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Molecular phylogeny and classification of Lyropaeini (Coleoptera: Lycidae) with description of larvae and new species of *Lyropaeus*

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Abstract. The generic classification of Lyropaeini is revised on the basis of molecular phylogeny. Two lineages mark the basal split of *Lyropaeus* Waterhouse, 1878: the Indian-Sri Lankan-Vietnamese clade (subgenus *Lyropaeus* s. str.) and the East Oriental clade (subgenus *Lyroneces* Kazantsev, 1998). *Lyroneces* is demoted to a subgenus of *Lyropaeus* due to the absence of reliable morphological characters. *Lyropaeus bicolor* Pic, 1911 (Java), *L. binotatus* Pic, 1926 (Java), *L. longipennis* Pic, 1911 (Java), *L. philippinensis* Kleine, 1926 (Philippines), *L. ritsemae* Gorham, 1882 (Sumatra), and *L. waterhousei* Gorham, 1882 (Sumatra) are placed in the subgenus *Lyroneces* Kazantsev, 1998. *Paralycus* Medvedev & Kazantsev, 1992 is a junior homonym of *Paralycus* Womersley, 1944 (Acari). The larvae of three *Lyropaeus* species are described and compared with neotenic larvae of *Platerodrilus* Pic, 1921. The independent origins of large-bodied neotenic larvae are hypothesized in *Lyropaeus* and *Platerodrilus* and the molecular evidence is supported by the differences in morphology. Two new *Lyropaeus* species are described: *Lyropaeus* (s. str.) *kejvali*, new species (India: Kerala), and *L.* (s. str.) *nepalensis*, new species (Nepal).

Key words. Coleoptera, Lycidae, Lyropaeini, phylogeny, new species, Oriental Region

INTRODUCTION

Asian neotenic larvae (Perty's or trilobite larvae) have attracted attention since the 19th century (Candèze, 1861). Their membership in the Lycidae was confirmed by Gravely (1915), who observed pupae and male larvae of *Lyropaeus biguttatus* Waterhouse, 1880 in India, and assigned them to large-bodied female larvae from the same locality. Gravely (1915) supposed that all large-bodied larvae from the Oriental region belong to the same genus, but Mjöberg (1925) named a mature larviform female from Sarawak *Duliticola paradoxa* Mjöberg, 1925, a species now placed in *Platerodrilus* Pic, 1921 (Kazantsev, 2002). Wong (1996) and Levkanicova & Bocak (2009) identified the larvae of further neotenic species of *Platerodrilus* Pic, 1921 and *Macrolibnetis* Pic, 1938. The morphology of neotenic female larvae of *Platerodrilus* was described in detail by Wong (1996) and Bocak & Matsuda (2003). Larvae of *Lyropaeus*, whose vouchers have not been located, have not been collected since Gravely (1915) and only the original description has been available.

The classification of Lyropaeinae was studied by Kazantsev (1998), Bocakova (2006), and Bocak et al. (2008). Kazantsev (1998) split *Lyropaeus* into three genera: *Lyropaeus* s. str., *Lybnopaeus* Kazantsev, 1998, and *Lyroneces* Kazantsev, 1998. We analyse the relationships within Lyropaeini, describe the larvae of three species of *Lyropaeus* from India and compare their morphology with trilobite larvae from Southeast Asia. The resulting molecular phylogeny provides further information for a revised concept of Lyropaeini genera and about the zoogeography of the lineage.

MATERIAL AND METHODS

DNA isolation, PCR amplification, and sequencing. Thoracic muscles from eight species were used for DNA isolation using the DNeasy Blood & Tissue kit (Qiagen, Inc.). PCR amplification was performed using 10× PCR buffer, 50 mM $MgCl_2$, Platinum 1 U Taq DNA polymerase (Invitrogen Inc.), 2 mM of each dNTP (Fermentas Inc.), 10 mM primers, distilled water to 50 µl and 10–30 ng of template. Five fragments were sequenced: the 18S rDNA (aligned length 1869 bp), a fragment of the 28S rDNA (631 bp), *rrnl* mtDNA (506 bp), *cox1* mtDNA (790 bp), and 1240 bp of *nad5* mtDNA with adjacent *tRNAs* (multiple gene fragments are referred as *rrnl* and *nad5* further). The primers used for amplification are those reported by Malohlava & Bocak (2010). The PCR products were purified using PCRµ96 Plates (Millipore Inc.), cycle sequencing was conducted according to the manufacturer's manual (Applied Biosystems, Inc.) using the Big Dye Sequencing Kit 1.1 and the product was sequenced by an ABI 3130 sequencer.

Sequence editing, alignment, and phylogenetic analyses. Sequences were edited using Sequencher 4.10 (Gene Codes Corp.) and merged with outgroup taxa published by Bocak et al. (2008). The newly sequenced fragments are listed in Table 1. Each fragment was aligned separately using ClustalW 1.83

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Table. 1. Material examined with distribution and Genbank accession numbers.

Species	Voucher	Locality	18S rRNA	28S rRNA	rrnL	cox1	nadh5
Lyropaeus (s.str.) sp. A	UPOLVP016	India	KC736893	KC736902	KC736885	KC736912	KC736921
Lyropaeus (s.str.) sp. B	UPOLVP017	India	KC736894	KC736903	KC736886	—	—
Lyropaeus (s.str.) sp. C	UPOLVP2312	India	KC736897	KC736906	KC736887	KC736915	KC736924
L. (Lyroneces) dominator	UPOLVP003	Malaysia	KC736890	KC736899	KC736882	KC736909	KC736918
L. (Lyroneces) optabilis	UPOLVP004	Malaysia	KC736891	KC736900	KC736883	KC736910	KC736919
L. (Lyroneces) optabilis	UPOL000585	Malaysia	DQ181088	DQ181162	DQ181014	DQ181236	DQ181390
L. (Lyroneces) philippinensis	UPOLVP018	Philippines	KC736895	KC736904	—	KC736913	KC736922
L. (Lyroneces) philippinensis	UPOLVP019	Philippines	KC736896	KC736905	—	KC736914	KC736923
L. (Lyroneces) ritsemae	UPOLVP001	Sumatra	KC736888	KC736898	KC736880	KC736907	KC736916
L. (Lyroneces) ritsemae	UPOLVP006	Sumatra	KC736892	KC736901	KC736884	KC736911	KC736920
L. (Lyroneces) rubrostriatus	UPOL000L11	Sabah	DQ181042	DQ181116	DQ180968	DQ181190	DQ181344
L. (Lyroneces) waterhousei	UPOLVP002	Sumatra	KC736889	—	KC736881	KC736908	KC736917
L. (Lyroneces) waterhousei	UPOL000584	Sumatra	DQ181087	DQ181161	DQ181013	DQ181235	DQ181389

