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Checklist of Passalidae Leach, 1815 (Coleoptera, Scarabaeoidea) of Laos with a key to their identification and a description of *Leptaulax pacholatkoi mutoniatus* ssp. nov.

by Christoph Neumann, Masahiro Kon & Kunio Araya

Abstract. The diversity of the Passalidae (Scarabaeoidea) of Laos is investigated, largely by means of material collected by the Beetle Diversity of Laos project undertaken by the Basel Natural History Museum (NHMB), as well from a Kyushu University expedition in 2003. Existing data from the literature to date are also included in this review. At present, 15 Passalidae species are recorded for Laos, two subspecies are potentially endemic, one of them, *Leptaulax pacholatkoi mutoniatus* Neumann et Kon ssp.nov., is described here for the first time. A key to species identification is provided.

Key words. Laos – Passalidae – checklist – key – ecological indicators – *Leptaulax pacholatkoi mutoniatus* ssp.nov.

Introduction

The Passalidae, also known as bess beetles, are a small family within Scarabaeoidea (Polyphaga), of predominantly pan-tropical distribution. They are of medium-to-large size and are notable in a number of respects: for their reliance on intact forests (e.g. SCHUSTER 1985); for their parent-offspring interactions (VALENZUELA-GONZALEZ & CASTILLO 1983, SCHUSTER & SCHUSTER 1997, ENTO *et al.* 2008); and for their sub-social behaviour patterns (REYES-CASTILLO & HALFFTER 1983, COSTA 2006). Gilbert J. Arrow has succinctly summarized the very special biology of the family: "Passalidae live together in all of their stages" (ARROW 1951). Almost all species rely on decaying wood as a food source as well a reproduction site, in which they live sub-socially in gallery systems with adults caring for their offspring through all stages of development. For just one species so far, the American *Odontotaenius disjunctus,* copulation during nuptial flight has been observed (MACGOWN & MACGOWN 1996).

The offspring's dependence on adults, combined with the long period before maturity for juvenile beetles (F1), i.e. complete sclerotization taking more than 8–10 weeks in some species, with additional time required finally to reach reproductive maturity, result in significant generation overlaps in the galleries that constitute a larger colony. The F1 generation is reported to support the next generation pre-pupal third instar larvae in preparing their protective pupal chambers, as well as in repair when these are damaged (SCHUSTER & SCHUSTER 1985, REYES-CASTILLO & HALFTTER 1994). Both adults and larvae communicate by complex stridulation signals in the contexts of courtship initiation, courtship, post-copulation, aggression and disturbance (SCHUSTER 1983). The larvae, in particular, have developed a special mechanism for stridulation, in which sound is generated by scraping the highly-modified and reduced metathoracic leg against pairs of ridges on the coxae of the mesothoracic leg (SCHIÖDTE 1874, OHAUS 1900).

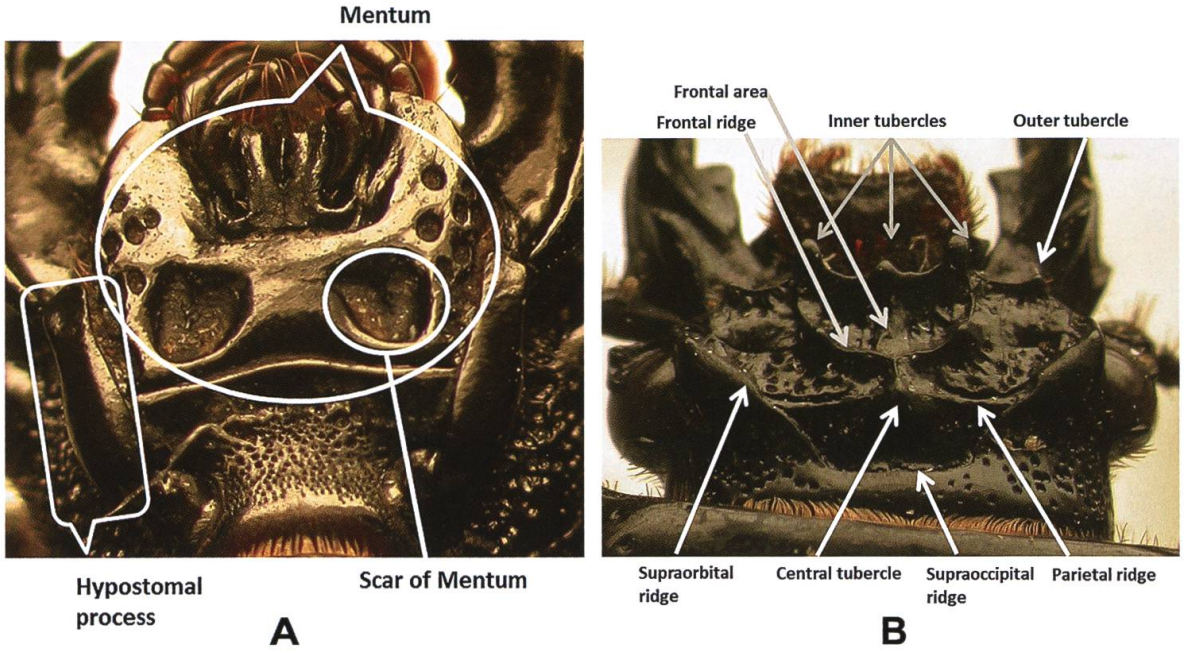
Passalidae are able to digest wood with the aid of micro-organisms, particularly the saccharomycete yeast strains required for the fermentation of xylose (SUH *et al.* 2003). Larvae and adults depend for their food upon a cocktail of wood chips bitten off, shredded and chewed from the galleries by the parents, together with the faeces of members of the colony. The mixture of faeces and wood chips is thought to undergo further external microbial metabolism of certain celluloses and hemicelluloses to glucose and xylose before re-ingestion, a process described by Mason and Odum as "external rumen" (MASON & ODUM 1969, ODUM 1971). Possibly as a result of their sub-sociality, the constraints and complexity of living in wood galleries and maintenance of the external rumen, few morphological differences exist between male and female Passalidae or even among species, contrasting with many scarabaeoid families, e.g. Dynastidae, Lucanidae (REYES-CASTILLO & HALFFTER 1984).

Given their biology as important primary decay mediators, mainly in moist tropical forests (CASTILLO & REYES-CASTILLO 2003), the Passalidae serve as excellent indicators for the ecological integrity of such habitats and have therefore been recommended for more frequent consideration (SCHUSTER 1985, SCHUSTER *et al.* 2000, BOUCHER 2005) as part of ecosystem audits. Until recently, about 700 species had been recorded globally; intensive research on some South American genera by Stephane Boucher has increased the number to about 800 species to date (BOUCHER 2005, HALLAN 2010). Asia has 45% of the species, of which currently about 30 valid species are recorded from Indochina*).

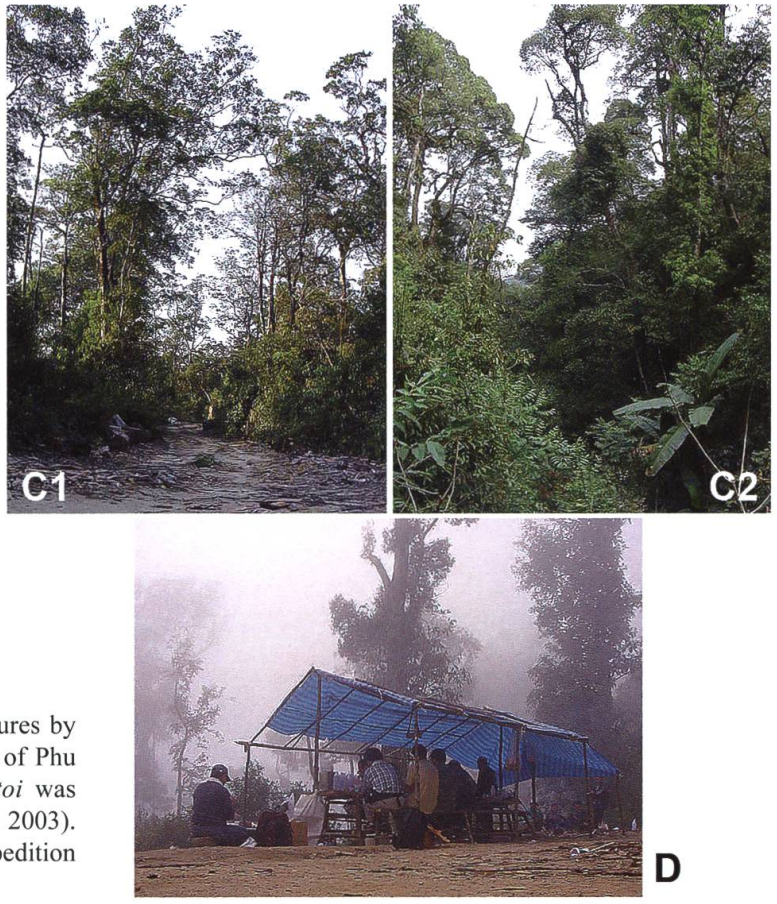
The Passalidae of Laos, as well as many other beetle and insect families, have not yet been addressed in comprehensive geographical or taxonomical terms. Although GRAVELY (1914, 1918) included specimens from all of Indochina in his monographs of Oriental and world Passalidae, the Laos fauna remained until recently far less investigated than that of the Indian subcontinent and Thailand. Only around the turn of the recent millennium did specimens of Passalidae from Laos (and adjacent Vietnam), collected occasionally together with other wood-associated insects, make their way more frequently into public and private collections. Systematic collecting started in 2003, with the Laos expedition(s) conducted by Kyushu University's exploration of Laotian insect diversity. This revealed some new and rare passalid species (KON *et al.* 2003b, 2006). Since 2003, the Natural History Museum in Basel, Switzerland, has engaged in concentrated scientific collecting expeditions led by the late Dr. Michel Brancucci who, with his colleagues, explored the fauna of Laos. Recently, this became a fully dedicated project, known as "The Beetle Diversity of Laos".

The aim of this contribution is to describe the current status of the Passalidae in Laos and to provide an identification key to the species of that country.

*) Indochina is considered here as a distinct sub-region of high endemism within the Oriental region, with unique and isolated ancestral groups of both fauna and flora. It comprises the countries of Thailand, Myanmar, Laos, Vietnam and Cambodia (GROOTAERT 2009).



Figs A, B. Key terms of Passalidae morphology (*sensu* GRAVELY 1914) used in the keys. A – Head ventral view. B – Head dorsal view.



