UNIVERZITA PALACKÉHO V OLOMOUCI

PŘÍRODOVĚDECKÁ FAKULTA

KATEDRA ZOOLOGIE

Molecular phylogeny and zoogeography of net-winged beetles (Coleoptera: Lycidae)

Ph.D. Thesis

Michal Mášek

P1527 – Biology

Zoology

Supervisor: Prof. Ing. Ladislav Bocák, Ph.D.

Olomouc 2017

Hereby, I declare that I prepared the thesis unders supervision by Dr. Ladislav Bocák using the literature cited in this study.

Olomouc, 16. February 2017

Mgr. Michal Mášek

Bibliographical identifications:
Author's first name and surname: Michal Mášek
Title: Molecular phylogeny and zoogeography of net-winged beetles (Coleoptera: Lycidae)
Type of thesis: Ph.D. Thesis
Department: Department of Zoology
Supervisor: Prof. Ing. Ladislav Bocák, Ph.D.
The year of presentation: 2017

Abstract:

The current study synthesizes the evidence from the molecular phylogenetics, extant distribution, paleoclimate and plate tectonics to provide an insight in ancestral areas, dispersal routes and the effectiveness of barriers for slowly dispersing net-winged beetles (Coleoptera: Lycidae). I assembled net-winged beetle samples from all zoogeographical regions and inferred the phylogenetic relationships for >600 species representing 25 tribal taxa using two nuclear rRNA and three mtDNA fragments. I used a general mixed Yule coalescent model to delimit putative species. The phylogenetic analyses revealed well-supported clades in agreement with the tribe-rank lineages in formal classifications. Conversely, a low support was inferred for deep relationships among major clades. The ancestral areas were identified separately for principal lineages: 17 tribes originated in interconnected eastern parts of the Oriental and Chino-Japanese realms, two tribes in the Panamannian realm, two in the Afrotropical realm, two in the Neotropical realm, and one in the South-Eastern Gondwana, i.e., present day India and Australia. The pattern of phylogenetic diversity fits with the origin of net-winged beetles in the southern parts of Eurasia and Amuria. The highest alpha-taxonomic diversity was identified in the tropical rain forests of present day Malesia. Three lineages Calochromini, Erotini and Dictyopterini colonized Nearctic region from Eastern Asia; Calochromini, Platerodini, and possibly Lycini colonized the Afrotropical region via northern coast of the Tethys sea in the Miocene, and Calochromini additionally reached the Wallacea and Australia. Four lineages, Metriorrhynchini, Calopterini, Slipinskiini and Dexorini, remained isolated in Gondwana after its definitive separation from northern continents. Metriorrhynchini colonized the Afrotropical and Oriental regions being transferred to the north by the drifting Indian subcontinent, Dexorinae and Lycinae: Slipinskiini remained limited to Afrotropical realm or its small part, Calopterini diversified in the Neotropical region and colonized the Nearctic region by a limited number of species. Using current analyses and previously published data, the effective dispersal barriers for net-winged beetles were identified. A few short distance inter-landmass dispersal events were inferred, the long-distance over-sea dispersal have not been indicated by the phylogeny, tectonics and extant distribution. Net-winged beetles and especially the neotenic lineages proved that distribution of poor dispersers enables reconstruction of dispersal and vicariance history over a long time-span. The ancient origins of most neotenic lineages were confirmed and monophyletic origin of neotenic lineages from Asia, the Guinea Gulf and the Caribbean is suggested for the first time by the current molecular analyses. These landmasses were located close to the equator and formed a continuous coast of the Tethys sea at the supposed time of the origin of these lineages. The new findings are reflected by the slightly modified classification, but further data are needed for building robust phylogeny of Lycidae.

Keywords: Coleoptera, Lycidae, phylogeny, zoogeography, rRNA, mtDNA, taxonomy.

Number of pages: 159
Number of appendices: –
Language: English

Content

Preface

The diversity of animals is extraordinary and yet mostly unknown. The estimation of the number of species currently living on the planet fluctuates between units to tens of millions of species. Although some groups have been already quite thoroughly studied, the insects belong into the group of animals, in which we have discovered a fragment of real diversity. Among most diverse orders are beetles (Coleoptera) with about 400,000 formally described species and here, I present a study focused on the family Lycidae. Net-winged beetles are among species rich, mostly tropical lineages and the last catalogue reported 2,819 species in early 1930's. More than a thousand species have been described since then and thousands still remain undescribed even in collections.

The Ph.D. thesis contains the set of six studies, one of them representing a comprehensive molecular phylogeny and zoogeography of the whole family and five previously published studies dealing with some restricted groups. Most studies in this disertation are using molecular phylogenetic approach and only a single publication represents a traditional morphology-based taxonomic work. The initial study deals with the phylogeny, classification and zoogeography of the family Lycidae. Its introductory part contains general information about the family, an overview of existing classifications and a summary of available informations on zoogeography and diversity. This information represents an introductory section for the whole study and is not repeated here. The first part of the dissertation has not yet been published and it is presented in the form which is ready for submission to an entomological journal. Further five studies have already been published in the journals registered in the database Web of Science (Thompson Scientific) in the category Zoology. The studies are aimed on various groups of Lycidae with an emphasis on groups with neotenic development (Articles 2–5), and a single study (6) is a co-authored work dealing with the reconstruction of ancestral areas of the tribe Calochromini.

All studies have in common the topics of diversity, classification and processes that are responsible for current distribution of individual lineages of the family Lycidae. Due to the chaotic species-level classification, the molecular approach was used. When necessary, the species were delimited using the structure of the mt DNA. Similarly, as the recent morphological studies brought further instability in the tribal and subfamiliar classification, here, I use exclusively the molecular phylogenies as a basis for natural classification and delimitation of higher taxa. Multiple DNA fragments, both nuclear and mitochondrial were produced and partly compiled from previous studies of the home laboratory to infer phylogenetic relationships and to reconstruct ancestral ranges. Based on the molecular phylogeny, distribution data, tectonic and paleoclimatic history of main dispersal routes and barriers were defined and compared with the current classification of zoogeographical regions based on the distribution of vertebrates.

The study demonstrates the power of the molecular approach in the contemporary phylogenetics, inferrence of natural classification and reconstruction of dispersal history. Taxonomy is a basic biological discipline and should provide information about the animal diversity on the Earth and construct natural and predictive classification system. Although such task is widely acknowledged and information provided by systematic biologists is needed for other fields in biology, the chances that we describe diversity before we destroy it are slim. Due to the burden of out-of-date taxonomic studies providing contentious information, general taxonomic impediment and the inaccessibility of many regions for scientific research, our knowledge remains limited for many groups. Lycidae are no exception, therefore the main task of this set of studies is to bring knowledge about phylogeny and classification on the new higher level. The current dataset containing more than 600 species is exceptional even in the time of the current explosive development in molecular phylogenetics and it enables phylogenetic and zoogeographic inference unthinkable previously. The principal outputs of this study are the delimitations of tribal level taxa, the inference of their relationships and distribution. Further, the research is focused on the diversity and speciation of neotenic lineages which have been incompletely known.

Part 1

Molecular phylogeny and zoogeography of net-winged beetles (Coleoptera: Lycidae)

Michal Masek

(unpublished manuscript)

Abstract

The current study synthesizes the evidence from the molecular phylogenetics, extant distribution, paleoclimate and plate tectonics to provide an insight in ancestral areas, dispersal routes and the effectiveness of barriers for slowly dispersing net-winged beetles (Coleoptera: Lycidae). I assembled net-winged beetle samples from all zoogeographical regions and inferred the phylogenetic relationships for >600 species representing 25 tribal taxa using two nuclear rRNA and three mtDNA fragments. I used a general mixed Yule coalescent model to delimit putative species. The phylogenetic analyses revealed well-supported clades in agreement with the tribe-rank lineages in formal classifications. Conversely, a low support was inferred for deep relationships among major clades. The ancestral areas were identified separately for principal lineages: 17 tribes originated in interconnected eastern parts of the Oriental and Chino-Japanese realms, two tribes in the Panamannian realm, two in the Afrotropical realm, two in the Neotropical realm, and one in the South-Eastern Gondwana, i.e., present day India and Australia. The pattern of phylogenetic diversity fits with the origin of net-winged beetles in the southern parts of Eurasia and Amuria. The highest alpha-taxonomic diversity was identified in the tropical rain forests of present day Malesia. Three lineages Calochromini, Erotini and Dictyopterini colonized Nearctic region from Eastern Asia; Calochromini, Platerodini, and possibly Lycini colonized the Afrotropical region via northern coast of the Tethys sea in the Miocene, and Calochromini additionally reached the Wallacea and Australia. Four lineages, Metriorrhynchini, Calopterini, Slipinskiini and Dexorini, remained isolated in Gondwana after its definitive separation from northern continents. Metriorrhynchini colonized the Afrotropical and Oriental regions being transferred to the north by the drifting Indian subcontinent, Dexorinae and Lycinae: Slipinskiini remained limited to Afrotropical realm or its small part, Calopterini diversified in the Neotropical region and colonized the Nearctic region by a limited number of species. Using current analyses and previously published data, the effective dispersal barriers for net-winged beetles were identified. A few short distance inter-landmass dispersal events were inferred, the long-distance over-sea dispersal have not been indicated by the phylogeny, tectonics and extant distribution. Net-winged beetles and especially the neotenic lineages proved that distribution of poor dispersers enables reconstruction of dispersal and vicariance history over a long time-span. The ancient origins of most neotenic lineages were confirmed and monophyletic origin of neotenic lineages from Asia, the Guinea Gulf and the Caribbean is suggested for the first time by the current molecular analyses. These landmasses were located close to the equator and formed a continuous coast of the Tethys sea at the supposed time of the origin of these lineages. The new findings are reflected by the slightly modified classification, but further data are needed for building robust phylogeny of Lycidae.

Introduction

The ultimate goal of systematic biology is to recover a robust species-level phylogeny. Such goal remains elusive for species-rich clades due to the chaotic traditional morphology-based taxonomy, the limited capacity of laboratories and the absence of material suitable for DNA isolation. Nevertheless, the recent progress in molecular phylogenetics opens a possibility to study the evolution of some clades with more resolution and better sampling. Here, the net-winged beetles (Coleoptera: Lycidae) are used as a model group for such study and I focus primarily on the origins of principal lineages, their species richness and dispersal history.

The dispersal propensity and ecological adaptability are very variable factors and they substantially affect the current distribution of animal lineages (e.g., Cruaud *et al*. 2011, Fabre *et al*. 2014, Gomez-Rodriguez *et al*. 2015). Consequently, the reconstruction of ancestral areas and dispersal routes of highly mobile groups with very diverse life history is often obscured by repeated episodes of faunal interchanges, by range shifts and by extinctions in dynamically changing environments. Conversely, the groups characteristic in a low dispersal propensity and ecological uniformity can serve as more appropriate models for the worldwide reconstruction of vicariance and dispersal history over a long-time span. Net-winged beetles have been demonstrated as a group with very limited dispersal propensity, and therefore they are suitable for a zoogeographic study (Sklenarova *et al.* 2014, Masek *et al*. 2015).

The phylogeography and origins of large clades with thousands of species have been seldom studied with a phylogenetic approach. Here, I present the phylogeny of several hundred species of net-winged beetles, one of major families of Elateroidea, i.e., click beetles and allies (Bocakova *et al*. 2007). Altogether 4224 valid species have been formally described and the most diverse lineages are the tribes Metriorrhynchini, Platerodini, Lycini, Calopterini, and Calochromini, each of them with at least several hundred species (Bocak & Bocakova 2008). The net-winged beetles have been reported from all zoogeographic regions except large deserts and polar regions (Kleine 1933) and they occur in forest and shrub habitats. The larvae live in upper soil layers rich with organic material, decaying roots in deeper soil layers, decaying tree trunks or in dead branches in the canopy of rain and cloud forests. The unique synapomorphy of net-winged beetles is their complex split mandible adapted for sucking up liquids containing rich microbial life (Cicero 1994, Bocak & Matsuda 2003). Therefore, these beetles are strictly limited to the regions where moisture is available in decaying wood or other organic materials at least for some part of the year (Bocak & Matsuda 2003). A prolonged dry season considerably limits abundance of net-winged beetles and only the draught tolerant lineages as Calochromini and Lycini are moderately abundant in such regions (Kleine 1933).

The net-winged beetles belong among soft-bodied elateroid families, a group corresponding with the historical concept of Cantharoidea (Crowson 1960, 1972). Their characteristic morphological trait is the incomplete sclerotization (Bocak *et al*. 2008) which limits their resistance to desiccation due to exposed inter-segmental membranes, an absent sub-elytral cavity, and delicate cuticle (Ahearn 1970, Bocak & Bocakova 2008).

Their soft integument provides inadequate framework for flight muscles and besides desiccation problem, further limits their ability to fly. Although most species are winged, they fly only slowly, in short distances and usually avoid open windy and sunny places and remain under the forest canopy (Bocak & Bocakova 2008, field observations). As a consequence, almost all net-winged beetles are poor dispersers. Sklenarova *et al.* (2014) showed that Metriorrhynchini only seldom crossed sea straits and Li *et al.* (2015a) identified high genetic differentiation between populations of Lyponiini in China and Japan despite the absence of apparent dispersal barriers. Similarly, the vicariant origin of Japanese Macrolycini fauna and the complete absence of recent dispersal between continent and the Japanese islands were documented by Li *et al*. (2015b, in press). The shift to the neotenic development is another factor further decreasing the dispersal propensity of Lycidae. The females of several net-winged beetle lineages do not metamorphose and they are sexually mature while retaining the complete larval morphology (Wong 1995, Levkanicova & Bocak 2009, Bocak & Bocakova 2008, Masek *et al*. 2014, McMahon & Hayward 2016). Their dispersal propensity is extremely limited and despite their ancient origin, their ranges are small (Bocak *et al*. 2008, Malohlava & Bocak 2010, Masek *et al*. 2015, Bray & Bocak 2016).

The aim of this paper is to analyze the phylogeny of net-winged beetles and discuss some relationships not yet indicated by the previous studies. Further, I focus on the distribution of main net-winged beetle clades identified by the molecular phylogeny and I try to define the areas with high phylogenetic and alpha-taxonomic diversity. Here, I use the largest up-to-date phylogeny of net-winged beetles to define robustly supported clades corresponding to the formally named tribes and analyze their areas of origin and evaluate the effectiveness of various barriers limiting their dispersal. Many internal relationships among Lycidae lineages remain ambiguous and similarly the species level classification has not been rigorously studied and mostly depends on historical uninformative descriptions. Therefore, I use tribes defined robustly by molecular phylogeny and morphology as natural entities and delimit species only on the basis of the phylogenetic tree.

Material and Methods

Sampling

Altogether 766 samples representing over 600 species were included in the phylogenetic analysis (Tab. S1). About 1900 sequences were taken from the previous studies dealing with the phylogeny of Lycidae (an earlier study containing 69 taxa, Bocak *et al*. 2008) and several taxonomically restricted studies (e.g., Sklenarova *et al*. 2014, Masek *et al.* 2015, Motyka *et al.* in press). Additional almost 800 fragments were newly produced for the present study and they form ~30% of the current dataset. Sequenced samples represent all major lineages of net-winged beetles except a few recently described monotypic lineages of an uncertain origin (Tab. S2). These were unavailable for the DNA extraction and their relationships cannot be inferred as they are deposited in a private collection and unavailable for study (Kazantsev, personal communication). The latest classification of Lycidae and the numbers of known taxa are listed in Fig. 5 and Tab. 1. As an alternative classification, I consider those published by Bocak & Bocakova (2008).

Laboratory methods

Whole genomic DNA was extracted from thoracic muscles using Wizard SV96 kit (Promega Inc.). The extraction yield was measured using a NanoDrop-1000 Spectrophotometer and PCR amplifications were performed in a 50 µl reaction volume using 0.5 U Taq polymerase, 1 mM $MgCl_2$, 50 mM of dNTPs, 0.2 mM of each primer, and typically 30 ng of template. Cycle conditions were 2 min at 94°C, 30–60 sec at 94°C, 30–60 sec at 45–52°C, 1–2 min at 72°C (steps 2–4 repeated 35–40 times), and 10 min at 72°C. I sequenced the complete nuclear 18S rRNA and the D2 region of 28S rRNA and three fragments of the mitochondrial genome (*rrnL*, *cox1-tRNA-Leu-cox2*, and *nad5-tRNAs* mtDNA, the multiple gene fragments are further referred as *cox1* and *nad5* only). The primers are listed in Tab. S3. PCR products were purified using PCRµ96 Plates (Millipore Inc.) and sequenced by an ABI3130 automated sequencer using the Big Dye Terminator Cycle Sequencing Kit 1.1 and setting recommended by the manufacturer.

Sequence handling and phylogenetic analyses

Sequences were edited using Sequencher 4.8 (Gene Codes Corp.). The protein-coding markers (*cox1*, *cox2*, and *nad5* mtDNA) were aligned by ClustalW 1.83 (Thompson *et al*. 1994) under 22.5 for gap opening and 0.83 for extension and the alignment was checked for amino acid reading frames. The length variable 18S rRNA, 28S rRNA, *rrnL*, and tRNA mtDNA fragments were aligned using MAFFT 7 (Katoh & Standley 2013), BlastAlign 1.2 (Belshaw & Katzourakis 2005) and MUSCLE 3.6 (Edgar 2004) under default settings. All aligned fragments were concatenated in a supermatrix for further analyses.

Phylogenetic trees were inferred under the maximum likelihood criterion (ML) using RAxML 7.2.5 (Stamatakis *et al*. 2005). The model was identified using jModelTest 2.1.7 (Darriba *et al*. 2012) and genes and protein coding positions were partitioned in all analyses. The bootstrap support values (BS) were obtained by analyzing 500 pseudoreplicates using the GTRCAT model (Stamatakis *et al*. 2008). The resulting phylogenetic trees were visualized using FigTree 1.4.2 (Rambaut 2009) and modified in the graphical software.

Geographical distribution and ancestral state reconstruction

The all available data on distribution were assembled from the latest catalogue of Lycidae (Kleine 1933) and the Zoological Record database till the end of 2014 (Thomson Reuters Inc.). Distribution maps for the whole family and major tribe level lineages were produced using the free vector map of the world (http://www.naturalearthdata.com/downloads/10m-physical-vectors/). Geographical coordinates of each beetle sample locality were edited in a csv file and analyzed on the 2-degrees vector grid. Final charts were visualized in the open source Geographic Information System QGIS Desktop 2.10.1 (https://www.qgis.org/en/site/forusers/download.html). I used the zoogeographical realms defined by Holt *et al*. (2013) for evaluation of species richness (Figs 3, S1–S20).

The ambiguous support for basal relationships excludes the formal reconstruction of the ancestral area for net-winged beetles (Fig. 2). Instead, I defined 20 clades which obtained high bootstrap support (BS ≥ 93%, the clades are marked in the Fig. S21) in the molecular phylogeny and they are simultaneously robustly supported by morphology. Ateliini and Dihammatini clades did not contain all terminals, in both cases a single terminal was placed at the base of their sister clade; these two terminals were omitted from further phylogeographic analyses. Further, I did not formally analyze five clades classified as tribes, but represented by a low number of taxa: Alyculini (1 sp.), Antennolycini (2 spp.), Dexorini (2 spp.), Leptolycini (4 spp.) or in case of Taphini (7 spp.) the tribe represented the group of species delimited only on the basis of morphology and was not recovered in the current analysis (Fig. 2). These five tribes are known either from a single region (the first four) or in the case of Taphini only a single species unavailable for study is reported from an adjacent area (Oriental Taphini and a single species reported from the Wallacea and Papua). The extant ranges of these clades are considered as their ancestral regions.

The putative species were identified algorithmically using the general mixed Yule-coalescent (GMYC) model and the preferred ML tree topology. Relative age of nodes was estimated using penalized likelihood and cross-validation analysis as implemented in r8s version 1.71 (Sanderson 2002). The GMYC approach applies the threshold time to separate DNA-based species. I used the algorithm implemented in the SPLITS package for R (http://r-forge.r-project.org/projects/splits/; Ezard *et al*. 2009).

The ancestral state reconstructions were performed only for clades with the sufficient number of terminals using discreet traits in the BEAST 2.3.0 (Bouckaert *et al*. 2014). The separate datasets were produced for the tribe-level monophyla identified in the phylogenetic analyses and outgroups were omitted. The best model of evolution for Bayesian phylogenetic analysis was selected using jModelTest 2.1.7 (Darriba *et al*. 2012). The analysis was set for 50 million generations using the coalescent model and constant population size as recommended in the manual (Drummond & Bouckaert 2015). For the ancestral reconstruction were generalized all species localities to defined areas: Neotropical; Panamanian; Nearctic realms; Afrotropical realm: continental Sub-Saharan Africa, no record for Madagascar in the current analyses; Sino-Japanese realm: continental China, incl. Taiwan and Hainan, Japan; Oriental realm: Indo-Burma, Indian, Sumatra, Borneo, the Philippines, Malay Peninsula, Wallacea; Oceanian realm: New Guinea and adjacent islands; Australian realm; Palearctic realm: West Palearctic, East Palearctic. The maximum credibility tree was generated using TreeAnnotator 2.2.0 (Bouckaert *et al*. 2014). Ancestral areas and directions of world distribution of each tribe were visualized using SPREAD 1.0.6 (Bielejec *et al*. 2011) and graphic outputs were finalized using Photoshop software. The analyses of dispersal history were not repeated for several clades, i.e., Ateliini, Calochromini, Dilophotini and Metriorrhynchini, whose relationships and phylogeography have been recently analyzed (Malohlava & Bocak 2010, Sklenarova *et al*. 2014, Motyka *et al*. in press).

Results

The representation of diversity in the dataset

The complete dataset contained 766 terminals of net-winged beetles representing 605 DNA-based putative species from all zoogeographical regions and 89 outgroup taxa from 9 families (Tab. S1). The concatenated dataset contained 18S rRNA sequences (569 terminals), 28S rRNA (567 terminals), *cox1* (699 terminals), *rrnL* (695 terminals) and *nad5* mtDNA (663 terminals). Altogether, 782 DNA fragments were produced newly for this study. The sequenced species of net-winged beetles represent 25 tribes; 7 tribes, combined representing 9 species, were not available for the study (Tab. S2). The sequenced species represent the equivalent of 14.4% of the described net-winged beetle diversity. Most species were identified only to the genus level as alpha-taxonomy of the tropical faunas remain chaotic and routine identification of species is impossible without the extensive study of types deposited in museums around the world. All zoogeographical regions were sampled approximately proportionate to their diversity (Tab. 1). The geographic information is reported for all samples and the highest number of samples was collected in the Oriental and Sino-Japanese realms (Tab. S1). The species-poor neotenic lineages were well represented due to the previous research focused on the taxonomy of these unique groups.

The tree topology

All analyses of the dataset consistently returned Lycidae as a monophyletic group and the clade was regularly supported by 100% bootstrap values (BS, Fig. S21). The topologies of major lineages, i.e., having the subfamily rank, was highly variable in the ML searches on various aligned datasets. Conversely, most major lineages which obtained the tribe rank in the formal classification (Bocak & Bocakova 2008) and were represented by a higher number of terminals, were recovered under all settings and they obtained bootstrap support 93–100% (Figs 2, S21). Only three terminals were placed in conflict with the formal classification in the tree in Fig. 2. As there is very little support for deep phylogeny of Lycidae, I chose a single tree consistent with the formal earlier published classification and it is shown in Figs 2 and S21. An additional tree with very different basal topology is shown in Fig. S22.

Libnetinae (BS 100%, 13 spp., but a single additional species misplaced) were variably found among the basal branches which include also the clade of neotenic lineages consisting of Antennolycini (BS 83%, 2 spp.), Alyculini (1 sp.), Dexorini (BS 100%, 2 spp.), Leptolycini (BS 32%, 4 spp.), Lyropaeini (BS 100%, 9 spp.), and Platerodrilini (BS 96%, 32 spp.) or in a variable terminal position (e.g., Fig. S22). Further, the subfamily Dictyopterinae was recovered (BS 97%, 25 spp.), but Taphini (8 spp.) rendered Dictyopterini paraphyletic and formed only a terminal branch in Dictyopterinae (Fig. 2). Metriorrhynchini were inferred as a clade with the robust support (BS 93%, 161 spp.). Dihammatini represented an independent clade of 9 species (BS 99%), but a single species was misplaced as a sister species of Slipinskiini (BS 100%, 4 spp.), the sister clade of Dihammatini. Lycoprogenthini (BS 100%, 9 spp.), Conderini (99%, 14 spp.), Thonalmini (BS 100%, 3 spp.), Eurrhacini (99%, 8 spp.), Platerodini (BS 93%, 48 spp.), Erotini (BS

100%, 18 spp.), Calochromini (BS 99%, 47 spp.), Calopterini (BS 96%, 15 spp.), Lycini (BS 100%, 34 spp.), Macrolycini (BS 100%, 14 spp.), Dilophotini (BS 97%, 30 spp.), Lyponiini (BS 100%, 17 spp.) were well supported and all terminals were placed in an agreement with their formal classification. Ateliinae were split in two clades: *Scarelus* (BS 99%, 18 spp.) and *Atelius* (1 sp.) which was misplaced as a sister taxon to Lyponiini. These two tribes formed a clade with a high support (BS 97%).

The distribution data were compiled for all species described till the end of 2014 and distribution maps were produced for the whole family, selected subfamilies and each tribe (Figs 3, S1–S20). The highest alpha-taxonomic diversity was identified in the rain forests of the Oriental region where have been recorded almost 1800 species (Fig. 3). The number of recorded species is much higher than in other realms when only ~500 species were recorded in the Afrotropical, Neotropical and Oceanian realms. In contrast with the Oriental realm, usually a single tribe dominates in each of these realms: Calopterini in the Neotropical realm (282 spp., 53% of the realm's diversity), Lycini in the Afrotropical realm (258 spp., 48%) and Metriorrhynchini in the Oceanian realm (471 spp., 73%; Fig. 3).

Additionally, the number of tribes was recorded in the geographic vector grid (Fig. 4). The highest number of tribes was identified in the eastern part of the Oriental realm, i.e., Indo-Burma, the Malay Peninsula, the Greater Sundas except Sulawesi and in the Philippines. Most of these tribes occur also in the transitional zone between the southern part of the Sino-Japanese realm (13 tribes in the Sino-Japanese realm) and the Oriental realm, but the number of tribes decreases substantially with the higher latitude. The northern part of the Sino-Japanese realm, especially the central and northern Chinese provinces (i.e., Gansu, Shanxi, Hebei, Shandong, Liaoning, Jilin, Heilongjiang) and the Korean Peninsula have impoverished fauna and only the Japanese islands display the diversity comparable to the southern China (12 tribes). The further realms with relatively high representation of tribes are the Palearctic realm (8 tribes, most of them in the costal area of the Russian Far East), Panamanian (7 tribes in the analysis and 3 tribes recently described for a few species, Tab. S2), Afrotropical (6 tribes), Neotropical (6 tribes), Nearctic (6 tribes) and Oceanian (5 tribes and the single monotypic tribe of unclear position, Tab. 1).