under settings of penalties 22.5 for gap opening and 0.83 for extension (Thompson et al., 1994). Data were partitioned for phylogenetic analyses by genes and codon positions. Each matrix was analysed using parsimony in TNT 1.1 (Goloboff et al., 2003) and 100 bootstrap trees were analysed and the results summarised in a majority consensus tree. Further, the dataset was analysed using maximum likelihood in RAxML 7.2.3 and 100 bootstrap trees (Stamatakis et al., 2005) and Bayesian analysis in the MrBayes 2.3.1 (Huelsenbeck, 2000). The Bayesian analysis was carried out for 40 × 10^6 generations using Markov chain Monte Carlo method (MCMC). MCMC method has been set for the independent parameters variability in individual protein-coding and non-coding genes according to GTR + I + G model as proposed by JModeltest 0.1 (Posada, 2008). Probability values were evaluated in Tracer 1.4 (Rambaut & Drummond, 2007) and generations before stationary phase were excluded.

Morphological methods. The morphological section is based on the male adult semaphoronts and larvae. Dry mounted specimens were softened for dissection of male genitalia. Photographs of diagnostic characters were taken by

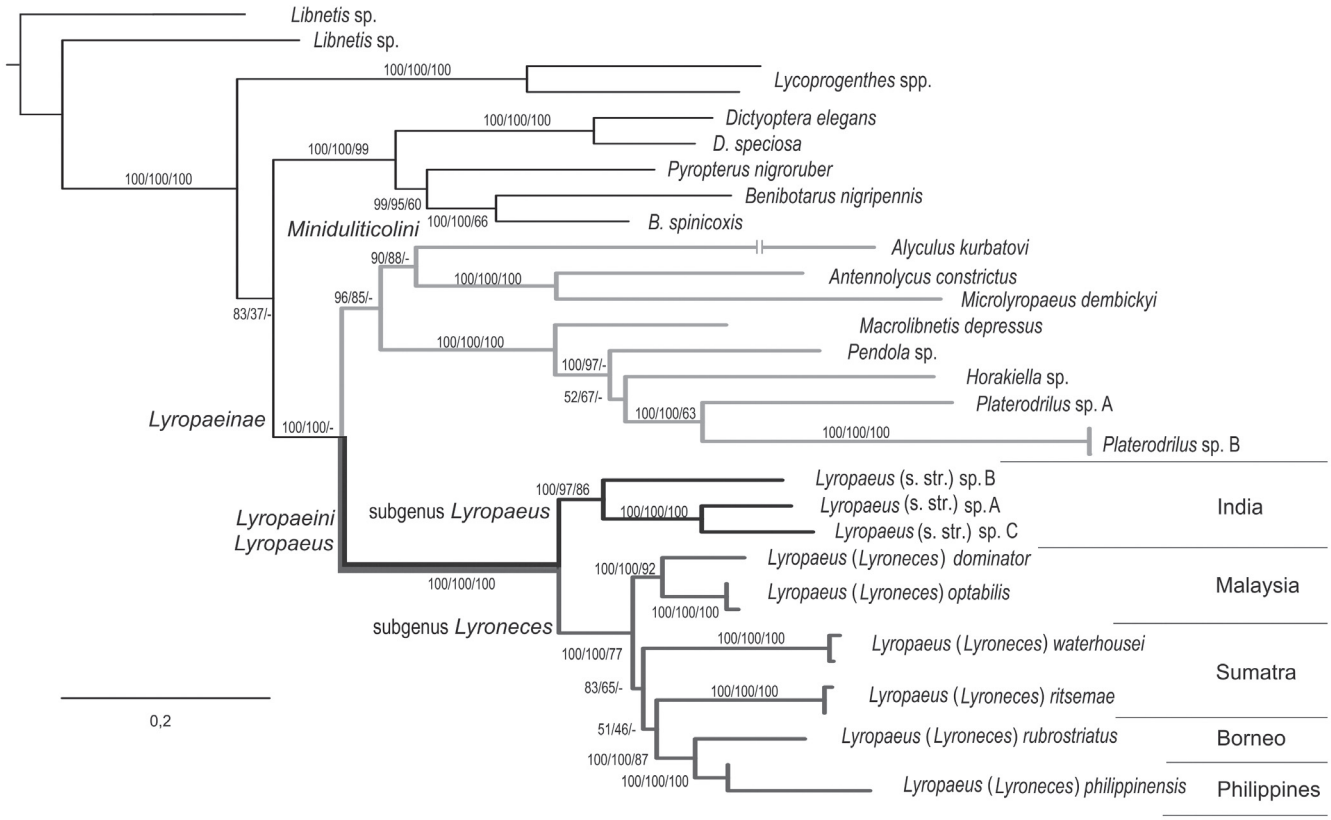


Fig. 1. Phylogenetic hypothesis for *Lyropaeus* Waterhouse, 1878 based on a maximum likelihood analysis of five fragments 18S and 28S rDNA, cox1, nad5 and rrnl mtDNA. Numbers at the branches are Bayesian frequencies and likelihood and parsimony bootstrap values.