Figs C–D. The collecting sites (pictures by Prof. K. Araya). A – The forest of Phu Pan where *Leptaulax matsumotoi* was collected for the first time (June 2003). B – The Kyushu University expedition researchers' camp (June 2003).

Material and Methods

Most of the specimens for this study were collected in the course of expeditions undertaken by the Kyushu University, Japan (2003) and by the late Michel Brancucci (Natural History Museum Basel = NHMB) and colleagues collecting within the larger Laotian Beetle Biodiversity project in the years 2003 to 2012. The specimens from the latter project are part of the collection of the NHMB. They are kept dry-mounted on pins or glued to pinned cards and are integrated into the main collection of the NHMB. Passalids were collected mainly by hand under bark or within wood; some were also attracted to light traps. A certain amount of earlier material held by the Natural History Museum in Basel was also examined for this contribution, including the Frey collection.

The authors also refer to HINCKS & DIBB (1935, 1958) and subsequent works for distribution records (referenced in Table 1). It is important to note that synonyms for species listed have already been covered by the work of KON *et al.* (2001b) on Thai Passalidae. For subfamily and tribe classification, the phylogenetic proposal for the family provided by BOUCHER 2005 is followed. The terminology for morphology in the keys (Figs A and B) generally follows GRAVELY (1914) .

Measurements of body length are taken from the anterior margin of the head to the apex of the elytra. Measurements of Passalidae should be approached with some care, since they are quite dependent on the extent to which the back of the head and the front of the metathorax have become telescoped into the prothorax (GRAVELY 2014). This is due to the special morphology of the mesothorax, which is produced into a tube upon which the pronotum may move in any direction, and the base of the pronotum not fitting closely into the base of the elytra (ARROW 1949).

All the photographs were taken with a Nikon Coolpix 4500 either directly or mounted on the Wild (Leica) M 8 stereomicroscope (Plan 1×) mainly used for the identification of specimens.

Classification key to passalid species of Laos

Key to subfamilies

1. Anterior coxae prominent, enlarged sufficiently for the intercoxal portion of the prosternum to be hidden; anterior margin of head without tubercles. ..... **Aulacocyclinae**
– Anterior coxae not enlarged, the intercoxal portion of the prosternum fully visible; anterior margin of head with tubercles. ..... **Passalinae**

Key to tribes of Aulacocyclinae

1. Head flat in front, mandibles without process (see Note below). .... (**Aulacocyclini**)
– Head bearing frontal horn; mandibles with erect frontal processes. .... **Ceracupini**

Note: No species of Aulacocyclini has yet been recorded for Laos; however there are records of *Taeniocerus* from India, Thailand and Myanmar, so the presence of this genus cannot be fully ruled out.

Key to species of Ceracupini (only one genus, *Ceracupes* Kaup, in Laos)

1. Anterior intermediate and lateral areas of metasternum impunctate and hairless; body length: 26 mm. ..... ***chingkini* Okano**
– Anterior intermediate and lateral areas of metasternum punctate and hairy. ..... 2.
2. Erect frontal process of mandible (upper tooth) almost as long as central tubercle in dorsal view; body length: 22–27 mm. .... ***fronticornis* (Westwood)**
– Erect frontal process of mandible longer, projecting beyond the central tubercle in dorsal view; body length: 25 mm. ..... ***arrowi* Heller**

Key to tribes of Passalinae

1. Antenna with 3 lamellae; head always symmetrical. ..... **Leptaulacini**
– Antenna with 6 lamellae, head asymmetrical (see Note) in some genera, i.e. right mandibles with incomplete dentation and/or frontal area of head with a prominent process on the left (see Figs 42, 43, 45, 46). .... **Macrolinini**

Note: Asymmetry is a frequent feature observed in some genera of the Macrolinini; it is particularly pronounced near Wallace's line (incl. Weber's line, etc.). What drives such asymmetry is still a matter for discussion (for introductory reference see GRAVELY 1914, ARROW 1949).

Key to genera of Macrolinini

1. Supraoccipital ridge extending beyond posterior end of supraorbital ridge; head symmetrical. ..... ***Macrolinus* Kaup**
– Supraoccipital ridge not extending beyond the posterior end of supraorbital ridge; if extending beyond (only one Laotian species) then outer tubercles asymmetrical (Fig. 43). ..... 2.
2. Mentum with scars; either tubercles of equal length or the right outer tubercle longer than the left, (see Note below). ..... (***Pelopides* Kuwert**)
– Mentum without scars; left outer tubercle (at least) somewhat longer than right (generally very obvious, in only one Laotian species weak). ..... 3.
3. Dentations of left and right mandible complete (Fig. 41). .... ***Ophrygonius* Zang**
– Dentation of right mandible incomplete, lowest terminal and lower anterior teeth of right mandible obsolete, or only present as very small denticles (Fig. 42). ..... ***Aceraius* Kaup**

Note: No species of genus *Pelopides* has yet been confirmed in Laos, but a potentially undescribed species was reported from Vietnam (IWASE 2009). According to Iwase, this is supposedly close to, but different from, *Pelopides dorsalis* (Kaup), but a description has yet to be published. *Pelopides* species are typically distributed in Sundaland, with *Pelopides monticulosus* reaching Thailand in the very south.

Key to species of Leptaulacini (single genus: *Leptaulax* Kaup)

1. Elytra laterally with distinct scalariform (transverse) punctation (Fig. 29); parietal ridge either not joined with the supraorbital ridge, sharply ending distally or not distinctly joined but tailing off towards it. ..... 2.
– Elytra laterally with normal, more-or-less rounded punctures (Fig. 30); parietal ridge either joined with the supraorbital ridge or fading to indistinct towards the supraorbital ridge, never sharply ending distally before it. ..... 4.
2. Parietal ridge not joining with the supraorbital ridge; sharply ending distally; hypostomal process grooved longitudinally, or with or without depression distally. ..... 3.
– Parietal ridge joining the supraorbital ridge although often indistinct; not ending sharply but gradually tailing off towards the supraorbital ridge; hypostomal process smooth with no depression or groove, metasternum with a group of punctures left and right of its centre (Fig. 33); male genitalia Figs 15–17; body length: 17–18 mm. .... ***matsumotoi* Kon, Johki et Araya**
3. Hypostomal process grooved longitudinally with fine punctures, (Fig. 32); mesosternum with very obvious, strong punctures (Fig. 31); male genitalia Figs 12–14; body length: 17–19.5 mm. .... ***cyclotaenius* Kuwert**
– Hypostomal process with or without some weak depressions, but without longitudinally grooved depression; mesosternum without punctures (if present, only very fine); body length 21–33 mm (Figs 6–7). ..... ***dentatus* (Fabricius) complex**
4. Anterior lower tooth simple; last abdominal sternite hairless or with an area of hairs in the centre of the 6th abdominal segment; the 5th sternite emarginate or not. ..... 5.
– Anterior lower tooth bidentate (Fig. 37); last abdominal sternite widely hairy (Fig. 38), 5th sternite straight, body length 23–25 mm (Fig. 11). ... . ***loebli* Kon, Johki et Araya**
5. 5th sternite emarginate at posterior margin. ..... 6.
– 5th sternite without emargination at posterior margin. ..... 7.
6. 6th abdominal sternite in males with hairy punctures concentrated as a median stripe and extending throughout, from the anterior base to the apex of the sternite, hairs short (Figs 55–56); male genitalia very characteristic (Figs 21–24), female unknown; body length: 22–23 mm (Fig. 8). ..... ***pacholatkoi mutoniatus* Neumann et Kon ssp.nov.**
– 6th abdominal sternite also with hairy punctures, but concentrated centrally in males, in between the anterior and posterior borders of the sternite but distant from them, appearing not as a stripe but as a more roundish area of punctures containing some longer hairs (Fig. 54); in females the hairs are also concentrated centrally but much more defined and dense (Fig. 53); male genitalia significantly different (Figs 18–20, 25); body length: 19–23 mm (Fig. 9). ... ***pacholatkoi pacholatkoi* Iwase**

7. Frontal area with some setiferous punctures (Fig. 34); body length: 14–16 mm. ..... ***riekoae* Iwase**
– Frontal area without setae; longer than 16 mm. ..... 8.
8. Elytra flattened on dorsal face; anterior marginal groove of pronotum fine without punctures or with only very few (max 4–5) small but distinct punctures (Fig. 36), lateral margin only with fine, single punctures in a row; lateral grooves of elytra with rounded punctures, narrower than the adjacent ribs; male genitalia with ventral face almost sclerous (Figs 26–28), body length: 18 mm (Fig. 10). ..... ***manis* Iwase**
– Elytra not flattened, more rounded on dorsal face; anterior marginal groove of pronotum more pronounced and broader in dorsal view, always with many large, distinct punctures; lateral margin with strong punctures, particularly in the anterior portion very closely lined up in pairs; lateral grooves of elytra with punctures more oblong, at least as large as ribs; body length: 21–23.5 mm. .... ***bicolor* (Fabricius) complex**

Further comments for *Leptaulax* Kaup

- *Leptaulax dentatus* and *L. bicolor* were recorded by Gravely as among the five most remarkably variable species in the Oriental region (Gravely 1914), which contrasts with the generally limited variability of Passalidae. This observation is also reflected in the large number of existing synonyms. Both species are also exceptionally widely distributed in the Oriental region, unlike most others recorded for Laos. Variation in *L. dentatus* is especially pronounced in terms of size; the largest Laotian specimen examined is 33 mm, the smallest 21 mm. While specimens from different localities present an apparently unbroken range of variation in length, this changes if specimens collected from single colonies or localities are viewed together, when they form homogeneous series (a trait that is often difficult to discern in material investigated retrospectively in collections). There are also certain obvious morphological differences within series for specimens from different colonies and/or localities, particularly with reference to the mentum, the terminal sternites, the hypostomal process, the proportions of the frontal area, and the punctation of the pronotum. Although many species related to *L. dentatus* described by Kuwert (1891, 1898) have been considered later to be synonyms for what are often very good reasons, there is a high likelihood that some specimens classified as *L. dentatus* today are actually a conglomerate of a distinct number of separate species; however, a review of the *dentatus* species complex is beyond the scope of this contribution, so all the Laotian specimens of this complex are treated here as *L. dentatus*. While a fresh taxonomical review for both species is necessary, this should be combined with thorough investigations at colony level. There appears to be a strong link between the variability and gregariousness and the size and lifetime of a colony, which could suggest that, to a certain degree, variability is driven by sub-social behaviour, i.e. colonies remaining together over several generations with a potentially high level of

inbreeding, as has been observed for *Aceraius helferi* (FOSTER & ELLWOOD 2010). Gravely has already suggested that classification of *Leptaulax* Kaup might potentially benefit if the colony were used as the basis for taxonomic work rather than single individuals. He hypothesized that there may be some strong, though as yet inconclusive, evidence that members of a colony are much more uniform than the species as a whole, at least for the markedly variable types (GRAVELY 1914). This supposition appears to be supported by the collection material examined, at least for the gregarious species *L. dentatus* and *L. bicolor*.