Geographical structure of diversity

The reconstruction of ancestral areas, previous studies and the distribution of clades known from a single region showed that 13 of 25 defined clades have started their differentiation in the Oriental realm, i.e., the south-eastern part of the Eurasian continent or their extant distribution is limited to this region. Additional four tribes started their evolution in the adjacent part of the Sino-Japanese realm (Tab. 1). Leptolycini and Thonalmini are endemic to the Panamanian realm, Eurrhacini and Calopterini to the Neotropical region, Dexorini and Slipinskiini to the Afrotropical realm. Macrolycini and Dilophotini are endemic to the Sino-Japanese region, except a single species known from northern Borneo (Levkanicova & Bocak 2009). The analyses specifically devoted to a single tribe were not repeated here. These involve Metriorrhynchini with the origin in East Gondwana (Sklenarova *et al*. 2014), Calochromini started their evolution in Indo-Burma, i.e., in the transitional region between the Oriental and the Sino-Japanese realms and Dilophotini in Indo-Burma

(Motyka *et al*. in press). The formal reconstruction of the dispersal history of Lycini cannot robustly support a single ancestral range due to the ambiguous deep relationships (Fig. 2).

Using distribution data, I defined six main dispersal barriers affecting distribution of net-winged beetles: the dry central Asian region separating the western Palearctic region and the eastern part of the Asian continent (i.e., the eastern Palearctic, the Sino-Japanese realm and the continental part of the Oriental realm (Fig. 8). This dry region separates very diverse eastern and extremely species-poor western fauna of the tribes Erotini, Dictyopterini, Calochromini, Lycini, and additionally several very diverse tribes in the eastern region which do not occur in the western part of Eurasia. Similarly, a low number of tribes is shared between the eastern Palearctic/Sino-Japanese and Nearctic realms (Fig. 8), when only five tribes are shared and only low numbers of Calochromini, Dictyopterini, Platerodini and Erotini occur in the New World. The faunas of the Nearctic and Panamanian + Neotropic realms share most tribes (six tribes are known from the Nearctic region and only Dictyopterini do not occur south of Northern Mexico), but the realms differ substantially in the species richness (81 versus 532 species). The Makassar strait in another effective barrier; in this case separating the highly diverse continental fauna of the Malay Peninsula and the islands of the continental Sunda shelf (Sumatra, Java, and Borneo) and the much poorer fauna of Sulawesi and the Moluccas (Fig. 8) which is predominantly of the Australian origin. Similarly, the sea straits between the southern Philippines and northern Sulawesi (including Sangir Besar and the Siau islands as stepping stones) stopped dispersal of the Philippine species with the Oriental origin to the islands with predominantly oceanic origin, i.e., Sulawesi and the Moluccas, and limited the dispersal of Australian fauna to the Philippines. A little difference at the tribal level was found between faunas of the Moluccas and Sulawesi. Substantial difference in species richness and phylogenetic composition was identified in the landmasses separated by the Mozambique strait. Only the metriorrhynchine genus *Cautires* has been recorded in the Madagascan realm (53 species) in contrast with six tribes and >500 species in the Afrotropical realm.

Discussion

Higher level phylogeny and classification of net-winged beetles

The current five-marker dataset of 766 terminals from 25 tribes considerably surpasses the latest six-marker phylogeny of net-winged beetles based on 73 terminals from 22 tribes (Bocak *et al*. 2008). Concerning the number of sequenced taxa, this phylogeny represents one of the most dense family-level phylogenies in Coleoptera and unlike other beetle studies, this phylogeny has the balanced representation of all geographical regions (Bocak *et al*. 2014). The monophyly of Lycidae obtained the high support. Nevertheless, despite much denser sampling and the high number of informative characters, basal subfamily-level relationships remain elusive, the recovered topologies differ among individual analyses and all deep splits obtained generally very low bootstrap supports. Therefore, no formal classificatory changes at the subfamily rank can be inferred from the current analyses. In the shallower levels of the tree, the monophyly of most tribes is robustly supported, but their mutual relationships remain similarly ambiguous and differs between individual analyses (Figs S21–22).

Libnetinae, a small and morphologically uniform Oriental lineage, was recovered at basal split of Lycidae or in the relationships with Dilophotini (Figs 2, S21, Bocak *et al*. 2008). Further deep splits are represented by the clade of neotenic lineages. These lineages were regularly found monophyletic, but without a sufficient bootstrap support (BS 26%). Unlike previous analysis, two critical neotenics, *Dexoris* and *Leptolycus* are newly included in the current dataset and for the first time their relationships with Oriental neotenic Lyropaeinae is indicated by molecular data (Fig. 2) in agreement with the morphology-based classification proposed originally by Bocak & Bocakova (1990) and later abandoned (Bocak *et al*. 2008, Kazantsev 2013). Dexoridae were given the family rank by Kazantsev (2005), lowered to the subfamily Dexorinae by Bocak & Bocakova (2008) and further lowered to Dexorini in Leptolycinae by Kazantsev (2013) (Fig. 1). Here, *Dexoris* is inferred as an internal branch within strongly supported Lycidae (Figs 2, S21–22). Hence, its position as a sister-group to remaining Lycidae is definitively falsified. The low support was obtained for the detailed position of *Dexoris* and *Leptolycus* within the neotenic clade. These taxa are either the sister-lineages of Lyropaeinae (incl. *Platerodrilus* and several related genera, Alyculini and Antennolycini, Fig. S22) or they were recovered as independent lineages within Leptolycinae *sensu lato* (i.e., Bocak & Bocakova 1990, but not Kazantsev 2013) in relationships to either Alyculini or Antennolycini (Fig. 2). Due to their long independent evolutionary history and morphological disparity, I keep subfamiliar ranks as in the previous classification (Bocak & Bocakova 2008), i.e., Leptolycinae for *Leptolycus* and closely related genera including Dominopterini and Electropterini from the Caribbean; Dexorinae incl. Mimolibnetini for the Afrotropical neotenic lineages (Kazantsev 2013, Mimolibnetinae synonymized with Dexorinae by Bocakova 2014) and Lyropaeinae with the tribes Alyculini, Antennolycini, Lyropaeini, Platerodrilini and the enigmatic Miniduliticolini based on a single heavily damaged specimen deposited in the private collection and unavailable for the study. Alyculini and Antennolycini were recovered as sister-groups of Dexorini in some analyses, but due to disagreement with the morphological evidence, I prefer to keep the subfamilies as they were earlier defined until further evidence is available (Fig. S22). All these subfamilies are clearly morphologically defined and they have allopatric distribution which provides additional support for their long independent evolutionary history. The classification proposed by Kazantsev (2013) placed the taxa which form the neotenic clade in four subfamilies: Mimolibnetinae (synonymized to Dexorinae by Bocakova (2014)), Miniduliticolinae (*Miniduliticola* which is unavailable for molecular analyses and Platerodrilini which were recovered as a terminal lineage of Lyropaeinae in all current analyses and surely do not deserve the subfamiliar status unless most Lyropaeinae genera get same high rank), Leptolycinae were formed by Antennolycini, Lyropaeini, Dexorini, Leptolycini, Dominopterini, Electropterini and Leptolycini, i.e., an assemblage of taxa, whose relationships did not get any support from the current analyses (Figs 2, S21–S22).

Dictyopterinae were found as the next extensive clade among principal lineages of net-winged beetles. Dictyopterinae (BS 97%) consist of Dictyopterini and Taphini, but

Taphini were recovered as a terminal lineage of Dictyopterinae in some analyses (Fig. 2). The current results did not provide any support for relationships between Erotini and Dictyopterinae suggested by earlier classification (e.g., Kleine 1933) and questioned already by the previous study (Bocak *et al*. 2008), but neither for the close relationships of Lycoprogenthini and Dictyopterinae (Lycoprogenthini were included in Dictyopterinae on the basis of morphology and recovered among basal clades by Bocak *et al*. 2008).

Further clade contains the tribes placed in the subfamilies Ateliinae and Lycinae as earlier delimited (Bocak & Bocakova 2008). The subfamily Ateliinae, i.e., Ateliini and Dilophotini, was not recovered as a monophylum and the neotenic lineage Ateliini, i.e., genera *Atelius* and *Scarelus*, formed a clade with Lyponiini (BS 97%). Lyponiini were found as a sister group of *Scarelus* with *Atelius* being a sister to them (Fig. S21). Considering the morphological similarity, I retain both *Atelius* and *Scarelus* in Ateliini till further molecular data are available to elucidate their relationships. The tribe Dilophotini, earlier hypothesized sister-group to Ateliini, was recovered as a sister to the Lyponiini + Ateliini clade (BS 47%, Fig. S21).

The Lycini + Calopterini clade was recovered in agreement with earlier studies although the support for their relationships remains very low (BS 36%). Calopterini contain lineages with presumed neotenic females (Miller 1991), but in contrast with the Oriental and Panamanian neotenic lineages, the calopterine neotenic species included in the analysis represents just a subclade with the quite recent origin as was proposed already by Miller (1988) and Bocak *et al*. (2008). Kazantsev (2013) included the calopterine neotenics (e.g., *Lycomorphon* etc.) in Leptolycini based on potentially homoplastic characters found in most small bodied males, whose females have neotenic development (Bocak *et al*. 2008). Similarly, the recently reported neotenic species *Cautires apterus* Bocak *et al*. 2014 represents another recent shift to the neotenic development. These findings support a scenario that neotenics evolve repeatedly in the elateroid lineages, including net-winged beetles (Bocakova *et al*. 2007, Kundrata & Bocak 2011, Kundrata *et al*. 2014, Bocak *et al*. 2008, 2016, McMahon & Hayward 2016) and that these lineages are apparently able to survive for a long time in stable habitats such as tropical rain forests (Bocak *et al*. 2008, Masek *et al*. 2015). Currently, at a minimum four independent origins of neoteny are hypothesized in Lycidae: the clade of Lyropaeinae, Dexorinae and Leptolycinae (incl. Miniduliticolinae and Mimolibnetinae, although their common origin is weakly supported), Ateliini (a clade with an independent origin based on morphological data, recovered as an independent terminal lineage by the present analyses), at least a single neotenic lineage in Calopterini (the terminal designated as *Pseudoceratoprion* in Fig. S21) and *Cautires apterus* in Metriorrhynchini (Bocak *et al*. 2014).

Concerning, the very low support for most relationships, I prefer to minimize formal changes of the previous classification and I keep the rank of subfamilies for Libnetinae, Dexorinae, Leptolycinae, Lyropaeinae, and Lycinae (Fig. 2). Ateliinae (Dilophotini + Ateliini) I propose to merge with Lycinae. Here, I apply a combined approach based on molecular phylogeny and earlier published information on morphology (Bocak & Bocakova 1990, Kazantsev 2005), although the formal morphological analysis is not presented. The monophyly of the Oriental neotenic lineages Alyculini, Antennolycini, Lyropaeini, Platerodrilini and Miniduliticolini does not have robust support, but I prefer this arrangement instead of elevating all of them to the rank of subfamilies as was partly proposed by Kazantsev (2013), who elevated the terminal lineage Platerodrilini (within his concept of the subfamily Miniduliticolinae) and terminal Alyculini to the subfamiliar rank. The very dense sampling did not substantially improve the topology of the Lycidae tree and only more genes in the analysis can provide further information to build the natural classification of Lycidae.

Diversity centers, ancestral areas and dispersal routes

The support for the basal topology remains ambiguous. Therefore, no formal analysis was conducted to infer the ancestral area of the whole family. Nevertheless, it is worth to note that split between Lycidae and Iberobaeniidae was inferred at 171.0 Ma (149.7–190.3, 95% HPD) (Bocak *et al*. 2016). Consequently, the origins of the most deeply rooted lineages can be expected at times when much higher connectivity between tropical regions is hypothesized (Seton *et al*. 2012). The endemism of neotenic Iberobaeniidae in the western Mediterranean and the distribution of neotenic Dexorinae, Leptolycinae and Lyropaeinae point to the southern coasts of Laurentia, Laurasia and Amuria as a potential area of the early diversification of net-winged beetles.

Libnetinae are restricted to the Oriental and Sino-Japanese regions with highest diversity known from the humid eastern tropical part of the Oriental region. The low diversity of Libnetini has been identified in India and Sri Lanka (Fig. S2) and it can be the result of either their delayed dispersal from the eastern part of the Oriental region to the newly accreted Indian subcontinent or unfavorable climatic conditions either in the connecting areas or at least temporarily in the substantial part of the Indian subcontinent. Relatively high diversity is known from the Sino-Japanese region, but diversity decreases rapidly in the northward direction and only a single species is known from the Japanese islands. The Sri Lankan and Indian species were unavailable for analysis and the origin of Libnetinae was inferred in the Malay Peninsula with multiple independent dispersal events leading to the extant distribution (Fig. 6A). Their distribution is in the clear contrast with their possible ancient origin and ability to fly.

The clade of neotenic lineages has the worldwide tropical distribution: Lyropaeinae in the Oriental and southernmost part of the Sino-Japanese realms, Dexorinae in the Afrotropical realm and Leptolycinae in the Panamanian realm (the Great Antilles and adjacent islands). Of these, only Dexorinae are Gondwanan, but their hypothesized dispersal from Eurasian craton to the current range in the Afrotropical region is possible, when ancient coastlines and positions of continents is considered (Smith *et al*. 2004, Seton *et al*. 2012). Neotenic lineages due to the extremely low dispersal ability, the long-distance dispersal across open sea is highly improbable and no dispersal have been documented even between closely situated landmasses (Malohlava & Bocak 2010, Masek *et al*. 2015). The only non-continental Lyropaeinae taxa are known from the northern Sulawesi and the central part of the island (Bocak 2002, Bocakova 2006). These taxa were not available for the phylogenetic analyses and I am not able to date their split from their Oriental relatives, therefore any scenario explaining their distribution lacks robust evidence. The morphological disparity of these neotenic lineages suggests an early split from the continental lineages and then the transfer of these lineages on the dry land fragments separated from the Asian continental plate in the Miocene (Hall 1998, 2002) is one of possible explanations. The zoogeographic analysis was limited to Lyropaeini for which several species were available (Masek *et al*. 2013). The origin of the tribe was inferred in Sumatra and with some exchanges among the Malay Peninsula, Sumatra and Borneo and dispersals to India and the Philippines. The dispersal history of *Platerodrilus* and closely related genera was studied by Masek *et al*. (2015) and similarly to *Lyropaeus*, the origin of the clade was inferred in the Greater Sundas with subsequent dispersal to the continental Asia and the Philippines. The colonization of the Philippines is old and was earlier dated to 31 mya when a connection was available between the Sunda shelf and southern Mindanao (Malohlava & Bocak 2010, Masek *et al*. 2013). The tectonic and climatic stability is supposedly the necessary condition for long term survival of these poor dispersers as these do not occur in adjacent northern parts of the Sino-Japanese realm (Li *et al*. in press).

Dictyopterinae are a species poor lineage with the predominantly Palearctic and Sino-Japanese distribution of Dictyopterini and Oriental distribution of Taphini (Figs S5-S6). Only a few species occur in the Nearctic region and a single species of Taphini is widely distributed in the Wallacea and New Guinea. Their phylogeny is still contentious when Dictyopterini and Taphini were not inferred as monophyla (Figs 2, S22). The highest diversity is present in the combined area of the eastern part of the Oriental region and the southern part of the Sino-Japanese region. Surprisingly, a single American species of *Dictyoptera* included in the analysis dispersed to the Nearctic region from Europe and the West and East Palearctic species of *Benibotarus* are closely related (Figs 2, 6C).

Platerodini are among the most diverse tribes of Lycidae (Tab. 1) and the highest alpha-diversity was found in the Oriental and Neotropical regions. Their origin was inferred in the Malay Peninsula and they dispersed to the Sino-Japanese realm, further north through the Bering strait to the Nearctic region and through southern coast of Asia to the Afrotropical realm. The deep topology obtained very poor support and all conclusions on the origin and dispersal of this tribe remain highly speculative.

Erotini is a group with a low number of described species, but very widely distributed tribe (Fig. S13). Their origin was inferred in Indo-Burma and they dispersed multiple times to the Sino-Japanese region which served as a source area for the West-Palearctic fauna. Only a single species was available from Northern America and its closest relative was found in Japan (Fig. 7A).

Dihammatini and Conderini belong to the group of tribes with the ancestral area in the Greater Sundas and the Malay Peninsula. Both dispersed to the Sino-Japanese realm and except *Xylobanellus erythropterus* (Baudi), they never dispersed to the west. Unlike these, Lyponiini and Macrolycini have a Sino-Japanese origin and they remained limited to this realm except a single species of *Lyponia* recorded from the Northern Borneo (Levkanicova & Bocak 2009).

The previously published analyses identified the origin of Calochrominae in Indo-Burma (Motyka *et al*. in press), Metriorrhynchini in India and the Australian realm when these landmasses were connected and with the dispersal using drifting India as a raft, when they colonized Madagascar, continental Africa and finally the Asian continent (Sklenarova *et al*. 2013). Finally, the origin of Dilophotini has been inferred to Indo-Burma and subsequent dispersal events were inferred to the Sino-Japanese realm, the Greater Sundas and the Philippines (Motyka *et al*. in press). The centers of origins were inferred in the Neotropical region for Calopterini and Eurrhacini and these dispersed to the north in a low number of species. The formal analysis of Lycini dispersal and more data are needed to solve their origin. Their origin can be placed either in the North America or East Asia; the topology clearly indicates that the origin of the Afrotropical fauna is recent and several dispersal events started diversification of Lycini in Africa (Figs 1, S21).

The current analyses are limited by the number of species included in the dataset. Some tribes need a much denser sampling, especially from the Nearctic, Panamanian and Neotropical regions to robustly infer the number of dispersal events and the age of vicariance events which shaped their current distribution. Nevertheless, I can conclude that the net-winged beetles never crossed a large distance across an open sea and all dispersal events crossed the present-day sea straits only when they were at least for some time subaerial or narrow. Similar dispersal routes have been inferred for *Metriorrhynchus,* one of Australian metriorrhynchine lineages which colonized the Philippines and the Greater Sundas (Bocak & Yagi 2010), or *Scarelus* (Malohlava & Bocak 2010).

The current analysis did not infer the ancestral area for the whole family. The individual clades were analyzed and many of them originate form the Greater Sundas, Indo-Burma or the Sino-Japanese realm. These regions are geographically close, never clearly isolated and have a common tectonic history as the stable margin of the Amuria and later Eurasia (Seton *et al*. 2012). Therefore, as a working hypothesis, I propose to place the origin of net-winged beetles to the southern, tropical south-eastern coast of Eurasia.

Major dispersal barriers

The animal diversity and representation of the major lineages were used for definition of the zoogeographical regions (Darlington 1966, Holt *et al.* 2013) and vertebrates are traditionally used as a principal model group. The comparison of inferred patterns has rarely been tested with large independent datasets despite the fact that the evolutionary history, dispersal ability and consequently the effectiveness of recovered barriers varies among groups. The biological characteristic is one of principal factors producing the observed diversity patterns. Many animals are highly mobile and can very easily in a very short time expand their range (Balke *et al*. 2009, Sota *et al*. 2008). Similarly, climatic fluctuations and submergence of dry land are likely to erase historical biogeographic signals. Here, using very poorly dispersing net-winged beetles I demonstrate effectiveness of some selected dispersal barriers, some of them representing a border between major zoogeographic regions (Wallace 1876, Darlington 1966, Holt *et al*. 2013) and some specific for Lycidae. Using molecular phylogeny, tectonics and climatic data, I discuss the differences in the diversity and phylogenetic structure of Lycidae in the regions separated by the hypothesized barriers.

Mozambique Strait

The Mozambique Strait is only 425 km wide and does not represent a major barrier for numerous animal lineages (Yoder & Nowak 2006). In case of net-winged beetles, the faunas are substantially different (Fig. 8). Altogether, six tribes are known from continental Africa, all of them are present in Eastern Africa, at the coast of the Mozambique strait. In contrast with them, only one tribe Metriorrhynchini, represented by a single terminal clade of *Cautires* is present in Madagascar and even the most mobile net-winged beetles such as flower-visiting Lycini and Calochromini and widely distributed Platerodini are absent in Madagascar. Additionally, the origin of Malagasy *Cautires* was hypothesized in India passing close to Madagascar about 62 mya (Sklenarova *et al*. 2014). Therefore, I conclude that no net-winged beetles were present in Madagascar when the island separated from other Gondwanan fragments 80 mya (Seton *et al*. 2012) and never any species dispersed across the Mozambique Strait despite its relative narrowness.

Bering Strait

The common pre-Pleistocene faunal exchanges between East Asia and North America via the Beringia Land Bridge have been documented for several plant and animal lineages in both directions from the early Paleocene until the late Miocene to early Pliocene (7.4 and 4.8 mya; e.g., Tiffney & Manchester 2001, Sota *et al*. 2008). Five tribes, Dictyopterini, Lycini, Calochromini, Erotini, and Platerodini contain both Asian and North American lineages and I was able to identify dispersal events only in a single direction from Asia to North America and dated them to the Lower Tertiary in Calochromini (two genera, *Lucaina* and *Lygistopterus*); the similar distribution of Lycini (*Lycus*, *Lycostomus*) in the Nearctic region might be the result of contemporary dispersal events. Dictyopterini were represented only by a single species which was inferred as a sister to the species from Europe (Fig. 6C). The current sampling is sparse for a robust reconstruction in other lineages. The common feature is the early occurrence of these dispersal events in agreement with previous study dealing with leaf beetles or frogs (Sota *et al*. 2008, *Li et al*. 2015). The Pleistocene low sea stands opened the land connection between these continents, but no such late dispersal event has been identified in the net-winged beetles. The cold and potentially dry climate probably prevented occurrence of net-winged beetles in these high latitudes.

Atrato Seaway (Panama)

The exchange between Nearctic and Neotropical realms has been identified in many animal groups and similarly, the dispersal from the Nearctic region was identified Calochromini (Motyka *et al*. in press) and can be supposed in Lycini based on a similar distribution pattern (Figs S14, S16). Conversely, the colonization starting from the south and reaching as far as southern Canada or Northern Mexico was inferred in Platerodini, Calopterini and Eurrhacini (Figs 6D, S12, S15). In these cases, the diversity is highly biased for the center of origin and the newly expanded parts of the range are colonized by a low number of species which in some cases remain very rare as Calochromini and Lycini in the Neotropical region (field observations). Despite the presence of the dry land and at least coastal regions with favorite biotopes, the exchange of net-winged beetles between these regions is only moderate.

Central Asia Dry Gap

The West Palearctic fauna of net-winged beetles is extremely poor when only 14 species are known from Europe and Caucasus and similarly only five species are known from the Saharo-Arabian realm. In contrast with these, the combined fauna of the Sino-Japanese and Eastern Palearctic region represents 18 tribes and 837 species (Fig. 8). Only 9 species from the western regions were included in the analysis and I can find their closest relatives in the eastern part of Eurasia, none in the Afrotropical and Nearctic realms. Both, desert areas and highly continental dry regions in central Asia represent impermeable barriers. The split of west Palearctic species from their closest relatives was dated to 23.6 mya for *Lygistopterus sanguineus* (Motyka *et al*. in press). Such split is relatively recent and the absence of other lineages in Europe is supported by the low diversity of net-winged beetle fauna in the Baltic amber. Only two genera *Lateralis* (Dictyopterini) and *Protolopheros* (Erotini), both with relatives known from the Sino-Japanese region, have been reported from the amber fossils and they are not known in the extant fauna (Winkler 1987, Kazantsev 2013). The Western Palearctic fauna suffered probably from aridization and glaciation in the Pleistocene and low dispersal ability excluded any recent re-colonization of the region.

North Africa Dry Gap

The desert area does not provide habitats for net-winged beetles and only two species of *Lycostomus* and three *Lygistopterus* are known in Africa north of Sahara, i.e., the western part of the Saharo-Arabian realm. The Afrotropical fauna is in contrast with the Saharo-Arabian (5 spp.) and Western Palearctic (14 spp.) faunas quite diverse (369 spp.) and represents 6 tribes (Fig. 4). The Afrotropical tribes represent two different groups concerning their origin: Dexorini and Slipinskiini are Afrotropical endemics with presumably ancient *in situ* origin, but the most diverse tribes Lycini and Calochromini are hypothesized as migrants from the Oriental region and they colonized the Afrotropical region about 25 mya during the period, when a belt of humid forest was present at the southern coast of the Tethys sea (Motyka *et al*. in press, Kosuch *et al*. 2001). Metriorrhynchini, another very diverse tribe in the Afrotropical region migrated from India about 65 mya (Sklenarova *et al*. 2014) from the drifting Indian subcontinent. Africa was isolated for long time and no out-of-Africa dispersal event was identified in net-winged beetles.

Wallace and Huxley lines (Wallace 1863, Mayr 1944, Huxley 1868)

a) Borneo/Sulawesi sector

The Wallace line lies within the newly defined Oriental realm (Holt *et al*. 2013), but I found almost complete turn over between the adjacent regions at genus level and also high turn over at the tribe level (Fig. 8). Metriorrhynchini are present on both sides of the Wallace line, but they belong mostly to different subtribes with Sulawesi and the Moluccas dominated by taxa with Australian origin (subtribe Metriorrhynchina) and the Sunda Shelf lands with taxa of the Indian origin (subtribes Cautirina and Metanoeina). Only a limited number of genera crossed this line (Bocak & Yagi 2010, Kubecek *et al*. 2015). Similarly to Cautirina, Calochromini (4 spp.) and Lycini (3 spp.) have a high number of their closest relatives in the Oriental region (Motyka *et al*. in press). A relatively low difference was found between faunas of the Moluccas and Sulawesi at the tribal level, although they belong to different realms in recent realm delimitation (Holt *et al*. 2013).

b) Sulawesi/Mindanao sector

The islands connecting Northern Sulawesi and Mindanao were hypothesized as a dispersal route for *Metriorrhynchus* (~10 mya, Bocak & Yagi 2010) and similarity between these faunas confirms effectiveness of this connection in Metriorrhynchini (genera *Leptotrichalus, Metriorrhynchus, Sulabanus* and others evolved in the Moluccas, Papua or Australia and a few species colonized the Philippines. Much less effective was dispersal from the Philippines to Sulawesi as many Oriental tribes are missing in the Philippines (Fig. 8).

c) Huxley line (Philippines/Borneo sector)

Similarly to the Wallace line, this line lies within the Oriental realm as defined by Holt *et al*. (2013) and two potential dispersal routes can be hypothesized within this area: the connection via Palawan which is separated from Borneo by the narrow although deep Balabac Strait and via the Sulu islands. The Sulu islands were hypothesized as a dispersal route for two neotenic lineages in the Lower Oligocene, when Palawan was much further in the north and probably submerged (31 mya, Malohlava & Bocak 2010, Masek *et al*. 2015). The more recent dispersal of neotenics between Borneo and the Philippines has not been identified by the current analyses. Palawan has a mixed fauna with taxa having their origin in the Wallacea and Papua being a minority. Palawan reached its position about 10 mya (Hall 2002) and the Philippines were the only adjacent region from which net-winged beetles with the Wallacean or New Guinean origin can migrate. These genera are rare or missing in Borneo. Neotenic lycids known from Palawan, i.e., *Scarelus* and *Platerodrilus*, were not available for DNA isolation, other neotenics are absent in Palawan.