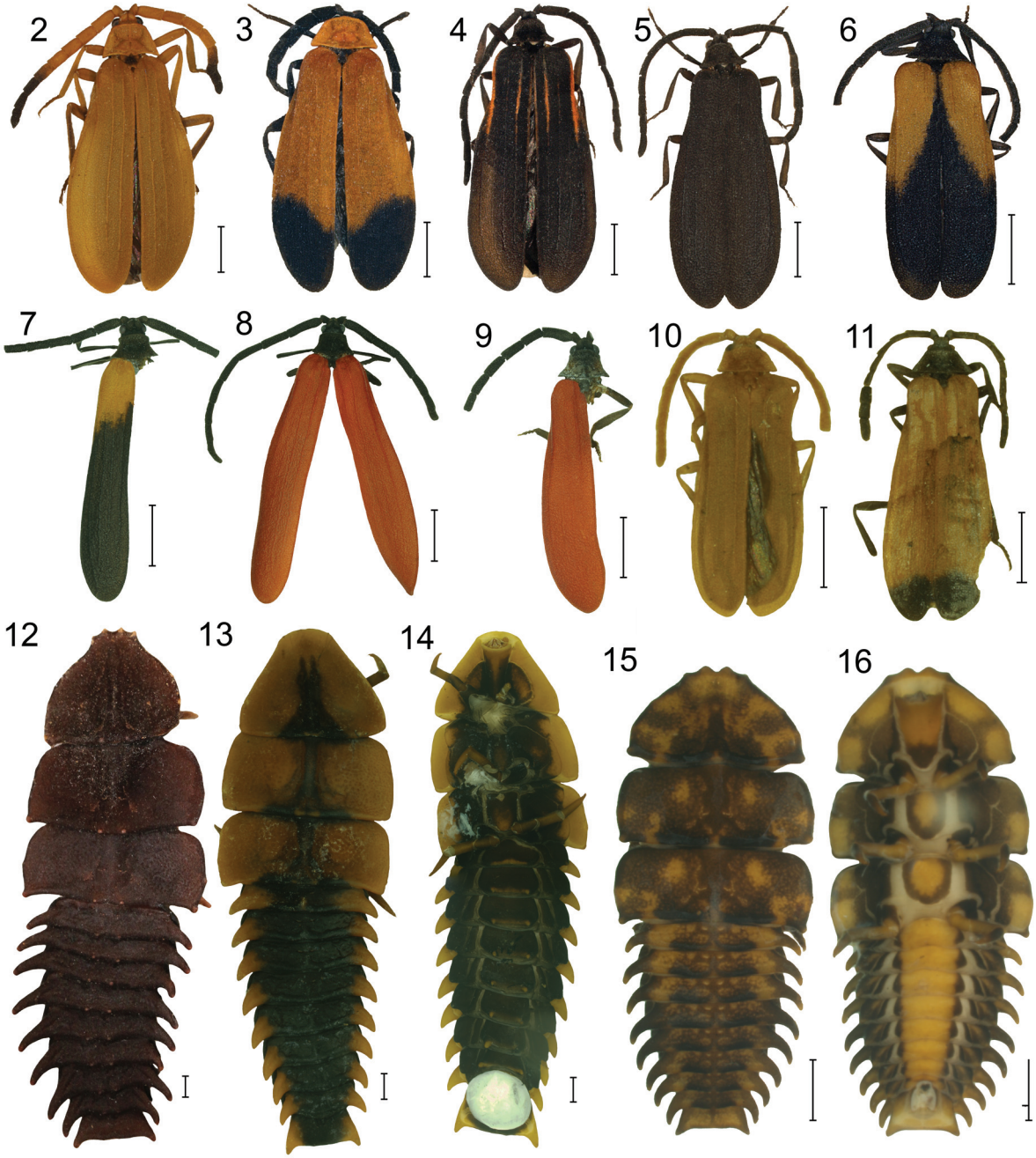
a digital camera attached to a stereoscopic microscope and line illustrations were derived from adjusted photographs. Morphometric data from adult males were measured with an ocular grid on an Olympus SZX-12 binocular dissecting microscope. The following measurements were taken: BL – body length; HW –width at the humeri; PW – pronotal width, measured at the widest part; PL – pronotal length at midline; Edist – minimum frontal distance between eyes; Ediam – maximum eye diameter in lateral view.

Depositories. BMNH – Natural History Museum, London, United Kingdom; LMBC – Department of Zoology, Palacky University, Olomouc, Czech Republic; MHNP – Museum d'histoire naturelle, Paris, France; MIZW – Museum and Institute of Zoology, Warszawa, Poland; MAIC – M. A. Ivie collection, Montana State University, Bozeman, USA.

TAXONOMY

Lyropaeini Bocak & Bocakova, 1989

Lyropaeini Bocak & Bocakova, 1989: 718.
Type genus: *Lyropaeus* Waterhouse, 1878.
Paralycinae Medvedev & Kazantsev, 1992: 55; Kazantsev, 2002: 18.
Type genus: *Paralycus* Medvedev & Kazantsev, 1992 (not *Paralycus* Womersley, 1944; Acari)



Figs. 2–16. Adult male, general appearance: 2, *Lyropaeus* (s. str.) *aurantiacus* Bourgeois; 3, *L.* (s. str.) *ceylonicus* Bocak & Bocakova; 4, *L.* (*Lyroneces*) *rubrostriatus* Kleine; 5, *L.* (*Lyroneces*) *optabilis* Kleine; 6, *L.* (*Lyroneces*) *philippinensis* Kleine; 7, *L.* (*Lyroneces*) *ritsemae* Gorham; 8, *L.* (*Lyroneces*) *waterhousei* Gorham; 9, *L.* (*Lyroneces*) *dominator* Kleine; 10, *L.* (s. str.) *kejvali*, new species; 11, *L.* (s. str.) *nepalensis*, new species. Larva, general appearance: 12, *Lyropaeus* (s. str.) sp. A; 13–14, *Lyropaeus* (s. str.) sp. B; 15, *Lyropaeus* (s. str.) sp. C. Scale bars = 2 mm.

Lyropaeus Waterhouse, 1878
(Figs. 2–24, 28–50)

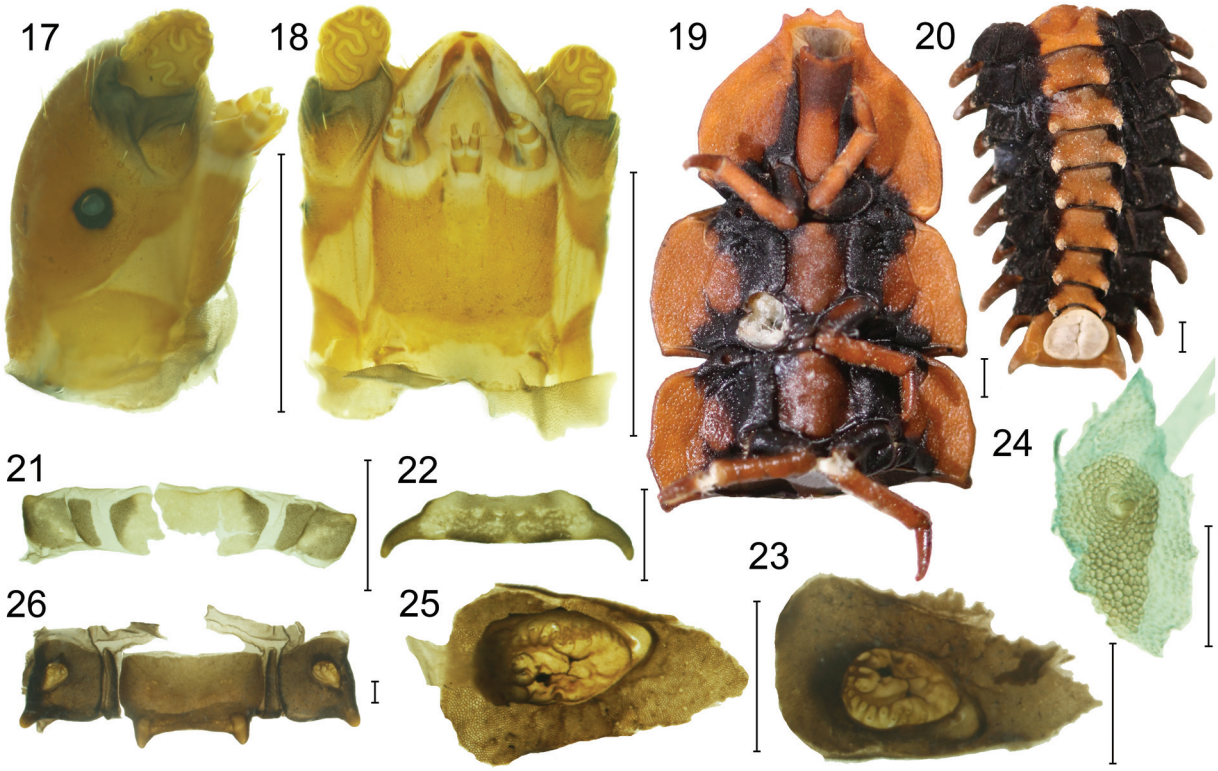
Adult. Differential diagnosis. Antennae 10-segmented, head hypognathous, mouthparts reduced and with merged basal palpomeres, pronotum without carinae, elytra with weak longitudinal costae, transverse costae absent. Only males winged (Figs. 2–11), females completely larviform (Figs. 12–24).