- *Leptaulax bicolor*, although more constant in length, is even more variable than *L. dentatus* at an entire-Oriental scale, in terms of body flatness, pattern of punctation, of certain morphologies as well as of the male genitalia. However, variations in specimens of the bicolour complex investigated from Laos seem to have a more constant pattern and could potentially be divided into clearly distinctive forms. This early observation may well accord with previous comments and arise out of the fact that the materials collected by the Basel expeditions, as well as earlier by our Czech colleague P. Pacholátko, of which some are held in Basel, generally comprise larger series of specimens from the same localities and often just a single colony. However, as is the case for *L. dentatus*, a revision of Indochina or Oriental *L. bicolor* is beyond the present work, so all specimens will be treated as belonging to the *bicolor* complex.
- *Leptaulax cyclotaenius*: Gravely also observed a high level of variability in this species, but this has not yet been observed in the material collected from Laos. All specimens show low variability and are easily recognized by the characters and figures provided in the key. However, it should be noted that there is larger variability within *L. cyclotaenius* from northern Thailand; consideration should be given to the reintroduction of some of the synonymous names of *L. cyclotaenius* specimens originally described by KUWERT (1896) (Neumann, in preparation). Specimens from Sundaland lack the strong punctures on the mesosternum.
- *Leptaulax loebli*: This species is easy to separate from all other known Laos and Indochina species by the widely hairy 6th sternite (Fig. 38) and the bifid anterior lower tooth of the mandibles (Fig. 37); the latter character is only shared within the entire genus by *L. sabahensis* from Borneo, which is separated however, by having the 6th abdominal sternite without dense hairs and in lacking a grooved hypostomal process.
- *Leptaulax riekoae riekoae*: This subspecies is among the smallest and flattest *Leptaulax* found in Laos; further, the characters provided in the key make it relatively easy to identify. The pronotal scar is distinct from most related species within the territory, i.e. it is deeply grooved but without, or only with very few, (1–3) distinct punctures, different from most other *Leptaulax* Kaup in the region (Fig. 35). For Laos only *L. matsumotoi*, probably a very closely-related species, has similar pronotal punctation and scar but the scar is grooved with discrete punctures. The colour of the adults appears to be a consistently lustrous reddish-brown, but the head is more dark brown, to almost black. For the north of Myanmar, the closely-related subspecies *kachinensis* has been described, which differs from the nominotypical subspecies only in having a small tubercle between

the outer tubercle and the anterior angle of head (Kon *et al.* 2003d, 2005a). The penis of the male genitalia is simple, truncated at the distal end in ventral view, whereas it is W-shaped in ventral view for the nominotypical subspecies. Recently specimens of *ssp. kachinensis* have also been recorded for the north of India (Assam, unpublished, Neumann in prep.).

- *Leptaulax matsumotoi*: In addition to the characters provided by the key (the parameres of the male genitalia are already quite unique in the shape of distal end), this species is also distinct in combining a number of features: the lateral surface of the mandibles has a marked hollow in the posterior portion, the frontal area has few punctures, bearing some hairs; and the shoulders of the elytra (humerus) have a number of hairs. The labrum is different from other Laos *Leptaulax* species in its distinct, sparse dorsal punctation. For *Leptaulax matsumotoi* to date, the nominotypical specimens were found within Laos on Phu Pan Mountain at an altitude of 1400–1700 m and are supposedly endemic to Laos. However, a subspecies has been described from Myanmar (*L. matsumotoi kangfangensis*), which is distinct in the following characters: sides of pronotum densely punctate throughout; humerus hairless; and male genitalia in the distal margin of the basal portion strongly incised (Kon & Abe 2008, Kon & Abe 2009). Variation for *Leptaulax m. matsumotoi* appears near negligible and what there is of it appears to be mainly in the extent of punctation of the sides of the pronotum, particularly behind the anterior margin. However, in much the same way as *L. bicolor* and *L. dentatus* variability, differences are minimal within specimens from one colony.
- *Leptaulax pacholatkoi pacholatkoi* and *L. pacholatkoi mutoniatus*: This is a species classified within the *bicolor* species group by having the 5th sternite distinctly emarginate at its anterior border, most of the anterior area between the inner tubercles visible in dorsal view, and showing some sexual dimorphism, which is generally rare in Passalidae. *Leptaulax pacholatkoi* was first described by Iwase from the south of Vietnam, but in the meantime has also been collected in the south of Laos as well in the north of Cambodia. The new subspecies (see Appendix A) resembles *L. p. pacholatkoi* but the male genitalia are strikingly different, possessing large parameres while the penis has a small concavity apically, almost making the apex appear bifurcated, which is clearly visible in ventral and dorsal view. When comparing available material from Vietnam (type location), Cambodia and Laos of specimens falling within the range of the description of *L. p. pacholatkoi*, there seems to be a relatively high degree of morphological variation in certain characters (scar of mentum, scar of mesosternum) between specimens. Thus some characters in even the detailed original description by Iwase (1998) need to be considered with a modicum of care and additional material may support a more in-depth review of this potential species group. However, the difference in the male genitalia alongside some other characters of the two specimens collected from Bolikhamxai and Xiangkhoang provinces are so significant as definitely to justify its status as a subspecies (see below), and also the collecting places are very much north of the original holotype locality.

- *Leptaulax manis*: This species is widely distributed in Sundaland and is also recorded south of the Wallace line in Sulawesi (IWASE 1998b). The specimens collected from Thailand and Laos, although matching the holotype description in all key characters, are consistently larger and the anterior marginal groove of the pronotum often has a few distinct punctures. The variation of punctation within a population of specimens from one single colony ranges from zero to up to four or five distinct but fine punctures. Whether this variation justifies its proposal as a subspecies of *L. manis* for the Indochina region needs to be re-evaluated with more material available. At this time we are satisfied to follow the treatment of specimens from Indochina as being *L. manis*, after JOHKI *et al.* (2001) and IWASE (2009).

Key to species of *Macrolinus* Kaup

– Only one species characterized by, other than the unique character of the genus, antenna with 6 moderately long lamellae; lateral grooves of elytra with transverse punctures; body length 30–34 mm (Fig. 44). .... ***sikkimensis* (Stoliczka)**

Key to species of *Ophrygonius* Zang

1. Supraoccipital ridge extending beyond the posterior end of the supraorbital ridge (this character renders *singapurae* distinct among genera of Macrolinini except for the genus *Macrolinus*); antenna with six lamellae, very long and slender (Fig. 49); labrum asymmetrical with the left anterior angle projected farther forward than the right, also the left concavity of the anterior margin more deeply scooped than the right; body length: 33–35 mm (Figs 4, 43). ..... ***singapurae* Gravely**
– Supraoccipital ridge not exceeding the supraorbital ridge, but joining at the end of it. ..... 3.
2. Antennae with 6 lamellae (Fig. 47), but the two first shorter than the terminal four, which are long and slender; labrum slightly asymmetrical, left anterior angle only slightly prolonged compared to a small central tooth and a right angle in the anterior border of the labrum; body length 29–34 mm (Fig. 5). ..... ***birmanicus* Gravely**
– Antennae with the first three lamellae short, of which the first is almost obsolete and the following two significantly shorter than the terminating three (Figs 49 and 50). ..... 4.
3. Body length: 30–34 mm, labrum almost symmetrical, anterior border concave, angular cut-off at left and right apices, and with a small projecting elevation (often obsolete) in the middle of the anterior border; sides straight, apices only shortly rounded laterally. .... ***cantori* (Percheron)**

– Body length: 27–29 mm, appearance very similar to previous species, but size difference constant for Laos specimens; labrum broadly rounded at apex laterally, only smoothly emarginate anteriorly, apices not cut off at angles but rounded, anterior margin straight, always lacking a projecting elevation. ..... ***convexifrons* (Zang)**

Further comments for *Ophrygonius* Zang

- The status of *Ophrygonius* (Zang 1904) *sensu* Gravely (1914), as well as redefined later by Boucher (1993), is not without debate. Although there may be good supporting reasons for some of the *Ophrygonius* species, in particular, being treated as *Aceraius* and potentially the genus *Basilianus* (Kaup 1871) as maintained within its original limits, in the current work the rationale for separation of *Ophrygonius* (including *Episphenus*) and *Aceraius* proposed by Boucher (1993) is maintained. This is also because no alternative rationale has yet been published in a peer-reviewed journal. Whatever the eventual outcome, the identification provided here works for classification to species level.
- *Ophrygonius convexifrons*: This species had been earlier synonymized with *O. cantori*, but according to Boucher it is a species proper (Boucher 1993); as well as characters mentioned in the key (described from Laos specimens), the punctation appears to be consistently less around the pronotal scar, the frontal area less concave, flat or appearing almost convex, and the posterior margin of the 4th sternite is emarginate. Another key difference is in the mesosternum, which has a scar at each side, rugosely shagreened, whereas the mesosternum looks highly polished in *O. cantori*, without a visible scar.
- *Ophrygonius cantori:* No records are available for Laos but as the species is recorded from all the neighbouring countries (although eventually confused with the previous species). It is probably present in the northern parts of Laos.

Key to species of *Aceraius* Kaup

1. Outer tubercles of the head almost symmetrical; labrum broadly rounded at sides, anterior frontal portion either very smoothly rounded off or appearing more or less straight, slightly asymmetrical, with the right angle lower, horizontally not in line with the left angle; body length: 27–32 mm (Fig. 1). ..... ***aequalis* (Gravely)**
– Outer tubercles of the head asymmetrical, the left significantly longer than the right; labrum with concavity, generally larger species. ..... 2.
2. Anterior left angle of head not prominently forward; upper margin of the left mandible with convexity behind upper tooth (Fig. 40); body length: 29–37 mm (Fig. 2). ..... ***helferi* Kuwert**
– Anterior left angle of head prominently forward (Figs 45, 46); upper margin of the left mandible without convexity behind upper tooth; body length: 40–55 mm (Fig. 3). ..... ***grandis* (Burmeister)**

Further comments for *Aceraius* Kaup

- Regarding the status of the genera *Aceraius* Kaup versus *Ophrygonius* Zang, see comment with species entry.
- One female of *Aceraius aequalis* has been recorded, from the Chin Hills in Myanmar, which differs to some extent from the Vietnam and Laos specimens (KON & FUKINUKI 2001a, KON 2002). However, whether this may be considered a new species or whether it is just a local form within the range of variation can only be ascertained when more material becomes available from Myanmar.
- Although *Aceraius grandis* is easily recognized by the characters provided in the key, it is probably a conglomerate of two closely-related species. It is also one of the species of the Oriental fauna that was listed by Gravely as having an exceptional range of variation; he even proposed the existence of two potential species (GRAVELY 1914). A more detailed review, particularly of the type species described by KUWERT (1891) close to *grandis*, would be required to draw conclusions, but that, once more, is beyond the scope of the current contribution.