Sea of Japan

The main Japanese islands have continental origin and although the sea of Japan opened ~15 mya (Maruyama *et al*. 1997, Barnes 2003), the Japanese islands were repeatedly connected with the Asian continent during low sea stands (Dobson & Kawamura 1998). Despite this connection, the separation of Japanese species from their closest continental relatives results from vicariance and dispersal across sea is absent (Li *et al*. 2015a, in press). Surprisingly, there are only a few lycid species known simultaneously from the continent and Japanese islands (98 spp. in Japan and a single species from both the continent and Japan). The genetic distance between continental and island populations remains unknown and the study of their identity is needed as recent studies showed high distance dependent differentiation within the Chinese and Japanese lycid species of *Lyponia* and *Macrolycus* (Li *et al*. 2015a, b).

Conclusions

The very high portion of diversity of a beetle family was analyzed when a dataset of 609 species, representing about 14% of world-wide fauna was assembled (Bocak *et al*. 2014). For the first time, the molecular analyses suggest monophyly of three neotenic lineages from distant regions: Leptolycinae (the Caribbean islands, Panamanian realm), Dexorinae (Afrotropical realm) and Lyropaeinae (Oriental realm). Tree topology and distribution confirms their ancient origin (Bocak *et al*. 2008). All these taxa have larviform females and their long-distance dispersal is highly improbable as was shown in species level studies (Malohlava & Bocak 2010, Masek *et al*. 2015, Bray & Bocak 2016). Ateliini, another neotenic lineage from the Oriental region was inferred in a distant position from remaining Asian neotenic lineages. The neotenic genera from the continental part of the Panamanian and Neotropical realm have much younger origin and a single representative was recovered as terminal lineages in Calopterini (Figs S21–S22). Further supposedly neotenic lineage is represented by a single species of *Cautires* (Metriorrhynchini, Bocak *et al*. 2014). The repeated origins of neoteny have been inferred in Elateroidea (Bocakova *et al*. 2007, Kundrata & Bocak 2011, Kundrata *et al*. 2014, Bocak *et al*. 2016) and similarly they were recovered by current analyses within the net-winged beetles. The current study supports the hypothesized long-term survival of these lineages in the ecologically stable habitats (Bocak *et al*. 2008).

The start of diversification in net-winged beetle clade is provisionally hypothesized in the southern tropical to subtropical regions of Laurasia. The origin of 17 major lineages was inferred in this area. Two lineages, Thonalmini and Leptolycini, are endemics of the Panamanian realm and concerning the inability to cross open sea. These lycids might have an old origin when the landmasses were more connected (Seton *et al*. 2012). Several tribes are distributed in the landmasses forming original Gondwana in the Upper Jurassic and Lower Cretaceous - Dexorini and Slipinskiini in the Afrotropical realm, Eurrhacini and Calopterini in the Neotropical realm and Metriorrhynchini with hypothesized origin in India and Australia (Sklenarova *et al*. 2014). Considering the observed distribution patterns, I do not consider as probable the long-distance dispersal of these groups from Eurasia with their subsequent extinction in the area of the origin and further analyses when dating is possible might infer the vicariance resulting from separation of Eurasia and Gondwana 138 mya (Seton *et al*. 2012).

The realms defined by Holt *et al*. (2013) are based on distribution of vertebrates and patterns identified in net-winged beetles are in conflict with this delimitation in some cases. The change of structure of the lycid fauna is gradual between the Oriental realm and the eastern regions of the Palearctic realm across the newly defined Sino-Japanese realm and only two tribes were identified as endemics of the Sino-Japanese realm with marginal dispersal to the Oriental realm. The high turn-over was identified along the Wallace line with the predominantly Australian and Oceanian origin of the Sulawesi fauna. A few species dispersed from continental Asia to Sulawesi are in deep contrast with several genera dispersed in the opposite direction. Some genus-level endemics were identified in the Oceanian and Australian realms and this finding supports their separation. Unlike vertebrate fauna (Holt *et al*. 2013), the net-winged beetle fauna of the Oceanian origin is distributed across the Moluccas and Sulawesi, the Wallace line represents a prominent dispersal barrier separating Oceanian/Australian and Oriental faunas of net-winged beetles.

The net-winged beetle distribution and phylogeny suggest that the Sino-Japanese realm as proposed by Holt *et al*. (2013) is a transitional zone (Kreft & Jetz 2013). Conversely, two rare tribes are endemic to the Panamanian real which otherwise is similarly characterized by the limited phylogenetic uniqueness. The Saharo-Arabian realm (Holt *et al*. 2013) is an arid zone with very limited number of net-winged beetle lineages, which are supposedly the relicts of earlier dispersal events from the Oriental realm, and no conclusion can be made using net-winged beetles as a model group. The inability of net-winged beetles to cross sea straits is documented by the effectiveness of barriers separating the close landmasses. One of the most prominent dispersal barriers is represented by the southern part of the Wallace line. Although the Makassar Strait was only about 100 km wide during the last glacial maximum (Voris 2000), it prevented dispersal of most Asian lineages to the Wallacea. Similarly, Madagascar has never been colonized by any continental African lineage and only a single colonization was identified from the passing Indian craton (Sklenarova *et al*. 2013). The Japanese fauna is a result of vicariance not of gradual colonization which could be expected due to the close position of these landmasses.

The current results show the power of net-winged beetles to identify centers of origin and dispersal routes across long time span. The conflict with patterns identified in other studies (Holt *et al*. 2013) should be evaluated when more large-scale phylogeographic analyses are available. Multiple recent studies identified the high dispersal propensity and the long-distance dispersal has been considered as a preferred explanation of the extant distribution. The present phylogeographic analysis of net-winged beetles indicates that these beetle lineages disperse seldom, slowly and without subsequent reversed colonization.

Acknowledgements

This project was supported by the funding provided by the Czech Science Foundation to the supervisor of this study (P506/11/1757), the European Social Fund, and the Faculty of Science UP (IGA Grants). I thank to many colleagues for collecting and providing specimens and to R. Bilkova for technical assistance.

References

Ahearn GA (1970) The control of water loss in desert tenebrionid beetles. Journal of Experimental Biology, 53: 573–595.

Balke M, Ribera I, Hendrich L, Miller MA, Sagata K, Posman A, Vogler AP, Meier R (2009) New Guinea highland origin of a wide spread arthropod supertramp. Proceedings of the Royal Society B, 276: 2359–2367.

Barnes GL (2003) Origins of the Japanese Islands: the new ‘big picture’. Japan Review, 15: 3–50.

Belshaw R & Katzourakis A (2005) BlastAlign: a program that uses blast to align problematic nucleotide sequences. Bioinformatics, 21: 122–123.

Bielejec F, Rambaut A, Suchard MA, Lemey P (2011) SPREAD: spatial phylogenetic reconstruction of evolutionary dynamics. Bioinformatics, 27(20): 2910–2912.

Bocak L (2002) *Pendola*, a new lycid genus (Coleoptera, Lycidae) from Australian region. Biologia, 57: 557–561.

Bocak L & Bocakova M (1990) Revision of the supergeneric classification of the family Lycidae (Coleoptera). Polskie Pismo Entomologiczne, 59: 623–676.

Bocak L & Bocakova M (2008) Phylogeny and classification of the family Lycidae (Insecta: Coleoptera). Annales Zoologici, 58: 695–720.

Bocak L & Matsuda K (2003) Review of the immature stages of the family Lycidae (Insecta: Coleoptera). Journal of Natural History, 37: 1463–1507.

Bocak L & Yagi T (2010) Evolution of mimicry patterns in *Metriorrhynchus* (Coleoptera: Lycidae): the history of dispersal and speciation in South East Asia. Evolution, 64(1): 39–52.

Bocak L, Bocakova M, Hunt T, Vogler AP (2008) Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. Proceedings of the Royal Society B, 275: 2015–2023.

Bocak L, Grebennikov VV, Sklenarova K (2014) *Cautires apterus*, a new species and the first record of wingless male Lycidae (Coleoptera) discovered in the North Pare Mountains, Tanzania. Annales Zoologici, 64(1): 1–7.

Bocak L, Kundrata R, Andújar Fernández C, Vogler AP (2016) The discovery of Iberobaeniidae (Coleoptera: Elateroidea): a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. Proceedings of the Royal Society of London B: Biological sciences, 283: 2350.

Bocakova M (2006) Review of the tribe Lyropaeini (Coleoptera: Lycidae). European Journal of Entomology, 103: 127–136.

Bocakova M (2014) *Lolodorfus*, a new genus of net-winged beetles (Coleoptera: Lycidae: Dexorinae) from Cameroon. Zootaxa, 3811(3): 374–380.

Bocakova M, Bocak L, Hunt T, Teravainen M, Vogler AP (2007) Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminiscence and neoteny. Cladistics, 23: 477–496.

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu C-H, Xie D, Suchard MA, Rambaut A, Drummond AJ (2014) BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. PLoS Computational Biology, 10(4): e1003537.

Bray TC & Bocak L (2016) Slowly dispersing neotenic beetles can speciate on a penny coin and generate space-limited diversity in the tropical mountains. Scientific Reports 6, 33579.

Cicero JM (1994) Composite, haustellate mouthparts in netwinged beetle and firefly larvae (Coleoptera, Cantharoidea: Lycidae, Lampyridae). Journal of Morphology, 219(2): 183–192.

Crowson RA (1960) The phylogeny of Coleoptera. Annual Review of Entomology, 5: 111–134.

Crowson RA (1972) A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families: Cneoglossidae and Omethidae. Revista de la Universidad de Madrid, 21: 35–71.

Cruaud A, Jabbour-Zahab R, Genson G, Couloux A, Yan-Qiong P, Rong YD, Ubaidillah R, Pereira RAS, Kjellberg F, Noort S, Kerdelhue C, Rasplus JY (2011) Out of Australia and back again: the world-wide historical biogeography of non-pollinating fig wasps (Hymenoptera: Sycophaginae). Journal of Biogeography, 38: 209–225.

Darlington PJ Jr (1966) Zoogeography: The Geographical Distribution of Animals. John Wiley & Sons, New York.

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2, more models, new heuristics and parallel computing. Nature Methods, 9(8): 772.

Dobson M & Kawamura Y (1998) Origin of the Japanese land mammal fauna: allocation of extant species to historically-based categories. The Quaternary Research, 37: 385–395.

Drummond AJ & Bouckaert RR (2015) Bayesian Evolutionary Analysis with Beast. Cambridge University Press, Cambridge.

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research, 32: 1792–1797.

Ezard T, Fujisawa T, Barraclough T (2009) splits: Species’ Limits by Threshold Statistics. R package version 1.0-11/r29. Available from http://R-Forge.R-project.org/projects/splits.

Fabre PH, Moltensen M, Fjeldsa J, Irestedt M, Lessard JP, Jonsson KA (2014) Multiple waves of colonization by monarch flycatchers (Myiagra, Monarchidae) across the Indo-Pacific and their implications for coexistence and speciation. Journal of Biogeography, 41: 274–286.

Gomez-Rodriguez C, Freijeiro A, Baselga A (2015) Dispersal and ecological traits explain differences in beta diversity patterns of European beetles. Journal of Biogeography, 42: 1526–1537.

Hall R (1998) The plate tectonics of Cenozoic Southeast Asia and the distribution of land and sea. Pp. 99–131. In: Hall R, Holloway JD (eds). Biogeography and geological evolution of Southeast Asia. Backhuys Publishers, Leiden, The Netherlands.

Hall R (2002) Cenozoic geological and plate tectonic evolution of Southeast Asia and the Southwest Pacific: computer-based reconstructions, model and animations. Journal of Asian Earth Sciences, 20: 353–434.

Holt B, Lessard JP, Borregaard MK, Fritz SA, Araujo MB, Dimitrov D, Fabre PH, Graham CH, Graves GR, Jonsson KA, Nogues-Bravo D, Wang ZH, Whittaker RJ, Fjeldsa J, Rahbek C (2013) An update of Wallace's zoogeographic regions of the world. Science, 339: 74–78.

Huxley TH (1868) On the classification and distribution of the Alectoromorphae and Heteromorpha. Proceedings of the Zoological Society of London, Pp 294–319.

Katoh K & Standley DM (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. Molecular Biology and Evolution, 30: 772–780.

Kazantsev SV (2005) Morphology of Lycidae with some considerations on evolution of the Coleoptera. Elytron, 19: 49–226.

Kazantsev SV (2013) A new fossil genus of net-winged beetles, with a brief review of amber Lycidae (Insecta: Coleoptera). Zootaxa, 20(13): 94–100.

Kleine R (1933) Coleopterorum Catalogus auspiciis et auxilio W. Junk editus S. Schenkling. Pars 128: Lycidae. W. Junk, Berlin.

Kosuch J, Vences M, Dubois A, Ohler A, Bohme W (2001) Out of Asia: Mitochondrial DNA evidence for an oriental origin of tiger frogs, genus *Hoplobatrachus*. Molecular Phylogenetics and Evolution, 21: 398–407.

Kreft H & Jetz W (2013) Comment on “An Update of Wallace’s Zoogeographic Regions of the World”. Science, 341: 343.

Kubecek V, Bray TC, Bocak L (2015) Molecular phylogeny of Metanoeina net-winged beetles identifies *Ochinoeus*, a new genus from China and Laos (Coleoptera: Lycidae). Zootaxa, 3955(1): 113–122.

Kundrata R & Bocak L (2011) The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? Zoologica Scripta, 40: 364–378.

Kundrata R, Bocakova M, Bocak L (2014) The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). Molecular Phylogenetics and Evolution, 76: 162–171.

Levkanicova Z & Bocak L (2009) Identification of net-winged beetle larvae (Coleoptera: Lycidae) using three mtDNA fragments: a comparison of their utility. Systematic Entomology, 34(2): 210–221.

Li JT, Wang JS, Nian HH, Litvinchuk SN, Wang JC, Li Y, Rao DQ, Klaus S (2015) Amphibians crossing the Bering Land Bridge: Evidence from holarctic treefrogs (*Hyla*, Hylidae, Anura). Molecular Phylogenetics And Evolution, 87: 80–90.

Li Y, Bocak L, Pang H (2015a) Molecular phylogeny of *Macrolycus* (Coleoptera: Lycidae) with description of new species from China. Entomological Science, 18: 319–329.

Li Y, Gunter N, Pang H, Bocak L (2015b) DNA-based species delimitation separates highly divergent populations within morphologically coherent clades of poorly dispersing beetles. Zoological Journal of the Linnean Society, 175: 59–72.

Li Y, Pang H, Bocak L (in press) Molecular phylogeny of Erotini with the description of a new genus from China (Coleoptera: Lycidae). Entomological Science.

Malohlava V & Bocak L (2010) Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. Molecular Ecology, 19(21): 4800–4811.

Maruyama S, Isozaki Y, Kimura G, Terabayashi M (1997) Paleogeographic maps of the Japanese Islands: plate tectonic synthesis from 750 Ma to the present. The Island Arc, 6: 121–142.

Masek M, Ivie MA, Palata V, Bocak L (2014) Molecular Phylogeny and classification of Lyropaeini (Coleoptera: Lycidae) with description of larvae and new species of *Lyropaeus*. Raffles Bulletin of Zoology, 62: 136–145.

Masek M, Palata V, Bray TC, Bocak L (2015) Molecular phylogeny reveals high diversity and geographic structure in Asian neotenic net-winged beetles *Platerodrilus* (Coleoptera: Lycidae). PLoS One, 10(4): e0123855.

Mayr E (1944) Wallace's Line in the Light of Recent Zoogeographic Studies. The Quarterly Review of Biology, 19(1): 1–14.

McMahon DP & Hayward A (2016) Why grow up? A perspective on insect strategies to avoid metamorphosis. Ecological Entomology, 41: 505–515.

Miller RS (1988) Behavior of *Calopteron reticulatum* (F.) larvae (Coleoptera: Lycidae). Ohio Journal of Science, 88: 119–120.

Miller RS (1991) A revision of the Leptolycini (Coleoptera: Lycidae) with a discussion of aedomorphosis. PhD Thesis. The Ohio State University, U. S. A.

Motyka M, Masek M, Bocak L (in press) Congruence between morphology and molecular phylogeny: the reclassification of Calochromini (Coleoptera: Lycidae) and their dispersal history. Zoological Journal of the Linnean Society.

Rambaut A (2009) FigTree 1.4.2. Retrieved from http://tree.bio.ed.ac.uk/software/figtree/.

Sanderson MJ (2002) Estimation absolute rates of molecular evolution and divergence times: a penalized likelihood approach. Molecular Biology and Evolution, 19: 101–109.

Seton M, Müller RD, Zahirovic S, Gaina C, Torsvik T, Shephard G, Talsma A, Gurnis M, Turner M, Maus S, Chandler M (2012) Global continental and ocean basin reconstructions since 200 Ma. Earth Science Reviews, 113: 212–270.

Sklenarova K, Chesters D, Bocak L (2013) Phylogeography of Poorly Dispersing Net-Winged Beetles: A Role of Drifting India in the Origin of Afrotropical and Oriental Fauna. PLoS One, 8(6): e67957.

Sklenarova K, Kubecek V, Bocak L (2014) Subtribal classification of Metriorrhynchini (Insecta: Coleoptera: Lycidae): an integrative approach using molecular phylogeny and morphology of adults and larvae. Arthropod Systematics & Phylogeny, 72(1): 37–54.

Smith AG, Smith DG, Funnell BM (2004) Atlas of Cenozoic and Mesozoic Coastlines. Cambridge University Press, Cambridge, UK.

Sota T, Bocak L, Hayashi M (2008) Molecular phylogeny and historical biogeography of the Holarctic wetland leaf beetle of the genus *Plateumaris*. Molecular Phylogenetics and Evolution, 46: 183–192.

Stamatakis A, Ludwig T, Meier H (2005) RAxML-III: a fast program for maximum likelihood-based inference of large phylogenetic trees. Bioinformatics, 21: 456–463.

Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML web servers. Systematic Biology, 57: 758–771.

Thompson J, Higgins D, Gibson T (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignments through sequence weighting, position specific gap penalties and weight matrix choice. Nucleic Acids Research, 22: 4673–4680.

Tiffney BH & Manchester SR (2001) The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the Northern Hemisphere Tertiary. International Journal of Plant Sciences, 162: 3–17.

Voris HK (2000) Maps of Pleistocene sea levels in south-east Asia: shorelines, river systems and time duration. Journal of Biogeography, 27: 1153–1167.

Wallace AR (1863) On the Physical Geography of the Malay Archipelago. Royal Geographical Society, 7: 205–212.

Wallace AR (1876) The Geographical Distribution of Animals. Harper and brothers, London.

Winkler JR (1987) Three new genera of fossil Lycidae from Baltic Amber. Mitteilungen der Monchner Entomologischen Gesellschaft, 77: 61–78.

Wong ATC (1995) Trilobite larvae: a new understanding. Nature Malaysiana, 20(1): 24–29.

Yoder AD & Nowak MD (2006) Has Vicariance or Dispersal Been the Predominant Biogeographic Force in Madagascar? Only Time Will Tell. Annual Review of Ecology, Evolution and Systematics, 37: 405–431.

Table 1. Overview of classification of Lycidae, their alpha-taxonomic diversity, distribution and inferred ancestral areas. The colonized areas as inferred from molecular analyses. The recently described tribe rank taxa unavailable for analysis are listed in the Supplementary Text. ^{n}-the neotenic lineage with proved or supposed larviform females at least in some species.

Subfamily	Tribe	No of species described/ sequenced		Distribution	Hypothesized ancestral area
LIBNETINAE	Libnetini	112	17	2–7, 11	Oriental (Fig. 6A)
LEPTOLYCINAE	Leptolycini^{n}	12	4	15	Panamanian (endemic)
DEXORINAE	Dexorini^{n}	15	2	12	Afrotropical (endemic)
LYROPAEINAE	Lyropaeini^{n}	43	9	4–8, 11	Oriental (Fig. 6B)
	Alyculini^{n}	3	1	6–7	Oriental (endemic)
	Antennolycini^{n}	3	2	6	Oriental (endemic)
	Platerodrilini^{n}	49	32	2, 4–7	Oriental (endemic)
DICTYOPTERINAE	Dictyopterini	73	25	1–7	Sino-Japanese (Fig. 6C)
	Lycoprogenthini	7	9	2,4–7	Oriental (endemic)
	Taphini	31	9	2,4-10	Oriental (except a single sp. endemic)
LYCINAE	Atelini^{n}	45	19	2, 4-7	Oriental (endemic, Malohlava & Bocak 2010)
	Dilophotini	81	30	2-7	Oriental (Motyka *et al.* in press)
	Calochromini	288	47	1-12, 14-15	Oriental (Motyka *et al.* 2017)
	Calopterini$^{(n)}$	367	15	14-16	Neotropical (endemic, a few species in the Nearctic reg.)
	Conderini	42	14	1-7	Oriental (Fig. 7C)
	Dihammatini	44	9	2-7	Oriental (Fig. 7B)
	Erotini	54	18	1-3, 14	Sino-Japanese (Fig. 7A)
	Slipinskiini	46	4	12	Afrotropical (endemic)
	Eurrhacini	102	8	15-16	Neotropical (endemic)
	Lycini	413	34	1-8	unresolved: Nearctic or Oriental
	Lyponiini	45	17	2-3,5,7,11	Sino-Japanese
	Macrolycini	69	14	2-3,5,11 S	Sino-Japanese
	Metriorrhynchini$^{(n)}$	1403	161	2-13	Australian (Sklenarova *et al.* 2013)
	Platerodini	861	48	1-12, 14-15	Oriental (Fig. 6D)
	Thonalmini	11	3	15	Panamanian (endemic)

Area codes: 1 Palearctic realm (PAL), western part, 2 Palearctic/Sino-Japanese realm (SIN-JAP) China, Korea, Taiwan, 3 SIN-JAP – Japan, 4 Oriental realm (OR), the Philippines, 5 OR, Indo-Burma, 6 OR, Malay Peninsula, 7 OR, Sunda Islands, 8 OR/Oceanian (OC) realm, Sulawesi, Moluccas, 9 OC, New Guinea, 10 Australian realm, 11 OR, India, 12 Afrotropical (AFR) realm, 13 AFR, Madagascar, 14 Neotropical realm, 15 Panamanian realm, Caribbean, 16 Neotropical realm.

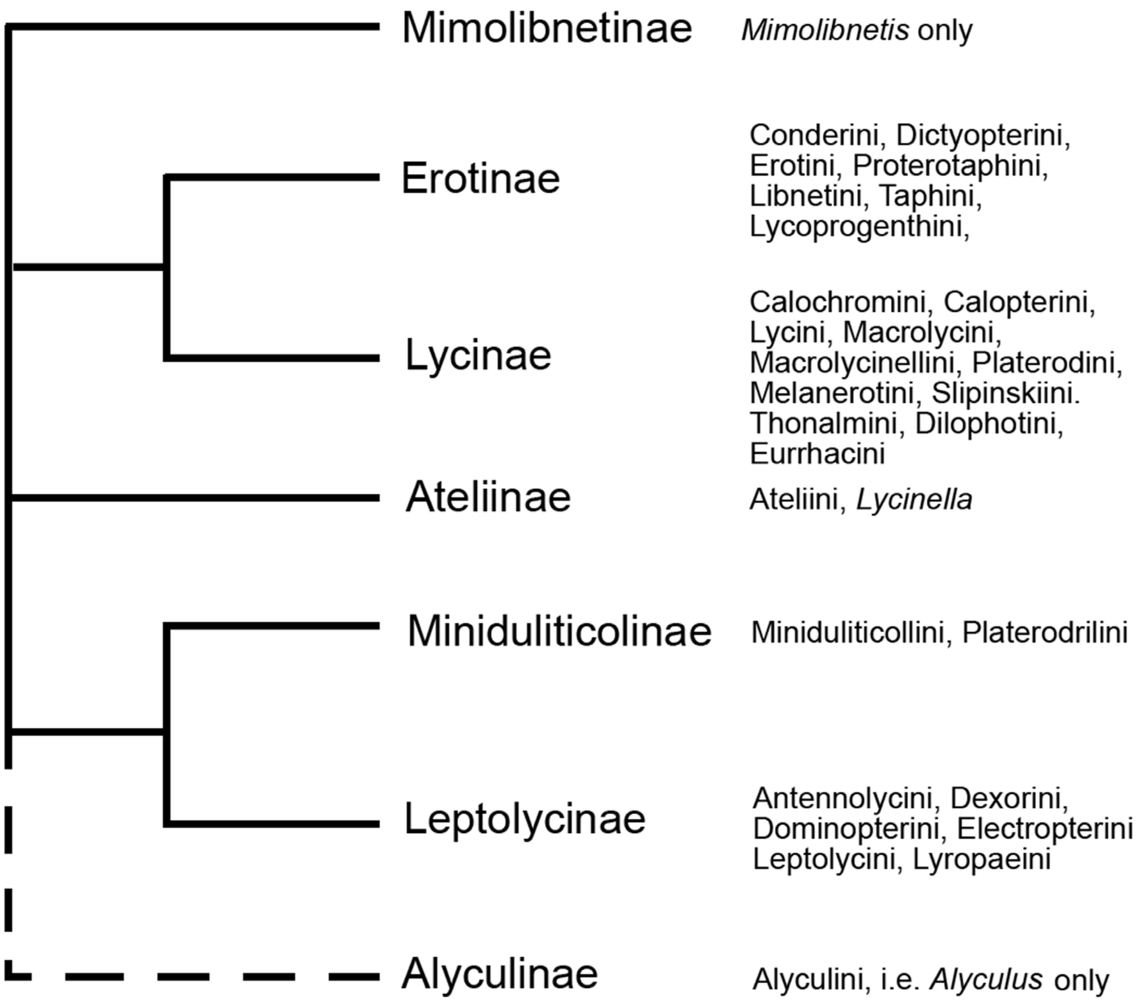


Figure 1. Classification of the family Lycidae proposed by Kazantsev (2013). Redrawn and modified.