Redescription. Male. Body 5.8–13.5 mm long, dorso-ventrally flattened, coloration variable from testaceous to black or aposematically colored (Figs. 2–11). Head small, hypognathous. Vertex horizontal, with prominent anterior antennal tubercles, frons vertical; antennal cavities proximate. Clypeus concave, labrum very small, slightly wider than long; hypopharynx plate-like, with antero-lateral processes, hypopharyngeal plate only slightly longer than wide. Mandibles vestigial, partially sclerotised, inner part membranous, without teeth (Fig. 49). Maxilla reduced, with small, setose mala, maxillary palpi short; 4-segmented (Fig. 48). Labium two-segmented, apical palpomere pointed at apex (Fig. 47). Eyes small. Antennae 10-segmented, flat; scapus twice longer than wide, pedicel very short; antennomeres 3–10 parallel-sided, similar in shape, getting shorter and less flattened, apical antennomere slender. Pronotum without carinae, at most with incomplete keel anteriorly along midline; disc of pronotum with punctures at margins (Fig. 50). Prosternum triangular, with widely rounded anterior margin and slender apical processes. Elytra flat, widened in apical third, weakly sclerotised. Each elytron with four weak primary longitudinal costae; secondary costae absent. Costa 4 basally forming elevated, well marked humerus, remaining costae much weaker, all costae diminishing apically, absent in apical fifth of elytral length. Elytral interstices with irregular net-like structure. Legs slender, laterally compressed, trochanters longer than one third of femoral length, tarsomeres 1–4 with gradually larger pulvillae, apical tarsomere slender, claws robust at base, with basal setae. Abdomen weakly sclerotised, much shorter and narrower than elytra, slender; tergites 5–7 with longitudinal keel, tergite 7 emarginate in middle, terminal segments slender. Phallus trilobate, slender; phallobase v-shaped, fused with bases of paramerae, paramerae wide, with apical processes (Figs. 28–38) or shortened with simple apex (Figs. 39–46). Females. No adult female has been collected, the large bodied larvae are assumed to be females, similar to the situation in *Platerodrilus* described by Wong (1996).

Lyropaeus **(s. str.) sp. A**
(Figs. 12, 17–24)

Material examined. 1 female larva, late instar (MAIC). India Kerala, Pon Mudi, 770 m, 8°45.592′N, 77°06.453′E, 28 June 2006 in forest, at night.

Differential diagnosis. The body flat, large, trilobite-like (Figs. 12–16) similar to those of *Platerodrilus* in general appearance. *Lyropaeus* larvae differ from other lycid larvae by the following diagnostic characters: fossa antennalis closed,



Figs. 17–26. Larva of *Lyropaeus* (s. str.) sp. A: 17, head in lateral view; 18, ditto in dorsal view; 19–20, general appearance in ventral view; 21, abdominal sternite and pleurites of segment 1; 22, abdominal tergite 1; 23, mesothoracic spiracular plate; 24, abdominal spiracle of the segment 1 from Fig. 21. Larva of *Platerodrilus* sp.: 25, spiracular plate of the segment 1 from Fig. 26; 26, abdominal sternite and pleurites of segment 1. Scale bars = 2 mm (Figs. 17–23, 25–26); scale bar = 0.25 mm (Fig. 24).

separated from mouth-parts by pleurostoma (similar only to *Platerodrilus*). The terminal antennal segment is unique in the whole family: the apical antennomere is divided into complex dorsal and ventral parts, each interdigitated with the opposite process and forming an ovoid with a brain-like appearance (Figs. 17–18).

The complex, oval meso- and metathoracic spiracles are cribriform, the sieve plate with 10 openings arranged in a circle. They are situated in large depressions (Fig. 23) which are different in form from the circular abdominal spiracles (Fig. 24), which are placed in the lateral membrane with the trachea attached at the center of the cavity rather than at the dorsal margin of the spiracular plate. In *Platerodrilus* the thoracic and abdominal spiracles are not so different, with a single opening at margin of the cavity and a linear row of additional openings along the main tracheal trunk; the abdominal spiracles placed in sclerotised pleurites and looking much like those of the thorax (Fig. 25). Sternites simple (Fig. 21), tergites A1–A8 with lateral processes at posterior margin (Fig. 22), without posterior sternal processes as in *Platerodrilus* (Fig. 26).