Leptaulax pacholatkoi mutoniatus Neumann et Kon ssp.nov. (Fig. 8)

Type material. Holotype: Boli Kham Xai, Ban Nape (8km NE) (18°21′N, 105°08′E), 1–18.i.2001, 600m, Pacholátko leg., 1 ♂; Paratype: Xieng Khouang, iv. 1996, leg. local collector, 1 ♂.

Description. Body length: 22 mm; width: 7.5 mm (broadest portion of elytra).

Integument: Lustrous brownish-black throughout.

Head: Anterior majority of head area visible in dorsal view between the inner tubercles, and between the inner and the outer tubercles as well; median tubercle small and blunt; inner tubercles triangular and about three times larger than the outer, apex rounded, not acute, pointing straight forward; outer tubercles triangular with acute apex pointing diagonally outwards; frontal area with longitudinal grooves bearing some large punctures grouped as pairs and the trace of a median keel; frontal ridges joining before the central tubercle, widely rounded, almost semicircular; parietal ridges joining the supraorbital ridges; anterior margin of labrum almost straight but with a small, scooped excavation in the anterior border sitting between the rounded anterior corners, sides laterally straight, dorsal surface rugose and covered with foveate setiferous punctures; scars of mentum V-shaped, lateral parts covered with dense punctures, median part without punctures and lustrous.

Pronotum: Anterior and lateral margin well developed, with strong punctures irregularly grouped in twos or threes, laterally almost appearing blanked out of the surface of the lateral margin; pronotal scar deep, rounded, covered in dense, foveate punctation; this punctation dorsally particularly concentrated behind the anterior angle and around the scar but spread throughout, within the area delimited by the lateral and anterior margins and an imagined line prolonged horizontally from the 5th elytral row, but impunctate for a small area along the lateral and anterior margin; anterior angle of pronotum not acute, while the anterior margin is curved widely; median groove distinct

throughout between the anterior and posterior border; width of central wrinkle of posterior margin (opposite base of elytra) covering two ribs left and right of the suture.

Elytra: Base of elytra with some hairs between rows 1–5, shoulders glabrous; lateral grooves with rounded punctures, 1/3 narrower than the adjoining ribs.

Mesothorax: Scar broad, almost triangular, inner wall only as long as 1/3 of the lustrous and polished middle part of the mesosternum.

Abdomen: 5th sternite distinctively emarginate (widely V-shaped) at its anterior border, 6th sternite with setiferous punctures concentrated in its centre portion (from base to apex), covered with short hairs throughout but not densely so (Fig. 55).

Male genitalia: The male genitalia are strikingly peculiar, possessing large parameres, and the penis has a small concavity apically, almost making the apex appear bifurcated, clearly visible in ventral and dorsal views (as in Figs 21–24).

Note: The paratype shows some minor variations, i.e. the scar of the mesosternum is longer and its inner wall extends to halfway along the adjoining and polished central area of the mesosternum and the scar of the mentum is somewhat more J- than V-shaped. However, these characters are assumed to be within the general range of variation typical of *Leptaulax* and of the particular features involved (e.g. the scars of the mesosternum).

Etymology. The name *mutoniatus* is a Latin adjective, derived from *muton* = penis, referring to the large and distinctive male genitalia of this subspecies of *Leptaulax pacholatkoi*.

Differential diagnosis. The new subspecies, although resembling *Leptaulax pacholatkoi* s.str. to a large extent, is easily recognized by its strikingly different male genitalia, as shown in Figs 21–24, a broader anterior and lateral margin of the pronotum (Figs 51, 52) and a larger extension of pronotal punctation in particular behind the anterior margin and around the lateral scar; width of wrinkle at posterior border of pronotum about twice as large, covering two ribs of each side of the suture, and the 6th abdominal segment with punctures and hairs throughout as a central band extending from the anterior to the posterior border.

The holotype will be placed in the main collection of the Natural History Museum in Basel, Switzerland; the paratype will be preserved in the private collection of Dr. Masahiro Kon, Kyoto in Japan.

Distribution. Known to date only from the holo- and paratype localities, potentially more widely distributed north of the triangle formed by Laos, Cambodia and Vietnam.

Passalidae fauna of Laos and comparisons with adjacent countries

The passalid species recorded in Laos are listed in Table 1. Fifteen species are recorded from Laos, with two subspecies that might be endemic, i.e. *Leptaulax matsumotoi matsumotoi* and *Leptaulax pacholatkoi mutoniatus*. Species having a distribution very much confined to the centre of the Indochina biogeographical area are *Ophrygonius birmanicus*, which is rarely collected or only locally distributed, and *Leptaulax loebli* which likewise has a distribution restricted to Thailand, Myanmar and Laos.

The current number of species known from Laos appears to be within the range of passalid inventories known from the better-investigated countries of Indochina, such as Thailand (KON *et al.* 2001b, 2003c), and Myanmar (KON *et al.* 1999a). However, any conclusion about the Laos fauna requires careful consideration in addressing certain particular differences in other species compositions that contrast with that of Laos.

Thailand and Myanmar both have overlaps, in addition to their typical Indochina fauna, with two other discrete biogeographical areas. Thailand's fauna in the south consists of some species already representative of Sundaland, i.e. *Aceraius laevicollis* and *Pelopides monticulosus* through which the fauna of northern Myanmar bears the genus *Tiberioides* Gravely of the tribe Macrolinini, which alone has radiated to the eastern Himalayas, i.e. all four of the known species are recorded only in this area. The very south of Myanmar is reached by *Leptaulax planus*, another typical Sundaland species, which is also recorded for the south of Thailand and Cambodia. Given the geography of Laos, landlocked in the centre of Indochina, almost no representative of these faunal elements is represented there, thus providing an easy rationale for some of the remarkable differences between the fauna of Laos and the adjacent countries to its west. Exceptions are *Leptaulax manis*, originally described from Malaysia and also recorded from Borneo, i.e. Sabah and Sarawak as well as Sulawesi (IWASE 1998b) and *Ophrygonius singapurae* with its centre of distribution in the Malayan peninsula and Borneo. *L. manis* was also recorded recently for Thailand and Laos (JOHKI *et al.* 2001, IWASE 2009), and *O. singapurae* is distributed in Thailand, Laos and Vietnam, but only rarely collected.

Looking to the eastern parts of Laos, these share a 2000-km border with Vietnam, mostly along the crest of the Annamite mountain chain in the north-east and the east. This chain might serve as some kind of natural border between the faunas of the two countries but it is also potentially an area with some elements of shared and high biodiversity. *Aceraius aequalis* might be used as an example of this, as it is distributed only along the two sides of the chain in the north of both countries.

Bearing these considerations in mind and in the knowledge that the faunas of Vietnam, Cambodia and Laos are not well enough known to draw final conclusions, the following examples might provide an indication of the current status of knowledge of the Laos passalid fauna:

- Vietnam fauna, in addition to four species of *Ophrygonius* Zang jointly shared with Laos, includes two additional species that have been described from locations fairly close to the Laos border (BOUCHER 1993). *Ophrygonius griveaui* has been found in the north, east of Hanoi, but there are also records for the south of Vietnam. The holotype of *Ophrygonius tanae*, the second species, was described from South Vietnam east of Dalat and appears closely related to the first species, likewise *Leptaulax pacholatkoi*, originally described from the south of Vietnam

Table 1. List of Laotian Passalidae and their adjacent distribution.

Abbreviations: BU= Bhutan, C = Cambodia, CN= China, IN= India, L= Laos, NE=Nepal, MY=Myanmar, T= Thailand, V=Vietnam, TW= Taiwan, GS = Greater Sunda; (S) = South, (N) = North, (Ti) = Tibet, (?) = status not clear, or not published in a peer reviewed journal yet. NHMB = Natural History Museum Basel, NMS = Naturkundemuseum Stuttgart. →