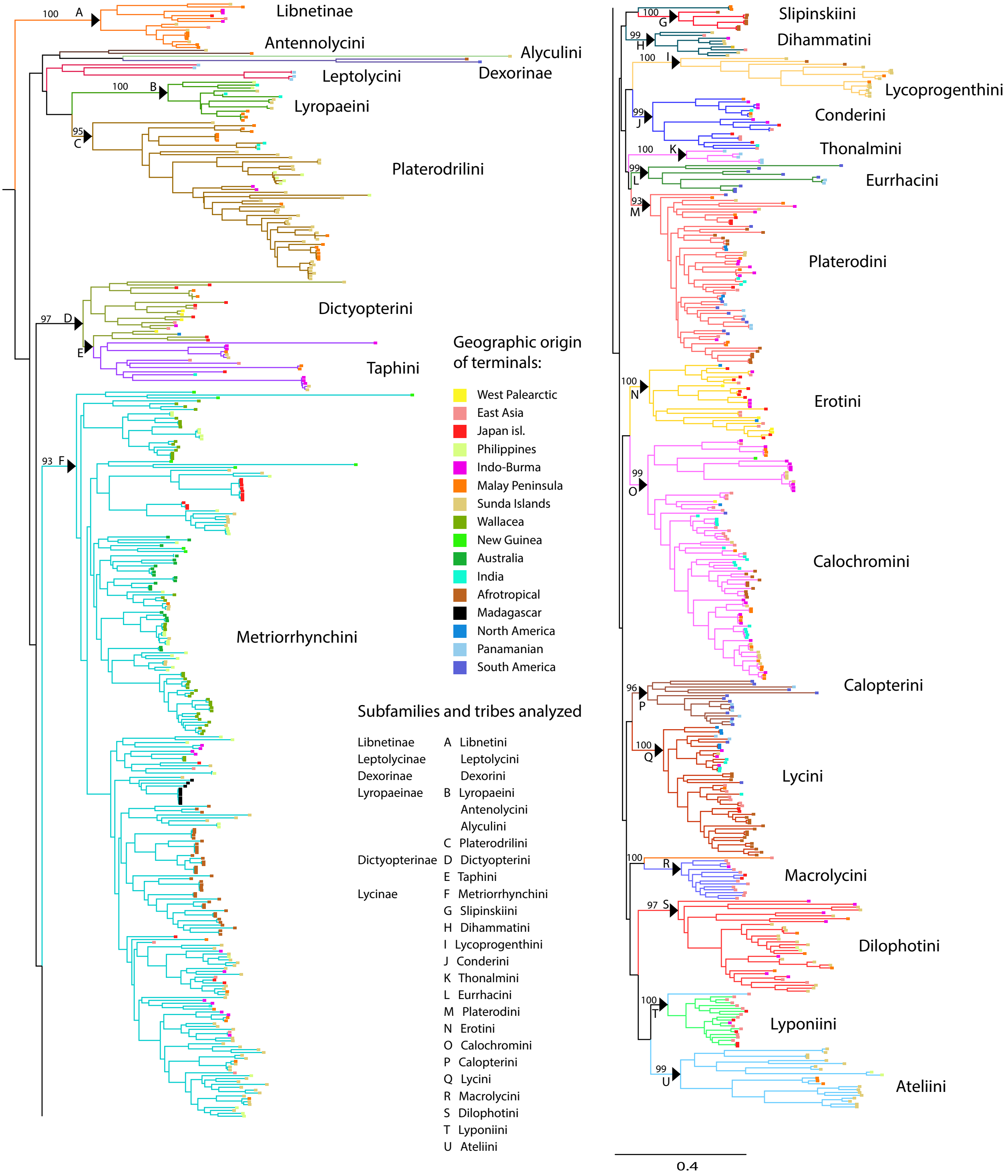


Figure 2. The phylogenetic hypothesis of Lycidae inferred from the Mafft alignment and maximum likelihood analysis.

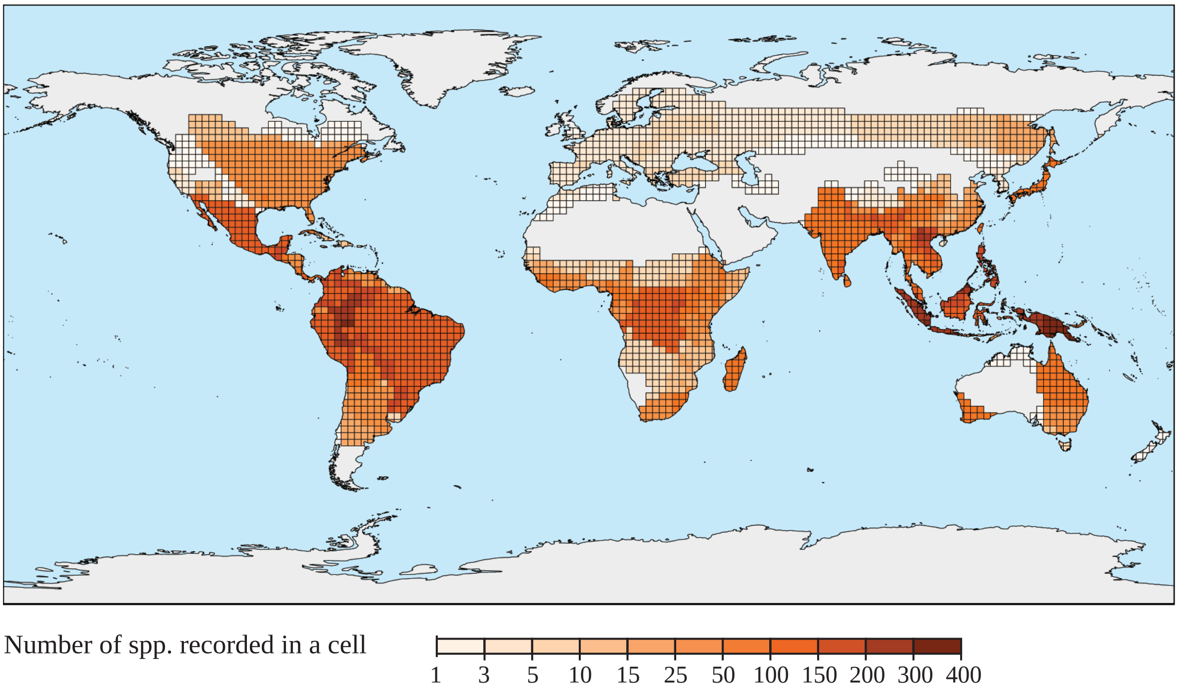


Figure 2. Distribution and species diversity of the family Lycidae.

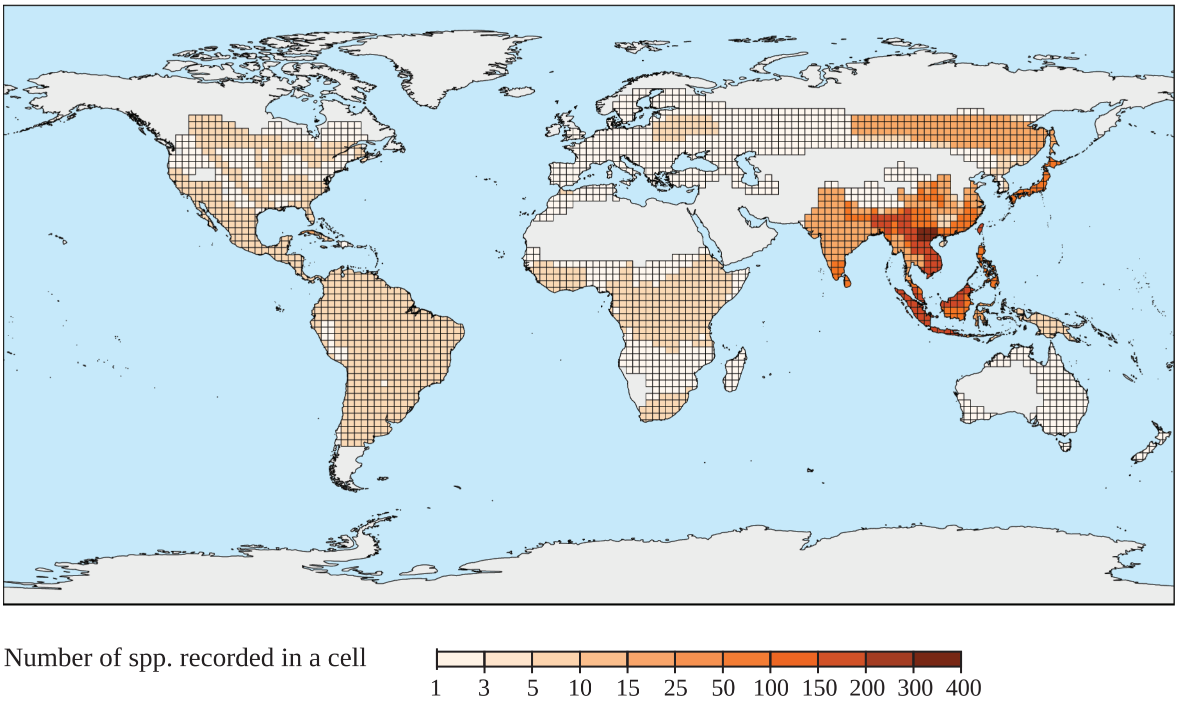


Figure 3. Distribution and species diversity of the family Lycidae.

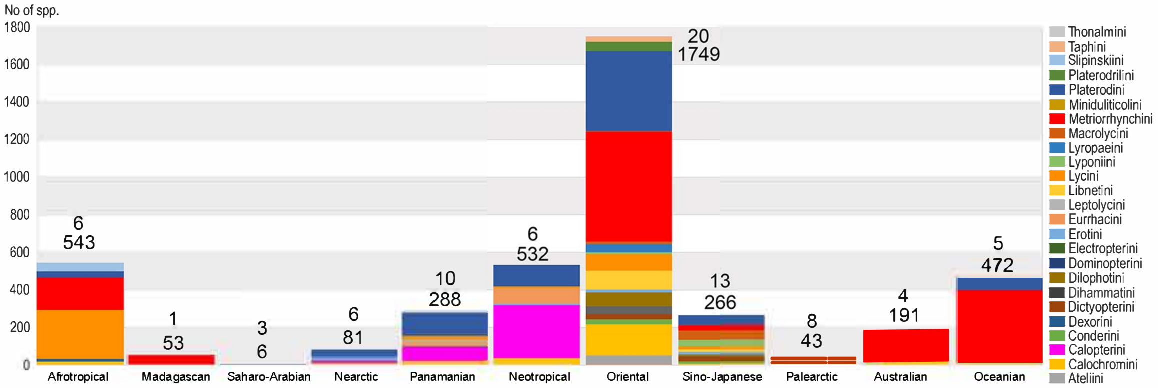


Figure 5. Number of tribes and species recorded in zoogeographic realms.

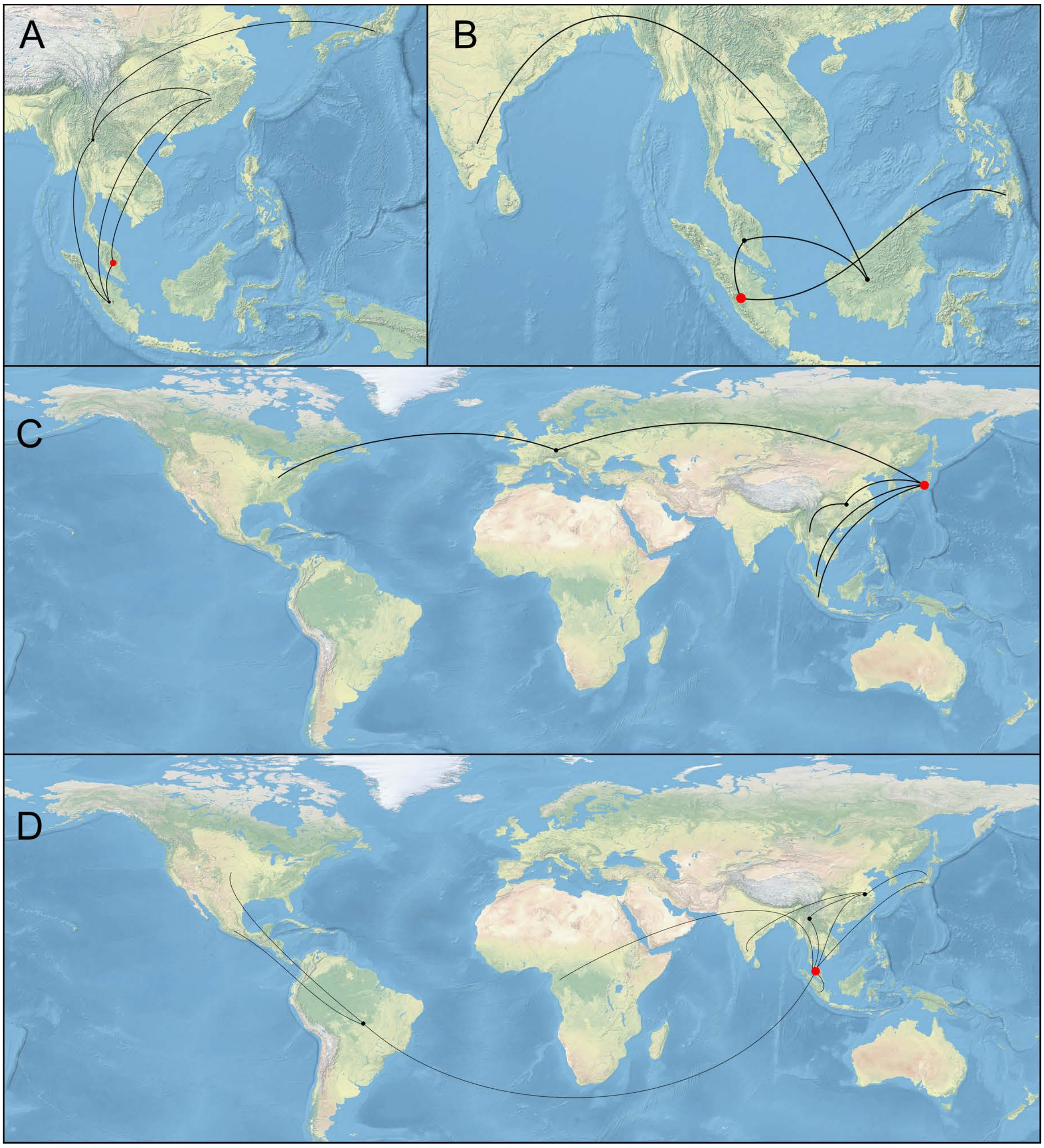


Figure 6. Reconstruction of ancestral ranges and dispersal events.
A Libnetini, B Lyropaeini, C Dictyopterini, D Platerodini.

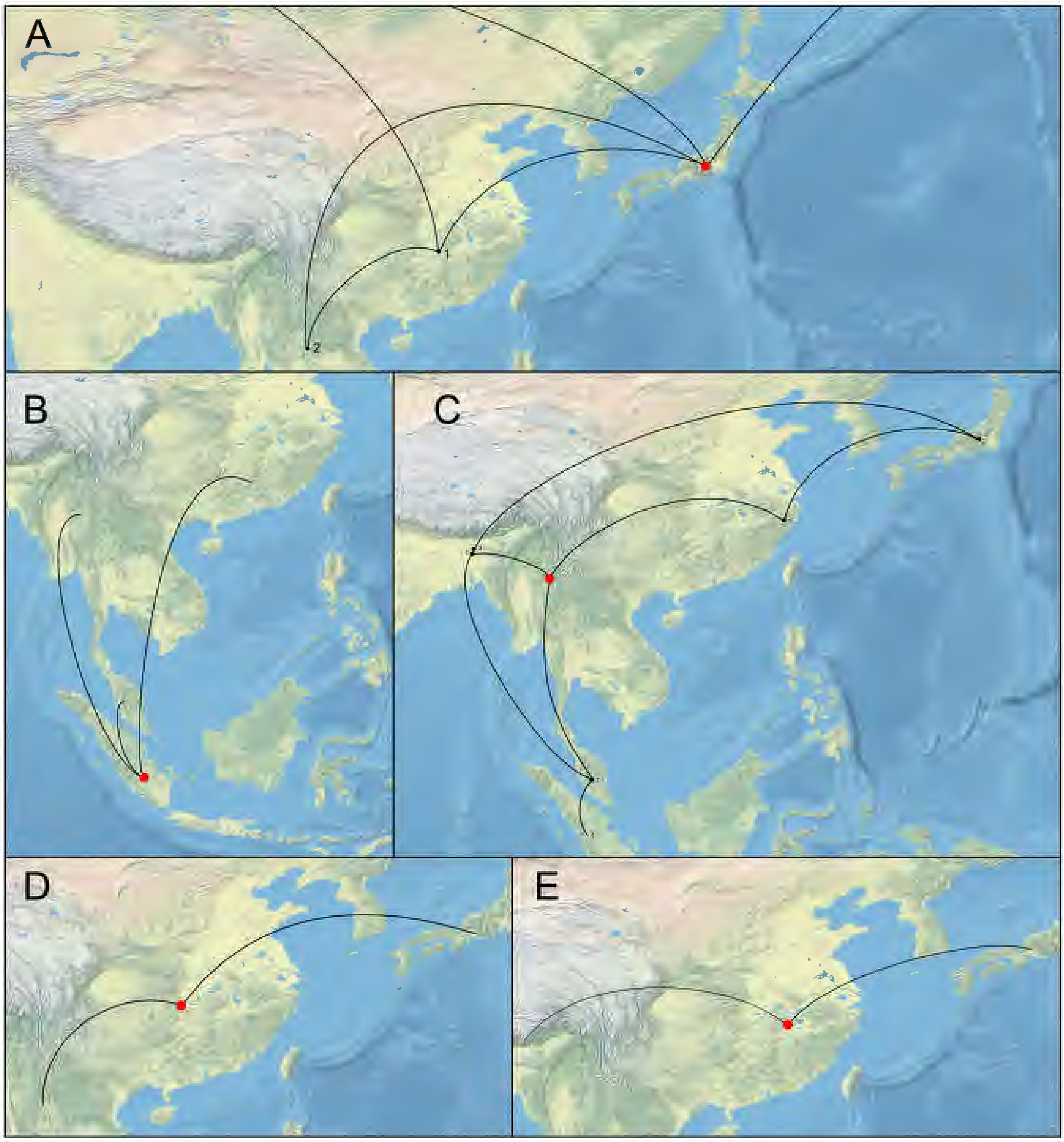


Figure 7. Reconstruction of ancestral ranges and dispersal events.
A Erotini, B Dihammatini, C Conderini, D Lyponiini, E Macrolycini.

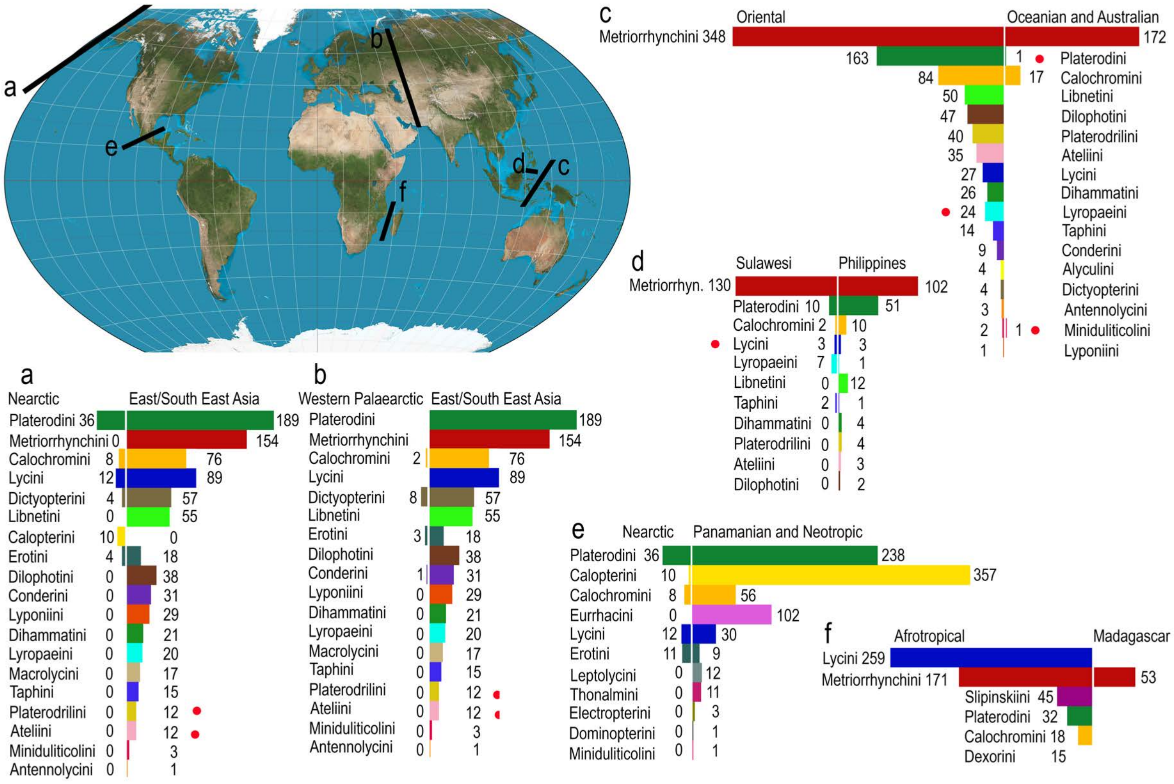


Figure 8. Principal dispersal and vicariance barriers and the number of tribes and species present in adjacent regions.

Supplements

Phylogeny and zoogeography phylogeography of net-winged beetles (Coleoptera: Lycidae)

by

Michal Masek

Supporting information

Table S1. The list of sequenced samples with GenBank Accession Numbers.
Table S2. Tribe-level taxa not included in the molecular analysis.
Table S3. Primers used for PCR amplification.

Figure S1. Distribution and species diversity of the tribes Leptolycini, Dexorini, and Lyropaeini.
Figure S2. Distribution and species diversity of the subfamily Libnetinae.
Figure S3. Distribution and species diversity of the tribe Lyropaeini.
Figure S4. Distribution and species diversity of the tribe Platerodrilini.
Figure S5. Distribution and species diversity of the tribe Dictyopterini.
Figure S6. Distribution and species diversity of the tribe Taphini.
Figure S7. Distribution and species diversity of the tribe Metriorrhynchini.
Figure S8. Distribution and species diversity of the tribe Slipinskiini.
Figure S9. Distribution and species diversity of the tribe Dihammatini.
Figure S10. Distribution and species diversity of the tribe Platerodini.
Figure S11. Distribution and species diversity of the tribe Conderini.
Figure S12. Distribution and species diversity of the tribe Eurrhacini.
Figure S13. Distribution and species diversity of the tribe Erotini.
Figure S14. Distribution and species diversity of the tribe Calochromini.
Figure S15. Distribution and species diversity of the tribe Calopterini.
Figure S16. Distribution and species diversity of the tribe Lycini.
Figure S17. Distribution and species diversity of the tribe Macrolycini.
Figure S18. Distribution and species diversity of the tribe Dilophotini.
Figure S19. Distribution and species diversity of the tribe Lyponiini.
Figure S20. Distribution and species diversity of the tribe Ateliini.
Figure S21. The complete RAxML tree inferred from the MAFFT alignment of all markers.
Figure S22. The complete RAxML tree inferred from the BlastAligned dataset of all markers.

Table S1. The list of sequenced samples with GenBank Accession Numbers.