Description of mature female larva (Voucher UPOLVP0017). Body wide, considerably flattened due to extensively projected lateral plates (Figs. 12, 19–20). Dark brown, only thoracic and abdominal sterna light brown, whole body heavily sclerotised, upper surface mat, with numerous small tubercles. Head slightly longer than wide, anterior margin projecting, rounded (Figs. 17–18). Epicranium consisting of dorsal and pleural plates, membranous between plates. Complete fossa antennalis present, dorsally limited by epicranium, ventrally by sclerotised pleurostoma, without longitudinal sclerite ventrad pleurostoma (sclerite present in *Platerodrilus*; Bocak & Matsuda, 2003, Fig. 27). Basal antennomere very short, ring-like; apical antennomere with ventral and dorsal processes, each branched, branches fitting together like puzzle pieces (Fig. 18). Maxillary mala sclerotised, with a peg-like process. Gulomentum almost rectangular, with short processes posteriorly, cervical sclerites free, slender, well sclerotised (Fig. 18). Pronotum trapezoidal, truncate at apex, with four small processes on frontal margin, indistinct tubercles at posterior and lateral margins, with marked but shallow longitudinal groove, continued on meso- and metathorax, less distinct on abdominal segments. Thoracic terga with strongly widened lateral plates. Prosternum long, more than four times longer than width in middle, episterna extensive, attached to prosternum. Meso- and metasternum gradually shorter, all sterna without tubercles (Fig. 19). Extensive spiracular plates fronto-laterally of episternum, distant from epimeron, with ~10 spiracles arranged in circle in bottom of extensive cavity in both, meso- and metathorax (Fig. 23). Robust trachea attached to bottom of cavity. Legs slender, relatively long, long trochanters divided into anterior and posterior part. Abdomen with large lateral processes, spiracles A1–A8 tiny, simple, in small feebly sclerotised plate in lateral membrane (Fig. 24). Sterna A1–A8 and pleurites without any processes (Fig. 21). Lower pleurites very small, upper pleurites larger. Segment A9 widest at apex, with short, fixed urogomphi (Figs. 12, 20).

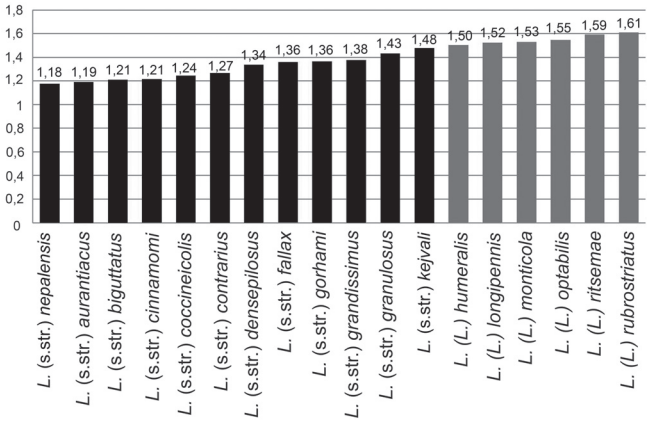


Fig. 27. Ratio between width at humeri and width of pronotum at basal margin in selected species of *Lyropaeus* (s. str.) (black bars) and *Lyropaeus* (*Lyroneces*) (gray bars).

Measurements. BL 46 mm, PL 10.5 mm, PW 12.5 mm.

Lyropaeus (s. str.) sp. B
(Figs. 13, 14)

Material examined. 1 female larva (MAIC). India Kerala, Pon Mudi, 770 m, 8°45.592'N, 77°06.453'E, 27 June 2006 in forest.

Differential diagnosis of late instar female larva (Voucher UPOL VP0016). Body shape similar to *Lyropaeus* sp. A, anterior margin of prothorax smooth, dorsal midline of thorax, sterna and parts of pleurae and abdomen except dorso-lateral processes dark brown to black, head, legs, lateral parts of thorax and postero-lateral processes of abdominal terga A1–A9 testaceous. Spiracular plates reaching epimeron posteriorly, abdominal sternal tubercles minute, lateral tergal processes short.

Measurements. BL 29 mm, PL 5.6 mm, PW 8.0 mm.

Lyropaeus (s. str.) sp. C
(Figs. 15, 16)

Material examined. 3 female larvae (MAIC, LMBC). India, Tamil Nadu, 2km NE Kotagiri, Longwood Shola, 1970 m, 11°26'10.97"N, 76°52'27"E, 2 July 2006, one feeding on mushy fungus, one possibly on snail.

Differential diagnosis of lower instar larvae (Species C, Voucher No. UPOL VP2312). Body shape similar to *Lyropaeus* sp. A, pronotum broader, 4 points on anterior margin of pronotum rounded, not acute, dark brown with symmetrical small irregular patches in thoracic terga, lateral parts of pleurae and parts of abdominal sterna, head, trochanters and femora, testaceous. Spiracular plates reach epimeron posteriorly, abdominal sternal tubercles of A2–A8 minute, lateral tergal processes short.

Measurements. BL 16.5 mm, PL 4.1 mm, PW 6.2 mm.

Remarks. The known 'trilobite larvae' known to date represent two genera: *Platerodrilus* (=*Duliticola* Mjöberg, 1925) and here redescribed *Lyropaeus*. Although they resemble each