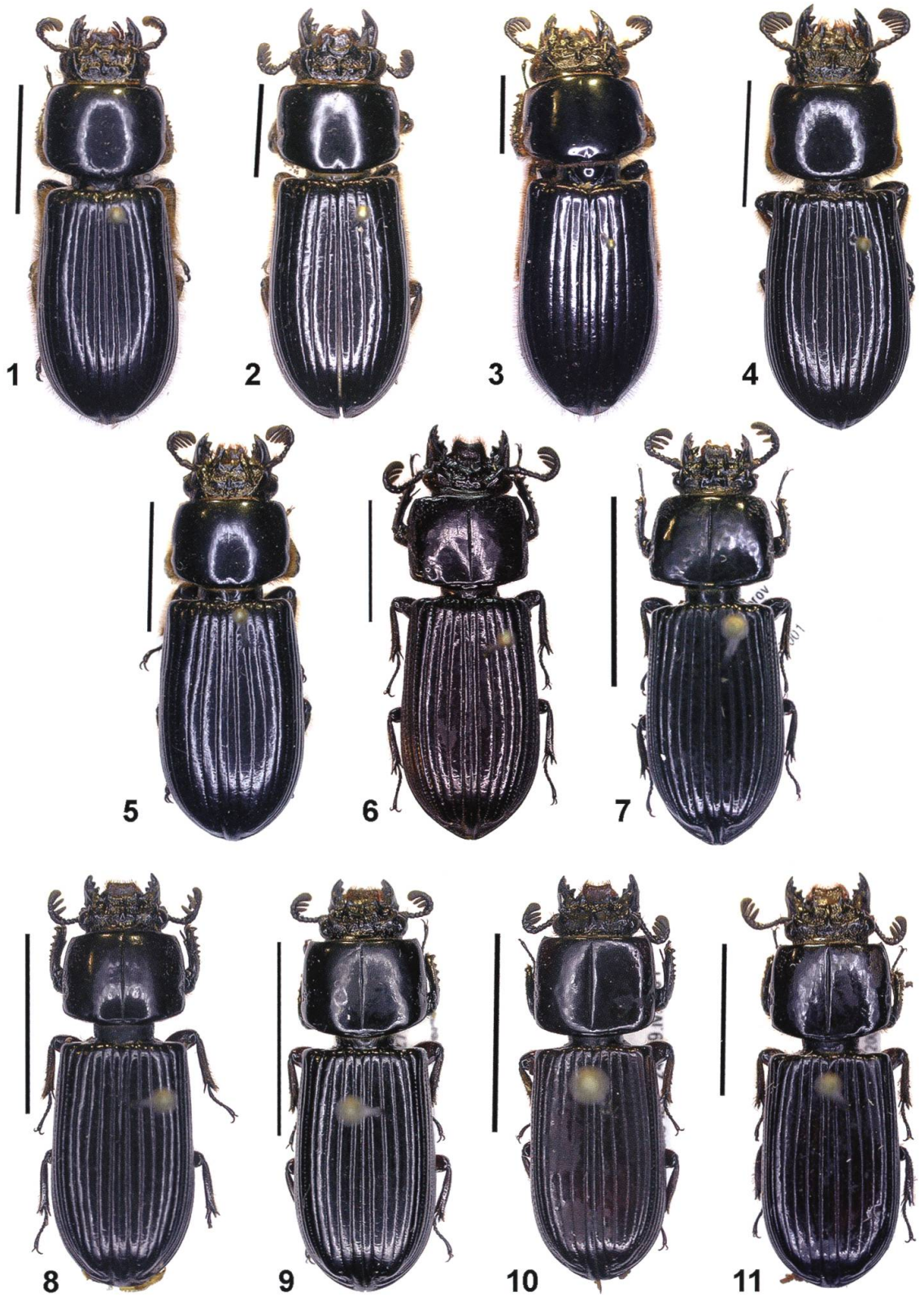
Genus	Species	Author	IN	NE	BU	T	MY	L	CA	VN	CN	TW	GS	References
Aulacocyclus	*andrewsi*	Gravely, 1914	X(S)											GRAVELY 1914, ARROW 1949
Taeniocerus	*bicuspis*	(Kaup, 1868)	X		X	X	X							BOUCHER 1998
Taeniocerus	*mourzinei*	Boucher, 1989					X							BOUCHER 1998, KON *et al.* 1999a
Ceracupes	*arrowi*	Heller, 1910								X		X		KON *et al.* 2005b, IWASE 2009
Ceracupes	*chingkini*	Okano, 1988				X	X			X	X	X		KON *et al.* 1995, KON *et al.* 1999a
Ceracupes	*fronticornis*	(Westwood, 1842)	X		X	X	X	**X**		X	X(S)			KON, *et al.* 1991, KON *et al.* 2001c
Ceracupes	*yui*	Okano, 1988										X		LÖBL & SMETANA 2006
Cylindrocaulus	*bucerus*	Fairmaire, 1880									X			BOUCHER & REYES CASTILLO 1996
Cylindrocaulus	*davidi*	Boucher et Reyes-Castillo, 1996									X			BOUCHER & REYES CASTILLO 1996, KON *et al.* 1997, 1999c
Tiberioides	*austeni*	Gravely, 1914	X		X		X							KON *et al.* 1999b
Tiberioides	*borealis*	Arrow, 1907	X				X							KON *et al.* 1999a
Tiberioides	*kerleyi*	Kon et Araya, 2007					X							KON & ARAYA 2007
Tiberioides	*kuwerti*	Arrow, 1907	X	X	X		X							KON *et al.* 1999a
Pleurarius	*brachyphyllus*	Stoliczka, 1873	X(S)											GRAVELY 1914, ARROW 1949
Leptaulax	*bicolor*	(Fabricius, 1801)	X		X	X	X	**X**	X	X	X		X	GRAVELY 1914, IWASE 2009
Leptaulax	*cyclotaenius*	Kuwert, 1891	X	X		X	X	**X**	X	X			X	KON *et al.* 1999, KON *et al.* 2003
Leptaulax	*dentatus*	(Fabricius, 1792)	X	X	X	X	X	**X**	X	X	X	X	X	GRAVELY 1914, IWASE 2009
Leptaulax	*formosanus*	van Doesburg, 1992										X		IWASE 2009
Leptaulax	*manis*	Iwase, 1996				X		**X**					X	IWASE 1998ab, 2009 & JOHKI *et al.* 2001
Leptaulax	*loebli*	Kon, Johki et Araya, 2003				X	X	**X**						KON *et al.* 2003C, KON *et al.* 2006
Leptaulax	*matsumotoi*	Kon, Johki et Araya, 2003						**X**						KON *et al.* 2003b
Leptaulax	*matsumotoi* ssp. *kangfangensis*	Kon et Abe, 2009					X							KON *et al.* 2008, KON *et al.* 2009
Leptaulax	*pacholatkoi*	Iwase, 1998						**X**	X	X				IWASE 1998, ARAYA *et al.* 2013
Leptaulax	*pacholatkoi* ssp. *mutoniatus*	Neumann et Kon, 2012						**X**						NEUMANN & KON (in this paper)
Leptaulax	*planus*	(Illiger, 1800)			X	X							X	KON *et al.* 2001b
Leptaulax	*riekoae*	Iwase, 1998				X		**X**						KON *et al.* 2003d, 2005a
Leptaulax	*riekoae.* ssp. *kachinensis*	Kon, Araya et Johki, 2005	X				X							KON *et al.* 2003d, 2005a; (NE India specimens in NMS, Neumann in prep.)
Leptaulax	*roepstorfi*	Kuwert, 1898	(X)											Andaman Islands (endemic)
Ophrygonius	*birmanicus*	Gravely, 1914	X		X	X	X	**X**	X	X				KON *et al.* 1999, 2001B, LÖBL & SMETANA 2006
Ophrygonus	*boxeri*	Boucher, 1993	X(S)											BOUCHER 1993
Ophrygonius	*cantori*	(Percheron, 1844)	X	X	X	X	X			X				GRAVELY 1918, KON *et al.* 1998, LÖBL & SMETANA 2006
Ophrygonius	*chinensis*	Endrödi, 1955									X			BOUCHER 1993
Ophrygonius	*convexifrons*	(Zang, 1904)	X		X	X	X				X(S)			LÖBL *et al.* 2006, IWASE 2009
Ophrygonius	*griveaui*	Boucher, 1993								X (N)				BOUCHER 1993
Ophrygonius	*indicus*	(Stoliczka, 1873)	X(S)											ARROW 1949, BOUCHER 1993
Ophyrgonius	*inopinus*	Boucher, 1997				X(S)								BOUCHER 1997
Ophrygonius	*neelgherriensis*	(Percheron, 1841)	X(S)											ARROW 1949, BOUCHER 1993
Ophrygonius	*singapurae*	Gravely, 1914				X		**X**		X			X	KON *et al.* 2001b, V specimen in coll. NHMB
Ophyrgonius	*tanae*	Boucher, 1993								X (S)				BOUCHER 1993
Aceraius	*aequalis*	Gravely, 1918					(X)	**X**		X				KON *et al.* 2001a, KON 2002
Aceraius	*grandis*	Burmeister, 1847	X			X	X	**X**	X	X	X	X	X	GRAVELY 1918, KON *et al.* 1999
Aceraius	*helferi*	Kuwert, 1891	X	X		X	X	**X**	X	X	X	?	X	GRAVELY 1914, KON *et al.* 2001b
Aceraius	*laevicollis*	Illiger, 1800				X(S)							X	KON *et al.* 2001B
(?) *Aceraius*	*annamensis*	Gravely, 1919												Indochina (?), IWASE 2009
(?) *Aceraius*	*chinensis*	Kuwert, 1898									X			IWASE 2009
(?) *Aceraius*	*hirsutus*	Kuwert, 1891	X	X	X									IWASE 2009; (spec. prop., Kon in prep.)
Macrolinus	*andamanensis*	Stoliczka, 1873	(X)											Andaman Islands (endemic)
Macrolinus	*foveolatus*	Ma, 1988										X(Ti)		IWASE 2009
Macrolinus	*medogensis*	Zhang, 1981										X(Ti)		IWASE 2009
Macrolinus	*sikkimensis*	(Stoliczka, 1873)	X	X		X	X	**X**						KON *et al.* 1999
Pelopides	*monticulosus*	(Smith, 1852)				X(S)							X	KON *et al.* 2001b

and recently recorded in the triangle formed by Laos, Vietnam and Cambodia. It is thus likely that more intensive searching will reveal more *Ophrygonius* species for Laos.