Family Subfamily tribe	**Species**	**Voucher number**	**Geographic origin**	**18S rRNA**	**28S rRNA**	***rrnL* mtDNA**	***cox1* mtDNA**	***nad5* mtDNA**
Outgroup								
Cantharidae	*Athemellus insulsus*	UPOL 001306	Japan	KF625620	KF626222	KF625912	KF625319	–
Cantharidae	*Athemus* sp.	UPOL 001301	USA	KF625615	KF626217	KF625907	KF625314	–
Cantharidae	*Cantharis* sp.	UPOL 001317	Slovakia	KF625631	KF626233	KF625923	KF625330	–
Cantharidae	*Cratosilis sicula*	UPOL RK0094	Italy	KF625587	KF626189	KF625882	KF625287	–
Cantharidae	*Habronychus* sp.	UPOL 001311	Japan	KF625625	KF626227	KF625917	KF625324	–
Cantharidae	Chauliognathinae indet.	UPOL 001393	Panama	KF625634	KF626236	KF625926	KF625333	–
Cantharidae	*Chauliognathus* sp.	UPOL 001250	USA	KF625600	KF626202	KF625892	KF625300	–
Cantharidae	*Ichthyurus* sp.	UPOL 001291	Indonesia	KF625605	KF626207	KF625897	KF625304	–
Cantharidae	*Inmalthodes* sp.	UPOL 001289	Indonesia	KF625603	KF626205	KF625895	KF625303	–
Cantharidae	*Lycocerus* sp.	UPOL RK0176	Laos	KF625591	KF626193	KF625886	KF625291	–
Cantharidae	*Malthinus* sp.	UPOL 001313	Czech Republic	KF625627	KF626229	KF625919	KF625326	–
Cantharidae	*Malthinus* sp.	UPOL RK0181	Morocco	KF625596	KF626198	KF625890	KF625296	–
Cantharidae	Malthodinae indet.	UPOL RK0178	Cameroon	KF625593	KF626195	KF625887	KF625293	–
Cantharidae	*Metacantharis haemorrhoidalis*	UPOL 000M14	Czech Republic	DQ100526	DQ198768	DQ198685	DQ198608	DQ181417
Cantharidae	*Micropodabrus* sp.	UPOL 001304	Japan	KF625618	KF626220	KF625910	KF625317	–
Cantharidae	*Podabrus temporalis*	UPOL 001307	Japan	KF625621	KF626223	KF625913	KF625320	–
Cantharidae	Silinae indet.	UPOL 001294	Indonesia	KF625608	KF626210	KF625900	KF625307	–
Cantharidae	Silinae indet.	UPOL 001296	Indonesia	KF625610	KF626212	KF625902	KF625309	–
Cantharidae	*Themus* sp.	UPOL 001302	Japan	KF625616	KF626218	KF625908	KF625315	–
Cantharidae	*Trypherus mutilatus*	UPOL 001308	Japan	KF625622	KF626224	KF625914	KF625321	–
Elateridae	*Adelocera* sp.	UPOL RK0041	Indonesia	HQ333794	HQ333889	KF626035	HQ333976	–
Elateridae	*Agriotes obscurus*	UPOL RK0052	Czech Republic	HQ333805	HQ333900	KF626039	KF625441	–
Elateridae	Cardiophorinae indet.	UPOL RK0031	Indonesia	HQ333784	HQ333879	KF626025	HQ333966	–
Elateridae	*Cebrio* sp.	UPOL RK0142	Italy	KF625745	KF626329	KF626040	KF625440	–
Elateridae	*Denticollis* sp.	UPOL RK0006	Japan	HQ333759	HQ333854	KF626041	HQ333943	–
Elateridae	*Dicronychus cinereus*	UPOL RK0023	Czech Republic	HQ333776	HQ333871	KF626024	HQ333959	–
Elateridae	*Diplophoenicus* sp.	UPOL RK0145	Madagascar	KF625753	KF626335	KF626050	KF625454	–
Elateridae	*Drilus concolor*	UPOL RK0074	Hungary	HQ333827	KF626322	HQ333734	HQ334007	–
Elateridae	Elaterinae indet.	UPOL RK0400	New Caledonia	KF625755	KF626339	KF626046	KF625455	–
Elateridae	Elaterinae indet.	UPOL RK0203	French Guyana	KF625752	KF626337	KF626052	KF625449	–
Elateridae	Elaterinae indet.	UPOL RK0406	Ethiopia	KF625759	KF626344	KF626049	KF625458	–
Elateridae	*Hemicrepidius hirtus*	UPOL RK0297	Bulgaria	KF625754	KF626340	KF626054	KF625448	–
Elateridae	*Chalcolepidius* sp.	UPOL RK0219	French Guyana	KF625743	KF626326	KF626031	KF625437	–
Elateridae	Lissominae indet.	UPOL RK0354	Cameroon	KF625750	KF626333	KF626045	KF625447	–
Elateridae	*Malacogaster passerinii*	UPOL RK0369	Italy	KF625741	KF626321	KF626029	KF625432	–
Elateridae	*Mulsanteus* sp.	UPOL 001414	Panama	HQ333744	HQ333839	KF626037	HQ333929	–
Elateridae	*Pyrophorus* sp.	UPOL 001423	Panama	HQ333753	HQ333848	HQ333672	KF625435	–
Elateridae	*Selasia* sp.	UPOL RK0172	Cameroon	KF625740	KF626324	KF626028	KF625434	–
Elateridae	*Tetrigus cyprius*	UPOL RK0228	Greece	KF625744	KF626327	KF626032	KF625438	–
Elateridae	Thylacosterninae indet.	UPOL RK0174	Cameroon	KF625760	KF626336	KF626051	KF625450	–
Eucnemidae	*Anischia kuscheli*	UPOL RK0119	New Caledonia	KF625545	KF626145	KF625845	KF625246	–
Eucnemidae	*Microrhagus* sp.	UPOL 001223	Slovakia	KF625569	KF626169	KF625866	KF625270	–
Eucnemidae	Macraulacinae indet.	UPOL 001332	Japan	KF625585	KF626186	KF625880	KF625284	–
Eucnemidae	Macraulacinae indet.	UPOL 001333	Malaysia	KF625586	KF626187	KF625881	KF625285	–
Eucnemidae	Macraulacinae indet.	UPOL 001236	Philippines	KF625581	KF626181	KF625876	KF625279	–
Eucnemidae	Macraulacinae indet.	UPOL RK0341	Cameroon	KF625556	KF626156	KF625856	KF625257	–
Eucnemidae	Macraulacinae indet.	UPOL RK0303	Panama	KF625554	KF626154	KF625854	KF625255	–
Eucnemidae	Melasinae indet.	UPOL 001230	Malaysia	KF625576	KF626176	KF625872	KF625275	–
Eucnemidae	*Melasis buprestoides*	UPOL RK0344	Greece	KF625558	KF626158	KF625858	KF625259	–
Eucnemidae	*Micorhagus pygmaeus*	UPOL 001224	Czech Republic	KF625570	KF626170	KF625867	KF625271	–
Iberebaneidae	Iberebaneina	UPOL RK0790	Spain	ab123456	ab123456	–	ab123456	–
Lampyridae	*Ceylanidrilus* sp.	UPOL 000156	India	DQ100524	DQ198765	DQ198682	DQ198605	–
Lampyridae	*Curtos* sp.	UPOL 000M16	Indonesia	DQ100513	DQ198761	DQ198671	DQ198594	–
Lampyridae	*Flabellotreta* sp.	UPOL 000M34	Indonesia	DQ100520	DQ198763	DQ198678	DQ198601	–
Lampyridae	Lampyridae gen.sp.	UPOL ZL2011	Japan	–	–	EF143221	EF143236	EF143250
Lampyridae	Lampyridae gen.sp.	UPOL ZL2019	Sulawesi	–	–	EF143228	EF143242	EF143256
Lampyridae	Lampyridae indet.	UPOL RK0093	RSA	KF625638	KF626239	KF625929	KF625337	–
Lampyridae	Lampyridae indet.	UPOL RK0396	Malaysia	KF625681	KF626268	KF625972	KF625380	–
Lampyridae	Lampyridae indet.	UPOL RK0096	Indonesia	KF625640	KF626240	KF625931	KF625339	–
Lampyridae	Lampyridae indet.	UPOL RK0378	Japan	KF625663	KF626253	KF625954	KF625362	–
Lampyridae	Lampyridae indet.	UPOL RK0173	Cameroon	KF625657	KF626250	KF625948	KF625356	–
Lampyridae	Lampyridae indet.	UPOL RK0111	Malaysia	KF625653	KF626248	KF625944	KF625352	–
Lampyridae	Lampyridae indet.	UPOL RK0106	Indonesia	KF625648	KF626244	KF625939	KF625347	–
Lampyridae	Lampyridae indet.	UPOL RK0392	Indonesia	KF625677	KF626264	KF625968	KF625376	–
Lampyridae	Lampyridae indet.	UPOL RK0375	French Guyana	KF625661	KF626252	KF625952	KF625360	–
Lampyridae	Lampyridae indet.	UPOL RK0391	Indonesia	KF625676	KF626263	KF625967	KF625375	–
Lampyridae	Lampyridae indet.	UPOL RK0118	Indonesia	KF625656	KF626249	KF625947	KF625355	–
Lampyridae	Lampyridae indet.	UPOL RK0099	Philippines	KF625643	KF626242	KF625934	KF625342	–
Lampyridae	Lampyridae indet.	UPOL RK0386	Panama	KF625671	KF626260	KF625962	KF625370	–
Lampyridae	Lampyridae indet.	UPOL RK0383	Indonesia	KF625668	KF626257	KF625959	KF625367	–
Lampyridae	Lampyridae indet.	UPOL RK0108	Ethiopia	KF625650	KF626246	KF625941	KF625349	–
Lampyridae	Lampyridae indet.	UPOL RK0381	Ethiopia	KF625666	KF626256	KF625957	KF625365	–
Lampyridae	Lampyridae indet.	UPOL RK0394	Indonesia	KF625679	KF626266	KF625970	KF625378	–
Lampyridae	*Luciola* sp.	UPOL 000M03	Indonesia	DQ100514	DQ198762	DQ198672	DQ198595	DQ181415
Lampyridae	*Vesta* sp.	UPOL 000M17	Indonesia	DQ100511	DQ198760	DQ198669	DQ198592	–
Omalisidae	*Omalisus fontisbellaquei*	UPOL 000377	Czech Republic	–	DQ198749	DQ198658	DQ198580	DQ181414
Omethidae	*Drilonius* sp.	UPOL 001274	Malaysia	KF625528	KF626129	KF625831	KF625228	–
Omethidae	*Drilonius* sp.	UPOL RK0132	Philippines	KF625523	KF626124	KF625832	KF625223	–
Omethidae	*Drilonius* sp.	UPOL RK0135	Malaysia	KF625524	KF626125	KF625833	KF625224	–
Omethidae	*Drilonius* sp.	UPOL RK0136	Indonesia	KF625525	KF626126	KF625834	KF625225	–
Omethidae	*Drilonius* sp.	UPOL RK0362	Laos	KF625526	KF626127	KF625835	KF625226	–
Omethidae	*Drilonius striatulus*	UPOL 001272	Japan	KF625527	KF626128	KF625830	KF625227	–
Omethidae	*Ginglymocladus* sp.	UPOL 001341	USA	KF625530	KF626131	KF625829	KF625230	–
Omethidae	*Troglomethes leechi*	UPOL 001340	USA	KF625529	KF626130	KF625828	KF625229	–
Phengodidae	*Bicladon* sp.	UPOL 000M35	China	DQ100507	DQ198755	DQ198664	DQ198586	DQ181419
Phengodidae	*Ochotyra* sp.	UPOL 000155	India	DQ100508	DQ198756	DQ198665	DQ198587	DQ181413
Phengodidae	*Phengodes* sp.	UPOL 000M29	USA	DQ100504	DQ198752	DQ198661	DQ198583	DQ181418
Telegeusidae	*Telegeusidae* sp.	UPOL RK0359	Belize	KF625769	KF626352	–	KF625464	–
Telegeusidae	*Telegeusidae* sp.	UPOL RK0360	Belize	KF625531	KF626132	–	KF625231	–

Lycidae (Ingroup)								
Alyculini	*Alyculus kurbatovi*	UPOL 000543	Java	DQ181072	DQ181146	DQ180998	DQ181220	DQ181374
Antennolycini	*Antenolycus constrictus*	UPOL 000L22*	Malaysia	DQ181051	DQ181125	DQ180977	DQ181199	DQ181353
Antennolycini	*Microlyropaeus dembickyi*	UPOL 000542	Sumatra	DQ181071	DQ181145	DQ180997	DQ181219	DQ181373
Ateliini	*Atelius* sp.	UPOL VK0733	China	–	–	KT752146	KT751822	KT751975
Ateliini	*Scarelus anthracinus*	UPOL VM0006	Malaysia	HM451125	HM451083	HM451002	HM451042	HM451211
Ateliini	*Scarelus baranciki*	UPOL VM0019	Borneo	HM451137	HM451093	HM451012	HM451051	–
Ateliini	*Scarelus brastagiensis*	UPOL VM0012	Sumatra	HM451131	HM451088	HM451006	HM451047	HM451217
Ateliini	*Scarelus cibodasensis*	UPOL VM0007	Java	HM451126	HM451084	HM451003	HM451043	HM451212
Ateliini	*Scarelus crudus*	UPOL VM0049	Philippines	HM451165	HM451118	HM451035	HM451076	HM451248
Ateliini	*Scarelus emasensis*	UPOL VM0022	Borneo	HM451140	–	HM451015	HM451054	HM451223
Ateliini	*Scarelus flavicolis*	UPOL VM0031	Sumatra	HM451149	HM451104	HM451021	HM451061	HM451232
Ateliini	*Scarelus loksadoensis*	UPOL VM0014	Borneo	HM451133	–	HM451008	HM451049	–
Ateliini	*Scarelus longicornis*	UPOL VM0026	Sumatra	HM451144	HM451099	HM451018	HM451057	HM451227
Ateliini	*Scarelus nigricornis*	UPOL VM0021	Borneo	HM451139	HM451095	HM451014	HM451053	HM451222
Ateliini	*Scarelus pahangensis*	UPOL VM0004	Malaysia	HM451123	HM451081	HM451000	HM451040	HM451209
Ateliini	*Scarelus pseudoumbosus*	UPOL VM0002	Malaysia	HM451121	HM451079	HM450999	HM451038	HM451207
Ateliini	*Scarelus ruficolis*	UPOL VM0033	Sumatra	HM451151	HM451106	HM451023	HM451063	HM451234
Ateliini	*Scarelus rufus*	UPOL VM0034	Sumatra	HM451152	HM451107	HM451024	HM451064	HM451235
Ateliini	*Scarelus salvani*	UPOL VM0050	Philippines	HM451166	HM451119	HM451036	HM451077	HM451249
Ateliini	*Scarelus sanguineus*	UPOL VM0023	Sumatra	HM451141	HM451096	HM451016	HM451055	HM451224
Ateliini	*Scarelus saranganensis*	UPOL VM0011	Java	HM451130	HM451087	HM451005	HM451046	HM451216
Ateliini	*Scarelus similis*	UPOL VM0005	Borneo	HM451124	HM451082	HM451001	HM451041	HM451210
Ateliini	*Scarelus* sp.	UPOL 000582	Borneo	DQ181085	DQ181159	DQ181011	DQ181233	DQ181387
Ateliini	*Scarelus* sp.	UPOL 000583	Borneo	DQ181086	DQ181160	DQ181012	DQ181234	DQ181388
Ateliini	*Scarelus* sp.	UPOL 000L15	Borneo	DQ181046	DQ181120	DQ180972	DQ181194	DQ181348
Calochromini	*Adoceta* sp.	UPOL MT0019	RSA	KU496010	KU496051	KU495971	KU496109	KU496202
Calochromini	*Adoceta* sp.	UPOL MT0020	Zambia	–	–	KU495973	KU496101	KU496205
Calochromini	*Adoceta* sp.	UPOL MT0021	Zambia	–	–	KU495974	KU496102	KU496170
Calochromini	*Adoceta* sp.	UPOL MT0022	RSA	–	–	KU495977	KU496115	KU496206
Calochromini	*Adoceta* sp.	UPOL MT0023	Kenya	–	–	KU495972	KU496116	KU496171
Calochromini	*Adoceta* sp.	UPOL MT0027	Kenya	–	–	KU495975	KU496110	KU496204
Calochromini	*Adoceta* sp.	UPOL MT0028	RSA	–	–	–	KU496144	–
Calochromini	*Adoceta* sp.	UPOL MT0029	RSA	–	–	–	KU496140	KU496207
Calochromini	*Adoceta* sp.	UPOL MT0033	Kenya	–	–	KU495976	KU496111	KU496203
Calochromini	*Adoceta* sp.	UPOL MT0060	RSA	KU496011	KU496052	–	KU496142	KU496201
Calochromini	*Calochromus* sp.	UPOL A00477	Malaysia	KT752159	KT752318	KT751987	KT751669	KT751829
Calochromini	*Calochromus* sp.	UPOL A00617	Laos	KT752282	KT752446	KT752115	KT751789	KT751948
Calochromini	*Calochromus* sp.	UPOL 000033	Borneo	DQ181060	DQ181134	DQ180986	DQ181208	DQ181362
Calochromini	*Calochromus* sp.	UPOL 000124	Borneo	DQ181061	DQ181135	DQ180987	DQ181209	DQ181363
Calochromini	*Calochromus* sp.	UPOL 000347	Borneo	DQ181068	DQ181142	DQ180994	DQ181216	DQ181370
Calochromini	*Calochromus* sp.	UPOL 000L16	China	DQ181047	DQ181121	DQ180973	DQ181195	DQ181349
Calochromini	*Calochromus* sp.	UPOL MT0001	China	KU496008	KU496036	KU495936	KU496068	KU496184
Calochromini	*Calochromus* sp.	UPOL MT0002	Borneo	KU496017	KU496038	KU495939	KU496070	KU496152
Calochromini	*Calochromus* sp.	UPOL MT0003	Laos	–	–	KU495998	KU496137	KU496196
Calochromini	*Calochromus* sp.	UPOL MT0004	Malaysia	KU496032	KU496060	KU495992	KU496122	KU496187
Calochromini	*Calochromus* sp.	UPOL MT0005	Sumatra	–	–	KU495942	KU496073	KU496155
Calochromini	*Calochromus* sp.	UPOL MT0006	China	–	–	KU495957	KU496079	KU496174
Calochromini	*Calochromus* sp.	UPOL MT0007	Borneo	–	–	KU495940	KU496071	KU496153
Calochromini	*Calochromus* sp.	UPOL MT0008	Laos	–	–	–	KU496118	KU496163
Calochromini	*Calochromus* sp.	UPOL MT0009	India	–	–	KU495960	–	KU496175
Calochromini	*Calochromus* sp.	UPOL MT0010	Malaysia	–	–	KU495994	KU496123	KU496188
Calochromini	*Calochromus* sp.	UPOL MT0011	Malaysia	–	–	KU495938	KU496100	KU496186
Calochromini	*Calochromus* sp.	UPOL MT0012	Borneo	KU496024	KU496045	KU495952	KU496082	KU496148
Calochromini	*Calochromus* sp.	UPOL MT0013	India	–	–	KU495937	KU496069	KU496185
Calochromini	*Calochromus* sp.	UPOL MT0014	Malaysia	KU496009	KU496037	KU495941	KU496072	KU496154
Calochromini	*Calochromus* sp.	UPOL MT0015	India	–	–	–	KU496086	KU496164
Calochromini	*Calochromus* sp.	UPOL MT0016	India	–	–	–	KU496087	KU496166
Calochromini	*Calochromus* sp.	UPOL MT0017	India	KU496014	KU496049	KU495968	KU496112	KU496172
Calochromini	*Calochromus* sp.	UPOL MT0025	Papua New Guinea	KU496035	KU496067	–	KU496129	KU496189
Calochromini	*Calochromus* sp.	UPOL MT0026	India	KU496012	KU496046	KU495963	–	–
Calochromini	*Calochromus* sp.	UPOL MT0031	India	–	–	–	KU496088	KU496165
Calochromini	*Calochromus* sp.	UPOL MT0032	Sumatra	KU496027	KU496063	KU496001	KU496130	KU496190
Calochromini	*Calochromus* sp.	UPOL MT0034	Laos	–	–	KU495953	KU496083	KU496149
Calochromini	*Calochromus* sp.	UPOL MT0035	Sumatra	–	–	KU495985	KU496105	KU496211
Calochromini	*Calochromus* sp.	UPOL MT0036	Laos	–	–	KU495999	KU496138	KU496195
Calochromini	*Calochromus* sp.	UPOL MT0037	Malaysia	–	–	KU495948	KU496078	KU496161
Calochromini	*Calochromus* sp.	UPOL MT0038	China	–	–	KU495980	–	–
Calochromini	*Calochromus* sp.	UPOL MT0039	Cambodia	–	–	KU495995	KU496125	
Calochromini	*Calochromus* sp.	UPOL MT0040	Malaysia	–	–	KU495954	KU496084	KU496150
Calochromini	*Calochromus* sp.	UPOL MT0041	Borneo	–	–	KU496002	KU496134	KU496192
Calochromini	*Calochromus* sp.	UPOL MT0043	Malaysia	–	–	KU495955	KU496085	KU496151
Calochromini	*Calochromus* sp.	UPOL MT0044	Borneo	–	–	KU496003	KU496135	KU496193
Calochromini	*Calochromus* sp.	UPOL MT0045	Borneo	–	–	KU496004	KU496136	KU496194
Calochromini	*Calochromus* sp.	UPOL MT0046	Laos	–	–	KU496005	KU496131	–
Calochromini	*Calochromus* sp.	UPOL MT0047	Laos	KU496029	KU496065	KU496000	KU496139	KU496197
Calochromini	*Calochromus* sp.	UPOL MT0048	China	–	–	KU495986	KU496104	KU496210
Calochromini	*Calochromus* sp.	UPOL MT0049	Malaysia	KU496018	KU496039	KU495945	KU496075	KU496158
Calochromini	*Calochromus* sp.	UPOL MT0050	Laos	–	–	KU495949	KU496106	KU496146
Calochromini	*Calochromus* sp.	UPOL MT0051	Laos	KU496020	KU496040	KU495946	KU496077	KU496160
Calochromini	*Calochromus* sp.	UPOL MT0052	Laos	–	–	KU495991	KU496090	KU496169
Calochromini	*Calochromus* sp.	UPOL MT0053	China	–	–	KU495958	KU496080	–
Calochromini	*Calochromus* sp.	UPOL MT0054	Laos	KU496028	KU496064	KU496006	KU496132	–
Calochromini	*Calochromus* sp.	UPOL MT0055	Malaysia	–	–	KU495950	KU496107	KU496147
Calochromini	*Calochromus* sp.	UPOL MT0056	China	–	–	KU495964	KU496094	–
Calochromini	*Calochromus* sp.	UPOL MT0057	Malaysia	KU496019	KU496041	KU495947	KU496076	–
Calochromini	*Calochromus* sp.	UPOL MT0058	Cambodia	–	–	KU496007	KU496133	KU496191
Calochromini	*Calochromus* sp.	UPOL MT0059	Malaysia	KU496021	KU496044	KU495943	KU496141	KU496156
Calochromini	*Calochromus* sp.	UPOL MT0061	China	–	–	KU495988	KU496143	KU496200
Calochromini	*Calochromus* sp.	UPOL MT0062	India	KU496013	KU496048	KU495961	KU496092	KU496176
Calochromini	*Calochromus* sp.	UPOL MT0063	India	–	–	KU495962	KU496093	KU496177
Calochromini	*Calochromus* sp.	UPOL MT0064	India	KU496023	KU496042	–	KU496089	KU496167
Calochromini	*Calochromus* sp.	UPOL MT0065	India	–	–	KU495966	KU496091	KU496178
Calochromini	*Calochromus* sp.	UPOL MT0066	India	–	–	KU495967	KU496119	KU496209
Calochromini	*Calochromus* sp.	UPOL MT0067	India	KU496016	KU496050	KU495969	KU496113	KU496208
Calochromini	*Calochromus* sp.	UPOL MT0068	Malaysia	KU496022	KU496043	KU495944	KU496074	KU496157
Calochromini	*Calochromus* sp.	UPOL MT0069	Malaysia	KU496033	KU496061	KU495993	KU496124	–
Calochromini	*Calochromus* sp.	UPOL MT0070	Laos	KU496030	KU496058	KU495951	KU496108	KU496145
Calochromini	*Calochromus* sp.	UPOL MT0071	India	–	–	KU495956	KU496103	KU496168
Calochromini	*Calochromus* sp.	UPOL MT0072	India	–	–	KU495970	KU496114	KU496173
Calochromini	*Calochromus* sp.	UPOL MT0074	California	KU496026	KU496066	KU495978	KU496121	KU496183