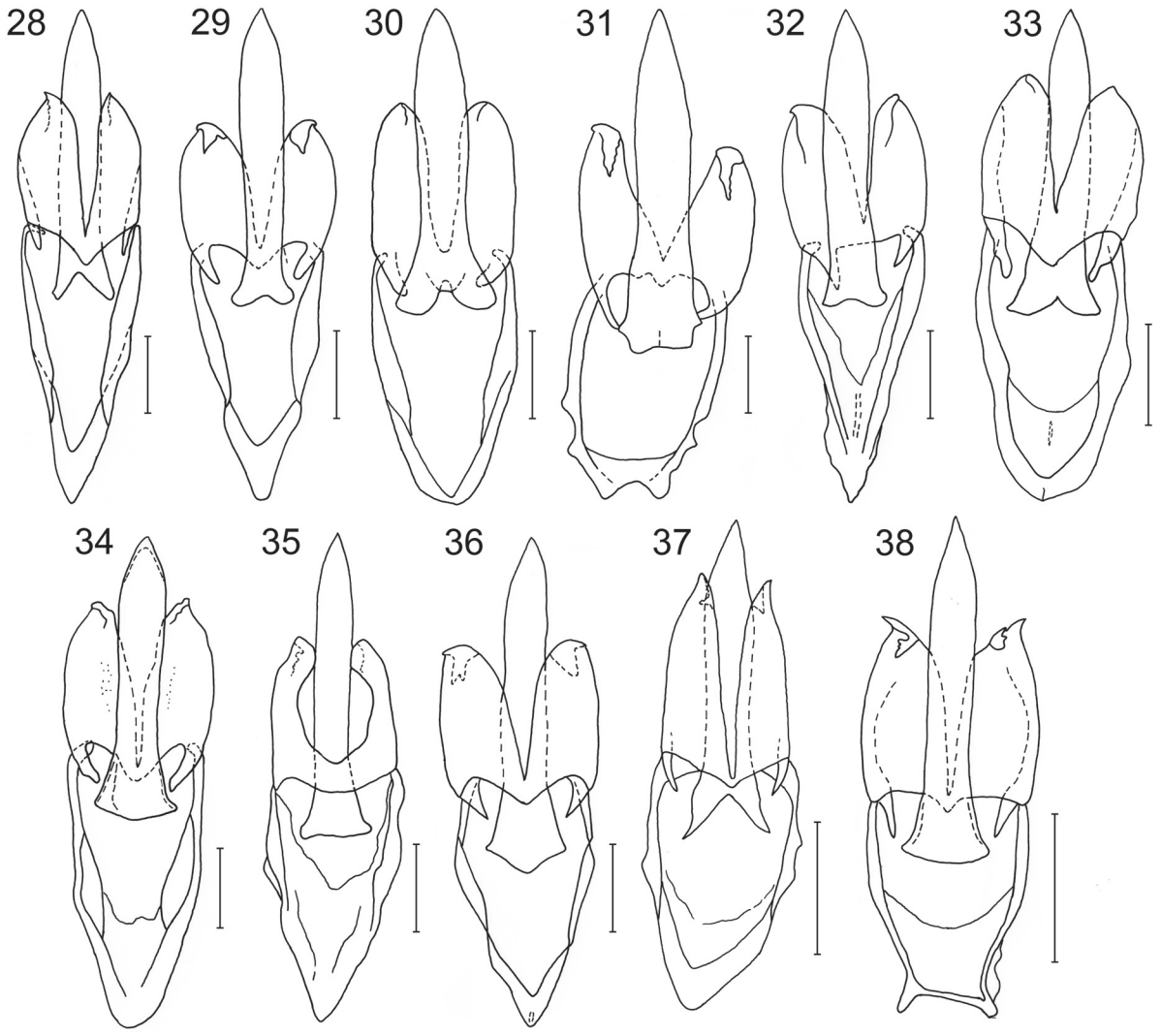
other in many characters, the analysis of molecular data shows that their similarity is a result of convergent evolution within Lyropaeinae. The unique spiracular sieve plate with 10 openings arranged in a circle was found only on the meso- and metathoracic segments in *Lyropaeus*, and they are placed in a distinct ovoid depression (Figs. 19, 23), unlike the circular spiracles of the abdomen that are small, simple, not depressed below the normal surface (Figs. 21, 24). This differs from the situation in *Platerodrilus* where the ovoid spiracular depression is present on both thoracic and abdominal segments (Fig. 26), and there is a linear group of openings on the sieve plate of the thoracic spiracles. Unlike *Lyropaeus*, in *Platerodrilus* a single opening is at upper margin of the cavity and the connecting trachea runs along the inner wall of sieve plate from the margin of the cavity to the opposite margin with several openings arranged in a row (Fig. 25). The origins of these large bodied larvae were ascribed to K-selection in a lineage with neotenic females (Bocak et al., 2008).

Gravely (1915) described a pupa of *Lyropaeus* which developed from a smaller larvae. We are not able to discriminate at the moment the male larvae from early instar female larvae and we can only say that the large bodied larvae (Voucher UPOLVP0016–7) must be females. We have only small-bodied specimens of the species C (Voucher UPOLVP2312) and these could be both late instar males and early instar females. Surprisingly, no Lyropaeini larvae have been collected in Southeast Asia (Wong, 1996) and large bodied larvae are now confirmed only in the south Indian *Lyropaeus*.

***Lyropaeus* (s. str.) *nepalensis*, new species**
(Figs. 11, 37)

Material examined. Holotype. Male (LMBC), Nepal, Gandrung, 2,050 m, coll. Tonxli, 10 October 1980.

Differential diagnosis. *M. nepalensis* is the only *Lyropaeus* species known from Nepal. It has the smallest extent of



Figs. 28–38. Male genitalia of *Lyropaeus* s. str.: 28, *L. aurantiacus* Bourgeois; 29, *L. biguttatus* Gorham; 30, *L. ceylonicus* Bocak & Bocakova; 31, *L. cinnamomi* Kleine; 32, *L. contrarius* Kleine; 33, *L. densepilosus* Kleine; 34, *L. fallax* Walker; 35, *L. grandissimus* Kleine; 36, *L. granulosus* Kleine; 37, *L. nepalensis*, new species; 38, *L. kejvali*, new species. Scale bars = 0.25 mm.

the apical dark patches in elytra and very long and slender paramerae (Figs. 11, 37).

Description. Body medium-sized, dark brown to black, only elytra except apical eighth testaceous, apex of elytra dark brown (Fig. 11). Head small, hypognathous, including eyes slightly narrower than frontal margin of pronotum. Eyes hemispherically prominent, eye diameter 0.64 times frontal interocular distance. Antennae robust, compressed, reaching two thirds of elytral length. Head and antennae with dense, short, recumbent pubescence. Pronotum flat, 2.53 times wider than long at midline. Posterior margin of pronotum bisinuate, longitudinal keel absent. Elytra almost parallel-sided, 6.86 times longer than width at humeri; slightly widened posteriorly, widest at apical fourth. Elytral costae well developed in basal two thirds of elytral length, costae 2 and three weaker, costa 3 inconspicuous in humeral part, but apparently running till dark apical patch. Legs compressed, with dense pubescence. Male genitalia 3.3 times longer than wide in middle part, paramerae with prominent apical processes (Fig. 37).

Measurements. BL 8.3 mm, PL 0.7 mm, PW 1.77 mm, HW 2.1 mm, Edist 0.48 mm, Ediam 0.31 mm.

Distribution. Nepal.

Etymology. The specific epithet refers to the type locality of the holotype.