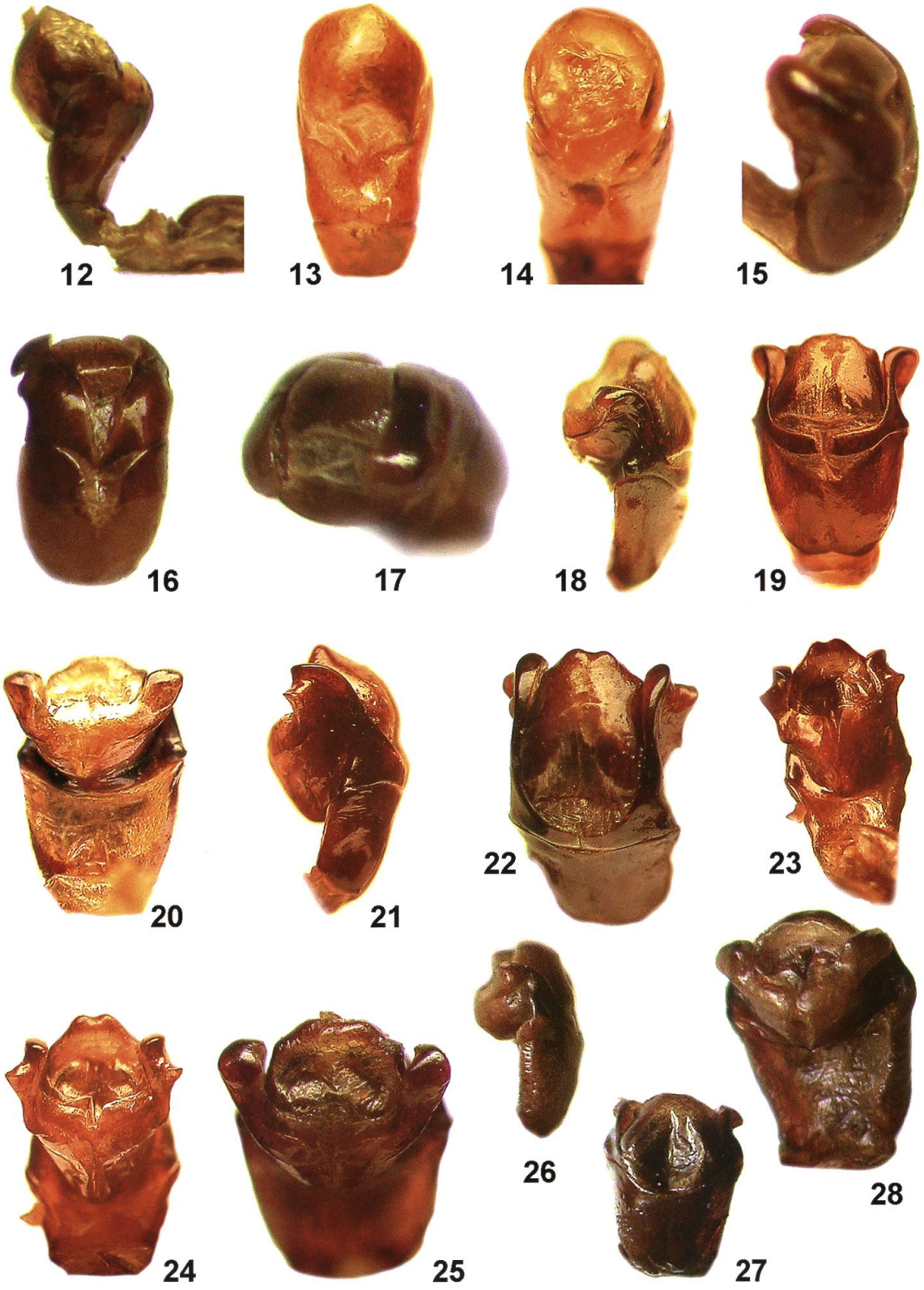
- Three species of the genus *Ceracupes* Kaup, i.e. *C. arrowi, C. chingkini*, and C. *fronticornis* inhabit the Indochina biogeograpical region. While *C. fronticornis*, the most widely-distributed species, has been recorded in Laos – albeit from only two locations – there are no collection data for the other two. This is particularly surprising for *C. chingkini* since it has been recorded for almost all the adjacent countries (see Table 1). Any reasons for this must be purely tentative, but it might well be that the peculiar habitats of *Ceracupes* Kaup, i.e. living deeply buried in detritus-like microhabitats of rotten wood (confirmed for *C. fronticornis,* assumed for *C. chingkini*), or even more specialized in detritus among the rhizomes of epiphytic ferns (*C. arrowi*) render it opaque – these are hardly the first choices of habitat for general collecting when checking for beetle biodiversity. In addition, *Ceracupes chingkini* and *C. fronticornis* live in colonies that consist of only a single male-female couple and all the various stages of their offspring , and never in larger colonies with a high number of specimens like the more frequently collected genera such as *Leptaulax* Kaup and *Aceraius* Kaup. *Ceracupes arrowi* has, however, been recorded in larger colonies but of course its unusual habitat still makes it likely to be overlooked (JOHKI & KON 1989, KON *et al.* 2001c).
- Although the genus *Leptaulax* Kaup is known to include the most variable species of Passalidae (see above, "Further comments on *Leptaulax* Kaup"), particularly in Laos, the complex of *Leptaulax bicolor* seems to have radiated into some clearly-distinguishable forms. Once more, dedicated and systematic collecting is required before conclusions can be drawn at species level. This observation also applies partially to some of the specimens of *Leptaulax dentatus* collected to date in Laos.

Based on a very small number of data points and the fact that the total area investigated for the Laos passalid fauna is still fairly limited, it should be assumed that the level of knowledge of Laotian passalids and their diversity might still have some major gaps. The relevance of Passalidae as indicators for the integrity of tropical forest ecosystems, given the rapidly progressing deforestation in Laos, makes further research imminent and urgent. Focus areas should be the forests along the border with Vietnam and the few remaining forests in the south of the country in the vicinity of the Mekong River and close to the border with Cambodia.

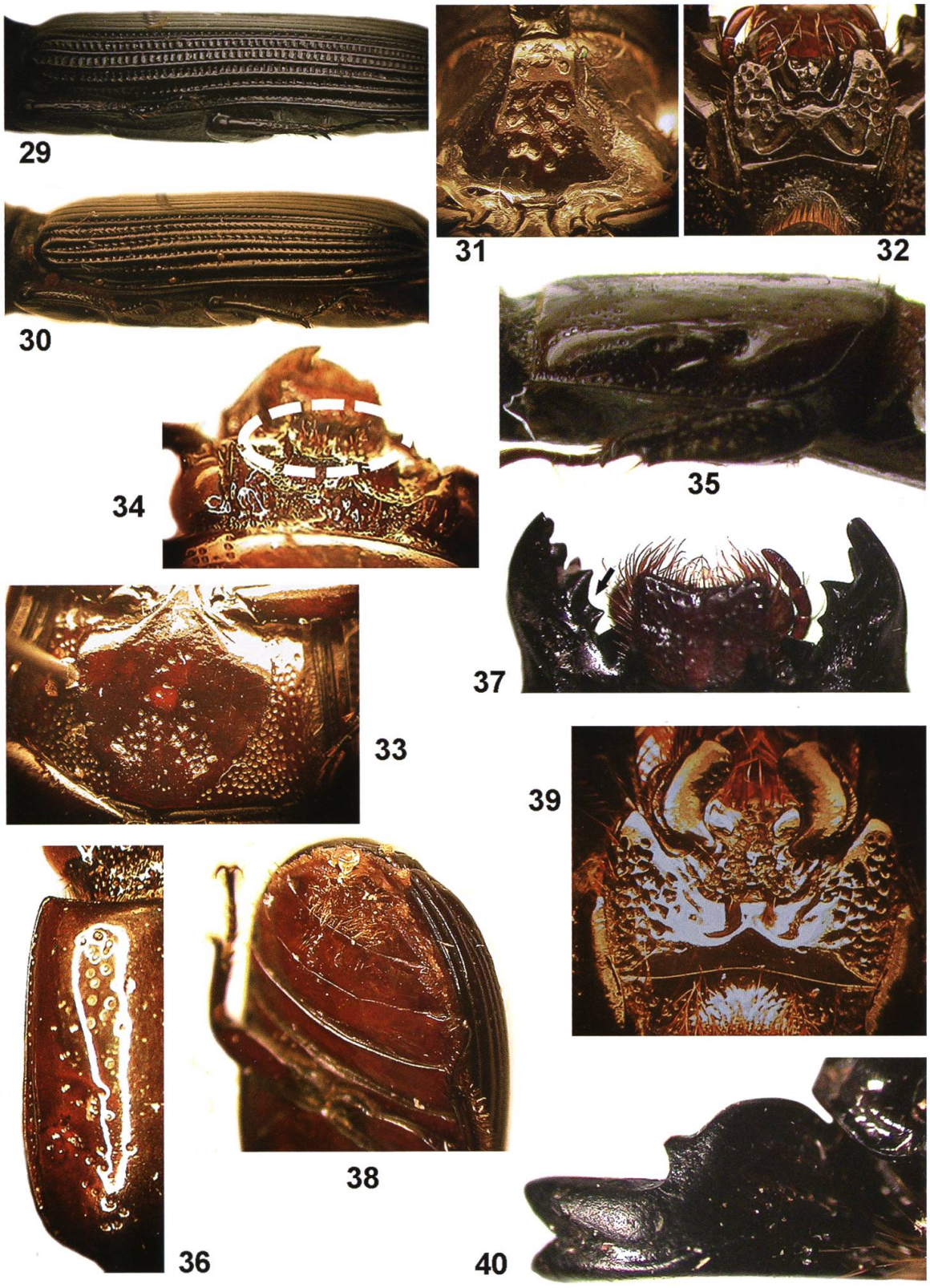
N o t e : The term Sundaland, as used here, "comprises the Malay Peninsula, the Malay archipelago, and the islands of Sumatra, Java, Bali and Borneo. The islands of Sundaland rest on the shallow continental shelf of Asia. The eastern border of Sundaland is formed by Wallace's line" (GROOTAERT 2009). We also consider the very southern parts of Thailand to be part of this biogeographical zone.



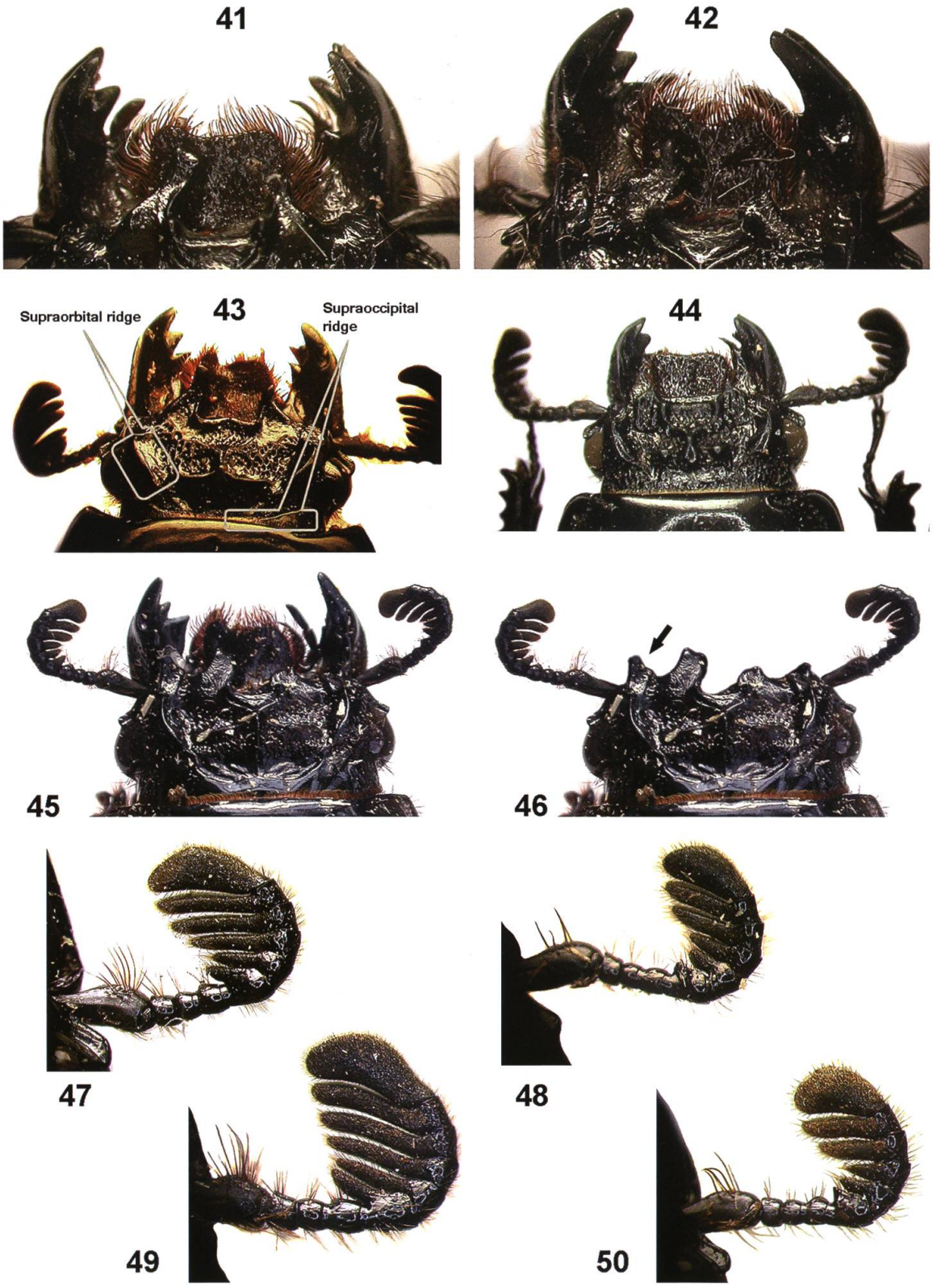
Figs 1–11. Representatives of Laotian Passalidae: 1 – *Aceraius aequalis*; 2 – *Aceraius helferi*; 3 – *Aceraius grandis*; 4 – *Ophrygonius singapurae*; 5 – *Ophrygonius birmanicus*; 6 – *Leptaulax dentatus* (large specimen); 7 – *L. dentatus* ("average" size specimen); 8 – *L. pacholatkoi mutoniatus*; 9 – *L. pacholatkoi pacholatkoi*; 10 – *L. manis*; 11 – *L. loebli*. Scale = 1 cm.