Calochromini	*Calochromus* sp.	UPOL MT0075	China	–	–	KU495989	KU496128	KU496199
Calochromini	*Calochromus* sp.	UPOL MT0076	China	KU496034	KU496062	KU495996	KU496126	–
Calochromini	*Calochromus* sp.	UPOL MT0077	China	KU496015	KU496047	KU495959	KU496081	KU496214
Calochromini	*Calochromus* sp.	UPOL MT0078	China	–	–	KU495965	–	KU496213
Calochromini	*Calochromus* sp.	UPOL MT0079	Laos	–	–	KU495997	KU496127	–
Calochromini	*Calochromus* sp.	UPOL MT0080	China	–	–	KU495990	–	KU496198
Calochromini	*Lygistopterus* sp.	UPOL MT0030	Greece	KU496025	KU496053	KU495979	KU496120	KU496182
Calochromini	*Macrolygistopterus* sp.	UPOL MT0073	Ecuador	KU496031	KU496059	KU495987	KU496099	KU496215
Calopterini	*Calopteron* sp.	UPOL A00621	Panama	KT752284	KT752449	KT752118	KT751792	KT751951
Calopterini	*Calopteron* sp.	UPOL A00628	Ecuador	–	–	KT752125	KT751798	KT751957
Calopterini	*Calopteron* sp.	UPOL A00629	Ecuador	–	–	KT752126	KT751799	KT751958
Calopterini	*Calopteron* sp.	UPOL A00630	Nicaragua	KT752289	KT752454	KT752127	KT751800	KT751959
Calopterini	*Calopteron* sp.	UPOL A00631	Ecuador	–	–	KT752128	KT751801	KT751960
Calopterini	*Calopteron* sp.	UPOL A00633	Ecuador	KT752291	KT752456	KT752129	KT751803	KT751962
Calopterini	*Calopteron* sp.	UPOL A00637	Argentina	–	–	KT752133	KT751807	–
Calopterini	*Calopteron* sp.	UPOL A00640	Nicaragua	KT752295	KT752460	KT752136	KT751809	KT751967
Calopterini	*Calopteron* sp.	UPOL A00645	Nicaragua	KT752296	KT752462	KT752139	KT751812	KT751970
Calopterini	*Calopteron* sp.	UPOL A00647	Bolivia	KT752298	KT752463	KT752141	KT751814	–
Calopterini	*Calopteron* sp.	UPOL A00650	Bolivia	KT752301	KT752466	KT752144	KT751817	KT751973
Calopterini	*Calopteron* sp.	UPOL A00651	Ecuador	–	–	KT752145	KT751818	KT751974
Calopterini	*Calopteron* sp.	UPOL 000L25	Ecuador	DQ181053	DQ181127	DQ180979	DQ181201	DQ181355
Calopterini	*Idiopteron biplagiatum*	UPOL 000M44	Ecuador	DQ181057	DQ181131	DQ180983	DQ181205	DQ181359
Calopterini	*Metapteron* sp.	UPOL IR2002	Peru	AF451946	DQ198757	–	DQ198588	–
Conderini	*Conderis rufohumeralis*	UPOL 000581	Japan	DQ181084	DQ181158	DQ181010	DQ181232	DQ181386
Conderini	*Conderis signicollis*	UPOL 000194	Malaysia	DQ181062	DQ181136	DQ180988	DQ181210	DQ181364
Conderini	*Conderis* sp.	UPOL A00601	Laos	KT752267	KT752431	KT752099	KT751774	KT751933
Conderini	*Conderis* sp.	UPOL A00602	China	KT752268	KT752432	KT752100	KT751775	KT751934
Conderini	*Conderis* sp.	UPOL A00603	China	KT752269	KT752433	KT752101	KT751776	KT751935
Conderini	*Conderis* sp.	UPOL A00605	Vietnam	KT752271	KT752435	KT752103	KT751778	KT751937
Conderini	*Conderis* sp.	UPOL A00606	India	KT752272	KT752436	KT752104	KT751779	KT751938
Conderini	*Conderis* sp.	UPOL A00607	China	KT752273	KT752437	KT752105	KT751780	KT751939
Conderini	*Conderis* sp.	UPOL A00609	Japan	KT752275	KT752439	KT752107	KT751782	KT751941
Conderini	*Conderis* sp.	UPOL A00610	Cambodia	KT752276	KT752440	KT752108	KT751783	KT751942
Conderini	*Conderis* sp.	UPOL A00612	India	KT752277	KT752441	KT752110	KT751784	KT751943
Conderini	*Conderis* sp.	UPOL A00613	Borneo	KT752278	KT752442	KT752111	KT751785	KT751944
Conderini	*Conderis* sp.	UPOL A00614	Malaysia	KT752279	KT752443	KT752112	KT751786	KT751945
Conderini	*Xylobanellus* sp.	UPOL A00604	China	KT752270	KT752434	KT752102	KT751777	KT751936
Conderini	*Xylobanellus* sp.	UPOL A00608	Japan	KT752274	KT752438	KT752106	KT751781	KT751940
Conderini	*Xylobanellus* sp.	UPOL A00611	China	–	–	KT752109	–	–
Conderini	*Xylobanellus* sp.	UPOL A00615	Laos	KT752280	KT752444	KT752113	KT751787	KT751946
Conderini	*Xylobanellus* sp.	UPOL A00616	Laos	KT752281	KT752445	KT752114	KT751788	KT751947
Dexorinae	*Dexoris chome*	UPOL A00654	Tanzania	KT752302	KT752467	KT752148	KT751819	–
Dexorinae	*Dexoris* sp.	UPOL VP0045	Cameroon	KT752309	KT752468	KT752147	KT751823	–
Dictyopterini	*Benibotarus nigripennis*	UPOL 000572	Japan	DQ181075	DQ181149	DQ181001	DQ181223	DQ181377
Dictyopterini	*Benibotarus spinicoxis*	UPOL 000573	Japan	DQ181076	DQ181150	DQ181002	DQ181224	DQ181378
Dictyopterini	*Benibotarus spinicoxis*	UPOL A00569	China	KT752235	KT752400	KT752067	KT751745	KT751902
Dictyopterini	*Benibotarus taygetanus*	UPOL A00568	Hungary	KT752234	KT752399	KT752066	KT751744	KT751901
Dictyopterini	*Benibotarus taygetanus*	UPOL 001285	Czech Republic	KF625694	KF626280	KF625983	KF625392	–
Dictyopterini	*Dictyoptera aurora*	UPOL 001276	Czech Republic	KF625687	KF626273	KF625977	KF625386	–
Dictyopterini	*Dictyoptera elegans*	UPOL 000570	Japan	DQ181073	DQ181147	DQ180999	DQ181221	DQ181375
Dictyopterini	*Dictyoptera* sp.	UPOL 001275	USA	KF625686	KF626272	KF625976	KF625385	–
Dictyopterini	*Dictyoptera speciosa*	UPOL 000571	Japan	DQ181074	DQ181148	DQ181000	DQ181222	DQ181376
Dictyopterini	*Dictyoptera* sp.	UPOL A00540	Sumatra	KT752209	KT752371	KT752038	–	–
Dictyopterini	Dictyopterini gen.sp.	UPOL ZL2013	Japan	–	–	EF143223	EF143238	EF143252
Dictyopterini	Dictyopterini indet.	UPOL A00519	China	KT752191	KT752352	KT752022	KT751703	–
Dictyopterini	Dictyopterini indet.	UPOL A00520	Malaysia	KT752192	KT752353	KT752023	KT751704	KT751862
Dictyopterini	Dictyopterini indet.	UPOL A00534	Malaysia	–	KT752365	KT752033	KT751716	KT751871
Dictyopterini	Dictyopterini indet.	UPOL A00597	Malaysia	KT752263	KT752427	KT752095	KT751771	KT751929
Dictyopterini	Dictyopterini indet.	UPOL 001283	Japan	KF625692	KF626278	KF625982	KF625391	–
Dictyopterini	Dictyopterini indet.	UPOL 001278	Malaysia	KF625689	KF626275	KF625979	KF625388	–
Dictyopterini	Dictyopterini indet.	UPOL 001282	Japan	KF625691	KF626277	KF625981	KF625390	–
Dictyopterini	*Helcophorus* sp.	UPOL A00570	Thailand	KT752236	KT752401	KT752068	–	KT751903
Dictyopterini	*Helcophorus* sp.	UPOL A00618	China	KT752283	KT752447	KT752116	KT751790	KT751949
Dictyopterini	*Helcophorus* sp.	UPOL 001369	China	KF625699	KF626285	KF625988	KF625397	–
Dictyopterini	*Pyropterus nigroruber*	UPOL 000574	Japan	DQ181077	DQ181151	DQ181003	DQ181225	DQ181379
Dictyopterini	*Pyropterus nigroruber*	UPOL 001277	Czech Republic	KF625688	KF626274	KF625978	KF625387	–
Dihammatini	*Dihammatus* sp.	UPOL A00546	China	KT752215	KT752377	KT752044	KT751724	KT751881
Dihammatini	*Dihammatus* sp.	UPOL A00594	Malaysia	KT752260	KT752424	KT752092	–	KT751926
Dihammatini	*Dihammatus* sp.	UPOL A00596	Sumatra	KT752262	KT752426	KT752094	KT751770	KT751928
Dihammatini	*Dihammatus* sp.	UPOL A00598	Malaysia	KT752264	KT752428	KT752096	–	KT751930
Dihammatini	*Dihammatus* sp.	UPOL A00599	China	KT752265	KT752429	KT752097	KT751772	KT751931
Dihammatini	*Dihammatus* sp.	UPOL A00600	Laos	KT752266	KT752430	KT752098	KT751773	KT751932
Dihammatini	*Dihammatus* sp.	UPOL A00625	Malaysia	KT752287	KT752452	KT752122	KT751796	KT751954
Dihammatini	*Dihammatus* sp.	UPOL 000L12	Borneo	DQ181043	DQ181117	DQ180969	DQ181191	DQ181345
Dihammatini	*Dihammatus* sp.	UPOL 001001	Sumatra	DQ181103	DQ181177	DQ181029	DQ181251	DQ181405
Dihammatini	*Dihammatus* sp.	UPOL 001009	Sumatra	DQ181106	DQ181180	DQ181032	DQ181254	DQ181408
Dihammatini	*Dihammatus* sp.	UPOL 001017	Sumatra	DQ181108	DQ181182	DQ181034	DQ181256	DQ181410
Dilophotini	*Dilophotes* sp.	UPOL 000244	Borneo	DQ181066	DQ181140	DQ180992	DQ181214	DQ181368
Dilophotini	*Dilophotes* sp.	UPOL TH0046	Laos	–	–	KJ404937	KJ405138	–
Dilophotini	*Dilophotes* sp.	UPOL TH0068	Malaysia	–	–	KJ404957	KJ405156	KJ405307
Dilophotini	*Dilophotes* sp.	UPOL TH0078	Laos	–	–	KJ404967	KJ405166	KJ405316
Dilophotini	*Dilophotes* sp.	UPOL TH0041	Sumatra	–	–	KJ404933	KJ405133	–
Dilophotini	*Dilophotes* sp.	UPOL TH0079	Laos	–	–	KJ404968	KJ405167	KJ405317
Dilophotini	*Dilophotes* sp.	UPOL TH0080	Laos	–	–	KJ404969	KJ405168	KJ405318
Dilophotini	*Dilophotes* sp.	UPOL TH0043	Sumatra	–	–	KJ404934	KJ405135	–
Dilophotini	*Dilophotes* sp.	UPOL TH0007	Sumatra	–	–	KJ404908	KJ405101	KJ405284
Dilophotini	*Dilophotes* sp.	UPOL A00060	Laos	KC538072	KC537863	KC538740	KC538359	KC538552
Dilophotini	*Dilophotes* sp.	UPOL TH0190	China	–	–	KJ405078	KJ405270	KJ405398
Dilophotini	*Dilophotes* sp.	UPOL TH0006	Sumatra	–	–	KJ404907	KJ405100	KJ405283
Dilophotini	*Dilophotes* sp.	UPOL TH0023	Sumatra	–	–	KJ404923	KJ405115	KJ405294
Dilophotini	*Dilophotes* sp.	UPOL TH0020	Sumatra	–	–	KJ404920	KJ405112	KJ405292
Dilophotini	*Dilophotes* sp.	UPOL TH0081	Laos	–	–	KJ404970	KJ405169	KJ405319
Dilophotini	*Dilophotes* sp.	UPOL TH0095	Laos	–	–	KJ404984	KJ405179	KJ405333
Dilophotini	*Dilophotes* sp.	UPOL TH0093	Borneo	–	–	KJ404982	KJ405177	KJ405331
Dilophotini	*Dilophotes* sp.	UPOL TH0101	Borneo	–	–	KJ404990	KJ405185	KJ405339
Dilophotini	*Dilophotes* sp.	UPOL TH0160	Malaysia	–	–	KJ405048	KJ405242	KJ405368
Dilophotini	*Dilophotes* sp.	UPOL TH0131	China	–	–	KJ405020	KJ405214	–
Dilophotini	*Dilophotes* sp.	UPOL TH0152	Malaysia	–	–	KJ405040	KJ405234	KJ405365
Dilophotini	*Dilophotes* sp.	UPOL TH0059	Sumatra	–	–	KJ404950	KJ405151	–
Dilophotini	*Dilophotes* sp.	UPOL TH0039	Java	–	–	KJ404931	KJ405131	–
Dilophotini	*Dilophotes* sp.	UPOL TH0069	Malaysia	–	–	KJ404958	KJ405157	–

Dilophotini	*Dilophotes* sp.	UPOL A00003	Sumatra	–	–	KJ404888	KJ405081	KJ405272
Dilophotini	*Dilophotes* sp.	UPOL TH0054	Java	–	–	KJ404945	KJ405146	–
Dilophotini	*Dilophotes* sp.	UPOL TH0036	Borneo	–	–	KJ404928	KJ405128	–
Dilophotini	*Dilophotes* sp.	UPOL TH0138	Malaysia	–	–	KJ405027	KJ405221	KJ405361
Dilophotini	*Dilophotes* sp.	UPOL TH0127	Mindanao	–	–	KJ405016	KJ405210	KJ405357
Dilophotini	*Dilophotes* sp.	UPOL A00013	Sumatra	–	–	KJ404898	KJ405091	–
Dilophotini	*Dilophotes* sp.	UPOL TH0076	Sumatra	–	–	KJ404965	KJ405164	KJ405314
Dilophotini	*Dilophotes* sp.	UPOL TH0125	Mindanao	–	–	KJ405014	KJ405208	KJ405356
Erotini	*Eropterus nothus*	UPOL 000579	Japan	DQ181082	DQ181156	DQ181008	DQ181230	DQ181384
Erotini	*Eropterus* sp.	UPOL A00548	China	KT752217	KT752379	KT752046	KT751725	KT751883
Erotini	*Eropterus* sp.	UPOL A00549	Laos	–	KT752380	KT752047	KT751726	KT751884
Erotini	*Eropterus* sp.	UPOL A00550	China	KT752218	KT752381	KT752048	KT751727	KT751885
Erotini	*Eropterus* sp.	UPOL A00551	Laos	KT752219	KT752382	KT752049	KT751728	KT751886
Erotini	*Eropterus* sp.	UPOL A00552	Laos	KT752220	KT752383	KT752050	KT751729	KT751887
Erotini	*Eropterus* sp.	UPOL A00553	Slovakia	–	KT752384	KT752051	KT751730	KT751888
Erotini	*Eropterus* sp.	UPOL A00554	Japan	–	KT752385	KT752052	KT751731	KT751889
Erotini	*Eropterus* sp.	UPOL A00558	Japan	KT752224	KT752389	KT752056	KT751735	KT751892
Erotini	*Eropterus* sp.	UPOL 000580	USA	DQ181083	DQ181157	DQ181009	DQ181231	DQ181385
Erotini	*Konoplatycis otome*	UPOL 000575	Japan	DQ181078	DQ181152	DQ181004	DQ181226	DQ181380
Erotini	*Lopheros* sp.	UPOL A00556	Japan	KT752222	KT752387	KT752054	KT751733	KT751891
Erotini	*Lopheros* sp.	UPOL A00567	Laos	KT752233	KT752398	KT752065	KT751743	KT751900
Erotini	*Lopheros* sp.	UPOL 000577	Japan	DQ181080	DQ181154	DQ181006	DQ181228	DQ181382
Erotini	*Lopheros* sp.	UPOL 000578	Japan	DQ181081	DQ181155	DQ181007	DQ181229	DQ181383
Erotini	*Lopheros* sp.	UPOL 001284	Japan	KF625693	KF626279	–	–	–
Erotini	*Platycis comardi*	UPOL A00559	Czech Republic	KT752225	KT752390	KT752057	KT751736	–
Erotini	*Platycis cosnardi*	UPOL 001286	Czech Republic	KF625695	KF626281	KF625984	KF625393	–
Erotini	*Platycis minutus*	UPOL 000348	Czech Republic	DQ181069	DQ181143	DQ181995	DQ181217	DQ181371
Erotini	*Platycis nasutus*	UPOL A00557	Korea	KT752223	KT752388	KT752055	KT751734	–
Erotini	*Platycis nasutus*	UPOL 000576	Japan	DQ181079	DQ181153	DQ181005	DQ181227	DQ181381
Erotini	*Platycis* sp.	UPOL A00547	China	KT752216	KT752378	KT752045	–	KT751882
Erotini	*Platycis* sp.	UPOL A00560	China	KT752226	KT752391	KT752058	–	KT751893
Erotini	*Platycis* sp.	UPOL ZL2008	Japan	–	–	EF143218	EF143233	EF143247
Erotini	*Platycis* sp.	UPOL 001366	USA	KF625697	KF626283	KF625986	KF625395	–
Erotini	*Platycis* sp.	UPOL 001365	China	KF625696	KF626282	KF625985	–	–
Eurrhacini	*Eurrhacini* sp.	UPOL A00622	Nicaragua	KT752285	KT752450	KT752119	KT751793	KT751952
Eurrhacini	*Eurrhacini* sp.	UPOL A00623	Ecuador	KT752286	KT752451	KT752120	KT751794	KT751953
Eurrhacini	*Eurrhacini* sp.	UPOL A00624	Ecuador	–	–	KT752121	KT751795	–
Eurrhacini	*Eurrhacini* sp.	UPOL A00627	Ecuador	–	–	KT752124	KT751797	KT751956
Eurrhacini	*Eurrhacini* sp.	UPOL A00636	Ecuador	KT752294	KT752459	KT752132	KT751806	KT751965
Eurrhacini	*Eurrhacini* sp.	UPOL A00638	Ecuador	–	–	KT752134	–	–
Eurrhacini	*Eurrhacini* sp.	UPOL A00641	Ecuador	–	–	KT752137	KT751810	KT751968
Eurrhacini	*Eurrhacini* sp.	UPOL A00648	Costa Rica	KT752299	KT752464	KT752142	KT751815	–
Eurrhacini	*Eurrhacini* sp.	UPOL A00649	Bolivia	KT752300	KT752465	KT752143	KT751816	KT751972
Eurrhacini	*Eurrhacus* sp.	UPOL 000M43	Ecuador	DQ181056	DQ181130	DQ180982	DQ181204	DQ181358
Leptolycini	Leptolycini sp.	UPOL 000592	Costa Rica	DQ181092	DQ181166	DQ181018	DQ181240	DQ181394
Leptolycini	*Leptolycus* sp.	UPOL VP0022	Puerto Rico	KT752303	KT752469	–	–	KT751976
Leptolycini	*Leptolycus* sp.	UPOL VP0023	Puerto Rico	KT752304	KT752470	–	–	–
Leptolycini	*Leptolycus* sp.	UPOL VP0024	Puerto Rico	KT752305	KT752471	KT752149	–	KT751977
Leptolycini	*Leptolycus* sp.	UPOL VP0025	Puerto Rico	KT752306	KT752472	–	KT751820	–
Leptolycini	*Leptolycus* sp.	UPOL VP0026	Puerto Rico	KT752307	KT752473	KT752150	–	KT751978
Leptolycini	*Leptolycus* sp.	UPOL VP0027	Puerto Rico	KT752308	KT752474	KT752151	KT751821	–
Libnetinae	*Libnetis granicollis*	UPOL 001012	Japan	DQ181107	DQ181181	DQ181033	DQ181255	DQ181409
Libnetinae	*Libnetis* sp.	UPOL A00577	Malaysia	KT752243	–	KT752075	KT751752	KT751909
Libnetinae	*Libnetis* sp.	UPOL A00578	China	KT752244	KT752408	KT752076	KT751753	KT751910
Libnetinae	*Libnetis* sp.	UPOL A00581	China	KT752247	KT752411	KT752079	KT751756	KT751913
Libnetinae	*Libnetis* sp.	UPOL A00582	Laos	KT752248	KT752412	KT752080	KT751757	KT751914
Libnetinae	*Libnetis* sp.	UPOL A00583	China	KT752249	KT752413	KT752081	KT751758	KT751915
Libnetinae	*Libnetis* sp.	UPOL A00584	Laos	KT752250	KT752414	KT752082	KT751759	KT751916
Libnetinae	*Libnetis* sp.	UPOL A00585	Malaysia	KT752251	KT752415	KT752083	KT751760	KT751917
Libnetinae	*Libnetis* sp.	UPOL A00586	Malaysia	KT752252	KT752416	KT752084	KT751761	KT751918
Libnetinae	*Libnetis* sp.	UPOL A00587	Malaysia	KT752253	KT752417	KT752085	KT751762	KT751919
Libnetinae	*Libnetis* sp.	UPOL A00588	Malaysia	KT752254	KT752418	KT752086	KT751763	KT751920
Libnetinae	*Libnetis* sp.	UPOL A00589	Sumatra	KT752255	KT752419	KT752087	KT751764	KT751921
Libnetinae	*Libnetis* sp.	UPOL A00590	Sumatra	KT752256	KT752420	KT752088	KT751765	KT751922
Libnetinae	*Libnetis* sp.	UPOL A00591	Laos	KT752257	KT752421	KT752089	KT751766	KT751923
Libnetinae	*Libnetis* sp.	UPOL 000L02	Borneo	DQ181038	DQ181112	DQ180964	DQ181186	DQ181340
Libnetinae	*Libnetis* sp.	UPOL 001002	Sumatra	DQ181104	DQ181178	DQ181030	DQ181252	DQ181406
Libnetinae	*Libnetis* sp.	UPOL 001008	Malaysia	DQ181105	DQ181179	DQ181031	DQ181253	DQ181407
Lycini	Lycini indet.	UPOL LF0428	Mexico	–	–	–	KF806789	KF806825
Lycini	Lycini indet.	UPOL LF0429	Nicaragua	–	–	KF806861	KF806790	KF806826
Lycini	Lycini indet.	UPOL LF0430	Ecuador	–	–	KF806862	KF806791	KF806827
Lycini	*Lycostomus* sp.	UPOL 000L27	China	DQ181055	DQ181129	DQ180981	DQ181203	DQ181357
Lycini	*Lycostomus* sp.	UPOL A00328	China	–	–	KF806834	KF806756	KF806798
Lycini	*Lycostomus* sp.	UPOL LF0303	Laos	–	–	KF806849	KF806773	–
Lycini	*Lycostomus* sp.	UPOL LF0304	Laos	–	–	KF806850	KF806774	–
Lycini	*Lycostomus* sp.	UPOL LF0308	Laos	–	–	KF806851	KF806775	–
Lycini	*Lycostomus* sp.	UPOL LF0319	India	–	–	–	KF806776	–
Lycini	*Lycostomus* sp.	UPOL LF0320	India	–	–	KF806852	KF806777	–
Lycini	*Lycostomus* sp.	UPOL LF0323	India	–	–	KF806853	KF806778	–
Lycini	*Lycostomus* sp.	UPOL LF0331	Indonesia	–	–	KF806854	KF806779	KF806815
Lycini	*Lycostomus* sp.	UPOL LF0340	Taiwan	–	–	KF806855	KF806780	KF806816
Lycini	*Lycostomus* sp.	UPOL LF0350	Japan	–	–	–	KF806781	KF806817
Lycini	*Lycostomus* sp.	UPOL LF0354	Japan	–	–	KF806856	KF806782	KF806818
Lycini	*Lycostomus* sp.	UPOL LF0359	Taiwan	–	–	–	KF806783	KF806819
Lycini	*Lycostomus* sp.	UPOL LF0365	Malaysia	–	–	KF806857	KF806784	KF806820
Lycini	*Lycostomus* sp.	UPOL LF0370	India	–	–	KF806858	KF806785	KF806821
Lycini	*Lycostomus* sp.	UPOL LF0381	India	–	–	–	KF806786	KF806822
Lycini	*Lycostomus* sp.	UPOL LF0388	Namibia	–	–	KF806859	KF806787	KF806823
Lycini	*Lycus arizonensis*	UPOL LF0451	USA	–	–	KF806864	KF806793	KF806829
Lycini	*Lycus arizonensis*	UPOL LF0452	USA	–	–	KF806865	KF806794	KF806830
Lycini	*Lycus arizonensis*	UPOL LF0454	USA	–	–	KF806866	KF806795	KF806831
Lycini	*Lycus loripes*	UPOL LF0464	USA	–	–	KF806867	KF806796	KF806832
Lycini	*Lycus loripes*	UPOL LF0466	USA	–	–	KF806868	KF806797	KF806833
Lycini	*Lycus* sp.	UPOL A00469	Zambia	KT752152	KT752310	KT751979	KT751662	KT751824
Lycini	*Lycus* sp.	UPOL 000L03	RSA	DQ181039	DQ181113	DQ180965	DQ181187	DQ181341
Lycini	*Lycus* sp.	UPOL LF0021	Ethiopia	–	–	KF806835	KF806757	KF806799
Lycini	*Lycus* sp.	UPOL LF0031	Cameroon	–	–	KF806836	KF806758	KF806800
Lycini	*Lycus* sp.	UPOL LF0035	Cameroon	–	–	KF806837	KF806759	KF806801
Lycini	*Lycus* sp.	UPOL LF0043	Ethiopia	–	–	KF806838	KF806760	KF806802
Lycini	*Lycus* sp.	UPOL LF0077	RSA	–	–	KF806839	KF806761	KF806803
Lycini	*Lycus* sp.	UPOL LF0093	Tanzania	–	–	–	KF806762	KF806804

