig. 8) includes species with remarkable morphology which can be identified solely on the basis of external characters. Species from this area range from very small to very large; stout and strongly convex to slender and slightly flattened; nearly impunctate to densely and coarsely punctate; with short, nearly recumbent vestiture or with very long and strongly erect setae; bearing sharply marked and deep or diffused and shallow ante-basal impressions on the pronotum; additionally some of them have various male secondary sexual characters on the vertex. Their aedeagi are similarly heterogenous (Fig. 9); general shapes and details of median lobes differ very much between species from Borneo, Sumatra and various parts of New Guinea.

A single female of an undescribed species was collected by the author in a subtropical moist forest in the Iriomote Island in the south-west part of the Japanese Ryukyus. Its morphology seems intermediate between the north-eastern group and some Sunda-Papuan *Paraneseuthia.* Undescribed species, known only from females, are also known from the southern Maluku Islands (Kai Besar and Yamdena), Morobe Province of the eastern part of Papua New Guinea and from Borneo; their morphology (Fig. 8) additionally supports the thesis of a more diverse radiation of Sunda-Papuan *Paraneseuthia* than of the north-eastern lineage.

The isolated Melanesian *P. peckorum* from the distant Fiji Islands has an external morphology similar to that of the Sunda-Papuan *P. bicolor*, *P. levigata*, *P. guineana*, sp. 4, sp. 6 and sp. 7, while the general appearance of the Australian *P. carltoni* and *P. booloumba* only remotely resembles the remaining members of the genus. However, the aedeagi of the Melanesian and especially Australian species are most similar to those of the north-eastern lineage.

DISCUSSION

Reconstructing the phylogeny and explaining the observed distribution of *Paraneseuthia* (and other Scydmaeninae) is hampered by several factors. One of them is the limited set of morphological characters available for analysis. The generally poor knowledge on the evolution and internal relationships within Scydmaeninae makes it difficult to interpret some potentially important characters and especially to identify homoplasies or parallelisms. Some characters used in the present study may therefore reflect poorly understood evolutionary events and their unambiguous interpretation is not possible with the current state of knowledge. For instance, some of the character states of the shape of tibiae (#21, modified vs. unmodified), the base of the median lobe (#26, symmetrical vs. asymmetrical) or the apex of the aedeagus (#27, symmetrical vs. asymmetrical) are likely homoplasies or reversals, and the ancestral state, although presumable (i.e., unmodified tibiae, symmetrical base and symmetrical apex of the aedeagus), is not obvious. The flattened and elongate body characteristic of the Australian *Paraneseuthia* may very likely represent a plesiomorphy of the Eutheiini and is the result of a reversal in *P. carltoni* and *P. booloumba*. A comprehensive study of all Eutheiini may clarify the status of some character polarities and result in more robust phylogenies of individual genera and species. In the case of such small and rare beetles, biogeographic analyses are also affected by missing data and unrecorded extinctions. Although the selected areas of SE Asia, the Far East or Australia are relatively well surveyed, it is probable that the distribution of *Paraneseuthia* is broader than reported and discussed in the present study and new findings would modify the hitherto obtained results. Fossil records of Eutheiini are exceptionally scarce and amber inclusions (the only available fossil record of such small insects) of *Paraneseuthia* or any possibly closely related taxa have never been described. Having in mind these constraints, the hypothesis presented below, accounting for the known distribution of this genus and its phylogenetic background, must be treated as preliminary and in need of verification.

A detailed comparative study of the morphology of north-eastern and Sunda-Papuan species of *Paraneseuthia* carried out recently confirmed that despite remarkable differences in general appearance they share a unique set of diagnostic characters (Jałoszyński, 2010). However, differences in structures associated with aedeagi were found to be a major problem in attempting an analysis of evolutionary relationships between northern and southern species. Discovery of *Paraneseuthia* in Australia not only filled a gap in the hitherto known distribution of this genus, but the genital characters of *P. carltoni* and *P. booloumba* turned out to be crucial for putting forward a hypothesis about the evolution of this enigmatic and apparently highly derived component of Eutheiini.

Although the phylogenetic analysis of species of *Paraneseuthia* must be treated as preliminary as the support values for most of the recovered branches were too low for the tree topology to be fully conclusive, these results combined with biogeographic data seem to have important implications for reconstructing the phylogeny of this genus. In Scydmaeninae in general, and in the (probably sister) tribes Eutheiini and Cephenniini, the morphology within genera is very uniform and attempts to clarify relationships between species on the basis of external characters most often result in highly polytomous trees (Jałoszyński, unpubl. data). On the other hand, the spectrum of shapes and details of aedeagi is so broad that the term "hyperdiverse" perfectly reflects intra- and intergeneric variation in male copulatory organs. One of the major problems in reconstructing the phylogeny of Scydmaeninae is the fact that the aedeagi are so different between genera that it is a major challenge to establish homologies between various structures. For instance, externally the most similar genera in Eutheiini, *Eutheia* and *Veraphis*, share a large number of unique apomorphies, but have very different aedeagi (e.g., Jałoszyński & Hoshina, 2005; Jałoszyński, 2008b), so that only their most plesiomorphic structures can be recognized as homologous with certainty – the parameres, the basal orifice and possibly also the ventral membranous area. Not only a general shape, but also details of the endophallus and apical structures of the median lobe are so different that characters associated with these important parts are not parsimony-informative when a genus-level analysis is carried out. *Paraneseuthia*, externally most similar to *Euthiconus*, and indeed recovered as a sister group to that genus, has the most complex aedeagus of all Eutheiini, which is quite different from that of *Euthiconus* (see Figs 5G–H in Jałoszyński, 2003), so that genital characters do not support a close relationship between these two genera.