Figs 12–28. Male genitalia of *Leptaulax* representatives in lateral, ventral and dorsal view (not to scale): 12–14 – *L. cyclotaenius*; 15–17 – *L. matsumotoi*; 18–20 – *L. pacholatkoi pacholatkoi*; 21–23 – *L. pacholatkoi mutoniatus*; 24 – 25 – *L. pacholatkoi mutoniatus* (24) and *L. p. pacholatkoi* (25), caudal view; 26–28 – *L. manis*.



Figs 29–40. Morphological details of selected species (1): 29–30 Lateral punctation of elytra *Leptaulax*: 29 – scalariform, 30 – "normal". 31–32 – Mesosternum and mentum, incl. hypostomal process of *L. cyclotaenius*; 33 – metasternum *of L. matsumotoi*; 34 – head of *L. rieokae* (frontal area with hairs); 35 – lateral view of pronotum of *L. rieokae*; 36 – lateral view of pronotum, *L. manis*; 37 – mandibles of *L. loebli* (arrow points the anterior lower tooth); 38 – 6th abdominal segment of *L. loebli*; 39 – mentum of *O. singapurae*; 40 – left mandible of *A. helferi*, lateral view.



Figs 41–50. Morphological details of selected species (2): 41–42 Dentation of mandibles: 41 – *Ophrygonius*, 42 – *Aceraius*. 43 – head of *O. singapurae*; 44 – head of *M. sikkimensis*. 45–46 Head of *A. grandis*: 45 – overview, 46 – anterior head. 47–50 Antennae and lamellae: 47 – *O. birmanicus*, 48 – *O. cantori*, 49 – *O. singapurae*, 50 – *O. convexifrons*.

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Figs 51–56. Morphological details of *Leptaulax p. pacholatkoi* and *L. pacholatkoi mutoniatus*. 51–52 Punctation of lateral margin: 51 – *L. p. pacholatkoi*, 52 – *L. p. mutoniatus*. 53 – 6th abdominal segment and posterior border of 5th segment of *L. p. pacholatkoi*, female; 54 – 6th abdominal segment of *L. p. pacholatkoi*, male (ventral and lateral ventral view); 55 – 6th abdominal segment of *L. pacholatkoi mutoniatus*, male (lateral ventral view); 56 – same, but ventral view.

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Summary

Fifteen species of Passalidae have been recorded from Laos to date. Although knowledge of this relatively small family of Scarabaeoidea has burgeoned in recent years for Laos, particularly through the collection expeditions undertaken by Michel Brancucci and colleagues from the Basel Natural History Museum, more systematic collection is required, particularly along the Vietnam border and in the south of the country. Two subspecies are potentially endemic, of which *Leptaulax pacholatkoi mutoniatus* ssp.nov. is described here for the first time.

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APPENDIX

List of detailed collection records for all species investigated

(If not otherwise mentioned, specimens are preserved in the main collection of Basel Natural History Museum, Switzerland and have been classified by the first author of this paper.)

Ceracupes fronticornis (Westwood 1842) (76 specimens)

Phongsaly, Ban Sano Mai (21°21′N, 102°03′E), 19.–26.v.2004, 1150m, Brancucci leg., 2 spec.; Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E), 04.–07.iii. 2003, 1800 m, Matsumoto, Iwata, Kon, Araya, Kitade, Richard, Koshikawa, Wakahara leg., 64 spec. (Kon det.); Houa Phan, Ban Saluei to Phou Pane Mt. (20°12–3′N, 103°59′–104°01′E), 15.iv.–15.v.2008, 1340–1870m, Lao collectors leg., 3 spec.; Houa Phan, Ban Saluei to Phou Pane Mt. (20°12–3′N, 103°59′–104°01′E) 10.v.–16.vi.2009, 1340–1870m, Brancucci and local coll. leg., 6 spec.; same locality: (20°13′N, 103°59′–104°00′E), 1.–16.vi.2009, 1480–1550m, Kraus leg., 1 spec.

Leptaulax bicolor (Fabricius 1801) (29 specimens)

Houa Phan, Phou Pane Mt. (20°13′N, 104°00′E), 1.–16.vi.2009, 1350–1500m, Brancucci leg., 2 spec.; same place, (20°13′N, 103°59′–104°00′E), 1.–16.vi.2009, 1480–1550m, Kraus leg., 5 spec.; same data, 9.–16.6.2009, Hauck leg., 1 spec.; Xieng Khouang, 30 km NE Phonsavan: Phou Sane Mt. (19°37–8′N, 103°20′E), 10–30.v.2009, 1400–1500m, Kraus leg., 19 spec.; same data, 1400–1700m, Hauck leg., 1 spec.; same data, 1300–1500m, Brancucci leg., 1 spec.

Leptaulax cyclotaenius Kuwert 1891 (39 specimens)

Bolikhamxai, Ban Nape (8km NE), (18°21′N, 105°08′E), 1–18.i.2001, 600 m, Pacholátko leg., 1 ♀; Phongsaly, Ban Sano Mai (21°21′N, 102°03′E), 19.–26.v.2004, 1150m, leg. Pacholátko leg, 1 ♂, 1 ♀; same data, Kuban leg., 2 ♀; Houa Phan, Phou Pane Mt. (20°13′N, 103°59′–104°00′E), 1.–16.vi.2009, 1480–1550m, Kraus leg., 2 spec.; Houa Phan, Phou Pane Mt. (20°13′N, 104°00′E), 1.–16.vi.2009, 1350–1500m, Brancucci leg., 5 spec.; Houa Phan, Ban Saluei to Phou Pane Mt. (20°12–3′N, 103°59′–104°01′E), 15.iv.–15.v.2008, 1340–1870m, Lao collectors leg., 4 spec.; Xieng Khouang, 30 km NE Phonsavan: Phou Sane Mt. (19°37–8′N, 103°20′E), 10–30.v.2009, 1400–1500m, Kraus leg., 18 spec.; same location and date, 1420m, Kraus leg., 2 spec.; same location and date, 1300–1500m, Brancucci leg., 2 spec.; same location and date, 1400–1700 m, Hauck leg., 3 spec. ; Champasak, Ban Nong Panouan env. (15°02′N, 106°31–4′E), 10–17.vi.2010, 770–800m, Geiser & Hauck leg., 1 spec.

Leptaulax dentatus (Fabricius 1792) (51specimens)

Louang Namtha, Ban Oudomsinh / B. Nam Det / B. Nam Mai env. (21°09–10′N, 101°13–15′E), 14.–20.v.2011, 750–1400m, Hauck & Geiser, 1 spec.; Phongsaly, Ban Sano Mai (21°21′N, 102°03′E), 19.–26.v.2004, 1150 m, Brancucci leg., 4 spec.; Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E), 04.–07.iii. 2003, 1800 m Matsumoto, Iwata, Kon, Araya, Kitade, Richard, Koshikawa, Wakahara leg., 15 spec. (Kon det.); Houa Phan, Ban Saluei to Phou Pane Mt. (20°12–3′N, 103°59′–104°01′E), 10.v.–16.vi.2009, 1340–1870m, Brancucci, local coll. leg., 1 spec.; Houa Phan, Phou Pane Mt. (20°13′N, 104°00′E), 1.–16.vi.2009, 1350–1500m, Brancucci leg., 2 spec.; Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E), 17.v.–3.vi.2007, 1500–1900m, Brancucci leg., 1 spec.; Xieng Khouang, Ban Thaviang env. (18°59′–19°03′N, 103°22–25′E), 17–21.v.2010, 400–600m, Geiser & Hauck leg., 8 spec.; Xieng Khouang, 30 km NE Phonsavan: Ban Na Lam to Phou Sane Mt. (19°37–8′N, 103°20′E), 10–30.v.2009, 1300–1500m, Brancucci leg., 4 spec.; same location

and date, 1400–1500 m, Kraus leg., 9 spec.; Bolikhamxai, Khamkheut, ca. 18°13′N/105°43′E, 1923, ex coll. Dussault, 5 spec.; Bolikhamxai, Pakkading (18°20′N, 104°00′ E), 27.v.2003, 200 m, Brancucci leg., 1 spec.; Champasak, Ban Nong Panouan env. (15°02′N, 106°31–4′E), 10–17.vi.2010, 770–800m, Geiser & Hauck, 2 spec.

Leptaulax loebli Kon, Johki et Araya 2003 (9 specimens)

Bolikhamxai, Ban Nape (8km NE) (18°21′N, 105°08′E), 1–18.i.2001, 600m, Pacholátko leg., 1 ♂; Oudomxay, Namo, 06.vii.2004, 5 spec. (Kon *et al.* 2006), Xieng Khouang, Ban Thaviang env. (18°59′–19°03′N, 103°22–25′E), 17–21.v.2010, 400–600m, Geiser & Hauck leg., 1 ♀; Bokeo, 5 km W Ban Toup, Bokeo Nature Reserve (20°27–28′N, 100°45′E), 4.–18.v.2011, 500–700m, Brancucci, Geiser, Hauck, Kraus, Phantala, Vongphachan leg., 1 ♂; Phongsaly, Ban Sano Mai (21°21′N, 102°03E), 19.–26.v.2004, 1150m, Kuban leg., 1 ♂.