Lycini	*Lycus* sp.	UPOL LF0110	Zambia	–	–	KF806840	KF806763	KF806805
Lycini	*Lycus* sp.	UPOL LF0116	RSA	–	–	KF806841	KF806764	KF806806
Lycini	*Lycus* sp.	UPOL LF0143	Zambia	–	–	KF806842	KF806765	KF806807
Lycini	*Lycus* sp.	UPOL LF0167	Ethiopia	–	–	KF806843	KF806766	KF806808
Lycini	*Lycus* sp.	UPOL LF0168	Ethiopia	–	–	KF806844	KF806767	KF806809
Lycini	*Lycus* sp.	UPOL LF0230	Zambia	–	–	–	KF806768	KF806810
Lycini	*Lycus* sp.	UPOL LF0262	Cameroon	–	–	KF806845	KF806769	KF806811
Lycini	*Lycus* sp.	UPOL LF0264	Cameroon	–	–	KF806846	KF806770	KF806812
Lycini	*Lycus* sp.	UPOL LF0266	Cameroon	–	–	KF806847	KF806771	KF806813
Lycini	*Lycus* sp.	UPOL LF0270	Cameroon	–	–	KF806848	KF806772	KF806814
Lycini	*Lycus* sp.	UPOL LF0394	Namibia	–	–	KF806860	KF806788	KF806824
Lycini	*Lycus* sp.	UPOL LF0444	Ethiopia	–	–	KF806863	KF806792	KF806828
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL A00523	Java	KT752193	KT752354	KT752024	KT751705	–
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL A00524	Malaysia	KT752194	KT752355	–	KT751706	KT751863
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL A00530	Malaysia	KT752200	KT752361	KT752029	KT751712	KT751867
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL A00532	Java	KT752202	KT752363	KT752031	KT751714	KT751869
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL A00533	Sumatra	KT752203	KT752364	KT752032	KT751715	KT751870
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL A00541	Sumatra	KT752210	KT752372	KT752039	KT751720	KT751876
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL A00542	Sumatra	KT752211	KT752373	KT752040	KT751721	KT751877
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL A00545	Sumatra	KT752214	KT752376	KT752043	–	KT751880
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL A00572	India	KT752238	KT752403	KT752070	KT751747	KT751904
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL A00626	India	KT752288	KT752453	KT752123	–	KT751955
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL 000358	Java	DQ181070	DQ181144	DQ180996	DQ181218	DQ181372
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL 000801	Sumatra	DQ181095	DQ181169	DQ181021	DQ181243	DQ181397
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL 000802	Java	DQ181096	DQ181170	DQ181022	DQ181244	DQ181398
Lycoprogenthini	*Lycoprogenthes* sp.	UPOL 000805	Sumatra	DQ181097	DQ181171	DQ181023	DQ181245	DQ181399
Lyponiini	*Lyponia debilis*	UPOL YL0296	China	–	–	ab123456	KJ650468	ab123456
Lyponiini	*Lyponia delicatula*	UPOL 000815	Japan	DQ181099	DQ181173	DQ181025	DQ181247	DQ181401
Lyponiini	*Lyponia kuatunensis*	UPOL YL0319	China	–	–	ab123456	KJ650482	ab123456
Lyponiini	*Lyponia muyuensis*	UPOL YL0314	China	–	–	ab123456	KJ650493	ab123456
Lyponiini	*Lyponia nigrohumeralis*	UPOL 000L17	China	DQ181048	DQ181122	DQ180974	DQ181196	DQ181350
Lyponiini	*Lyponia quadricollis*	UPOL 000817	Korea	DQ181101	DQ181175	DQ181027	DQ181249	DQ181403
Lyponiini	*Lyponia* sp.	UPOL A00571	Laos	KT752237	KT752402	KT752069	KT751746	–
Lyponiini	*Lyponia* sp.	UPOL ZL2014	Japan	–	–	FJ390408	FJ390410	FJ390412
Lyponiini	*Lyponia* sp.	UPOL ZL2016	Japan	–	–	EF143225	EF143240	EF143253
Lyponiini	*Lyponia* sp.	UPOL 000816	China	DQ181100	DQ181174	DQ181026	DQ181248	DQ181402
Lyponiini	*Lyponia* sp.	UPOL A00467	China	KU184276	KU184284	ab123456	KJ650453	ab123456
Lyponiini	*Lyponia tianquanensis*	UPOL A00468	China	KU184277	KU184285	ab123456	KJ650450	ab123456
Lyponiini	*Ponyalis alternata*	UPOL YL0217	China	–	–	ab123456	KJ650408	ab123456
Lyponiini	*Ponyalis fukiensis*	UPOL YL0282	China	–	–	ab123456	KJ650420	ab123456
Lyponiini	*Ponyalis gracilis*	UPOL YL0409	China	–	–	ab123456	KJ650437	ab123456
Lyponiini	*Ponyalis ishigakiana*	UPOL YL0259	Japan	–	–	ab123456	KJ650438	ab123456
Lyponiini	*Ponyalis laticornis*	UPOL A00460	China	KU184270	KU184278	ab123456	KJ650401	ab123456
Lyponiini	*Ponyalis oshimana*	UPOL YL0263	Japan	–	–	ab123456	KJ650415	ab123456
Lyropaeini	*Lyropaeus dominator*	UPOL VP0003	Malaysia	KC736890	KC736899	KC736882	KC736909	KC736918
Lyropaeini	*Lyropaeus optabilis*	UPOL 000585	Malaysia	DQ181088	DQ181162	DQ181014	DQ181236	DQ181390
Lyropaeini	*Lyropaeus optabilis*	UPOL VP0004	Malaysia	KC736891	KC736900	KC736883	KC736910	KC736919
Lyropaeini	*Lyropaeus philippinensis*	UPOL VP0018	Philippines	KC736895	KC736904	–	KC736913	KC736922
Lyropaeini	*Lyropaeus philippinensis*	UPOL VP0019	Philippines	KC736896	KC736905	–	KC736914	KC736923
Lyropaeini	*Lyropaeus ritsemae*	UPOL VP0001	Sumatra	KC736888	KC736898	KC736880	KC736907	KC736916
Lyropaeini	*Lyropaeus ritsemae*	UPOL VP0006	Sumatra	KC736892	KC736901	KC736884	KC736911	KC736920
Lyropaeini	*Lyropaeus rubrostriatus*	UPOL 000L11	Borneo	DQ181042	DQ181116	DQ180968	DQ181190	DQ181344
Lyropaeini	*Lyropaeus* sp.	UPOL A00574	Malaysia	KT752240	KT752405	KT752072	KT751749	KT751906
Lyropaeini	*Lyropaeus* sp.	UPOL VP0016	India	KC736893	KC736902	KC736885	KC736912	KC736921
Lyropaeini	*Lyropaeus* sp.	UPOL VP0017	India	KC736894	KC736903	KC736886	–	–
Lyropaeini	*Lyropaeus* sp.	UPOL VP2312	India	KC736897	KC736906	KC736887	KC736915	KC736924
Lyropaeini	*Lyropaeus waterhouesi*	UPOL VP0002	Sumatra	KC736889	–	KC736881	KC736908	KC736917
Lyropaeini	*Lyropaeus waterhousei*	UPOL 000584	Sumatra	DQ181087	DQ181161	DQ181013	DQ181235	DQ181389
Macrolycini	*Macrolycus atronotatus*	UPOL A00465	China	KU184274	KU184282	ab123456	ab123456	ab123456
Macrolycini	*Macrolycus bicolor*	UPOL YL0403	China	–	–	ab123456	ab123456	ab123456
Macrolycini	*Macrolycus bowringi*	UPOL A00461	China	KU184271	KU184279	ab123456	ab123456	ab123456
Macrolycini	*Macrolycus dotatus*	UPOL YL0185	China	–	–	ab123456	ab123456	ab123456
Macrolycini	*Macrolycus flabellatus*	UPOL YL0032	Japan	–	–	ab123456	ab123456	ab123456
Macrolycini	*Macrolycus galinae*	UPOL A00464	China	KU184273	KU184281	ab123456	ab123456	ab123456
Macrolycini	*Macrolycus ligulatus*	UPOL A00462	China	–	–	ab123456	ab123456	ab123456
Macrolycini	*Macrolycus mucronatus*	UPOL YL0206	China	–	–	ab123456	ab123456	ab123456
Macrolycini	*Macrolycus ochraceus*	UPOL YL0192	China	–	–	ab123456	KJ650495	ab123456
Macrolycini	*Macrolycus oreophilus*	UPOL A00466	China	KU184275	KU184283	ab123456	ab123456	ab123456
Macrolycini	*Macrolycus sichuanensis*	UPOL A00463	China	KU184272	KU184280	ab123456	ab123456	ab123456
Macrolycini	*Macrolycus* sp.	UPOL ZL2005	Japan	–	–	EF143217	EF143232	EF143246
Macrolycini	*Macrolycus* sp.	UPOL 000828	Thailand	DQ181102	DQ181176	DQ181028	DQ181250	DQ181404
Macrolycini	*Macrolycus* sp.	UPOL 000L18	China	DQ181049	DQ181123	DQ180975	DQ181197	DQ181351
Metriorrhynchini	*Broxylus kalamensis*	UPOL MD0107	Sulawesi	KC538221	KC538010	KC538793	KC538414	KC538607
Metriorrhynchini	*Broxylus malinensis*	UPOL MD0101	Sulawesi	KC538219	KC538008	HQ456958	HQ456981	HQ457003
Metriorrhynchini	*Broxylus pendolensis*	UPOL MD0106	Sulawesi	KC538220	KC538009	KC538792	KC538413	KC538606
Metriorrhynchini	*Broxylus pfeifferi*	UPOL MD0099	Sulawesi	KC538218	KC538007	HQ456957	HQ456980	HQ457002
Metriorrhynchini	*Cautires apterus*	UPOL A00652	Tanzania	–	–	KF588381	–	KF588386
Metriorrhynchini	*Cautires apterus*	UPOL A00653	Tanzania	–	–	KF588382	–	KF588387
Metriorrhynchini	*Cautires apterus*	UPOL A00655	Tanzania	–	–	–	KF588384	KF588388
Metriorrhynchini	*Cautires apterus*	UPOL A00656	Tanzania	–	–	KF588383	KF588385	KF588389
Metriorrhynchini	*Cautires cf. montanus*	UPOL 000L06	Borneo	DQ181041	DQ181115	DQ180967	DQ181189	DQ181343
Metriorrhynchini	*Cautires* sp.	UPOL ZL2009	Sumatra	–	–	EF143219	EF143234	EF143248
Metriorrhynchini	*Cautires* sp.	UPOL 000L14	RSA	DQ181045	DQ181119	DQ180971	DQ181193	DQ181347
Metriorrhynchini	*Cautires* sp.	UPOL 000030	Borneo	KC538128	KC537918	KC538632	KC538245	KC538437
Metriorrhynchini	*Cautires* sp.	UPOL 000037	Borneo	KC538129	KC537919	KC538633	KC538246	KC538438
Metriorrhynchini	*Cautires* sp.	UPOL 000040	Borneo	KC538130	KC537920	KC538634	KC538247	KC538439
Metriorrhynchini	*Cautires* sp.	UPOL 000043	Borneo	KC538131	KC537921	KC538635	KC538248	KC538440
Metriorrhynchini	*Cautires* sp.	UPOL 000044	Borneo	KC538132	KC537922	KC538636	KC538249	KC538441
Metriorrhynchini	*Cautires* sp.	UPOL 000047	Sumatra	KC538133	KC537923	KC538637	KC538250	KC538442
Metriorrhynchini	*Cautires* sp.	UPOL 000048	Sumatra	KC538134	KC537924	KC538638	KC538251	KC538443
Metriorrhynchini	*Cautires* sp.	UPOL 000050	Sumatra	KC538135	KC537925	KC538639	KC538252	KC538444
Metriorrhynchini	*Cautires* sp.	UPOL 000052	Sumatra	KC538136	KC537926	KC538640	KC538253	KC538445
Metriorrhynchini	*Cautires* sp.	UPOL 000056	Sumatra	KC538137	KC537927	KC538641	KC538254	KC538446
Metriorrhynchini	*Cautires* sp.	UPOL 000060	Sumatra	KC538138	KC537928	KC538642	KC538255	KC538447
Metriorrhynchini	*Cautires* sp.	UPOL 000064	Laos	KC538139	KC537929	KC538643	KC538256	KC538448
Metriorrhynchini	*Cautires* sp.	UPOL 000066	Laos	KC538140	KC537930	KC538644	KC538257	KC538449
Metriorrhynchini	*Cautires* sp.	UPOL 000068	Borneo	KC538141	KC537931	KC538645	KC538258	KC538450
Metriorrhynchini	*Cautires* sp.	UPOL 000069	Borneo	KC538142	KC537932	KC538646	KC538259	KC538451
Metriorrhynchini	*Cautires* sp.	UPOL 000070	Malaysia	KC538143	KC537933	KC538647	KC538260	KC538452
Metriorrhynchini	*Cautires* sp.	UPOL 000074	Borneo	KC538145	KC537935	KC538649	KC538262	KC538454
Metriorrhynchini	*Cautires* sp.	UPOL 000075	Laos	KC538146	KC537936	–	KC538263	KC538455

Metriorrhynchini	*Cautires* sp.	UPOL 000079	Borneo	KC538147	KC537937	KC538650	KC538264	KC538456
Metriorrhynchini	*Cautires* sp.	UPOL 000080	Borneo	KC538148	KC537938	KC538651	KC538265	KC538457
Metriorrhynchini	*Cautires* sp.	UPOL 000081	Borneo	KC538149	KC537939	KC538652	KC538266	KC538458
Metriorrhynchini	*Cautires* sp.	UPOL 000084	Borneo	KC538150	KC537940	KC538653	KC538267	KC538459
Metriorrhynchini	*Cautires* sp.	UPOL 000088	Malaysia	KC538151	KC537941	KC538654	KC538268	KC538460
Metriorrhynchini	*Cautires* sp.	UPOL 000090	Borneo	KC538152	KC537942	KC538655	KC538269	KC538461
Metriorrhynchini	*Cautires* sp.	UPOL 000104	Borneo	KC538153	KC537943	KC538656	KC538270	KC538462
Metriorrhynchini	*Cautires* sp.	UPOL 000109	Borneo	–	KC537945	KC538658	KC538272	KC538464
Metriorrhynchini	*Cautires* sp.	UPOL 000122	Borneo	KC538157	KC537948	KC538661	KC538275	KC538467
Metriorrhynchini	*Cautires* sp.	UPOL 000123	Java	KC538158	KC537949	–	KC538276	–
Metriorrhynchini	*Cautires* sp.	UPOL 000147	India	KC538161	KC537952	KC538664	KC538278	KC538470
Metriorrhynchini	*Cautires* sp.	UPOL 000164	Laos	KC538165	KC537956	KC538667	KC538282	KC538473
Metriorrhynchini	*Cautires* sp.	UPOL 000174	Malaysia	KC538166	KC537957	–	KC538283	KC538474
Metriorrhynchini	*Cautires* sp.	UPOL 000177	Malaysia	KC538167	–	KC538668	KC538284	KC538475
Metriorrhynchini	*Cautires* sp.	UPOL 000178	Malaysia	KC538168	KC537958	KC538669	KC538285	KC538476
Metriorrhynchini	*Cautires* sp.	UPOL 000188	Laos	KC538170	KC537960	KC538671	KC538287	KC538478
Metriorrhynchini	*Cautires* sp.	UPOL 000189	Laos	KC538171	KC537961	KC538672	KC538288	KC538479
Metriorrhynchini	*Cautires* sp.	UPOL 000195	RSA	KC538172	KC537962	KC538673	KC538289	KC538480
Metriorrhynchini	*Cautires* sp.	UPOL 000205	Sumatra	KC538174	KC537964	KC538675	KC538291	KC538482
Metriorrhynchini	*Cautires* sp.	UPOL 000206	Sumatra	KC538175	KC537965	KC538676	KC538292	KC538483
Metriorrhynchini	*Cautires* sp.	UPOL 000217	Japan	KC538176	KC537966	KC538678	KC538293	KC538484
Metriorrhynchini	*Cautires* sp.	UPOL 000219	Japan	KC538177	KC537967	KC538679	KC538294	KC538485
Metriorrhynchini	*Cautires* sp.	UPOL 000220	Japan	KC538178	KC537968	KC538680	KC538295	KC538486
Metriorrhynchini	*Cautires* sp.	UPOL 000246	Sumatra	KC538181	KC537970	KC538683	KC538298	KC538489
Metriorrhynchini	*Cautires* sp.	UPOL 000290	Laos	KC538184	KC537974	KC538687	KC538302	KC538493
Metriorrhynchini	*Cautires* sp.	UPOL 000294	Sumatra	KC538185	KC537975	KC538688	KC538303	KC538494
Metriorrhynchini	*Cautires* sp.	UPOL 000295	Sumatra	KC538186	KC537976	KC538689	KC538304	KC538495
Metriorrhynchini	*Cautires* sp.	UPOL 000297	Sumatra	KC538187	KC537977	KC538690	KC538305	KC538496
Metriorrhynchini	*Cautires* sp.	UPOL 000314	Sumatra	KC538188	KC537978	KC538691	KC538306	KC538497
Metriorrhynchini	*Cautires* sp.	UPOL 000335	Borneo	–	–	KC538693	KC538308	KC538499
Metriorrhynchini	*Cautires* sp.	UPOL 000339	Borneo	KC538190	KC537980	KC538694	KC538309	KC538500
Metriorrhynchini	*Cautires* sp.	UPOL 000342	Borneo	KC538191	KC537981	KC538695	KC538310	KC538501
Metriorrhynchini	*Cautires* sp.	UPOL 000346	Borneo	KC538192	KC537982	KC538696	KC538311	KC538502
Metriorrhynchini	*Cautires* sp.	UPOL 000355	Java	–	KC537983	KC538697	KC538312	KC538503
Metriorrhynchini	*Cautires* sp.	UPOL 000395	Palawan	–	–	KC538706	KC538319	KC538510
Metriorrhynchini	*Cautires* sp.	UPOL 000403	Palawan	–	KC537990	KC538709	KC538323	KC538514
Metriorrhynchini	*Cautires* sp.	UPOL 000411	Palawan	KC538201	–	KC538710	KC538324	KC538515
Metriorrhynchini	*Cautires* sp.	UPOL 000425	Palawan	–	–	KC538713	KC538327	KC538518
Metriorrhynchini	*Cautires* sp.	UPOL A00017	Taiwan	–	KC537824	–	–	–
Metriorrhynchini	*Cautires* sp.	UPOL A00019	Taiwan	KC538034	KC537826	KC538715	KC538329	KC538520
Metriorrhynchini	*Cautires* sp.	UPOL A00020	Taiwan	KC538035	KC537827	–	–	–
Metriorrhynchini	*Cautires* sp.	UPOL A00021	Taiwan	KC538036	KC537828	HQ456947	HQ456965	–
Metriorrhynchini	*Cautires* sp.	UPOL A00022	Madagascar	KC538037	KC537829	KC538716	HQ456966	HQ456989
Metriorrhynchini	*Cautires* sp.	UPOL A00023	Madagascar	KC538038	KC537830	KC538717	KC538330	KC538521
Metriorrhynchini	*Cautires* sp.	UPOL A00024	Madagascar	KC538039	KC537831	KC538718	KC538331	KC538522
Metriorrhynchini	*Cautires* sp.	UPOL A00025	Madagascar	KC538040	KC537832	KC538719	KC538332	KC538523
Metriorrhynchini	*Cautires* sp.	UPOL A00026	Madagascar	KC538041	KC537833	–	KC538333	KC538524
Metriorrhynchini	*Cautires* sp.	UPOL A00027	Madagascar	KC538042	KC537834	–	KC538334	KC538525
Metriorrhynchini	*Cautires* sp.	UPOL A00028	Madagascar	KC538043	KC537835	–	KC538335	–
Metriorrhynchini	*Cautires* sp.	UPOL A00029	Madagascar	KC538044	KC537836	–	KC538336	KC538526
Metriorrhynchini	*Cautires* sp.	UPOL A00030	Madagascar	KC538045	KC537837	KC538720	KC538337	KC538527
Metriorrhynchini	*Cautires* sp.	UPOL A00048	Malaysia	KC538063	KC537855	HQ456948	HQ456967	HQ456990
Metriorrhynchini	*Cautires* sp.	UPOL A00050	Malaysia	KC538065	KC537857	–	–	KC538546
Metriorrhynchini	*Cautires* sp.	UPOL A00057	Philippines	KC538069	KC537860	–	KC538356	KC538549
Metriorrhynchini	*Cautires* sp.	UPOL A00058	Philippines	KC538070	KC537861	–	KC538357	KC538550
Metriorrhynchini	*Cautires* sp.	UPOL A00062	Philippines	KC538074	KC537865	KC538742	KC538361	KC538554
Metriorrhynchini	*Cautires* sp.	UPOL A00078	Cameroon	KC538089	KC537880	KC538754	KC538375	KC538567
Metriorrhynchini	*Cautires* sp.	UPOL A00079	Cameroon	KC538090	KC537881	KC538755	KC538376	KC538568
Metriorrhynchini	*Cautires* sp.	UPOL A00080	Cameroon	KC538091	KC537882	HQ456950	HQ456969	HQ456992
Metriorrhynchini	*Cautires* sp.	UPOL A00081	Cameroon	KC538093	KC537884	KC538756	KC538377	KC538569
Metriorrhynchini	*Cautires* sp.	UPOL A00082	Cameroon	KC538092	KC537883	KC538757	KC538378	–
Metriorrhynchini	*Cautires* sp.	UPOL A00083	Cameroon	KC538094	KC537885	KC538758	KC538379	KC538570
Metriorrhynchini	*Cautires* sp.	UPOL A00084	Cameroon	KC538095	KC537886	KC538759	KC538380	KC538571
Metriorrhynchini	*Cautires* sp.	UPOL A00085	Cameroon	KC538096	KC537887	KC538760	KC538381	KC538572
Metriorrhynchini	*Cautires* sp.	UPOL A00086	Cameroon	KC538097	KC537888	KC538761	KC538382	KC538573
Metriorrhynchini	*Cautires* sp.	UPOL A00087	Cameroon	KC538098	KC537889	KC538762	KC538383	KC538574
Metriorrhynchini	*Cautires* sp.	UPOL A00088	Cameroon	KC538099	KC537890	KC538763	KC538384	KC538575
Metriorrhynchini	*Cautires* sp.	UPOL A00089	Cameroon	KC538100	KC537891	KC538764	KC538385	KC538576
Metriorrhynchini	*Cautires* sp.	UPOL A00090	Cameroon	KC538101	KC537892	KC538765	KC538386	KC538577
Metriorrhynchini	*Cautires* sp.	UPOL A00092	Cameroon	KC538103	KC537894	KC538766	KC538388	KC538579
Metriorrhynchini	*Cautires* sp.	UPOL A00093	Cameroon	KC538104	KC537895	KC538767	KC538389	KC538580
Metriorrhynchini	*Cautires* sp.	UPOL A00099	Cameroon	KC538110	KC537901	KC538773	KC538393	KC538586
Metriorrhynchini	*Cautires* sp.	UPOL A00100	Cameroon	KC538111	–	KC538774	KC538394	KC538587
Metriorrhynchini	*Cautires* sp.	UPOL A00101	Cameroon	KC538112	KC537902	–	KC538395	–
Metriorrhynchini	*Cautires* sp.	UPOL A00102	Cameroon	KC538113	KC537903	–	KC538396	KC538588
Metriorrhynchini	*Cautires* sp.	UPOL A00103	Cameroon	KC538114	KC537904	–	KC538397	–
Metriorrhynchini	*Cautires* sp.	UPOL A00105	Cameroon	KC538116	KC537906	KC538776	–	KC538590
Metriorrhynchini	*Cautires* sp.	UPOL A00106	Cameroon	KC538117	KC537907	KC538777	KC538398	KC538591
Metriorrhynchini	*Cautires* sp.	UPOL A00107	Cameroon	KC538118	KC537908	–	KC538399	–
Metriorrhynchini	*Cautires* sp.	UPOL A00109	Cameroon	KC538119	KC537909	KC538778	KC538400	KC538592
Metriorrhynchini	*Cautires* sp.	UPOL A00110	Cameroon	KC538120	KC537910	KC538779	–	KC538593
Metriorrhynchini	*Cautires* sp.	UPOL A00111	Cameroon	KC538121	KC537911	KC538780	KC538401	KC538594
Metriorrhynchini	*Cautires* sp.	UPOL A00112	Cameroon	KC538122	KC537912	KC538781	KC538402	KC538595
Metriorrhynchini	*Cautiromimus* sp.	UPOL 000388	Palawan	–	–	–	KC538318	KC538509
Metriorrhynchini	*Ditua* sp.	UPOL A00033	Australia	KC538048	KC537840	KC538723	–	KC538530
Metriorrhynchini	*Leptotrichalus* sp.	UPOL ZL2002	Java	–	–	EF143215	EF143230	EF143244
Metriorrhynchini	*Leptotrichalus* sp.	UPOL 000208	Borneo	DQ181064	DQ181138	DQ180990	DQ181212	DQ181366
Metriorrhynchini	*Leptotrichalus* sp.	UPOL 000396	Palawan	–	–	KC538707	KC538320	KC538511
Metriorrhynchini	*Leptotrichalus* sp.	UPOL 000419	Palawan	KC538203	KC537992	KC538712	KC538326	KC538517
Metriorrhynchini	*Leptotrichalus* sp.	UPOL A00052	Philippines	KC538066	KC537858	HQ456949	HQ456968	HQ456991
Metriorrhynchini	*Leptotrichalus* sp.	UPOL A00059	Philippines	KC538071	KC537862	KC538739	KC538358	KC538551
Metriorrhynchini	*Leptotrichalus* sp.	UPOL A00061	Philippines	KC538073	KC537864	KC538741	KC538360	KC538553
Metriorrhynchini	*Matsudanoeus yuasai*	UPOL VK0248	Japan	–	–	KF652136	–	KF652130
Metriorrhynchini	*Matsudanoeus yuasai*	UPOL VK0249	Japan	–	–	KF652137	KF652120	KF652131
Metriorrhynchini	*Matsudanoeus yuasai*	UPOL VK0395	Japan	–	–	–	–	KF652132
Metriorrhynchini	*Metanoeus* sp.	UPOL 000026	Borneo	KC538127	KC537917	KC538631	KC538244	KC538436
Metriorrhynchini	*Metanoeus* sp.	UPOL 000105	Borneo	KC538154	KC537944	KC538657	KC538271	KC538463
Metriorrhynchini	*Metanoeus* sp.	UPOL 000121	Sumatra	KC538156	KC537947	KC538660	KC538274	KC538466
Metriorrhynchini	*Metanoeus* sp.	UPOL 000125	Sumatra	KC538159	KC537950	KC538662	KC538277	KC538468
Metriorrhynchini	*Metanoeus* sp.	UPOL 000248	Sumatra	KC538182	KC537971	KC538684	KC538299	KC538490
Metriorrhynchini	*Metanoeus* sp.	UPOL 000434	Palawan	–	–	KC538714	KC538328	KC538519