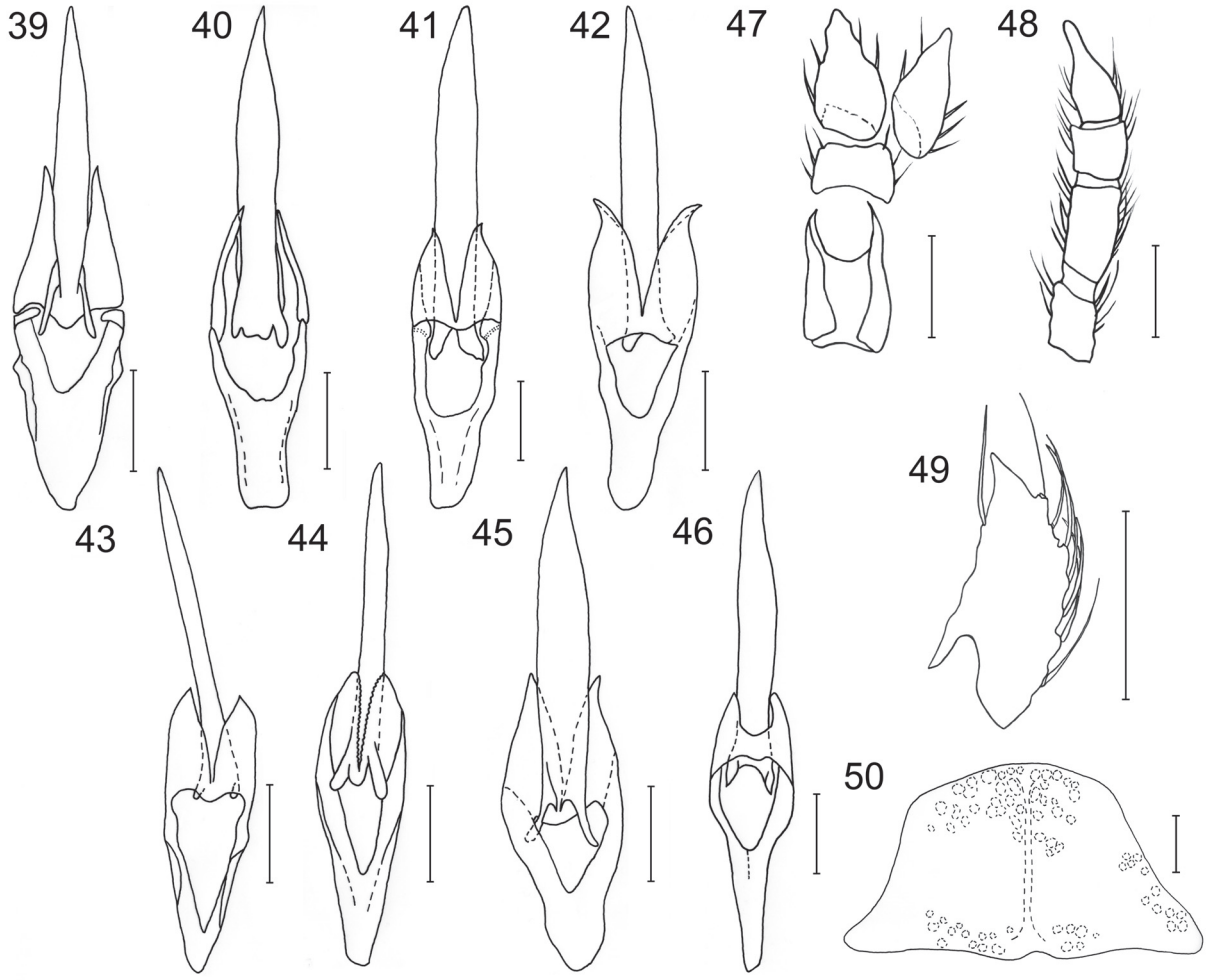
Lyropaeus (s. str.) *kejvali*, new species

(Figs. 10, 38)

Material examined. Holotype. Male (LMBC), India, Kerala, Cardamom Hills, Pamba env., 77°05'E, 9°25'N, 300 m, 15 May 1999, colls. Z. Kejval & M. Tryzna; Paratype. Male (LMBC), same data.

Differential diagnosis. *M. kejvali* has the smallest body of all Indian species. It resembles *L. aurantiacus* in the unicolour upper side of the body, but these species differ in the shape of apical processes of paramerae (Fig. 38).

Description. Body small. Head, thorax, elytra, and appendices testaceous, abdomen dark brown. Head small, hypognathous, including eyes slightly narrower than frontal margin of pronotum. Eyes hemispherically prominent, eye diameter 0.59 times frontal interocular distance. Antennae robust, compressed, reaching over middle of elytral length. Pronotum flat, 2.73 times wider than long at midline, widest at



Figs. 39–50. Male genitalia of *Lyropaeus* (*Lyroneces*): 39, *L. dominator* Kleine; 40, *L. humeralis* Kleine; 41, *L. monticola* Kleine; 42, *L. optabilis* Kleine; 43, *L. philippinensis* Kleine; 44, *L. ritsemae* Gorham; 45, *L. rubrostriatus* Kleine; 46, *L. waterhousei* Gorham. Mouth parts of *L. (Lyroneces) optabilis*: 47, labium; 48, maxillary palpus; 49, mandible. Pronotum: 50, *L. (Lyroneces) optabilis*. Scale bars = 0.25 mm (Figs. 39–46, 47–49); scale bar = 0.5 mm (Fig. 50).

basal margin. Posterior margin of pronotum bisinuate. Median longitudinal keel well marked in frontal and posterior parts, interrupted in middle. Scutellum deeply emarginate at apex. Elytra almost parallel-sided, 5.71 times longer than width at humeri; humeri marked by sharp costae 4, epipleura vertical in humeral fourth of elytra, rest of elytra flat, elytra widest at apical third. Elytral costae 1 and 4 strong in basal two thirds, costa 2 weak, costa fourth inconspicuous, absent in most of elytral length. Legs compressed, with dense pubescence. Male genitalia with wide, slightly shortened paramerae and basal processes of phallobase (Fig. 38).

Measurements. BL 6.9 mm, PL 0.68 mm, PW 1.41 mm, HW 2.1 mm, Edist 0.50 mm, Ediam 0.30 mm.

Distribution. India: Kerala.

Etymology. The specific epithet is a patronym in honour of Z. Kejval, the collector of the holotype.

PHYLOGENETIC ANALYSIS RESULTS

Thirteen ingroup samples (Table 1) were sequenced for 18S, 28S rRNA, *rrnl*, *cox1* and *nad5* mtDNA fragments and the fragments were aligned with eighteen outgroup taxa (Bocak et al., 2008) along 5,036 homologous positions. The newly described species in this paper were not fixed for DNA isolation and therefore they were not included in the molecular analysis. The clade represented by *Lyropaeus* s. l. obtained high support in all analyses as was the basal split between subgenera *Lyropaeus* s. str. and *Lyroneces* (Fig. 1). The topology of the *Lyroneces* clade suggests independent monophyla occurring in Peninsular Malaysia, Sumatra, and Borneo + the Philippines. These *Lyroneces* clades were mostly characterised by high bootstrap values, although the position of the Sumatran and Malayan clade was inferred differently in the parsimony analysis relative to the maximum likelihood and Bayesian analyses. All analyses suggested close relationships between Lyropaeini (*Lyropaeus* s. l.) and Miniduliticolini (*Platerodrilus*, *Pendola*, *Macrolibnetis* etc.). The large bodied females known in *Macrolibnetis*, *Platerodrilus*, and *Lyropaeus* originated independently in the respective clades (Fig. 2).