Leptaulax matsumotoi Kon, Johki et Araya 2003 (110 specimens)

Type location: (Holotype) Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E), 04.iii.2003, 1800 m, Matsumoto leg., 1 ♂; (Paratypes) same location, 04.–07.iii. 2003, Matsumoto, Iwata, Kon, Araya, Kitade, Richard, Koshikawa, Wakahara and local collectors leg., 16 ♂, 19 F (Kon et.al. 2003b), Holotype deposited in the National Science Museum (Natural History), Tokyo; Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E), 17.v.–3.vi.2007, 1500–1900m, Brancucci leg., 58 spec.; Houa Phan, Ban Saluei to Phou Pane Mt. (20°12–13.5N, 103.5), 15.iv.–15.v.2008, 1340–1870m, Lao collectors, 11 spec.; Houa Phan, Phou Pane Mt. (20°13′N, 103°59′–104°00′E), 1.–16.6.2009, 1480–1550m, Kraus leg., 4 spec.; same location and date, 1350–1500m, Brancucci leg., 1 spec.

Leptaulax manis Iwase 1996 (16 specimens)

Salavan, Datai Ban Ralao, 24–27. Xii. 2000, 3 ♂, 3 ♀ (Johki *et al.* 2001); Kham Mouan, Ban Khoun Ngeun (18°07′N, 104°29′S), 24–29.vi.2001, 200m, Pacholátko leg., 4 ♂, 7 ♀.

Leptaulax pacholatkoi Iwase 1998 (6 specimens)

Attapeu, Thong Kai Ohk, Ban Kachung (Mai) env. (15°01–02′N, 107°26–27′E), 10–24.vi.2011, 1200–1450m, Brancucci, Geiser, Hauck, Kraus, Phantala, Vongphachan leg., 5 spec.

Leptaulax pacholatkai ssp. mutoniatus Neumann et Kon 2012 (2specimens)

Boli Kham Xai, Ban Nape (8km NE) (18°21′N, 105°08′E), 1–18.i.2001, 600m, Pacholátko leg., 1 ♂; Xieng Khouang, iv. 1996, ### leg., 1m.

Leptaulax riekoae Iwase 1998 (5 specimens)

Luang Prabang Luang Phrabang, 24.iv.–16.v.1999, 1200m, local collector leg., 3 ♂, 1 ♀ (Kon *et al.* 2005) ; Bolikhamxai, Ban Nape (8km NE) (18°21′N, 105°08′E), 1–18.i.2001, 600 m, Pacholátko leg., 1 spec.

Macrolinus sikkimensis (Stoliczka 1873) (4 specimens)

Bokeo, 5 km W Ban Toup, Bokeo Nature Reserve (20°27–28′N, 100°45′E), 4.–18.v.2011, 500–700m, Brancucci, Geiser, Hauck, Kraus leg., 4 spec.

*Ophrygonius birmanicus (*Gravely 1914) (44 specimens)

Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E), 04.–07.iii. 2003, 1800 m Matsumoto, Iwata, Kon, Araya, Kitade, Richard, Koshikawa, Wakahara leg., 16 spec. (Kon det.); Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E), 17.v.–3.vi.2007, 1500–1900m, Brancucci leg., 27 spec.; same place, (20°13′N, 103°59′–104°00′E), 1.–16.vi.2009, 1480–1550m, Kraus leg., 1 spec.

Ophrygonius singapurae (Gravely 1914) (3 specimens)

Savannakhet, Phou Xang He NBCA, ca. 5 km SW Ban Pa Phaknau (17°00′N, 105°38′E), 31.v.–6.vi.2011, 250–400m, Brancucci, Geiser, Hauck, Kraus, Phantala, Vongphachan leg., 3 spec.

Aceraius aequalis (Gravely 1918) (278 specimens)

Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E), 04.–07.iii. 2003, 1800 m, Matsumoto, Iwata, Kon, Araya, Kitade, Richard, Koshikawa, Wakahara leg., 247 spec. (Kon det.); Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E) 17.v.–3.vi.2007, 1500–1900m, Brancucci leg., 29 spec.; Houa Phan, Ban Saluei to Phou Pane Mt. (20°12–3′N, 103°59′–104°01′E), 10.v.–16.vi.2009, 1340–1870m, Brancucci, local coll. leg., 1 spec.; Houa Phan, Phou Pane Mt. (20°13′N, 103°59′–104°01'E), 1.–16.vi.2009, 480–1550m, Kraus leg., 1 spec.

Aceraius grandis (Burmeister 1847) (108 specimens)

Bolikhamxai, Ban Nape (8km NE) (18°21'N, 105°08′E), 1–18.i.2001, 600m, Pacholátko leg., 9 spec.; Phongsaly, Ban Sano Mai, (21°21′N, 102°03′E, 19.–26.v.2004), 1150m, Kuban leg., 3 spec. (NHMB); same location and date, Brancucci leg., 1 spec. (NHMB); Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E), 04.–07.iii. 2003, 1800 m, Matsumoto, Iwata, Kon, Araya, Kitade, Richard, Koshikawa, Wakahara leg., 40 spec. (Kon det.); Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E) 17.v.–3.vi.2007, 1500–1900m , Brancucci leg, 15 spec.; Houa Phan, Phou Pane Mt. (20°13′N, 104°00′E), 1.–16.vi.2009, 1350–1500m, Brancucci leg., 5 spec.; Houa Phan, Phou Pane Mt. (20°13′N, 103°59′–104°00′E), 1.–16.vi.2009, 1480–1550m, Kraus leg. , 6 spec.; same location and date, Hauck leg., 1 spec.; Houa Phan, Ban Saluei to Phou Pane Mt. (20°11–3′N, 103°59′–104°01′E), 9.–17.vi.2009, 1300–1900 m, Geiser leg, 2 spec.; same locality, 10.vi.–16.vi.2009, 1340–1870 m, Brancucci, local coll. leg., 1 spec.; Xieng Khouang, 30 km NE Phonsavan: Ban Na Lam to Phou Sane Mt. (19°37–8′N, 103°20′E), 10–30.v.2009, 1300–1500 m, Brancucci leg. 5 spec.; same data and location, 1400–1500m, Kraus leg., 7 spec.; Champasak,Ban Nong Panouan env. (15°02′N, 106°31–4′E), 10–17.vi.2010, 770–800m, Geiser & Hauck leg., 5 spec.; Attapeu, Thong Kai Ohk, Ban Kachung (Mai) env. (15°01–02′N, 107°26–27′E), 10–24.vi.2011, 1200–1450 m, Brancucci, Geiser, Hauck, Kraus, Phantala, Vongphachan leg., 9 spec.

Aceraius helferi Kuwert 1891(165 specimens)

Bokeo, 5 km W Ban Toup, Bokeo Nature Reserve (20°27–28′N, 100°45′E), 4.–18.v.2011, 500–700m, Brancucci, Geiser, Hauck, Kraus, Phantala, Vongphachan leg., 7 spec; Louang Namtha, Ban Oudomsinh / B. Nam Det / B. Nam Mai env. (21°09–10′N, 101°13–15′E), 14.–20.v.2011, 750–1400, Hauck & Geiser leg, 1 spec.; Oudomxai, Pak Beng (19°53′N, 101°, 07′E), 12–27.v.2001, 450m, Kolibac leg., 1 spec.; Phongsaly, Ban Sano Mai (21°21′N, 102°03′E), 19.–26.v.2004, 1150m, Brancucci & Kuban leg., 22 spec.; Phongsaly, Phongsaly env. (21°41–2′N, 102°06–8′E), 28.v.–20.vi.2003, 1500m, Pacholátko leg., 5 spec.; same data, Brancucci leg., 1 spec.; Phongsaly, 4 km E Boun Neua (21°38′N, 101°57′E), 26.v.2004, 1100m, Brancucci leg., 1 spec; Phongsaly, Boun Tai (21°38′N, 101°57′E), 18.v.2004, 580m , Brancucci leg., 4 spec.; Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E), 04.–07.iii. 2003, 1800 m, Matsumoto, Iwata, Kon, Araya, Kitade, Richard, Koshikawa, Wakahara leg., 44 spec. (Kon det.); Houa Phan, Phou Pane Mt. (20°12′N, 104°01′E), 17.v.–3.vi.2007, 1500–1900m, Brancucci leg., 21 spec.; Houa Phan, Phou Pane Mt. (20°13′N, 103°59′–104°00′E), 1.–16.vi.2009, 1480–1550 m, Kraus leg., 4 spec.; same location, 9.–16.vi.2009, Hauck

leg., 1 spec.; Houa Phan, Phou Pane Mt. (20°13′N, 104°00′E), 1.–16.vi.2009, 1350–1500m, Brancucci leg., 4 spec.; Bolikhamxai, Nam Kading NBCA, Tad Paloy campsite (18°20′N, 104°08′E), 7.–12.vii.2010, 280–400m, Brancucci & Geiser leg., 1 spec.; Bolikhamxai, Pakkading, Ban Phone Kham (18°19′N, 104°08′E), 23.–29.v.2011, 200–300m, Brancucci, Geiser, Hauck, Kraus, Phantala, Vongphachan leg., 1 spec.; Xieng Khouang, 30 km NE Phonsavan: Ban Na Lam to Phou Sane Mt. (19°37–8′N, 103°20′E), 10–30.v.2009, 1300–1500m, Brancucci leg., 4 spec.; same location and date, 1400–1500m, Kraus leg., 2 spec.; same location and date, 1400–1700m, Hauck leg., 2 spec.; Savannakhet, Phou Xang He NBCA, ca. 5 km SW Ban Pa Phaknau (17°00′N, 105°38′E), 31.v.–6.vi.2011, 250–400m, Brancucci, Geiser, Hauck, Kraus, Phantala, Vongphachan leg., 2 spec.; Champasak, Ban Nong Panouan env. (15°02′N, 106°31–4′E), 10–17.vi.2010, 770–800m , Geiser & Hauck leg., 11 spec.; Champasak, Ban Nam Touad env. (near Xe Katamtok) (15°06′N, 106°35–8′E), 8.–10. vi.2010, 500–800m, Geiser & Hauck leg., 3 spec.; Attapeu, Thong Kai Ohk, Ban Kachung (Mai) env. (15°01–02′N, 107°26–27′E), 10–24.vi.2011, 1200–1450m, Brancucci, Geiser, Hauck, Kraus, Phantala, Vongphachan leg., 23 spec.