On the other hand, it is common in the Scydmaeninae for species with similar aedeagi to be dissimilar in appearance. *Paraneseuthia bicolor* and *P. spinosa* have nearly identical aedeagi, but externally they are obviously different species. Their distribution (along the Barisan mountain range in Sumatra) and the similarities in their aedeagi suggest a close evolutionary relationship despite their external dissimilarities. The very small West Papuan *Paraneseuthia devia* and much larger *P. guineana* is another example of such a pair, although in this case the morphological differences are not as striking as in the Sumatran species.

When the genital characters of individual species are compared, the Australasian distribution of *Paraneseuthia* shows an interesting anomaly. The characters associated with aedeagi, and the most derived position on the obtained tree, bind together geographically distant Palearctic (north-eastern) and Australian (south-eastern) species. All of them have lateral subapical lobes on the median lobe (#32(1)) and in most of them (with *P. paradoxa* being the only exception) the apex of the median lobe is strongly emarginated, so that the lateral parts form lateral apical projections (unique combination of characters #36(1) and #37(1)). When these species are compared with *P. devia* and *P. guineana*, it is difficult to find homologous structures associated with the apical and subapical part of the median lobe. Interestingly, aedeagi most similar to those of the Palearctic and Australian species are found in *P. quadrifoveata*, a species geographically closest to the north-eastern group, and in *P. peckorum*, a Melanesian species geographically close to the Australian lineage. In species from Sumatra and West Papua the aedeagi are strongly elongate (#25(0)), with symmetrical bases (26(0)) and with different apical and subapical structures. The aedeagus of West Papuan *P. levigata* shows some intermediary characters – it is strongly elongate (#25(0)), but its base is slightly asymmetrical (26(1)) and the apical part bears a pair of apical projections (37(1)).

The most plausible region of origin of *Paraneseuthia* seems to be the western part of the Sundaland area. This genus occurs on volcanic islands that were never connected to any large land mass, such as the southern part of the Maluku Archipelago and Fiji. Therefore, dispersal without a doubt has played an important role in the evolution of *Paraneseuthia*. The aedeagi of Sumatran *P. bicolor* and *P. spinosa* seem to be the most plesiomorphic, entirely symmetrical (as in all the species of the most basal *Eutheia* and *Veraphis* and the sister genus *Euthiconus*), with only slightly emarginated apices and simple endophalli. The common ancestor of the north-eastern and south-eastern lineages must have acquired the remarkable asymmetry of the basal part of the aedeagus, a deeper apical emargination and the subapical lateral lobes, which was later inherited by and conserved in most Palearctic and Australian descendants. Fiji might have been colonized via the Outer-Melanesian Arc. It has been demonstrated that the series of island arcs formed during the Quaternary served as an important dispersal route from New Guinea to the area of the present-day Tonga Trench (Keast & Miller, 1996). Therefore, it is very likely that the Melanesian *P. peckorum*, a sister taxon to the north-eastern + south-eastern lineages, is an offshoot of a Sundaland ancestor and not derived from the Australian *Paraneseuthia*. This explains why the aedeagus of *P. peckorum* has the general plan of the north-eastern and south-eastern lineages, but the external morphology of this species resembles that of some Sunda-Papuan *Paraneseuthia* (e.g., *P. bicolor*). It is likely that the common ancestor of all Palearctic, Australian and Melanesian species might have had an aedeagus with an asymmetrical base, but without subapical lateral lobes and with a weakly emarginated apex. The aedeagus of East Papuan *P. levigata* (strongly elongate but with a slightly asymmetrical base and bifurcated apex of the median lobe) and the unusual aedeagi of West Papuan *P. guineana* and *P. devia* may represent forms evolved during the radiation that occurred only in the Sundaland area.

The Palearctic branch of *Paraneseuthia*, derived from a Sundaland ancestor, is interesting from an ecological and biogeographical point of view. This is a group adapted to a cool climate, and a comparative study of possible morphological and physiological adaptations to northern latitudes may provide interesting results. The north-eastern colonization route also remains unclear. Species from the Japanese Archipelago (including Kunashir) are very similar to *P. trepida* that occurs in the continental part of the Far East, but taking into account the ability of *Paraneseuthia* to disperse and colonize islands, two expansion routes seem equally plausible. Ancestors of the north-eastern lineage might have colonized Japan after this archipelago had separated from continental Asia 15 mya ago (Barnes, 2003), via the Philippines (from Borneo), Taiwan and the present-day Ryukyus. In this scenario, the colonization of Primorsky Krai was possible from the Japanese stock. The other possible variant is a continental dispersal from SE Asia to the Palearctic Far East, so that the Japanese species would have been vicariants derived from a continental ancestor. It cannot be excluded that both routes contributed to the north-eastern colonization. *Paraneseuthia* (as all Eutheiini) is a very rare genus and the gaps in its distribution can partly be attributed to the inadequate knowledge of Scydmaeninae in this part of Asia, especially in the Philippines and other islands of Wallacea, Taiwan, East China, Korea and the Russian Far East. Therefore, our current understanding of the dispersal routes and major events in the evolution of *Paraneseuthia* is very fragmentary. A number of undescribed species and possibly new genera of Eutheiini from SE Asia, especially from India and the Sunda Archipelago, are known to the author. Study of their morphology and a complete phylogenetic analysis may help in clarifying the evolution of the genera, and finding males of species known so far only from females may contribute to a more precise clarification of the relationships within *Paraneseuthia*.

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