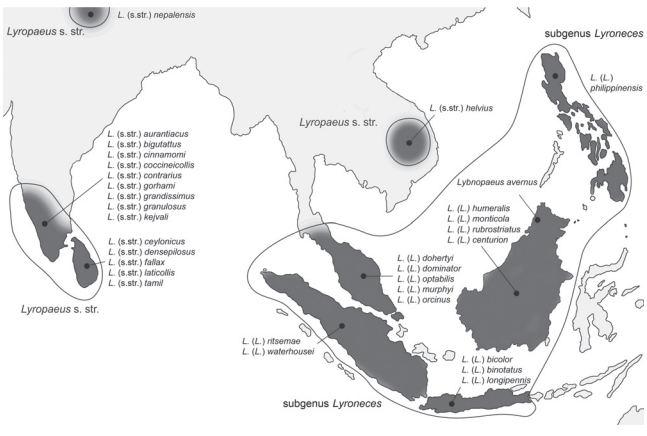


Fig. 51. Geographical distribution of Lyropaeini.

DISCUSSION

Relationships and classification. *Lyropaeus* were originally classified in Dilophotini (Kleine, 1933) and Bocak & Bocakova, 1989 proposed the tribe Lyropaeini within Leptolycinae. Bocak et al. (2008) inferred Lyropaeini among the basal branches of Lycidae. This position is supported by the present results which place Lyropaeini as a sister group to *Platerodrilus* and related genera (Fig. 1). The tree suggests that the large bodied neotenic females evolved as a parallelism. Their independent origin is supported by several unique morphological modifications described above (Figs. 21–26).

The tribe Lyropaeini originally contained only *Lyropaeus*. Later, Kazantsev (1998) studied several species of *Lyropaeus* and split the genus in three genera: *Lyropaeus* Waterhouse, 1878; *Lybnopeus* Kazantsev, 1998; and *Lyroneces* Kazantsev, 1998. The concept of *Lyroneces* was based on: 1) significantly smaller pronotum; 2) the humera considerably wider than the pronotum; 3) the phallobase and parameres fused; and 4) parameres not hooked outwardly at apex (Kazantsev, 1998; Figs. 28–46). Unfortunately, Kazantsev (1998) did not examine the morphology of most species of *Lyropaeus* and classified only six species as *Lyroneces*. The topology inferred from DNA fragments shows that *Lyroneces* needs to be more widely defined to include all species of the eastern clade of *Lyropaeus* s. l. When more species are examined, some characters given are not as clear as proposed by Kazantsev (1998). The first two characters are correlated and we found a gradation toward the smaller pronotum without any abrupt change between *Lyropaeus* and *Lyroneces* (Fig. 27). Therefore, the relative size of the pronotum can be used only in the extremes of the range. Similarly the shape of apical part of paramerae is quite variable and in some cases the placement of a species might be ambiguous, as in case of *L. monticola* or *L. optabilis* (Figs. 41–42). This is supported by the fact that Kazantsev (1998) placed only a few species in *Lyroneces* and the other members of the eastern clade were left in *Lyropaeus*. The fused paramerae and phallobase are similarly unclear in several species (Figs. 39–41). When the phallus is observed in lateral view at higher magnification, a clear division between phallobase and paramerae is visible. As a consequence, some species can be placed in either group only using molecular and distributional data. The original diagnostic characters are invalid and only the shorter paramerae support the definition of *Lyroneces* (Figs. 28–46). Given the finding of an eastern and a western clade in the molecular phylogeny we propose to retain the name *Lyroneces* as a redefined subgenus of *Lyropaeus* until further information on the Indian and Vietnamese species is available. Although there is no objective rule as to whether or not a given lineage should be recognised as a genus or subgenus, our view is that the genus should be clearly defined to enable non-specialist to place a species without any doubts.

Based on this expanded concept we transfer to the subgenus *Lyroneces* the following species formerly classified in *Lyropaeus*: *Lyropaeus (Lyroneces) bicolor* Pic, 1911 (Java); *L. (Lyroneces) binotatus* Pic, 1926 (Java); *L. (Lyroneces)*

longipennis Pic, 1911 (Java); *L. (Lyroneces) philippinensis* Kleine, 1926 (Philippines); *L. (Lyroneces) ritsemae* Gorham, 1882 (Sumatra); and *L. (Lyroneces) waterhousei* Gorham, 1882 (Sumatra). The male genitalia of most species have not yet been studied, therefore available species are illustrated in Figs. 28–46.

Paralycus Medvedev & Kazantsev, 1992 is a junior homonym of *Paralycus* Womersley, 1944 in Acari (a new homonymy proposed here). *Lybnopeus* was not available for examination and we retain its generic status as proposed by Kazantsev (1998) in the Lyropaeini.

Distribution. An apparent trait of the lineage is high local endemism at the species level (Fig. 51). The range of *Lyropaeus* is discontinuous: *Lyropaeus* s. str. is recorded from Sri Lanka, Southern India, the Himalayas, and Vietnam while *Lyropaeus* (*Lyroneces*) occurs in the Malay Peninsula, the Greater Sundas, and the Philippines. The above described distribution is similar to those of Ateliinae represented by *Atelius* Waterhouse, 1878 (Ceylon, Northern Vietnam, Hainan) and *Scarelus* Waterhouse, 1878 (the Malay Peninsula, Greater Sundas and Philippines). The terminal position of the Philippine species in a sister position with the *L. rubrostriatus* suggests colonisation of the Philippines from Borneo similarly to *Scarelus* (Malohlava & Bocak, 2010).

We have examined material from major European collections and we found that all species are restricted to a single island (Sumatra, Borneo, Java, the Philippines, Sri Lanka) or in areas defined by mountain systems or biomes (the Malay Peninsula, Central Highlands in Vietnam, the Himalayas, and the Ghats of Southern India). The report of the Malayan species *L. dohertyi* from Assam by Kleine (1933) is therefore very doubtful and we have not found any specimen of *L. dohertyi* from India. The range of *Lyropaeus* seems limited to the rain forests of the Oriental region despite the absence of natural barriers to the north. Although Southern China forms a continuous landmass with Southeast Asia, *Lyropaeus* apparently does not occur in these regions, which were affected by climatic fluctuations (Jiang et al., 2008). Therefore, we suppose that the extremely limited dispersal propensity of flightless females limits dispersal over long time spans. The diversity also depends on the tectonic stability of the area where these beetles occur. Most parts of Java and Sumatra were submerged from the late Oligocene until the middle Miocene (Hall, 2011) and fauna of these islands is less diverse than those of Borneo (5 spp.), the Malay Peninsula (5 spp.), Southern India (9 spp.) and Sri Lanka (5 spp.). Only two species from isolated localities are known from Indochina and Northern India (Fig. 51), but these were not available for sequencing and their detailed relationships could not be studied.

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