Metriorrhynchini	*Metanoeus* sp.	UPOL A00063	Philippines	KC538075	KC537866	–	KC538362	KC538555
Metriorrhynchini	*Metanoeus* sp.	UPOL A00064	Philippines	KC538076	KC537867	–	KC538363	KC538556
Metriorrhynchini	*Metanoeus* sp.	UPOL A00065	Philippines	KC538077	KC537868	–	KC538364	KC538557
Metriorrhynchini	*Metriorrhynchus palawensis*	UPOL 000366	Palawan	–	–	KC538698	DQ144665	DQ144691
Metriorrhynchini	*Metriorrhynchus lineatus*	UPOL 000L05	Borneo	DQ181040	DQ181114	DQ180966	DQ181188	DQ181342
Metriorrhynchini	*Metriorrhynchus lineatus*	UPOL 000009	Sumatra	KC538123	KC537913	KC538628	DQ904297	DQ904259
Metriorrhynchini	*Metriorrhynchus lobatus*	UPOL 000017	Sulawesi	KC538126	KC537916	KC538630	DQ144662	DQ144688
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL 000010	Sulawesi	KC538124	KC537914	–	DQ144659	DQ144685
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL 000011	Sulawesi	KC538125	KC537915	KC538629	DQ144660	DQ144686
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL 000374	Australia	KC538195	KC537986	KC538701	KC538314	KC538505
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00034	Australia	KC538049	KC537841	KC538724	KC538340	KC538531
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00038	Australia	KC538053	KC537845	KC538728	KC538344	KC538535
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00039	Australia	KC538054	KC537846	KC538729	KC538345	KC538536
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00043	Australia	KC538058	KC537850	KC538732	KC538349	KC538540
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00046	Australia	KC538061	KC537853	KC538735	KC538352	KC538543
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00049	Malaysia	KC538064	KC537856	KC538736	KC538354	KC538545
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00116	Papua New Guinea	ab123456	ab123456	ab123456	–	ab123456
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00120	Papua New Guinea	ab123456	ab123456	ab123456	–	ab123456
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00128	Papua New Guinea	ab123456	ab123456	ab123456	ab123456	ab123456
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00132	Papua New Guinea	ab123456	ab123456	ab123456	ab123456	ab123456
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00148	Papua New Guinea	ab123456	ab123456	ab123456	ab123456	ab123456
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00160	Papua New Guinea	ab123456	ab123456	–	ab123456	ab123456
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00164	Papua New Guinea	ab123456	ab123456	ab123456	ab123456	ab123456
Metriorrhynchini	*Metriorrhynchus* sp.	UPOL A00185	Papua New Guinea	ab123456	ab123456	ab123456	ab123456	–
Metriorrhynchini	*Microtrichalus* sp.	UPOL 000L23	Borneo	DQ181052	DQ181126	DQ180978	DQ181200	DQ181354
Metriorrhynchini	*Microtrichalus* sp.	UPOL 000199	Sulawesi	KC538173	KC537963	KC538674	KC538290	KC538481
Metriorrhynchini	*Microtrichalus* sp.	UPOL 000373	Australia	KC538194	KC537985	KC538700	KC538313	KC538504
Metriorrhynchini	*Microtrichalus* sp.	UPOL 000375	Australia	KC538196	KC537987	KC538702	KC538315	KC538506
Metriorrhynchini	*Microtrichalus* sp.	UPOL 000376	Australia	KC538197	KC537988	KC538703	KC538316	KC538507
Metriorrhynchini	*Microtrichalus* sp.	UPOL 000412	Palawan	KC538202	KC537991	KC538711	KC538325	KC538516
Metriorrhynchini	*Microtrichalus* sp.	UPOL A00068	Philippines	KC538080	KC537871	KC538745	KC538367	KC538560
Metriorrhynchini	*Microtrichalus* sp.	UPOL A00069	Philippines	KC538081	KC537872	KC538746	KC538368	KC538561
Metriorrhynchini	*Microtrichalus* sp.	UPOL A00073	Philippines	KC538084	KC537875	KC538749	KC538371	–
Metriorrhynchini	*Microtrichalus* sp.	UPOL MD0097	Sulawesi	KC538216	KC538005	KC538791	HQ456978	HQ457000
Metriorrhynchini	*Microtrichalus* sp.	UPOL MD0098	Sulawesi	KC538217	KC538006	HQ456956	HQ456979	HQ457001
Metriorrhynchini	*Porrostoma haemorrhoidalis*	UPOL 000378	Australia	KC538198	KC537989	KC538704	DQ144679	DQ144703
Metriorrhynchini	*Porrostoma rhipidum*	UPOL 000372	Australia	KC538193	KC537984	KC538699	DQ144678	DQ144702
Metriorrhynchini	*Porrostoma* sp.	UPOL A00035	Australia	KC538050	KC537842	KC538725	KC538341	KC538532
Metriorrhynchini	*Porrostoma* sp.	UPOL A00036	Australia	KC538051	KC537843	KC538726	KC538342	KC538533
Metriorrhynchini	*Porrostoma* sp.	UPOL A00037	Australia	KC538052	KC537844	KC538727	KC538343	KC538534
Metriorrhynchini	*Porrostoma* sp.	UPOL A00040	Australia	KC538055	KC537847	KC538730	KC538346	KC538537
Metriorrhynchini	*Porrostoma* sp.	UPOL A00041	Australia	KC538056	KC537848	KC538731	KC538347	KC538538
Metriorrhynchini	*Porrostoma* sp.	UPOL A00042	Australia	KC538057	KC537849	–	KC538348	KC538539
Metriorrhynchini	*Porrostoma* sp.	UPOL A00044	Australia	KC538059	KC537851	KC538733	KC538350	KC538541
Metriorrhynchini	*Porrostoma* sp.	UPOL A00045	Australia	KC538060	KC537852	KC538734	KC538351	KC538542
Metriorrhynchini	*Sulabanus cordatus*	UPOL MD0069	Sulawesi	KC538213	KC538002	KC538788	KC538410	KC538603
Metriorrhynchini	*Sulabanus cordatus*	UPOL MD0081	Sulawesi	KC538215	KC538004	KC538790	KC538412	KC538605
Metriorrhynchini	*Sulabanus gracilis*	UPOL MD0064	Sulawesi	KC538210	KC537999	KC538786	KC538407	KC538600
Metriorrhynchini	*Sulabanus gracilis*	UPOL MD0067	Sulawesi	KC538212	KC538001	KC538787	KC538409	KC538602
Metriorrhynchini	*Sulabanus gracilis*	UPOL MD0071	Sulawesi	KC538214	KC538003	KC538789	KC538411	KC538604
Metriorrhynchini	*Sulabanus katarinae*	UPOL MD0033	Sulawesi	KC538206	KC537995	KC538783	KC538404	KC538597
Metriorrhynchini	*Sulabanus lalui*	UPOL MD0030	Sulawesi	KC538205	KC537994	–	KC538403	KC538596
Metriorrhynchini	*Sulabanus lineatus*	UPOL MD0034	Sulawesi	KC538207	KC537996	KC538784	KC538405	KC538598
Metriorrhynchini	*Sulabanus mamasensis*	UPOL MD0044	Sulawesi	KC538209	KC537998	KC538785	KC538406	KC538599
Metriorrhynchini	*Sulabanus similis*	UPOL MD0065	Sulawesi	KC538211	KC538000	–	KC538408	KC538601
Metriorrhynchini	*Sulabanus* sp.	UPOL ZL2010	Sulawesi	–	–	EF143220	EF143235	EF143249
Metriorrhynchini	*Sulabanus* sp.	UPOL A00066	Philippines	KC538078	KC537869	KC538743	KC538365	KC538558
Metriorrhynchini	*Sulabanus* sp.	UPOL A00067	Philippines	KC538079	KC537870	KC538744	KC538366	KC538559
Metriorrhynchini	*Sulabanus* sp.	UPOL A00070	Philippines	KC538082	KC537873	KC538747	KC538369	KC538562
Metriorrhynchini	*Sulabanus* sp.	UPOL A00071	Philippines	KC538083	KC537874	KC538748	KC538370	KC538563
Metriorrhynchini	*Sulabanus* sp.	UPOL A00075	Philippines	KC538086	KC537877	KC538751	KC538372	KC538564
Metriorrhynchini	*Sulabanus* sp.	UPOL A00077	Philippines	KC538088	KC537879	KC538753	KC538374	KC538566
Metriorrhynchini	*Synchonnus* sp.	UPOL A00031	Australia	KC538046	KC537838	KC538721	KC538338	KC538528
Metriorrhynchini	*Trichalus* sp.	UPOL A00032	Australia	KC538047	KC537839	KC538722	KC538339	KC538529
Metriorrhynchini	*Wakarumbia aurea*	UPOL MD0136	Sulawesi	KC538235	KC538024	KC538804	KC538427	KC538619
Metriorrhynchini	*Wakarumbia aurea*	UPOL MD0137	Sulawesi	KC538236	KC538025	KC538805	KC538428	KC538620
Metriorrhynchini	*Wakarumbia fasciata*	UPOL MD0121	Sulawesi	KC538226	KC538015	KC538796	KC538418	KC538610
Metriorrhynchini	*Wakarumbia fascicularis*	UPOL MD0140	Sulawesi	KC538237	KC538026	KC538806	KC538429	KC538621
Metriorrhynchini	*Wakarumbia fascicularis*	UPOL MD0145	Sulawesi	KC538239	KC538028	KC538808	KC538431	KC538623
Metriorrhynchini	*Wakarumbia grisea*	UPOL MD0127	Sulawesi	KC538228	KC538017	–	KC538420	KC538612
Metriorrhynchini	*Wakarumbia grisea*	UPOL MD0156	Sulawesi	KC538241	KC538030	KC538810	KC538433	KC538625
Metriorrhynchini	*Wakarumbia kalamensis*	UPOL MD0133	Sulawesi	KC538232	KC538021	KC538801	KC538424	KC538616
Metriorrhynchini	*Wakarumbia kalamensis*	UPOL MD0169	Sulawesi	KC538243	KC538032	KC538812	KC538435	KC538627
Metriorrhynchini	*Wakarumbia kundratai*	UPOL MD0130	Sulawesi	KC538230	KC538019	KC538799	KC538422	KC538614
Metriorrhynchini	*Wakarumbia linearis*	UPOL MD0134	Sulawesi	KC538233	KC538022	KC538802	KC538425	KC538617
Metriorrhynchini	*Wakarumbia mamasensis*	UPOL MD0155	Sulawesi	KC538240	KC538029	KC538809	KC538432	KC538624
Metriorrhynchini	*Wakarumbia mamasensis*	UPOL MD0157	Sulawesi	KC538242	KC538031	KC538811	KC538434	KC538626
Metriorrhynchini	*Wakarumbia monacha*	UPOL MD0111	Sulawesi	KC538223	KC538012	KC538795	KC538416	KC538609
Metriorrhynchini	*Wakarumbia montana*	UPOL MD0119	Sulawesi	KC538225	KC538014	HQ456961	HQ456984	HQ457006
Metriorrhynchini	*Wakarumbia nepeensis*	UPOL MD0129	Sulawesi	KC538229	KC538018	KC538798	KC538421	KC538613
Metriorrhynchini	*Wakarumbia nepeensis*	UPOL MD0135	Sulawesi	KC538234	KC538023	KC538803	KC538426	KC538618
Metriorrhynchini	*Wakarumbia pendolensis*	UPOL MD0109	Sulawesi	KC538222	KC538011	KC538794	KC538415	KC538608
Metriorrhynchini	*Wakarumbia pendolensis*	UPOL MD0143	Sulawesi	KC538238	KC538027	KC538807	KC538430	KC538622
Metriorrhynchini	*Wakarumbia petri*	UPOL MD0118	Sulawesi	KC538224	KC538013	HQ456960	HQ456983	HQ457005
Metriorrhynchini	*Wakarumbia* sp.	UPOL MD0126	Sulawesi	KC538227	KC538016	KC538797	KC538419	KC538611
Metriorrhynchini	*Wakarumbia* sp.	UPOL MD0132	Sulawesi	KC538231	KC538020	KC538800	KC538423	KC538615
Metriorrhynchini	*Xylobanus basivittatus*	UPOL 000222	Japan	–	–	–	–	KF652128
Metriorrhynchini	*Xylobanus basivittatus*	UPOL 000223	Japan	–	–	–	–	KF652129
Metriorrhynchini	*Xylobanus basivittatus*	UPOL VK0075	Japan	–	–	KF652135	KF652115	KF652123
Metriorrhynchini	*Xylobanus basivittatus*	UPOL 000221	Japan	KC538179	–	KC538681	KC538296	KC538487
Metriorrhynchini	*Xylobanus kundratai*	UPOL MD0029	Sulawesi	KC538204	KC537993	–	HQ456972	HQ456994
Metriorrhynchini	*Xylobanus kundratai*	UPOL MD0036	Sulawesi	KC538208	KC537997	–	HQ456973	HQ456995
Metriorrhynchini	*Xylobanus* sp.	UPOL 000071	Borneo	KC538144	KC537934	KC538648	KC538261	KC538453
Metriorrhynchini	*Xylobanus* sp.	UPOL 000120	Laos	KC538155	KC537946	KC538659	KC538273	KC538465
Metriorrhynchini	*Xylobanus* sp.	UPOL 000132	Sumatra	KC538160	KC537951	KC538663	HQ456987	HQ457009
Metriorrhynchini	*Xylobanus* sp.	UPOL 000152	Laos	KC538162	KC537953	KC538665	KC538279	KC538471
Metriorrhynchini	*Xylobanus* sp.	UPOL 000153	Laos	KC538163	KC537954	KC538666	KC538280	KC538472
Metriorrhynchini	*Xylobanus* sp.	UPOL 000154	Laos	KC538164	KC537955	–	KC538281	–
Metriorrhynchini	*Xylobanus* sp.	UPOL 000184	Borneo	KC538169	KC537959	KC538670	KC538286	KC538477
Metriorrhynchini	*Xylobanus* sp.	UPOL 000224	Japan	KC538180	KC537969	KC538682	KC538297	KC538488
Metriorrhynchini	*Xylobanus* sp.	UPOL 000262	Borneo	–	KC537972	KC538685	KC538300	KC538491

Metriorrhynchini	*Xylobanus* sp.	UPOL 000274	Borneo	KC538183	KC537973	KC538686	KC538301	KC538492
Metriorrhynchini	*Xylobanus* sp.	UPOL 000315	Sumatra	KC538189	KC537979	KC538692	KC538307	KC538498
Metriorrhynchini	*Xylobanus* sp.	UPOL 000379	Palawan	KC538199	–	KC538705	KC538317	KC538508
Metriorrhynchini	*Xylobanus* sp.	UPOL 000402	Palawan	KC538200	–	KC538708	KC538322	KC538513
Metriorrhynchini	*Xylobanus* sp.	UPOL A00018	Taiwan	KC538033	KC537825	HQ456946	HQ456964	HQ456988
Metriorrhynchini	*Xylobanus* sp.	UPOL A00053	Palawan	KC538067	KC537859	KC538737	KC538355	KC538547
Metriorrhynchini	*Xylobanus* sp.	UPOL A00054	Palawan	KC538068	–	KC538738	–	KC538548
Metriorrhynchini	*Xylobanus* sp.	UPOL A00074	Philippines	KC538085	KC537876	KC538750	–	–
Metriorrhynchini	*Xylobanus* sp.	UPOL A00076	Philippines	KC538087	KC537878	KC538752	KC538373	KC538565
Metriorrhynchini	*Xylobanus* sp.	UPOL A00091	Cameroon	KC538102	KC537893	–	KC538387	KC538578
Metriorrhynchini	*Xylobanus* sp.	UPOL A00094	Cameroon	KC538105	KC537896	KC538768	KC538390	KC538581
Metriorrhynchini	*Xylobanus* sp.	UPOL A00095	Cameroon	KC538106	KC537897	KC538769	–	KC538582
Metriorrhynchini	*Xylobanus* sp.	UPOL A00096	Cameroon	KC538107	KC537898	KC538770	–	KC538583
Metriorrhynchini	*Xylobanus* sp.	UPOL A00097	Cameroon	KC538108	KC537899	KC538771	KC538391	KC538584
Metriorrhynchini	*Xylobanus* sp.	UPOL A00098	Cameroon	KC538109	KC537900	KC538772	KC538392	KC538585
Metriorrhynchini	*Xylobanus* sp.	UPOL A00104	Cameroon	KC538115	KC537905	KC538775	–	KC538589
Metriorrhynchini	*Xylometanoeus japonicus*	UPOL VK0038	Japan	–	–	–	KF652116	KF652124
Metriorrhynchini	*Xylometanoeus japonicus*	UPOL VK0039	Japan	–	–	–	KF652117	KF652125
Metriorrhynchini	*Xylometanoeus japonicus*	UPOL VK0090	Japan	–	–	–	KF652118	KF652126
Metriorrhynchini	*Xylometanoeus japonicus*	UPOL VK0093	Japan	–	–	–	KF652119	KF652127
Platerodini	*Plateros* sp.	UPOL A00470	Malaysia	KT752153	KT752311	KT751980	KT751663	KT751825
Platerodini	*Plateros* sp.	UPOL A00471	Malaysia	KT752154	KT752312	KT751981	KT751664	KT751826
Platerodini	*Plateros* sp.	UPOL A00472	Malaysia	KT752155	KT752313	KT751982	KT751665	–
Platerodini	*Plateros* sp.	UPOL A00473	Malaysia	–	KT752314	KT751983	KT751666	KT751827
Platerodini	*Plateros* sp.	UPOL A00474	Malaysia	KT752156	KT752315	KT751984	KT751667	–
Platerodini	*Plateros* sp.	UPOL A00475	Malaysia	KT752157	KT752316	KT751985	–	KT751828
Platerodini	*Plateros* sp.	UPOL A00476	Malaysia	KT752158	KT752317	KT751986	KT751668	–
Platerodini	*Plateros* sp.	UPOL A00478	Vietnam	KT752160	KT752319	KT751988	KT751670	KT751830
Platerodini	*Plateros* sp.	UPOL A00479	Vietnam	KT752161	KT752320	KT751989	KT751671	KT751831
Platerodini	*Plateros* sp.	UPOL A00480	Laos	KT752162	KT752321	KT751990	KT751672	KT751832
Platerodini	*Plateros* sp.	UPOL A00481	Laos	KT752163	KT752322	KT751991	–	KT751833
Platerodini	*Plateros* sp.	UPOL A00482	Laos	–	KT752323	KT751992	KT751673	KT751834
Platerodini	*Plateros* sp.	UPOL A00483	Laos	KT752164	–	KT751993	KT751674	KT751835
Platerodini	*Plateros* sp.	UPOL A00484	Thailand	KT752165	KT752324	KT751994	KT751675	KT751836
Platerodini	*Plateros* sp.	UPOL A00485	India	KT752166	KT752325	KT751995	KT751676	KT751837
Platerodini	*Plateros* sp.	UPOL A00486	India	–	KT752326	KT751996	KT751677	KT751838
Platerodini	*Plateros* sp.	UPOL A00487	India	KT752167	KT752327	KT751997	KT751678	KT751839
Platerodini	*Plateros* sp.	UPOL A00488	Taiwan	–	KT752328	KT751998	KT751679	KT751840
Platerodini	*Plateros* sp.	UPOL A00489	Taiwan	KT752168	KT752329	KT751999	KT751680	KT751841
Platerodini	*Plateros* sp.	UPOL A00490	Taiwan	KT752169	KT752330	KT752000	KT751681	KT751842
Platerodini	*Plateros* sp.	UPOL A00491	Japan	KT752170	KT752331	KT752001	KT751682	KT751843
Platerodini	*Plateros* sp.	UPOL A00492	Japan	KT752171	KT752332	KT752002	KT751683	KT751844
Platerodini	*Plateros* sp.	UPOL A00493	Kenya	KT752172	KT752333	KT752003	KT751684	KT751845
Platerodini	*Plateros* sp.	UPOL A00494	Cameroon	KT752173	KT752334	KT752004	KT751685	KT751846
Platerodini	*Plateros* sp.	UPOL A00495	Cameroon	KT752174	KT752335	KT752005	KT751686	KT751847
Platerodini	*Plateros* sp.	UPOL A00496	Cameroon	KT752175	KT752336	KT752006	KT751687	–
Platerodini	*Plateros* sp.	UPOL A00497	Cameroon	KT752176	KT752337	KT752007	KT751688	–
Platerodini	*Plateros* sp.	UPOL A00498	Cameroon	KT752177	KT752338	KT752008	KT751689	KT751848
Platerodini	*Plateros* sp.	UPOL A00499	Zambia	KT752178	KT752339	KT752009	KT751690	KT751849
Platerodini	*Plateros* sp.	UPOL A00500	Zambia	KT752179	KT752340	KT752010	KT751691	KT751850
Platerodini	*Plateros* sp.	UPOL A00501	RSA	KT752180	KT752341	KT752011	KT751692	KT751851
Platerodini	*Plateros* sp.	UPOL A00502	Cameroon	KT752181	KT752342	KT752012	KT751693	KT751852
Platerodini	*Plateros* sp.	UPOL A00503	Cameroon	KT752182	KT752343	KT752013	KT751694	KT751853
Platerodini	*Plateros* sp.	UPOL A00504	Cameroon	KT752183	KT752344	KT752014	KT751695	KT751854
Platerodini	*Plateros* sp.	UPOL A00505	Canada	KT752184	KT752345	KT752015	KT751696	KT751855
Platerodini	*Plateros* sp.	UPOL A00507	Canada	KT752185	KT752346	KT752016	KT751697	KT751856
Platerodini	*Plateros* sp.	UPOL A00509	Argentina	KT752186	KT752347	KT752017	KT751698	KT751857
Platerodini	*Plateros* sp.	UPOL A00510	Argentina	KT752187	KT752348	KT752018	KT751699	KT751858
Platerodini	*Plateros* sp.	UPOL A00511	Costa Rica	KT752188	KT752349	KT752019	KT751700	KT751859
Platerodini	*Plateros* sp.	UPOL A00512	Costa Rica	KT752189	KT752350	KT752020	KT751701	KT751860
Platerodini	*Plateros* sp.	UPOL A00513	Panama	KT752190	KT752351	KT752021	KT751702	KT751861
Platerodini	*Plateros* sp.	UPOL A00555	Thailand	KT752221	KT752386	KT752053	KT751732	KT751890
Platerodini	*Plateros* sp.	UPOL A00579	Nicaragua	KT752245	KT752409	KT752077	KT751754	KT751911
Platerodini	*Plateros* sp.	UPOL A00580	USA	KT752246	KT752410	KT752078	KT751755	KT751912
Platerodini	*Plateros* sp.	UPOL A00619	Ecuador	–	KT752448	KT752117	KT751791	KT751950
Platerodini	*Plateros* sp.	UPOL A00632	Ecuador	KT752290	KT752455	–	KT751802	KT751961
Platerodini	*Plateros* sp.	UPOL A00634	Ecuador	KT752292	KT752457	KT752130	KT751804	KT751963
Platerodini	*Plateros* sp.	UPOL A00635	Nicaragua	KT752293	KT752458	KT752131	KT751805	KT751964
Platerodini	*Plateros* sp.	UPOL A00639	Ecuador	–	–	KT752135	KT751808	KT751966
Platerodini	*Plateros* sp.	UPOL A00643	Ecuador	–	KT752461	KT752138	KT751811	KT751969
Platerodini	*Plateros* sp.	UPOL A00646	Ecuador	KT752297	–	KT752140	KT751813	KT751971
Platerodini	*Plateros* sp.	UPOL ZL2012	Japan	–	–	EF143222	EF143237	EF143251
Platerodini	*Plateros* sp.	UPOL ZL2018	Japan	–	–	EF143227	EF143241	EF143255
Platerodini	*Plateros* sp.	UPOL 000031	Borneo	DQ181059	DQ181133	DQ180985	DQ181207	DQ181361
Platerodini	*Plateros* sp.	UPOL 000243	Borneo	DQ181065	DQ181139	DQ180991	DQ181213	DQ181367
Platerodini	*Plateros* sp.	UPOL 000303	Sumatra	DQ181067	DQ181141	DQ180993	DQ181215	DQ181369
Platerodini	*Plateros* sp.	UPOL 000L13	Borneo	DQ181044	DQ181118	DQ180970	DQ181192	DQ181346
Platerodini	*Plateros* sp.	UPOL 001031	USA	DQ181109	DQ181183	DQ181035	DQ181257	DQ181411
Platerodini	*Plateros* sp.	UPOL RK0377	French Guyana	KF625685	KF626271	KF625975	KF625384	–
Platerodrilini	*Horakiella emasensis*	UPOL 001043	Borneo	DQ181110	DQ181184	DQ181036	DQ181258	DQ181412
Platerodrilini	*Macrolibnetis depressus*	UPOL 000515	Malaysia	–	–	–	FJ390411	FJ390413
Platerodrilini	*Macrolibnetis depressus*	UPOL 000L21	Malaysia	DQ181050	DQ181124	DQ180976	DQ181198	DQ181352
Platerodrilini	*Macrolibnetis depressus*	UPOL VP0050	Malaysia	KF802504	KF802506	KF802467	–	KF802538
Platerodrilini	*Pendola* sp.	UPOL 000M45	Java	DQ181058	DQ181132	DQ180984	DQ181206	DQ181360
Platerodrilini	*Platerodrilini* gen. sp.	UPOL VP0009	Malaysia	KF802497	KF802507	KF802457	KF802527	KF802539
Platerodrilini	*Platerodrilini* gen. sp.	UPOL VP0010	Sumatra	KF802498	KF802508	KF802480	KF802533	KF802542
Platerodrilini	*Platerodrilini* gen. sp.	UPOL VP0012	Malaysia	KF802499	KF802509	KF802458	KF802528	KF802541
Platerodrilini	*Platerodrilini* gen. sp.	UPOL VP0013	Malaysia	KF802500	KF802510	–	KF802529	KF802540
Platerodrilini	*Platerodrilini* gen. sp.	UPOL VP0030	India	KF802493	KF802511	KF802462	KF802530	KF802543
Platerodrilini	*Platerodrilini* gen. sp.	UPOL VP0031	India	KF802495	KF802512	KF802463	KF802531	–
Platerodrilini	*Platerodrilini* gen. sp.	UPOL VP0034	India	KF802496	KF802513	KF802464	KF802532	KF802544
Platerodrilini	*Platerodrilus angustatus*	UPOL 001388	Sumatra	KF625713	KF626299	KF626001	KF625406	–
Platerodrilini	*Platerodrilus atricolor*	UPOL 001384	Malaysia	KF625710	KF626296	–	–	–
Platerodrilini	*Platerodrilus corporaali*	UPOL 001373	Sumatra	KF625702	KF626288	KF625991	KF625400	–
Platerodrilini	*Platerodrilus curtus*	UPOL 001380	Philippines	KF625708	KF626294	KF625997	KF625404	–
Platerodrilini	*Platerodrilus curtus*	UPOL 001381	Philippines	KF625781	KF626365	KF626073	–	–
Platerodrilini	*Platerodrilus curtus*	UPOL 001383	Philippines	KF625782	KF626366	KF626074	KF625474	–
Platerodrilini	*Platerodrilus foliaceus*	UPOL 000588	Borneo	DQ181091	DQ181165	DQ181017	DQ181239	DQ181393
Platerodrilini	*Platerodrilus foliaceus*	UPOL 000589	Borneo	–	–	EF143214	EF143229	EF143243
Platerodrilini	*Platerodrilus ijenensis*	UPOL 000586	Java	DQ181089	DQ181163	DQ181015	DQ181237	DQ181391
Platerodrilini	*Platerodrilus luteus*	UPOL 001379	Sumatra	KF625707	KF626293	KF625996	KF625403	–

Platerodrilini	*Platerodrilus major*	UPOL 001387	Sumatra	KF625712	KF626298	KF626000	–	–
Platerodrilini	*Platerodrilus maninjauensis*	UPOL 001374	Sumatra	KF625703	KF626289	KF625992	KF625401	–
Platerodrilini	*Platerodrilus maninjauensis*	UPOL 001377	Sumatra	KF625705	KF626291	KF625994	–	–
Platerodrilini	*Platerodrilus maninjauensis*	UPOL VP2303	Sumatra	KF802485	KF802514	KF802470	–	KF802545
Platerodrilini	*Platerodrilus maninjauensis*	UPOL VP2306	Sumatra	KF802487	KF802515	KF802473	–	KF802546
Platerodrilini	*Platerodrilus maninjauensis*	UPOL VP2307	Sumatra	KF802488	KF802516	KF802474	–	KF802547
Platerodrilini	*Platerodrilus montanus*	UPOL 001371	Sumatra	KF625700	KF626286	KF625989	KF625398	–
Platerodrilini	*Platerodrilus montanus*	UPOL VP2308	Sumatra	KF802489	KF802517	KF802475	–	KF802549
Platerodrilini	*Platerodrilus ngi*	UPOL VP0021	Singapore	KF802481	KF802520	KF802461	–	–
Platerodrilini	*Platerodrilus palawanensis*	UPOL 000371	Philippines	–	–	–	–	KF802552
Platerodrilini	*Platerodrilus ranauensis*	UPOL 000587	Sumatra	DQ181090	DQ181164	DQ181016	DQ181238	DQ181392
Platerodrilini	*Platerodrilus robinsoni*	UPOL 001378	Sumatra	KF625706	KF626292	KF625995	–	–
Platerodrilini	*Platerodrilus sibayakensis*	UPOL 001372	Sumatra	KF625701	KF626287	KF625990	KF625399	–
Platerodrilini	*Platerodrilus sibayakensis*	UPOL 001389	Sumatra	KF625784	KF626367	–	KF625475	–
Platerodrilini	Platerodrilus sp.	UPOL 000L01	Borneo	DQ181037	DQ181111	DQ180963	DQ181185	DQ181339
Platerodrilini	*Platerodrilus* sp.	UPOL VP0014	Philippines	KF802482	KF802519	KF802459	–	KF802553
Platerodrilini	*Platerodrilus* sp.	UPOL VP0020	Malaysia	KF802501	–	KF802460	KF802535	KF802554
Platerodrilini	*Platerodrilus* sp.	UPOL VP0044	Borneo	KF802505	–	KF802465	–	KF802550
Platerodrilini	*Platerodrilus* sp.	UPOL VP0047	Sumatra	KF802502	–	KF802466	–	KF802555
Platerodrilini	*Platerodrilus* sp.	UPOL VP2301	Borneo	KF802483	KF802518	KF802468	–	KF802551
Platerodrilini	*Platerodrilus* sp.	UPOL VP2302	Malaysia	KF802484	KF802521	KF802469	–	KF802556
Platerodrilini	*Platerodrilus* sp.	UPOL VP2304	Thailand	KF802486	KF802522	KF802471	–	–
Platerodrilini	*Platerodrilus* sp.	UPOL VP2309	Malaysia	KF802490	KF802524	KF802476	–	KF802557
Platerodrilini	*Platerodrilus* sp.	UPOL VP2310	Malaysia	KF802491	KF802525	KF802477	KF802536	KF802558
Platerodrilini	*Platerodrilus* sp.	UPOL VP2311	Laos	KF802503	–	KF802478	–	KF802559
Platerodrilini	*Platerodrilus* sp.	UPOL VP2316	Philippines	KF802492	KF802526	KF802479	–	KF802560
Platerodrilini	*Platerodrilus* sp.	UPOL A00575	Malaysia	KT752241	KT752406	KT752073	KT751750	KT751907
Platerodrilini	*Platerodrilus* sp.	UPOL A00576	Malaysia	KT752242	KT752407	KT752074	KT751751	KT751908
Platerodrilini	*Platerodrilus strbai*	UPOL 000472	Borneo	–	–	–	KF802537	KF802561
Platerodrilini	*Platerodrilus talamauensis*	UPOL 001375	Sumatra	KF625780	KF626364	KF626072	KF625473	–
Platerodrilini	*Platerodrilus talamauensis*	UPOL 001376	Sumatra	KF625704	KF626290	KF625993	KF625402	–
Platerodrilini	*Platerodrilus tujuhensis*	UPOL 001385	Sumatra	KF625711	KF626297	KF625999	KF625405	–
Platerodrilini	*Platerodrilus tujuhensis*	UPOL VP2305	Sumatra	KF802494	KF802523	KF802472	–	KF802548
Slipinskiini	*Flagrax* sp.	UPOL A00561	RSA	KT752227	KT752392	KT752059	KT751737	KT751894
Slipinskiini	*Flagrax* sp.	UPOL A00562	Cameroon	KT752228	KT752393	KT752060	KT751738	KT751895
Slipinskiini	*Flagrax* sp.	UPOL A00563	Cameroon	KT752229	KT752394	KT752061	KT751739	KT751896
Slipinskiini	*Flagrax* sp.	UPOL A00564	RSA	KT752230	KT752395	KT752062	KT751740	KT751897
Slipinskiini	*Flagrax* sp.	UPOL A00565	RSA	KT752231	KT752396	KT752063	KT751741	KT751898
Slipinskiini	*Flagrax* sp.	UPOL A00566	RSA	KT752232	KT752397	KT752064	KT751742	KT751899
Slipinskiini	*Flagrax* sp.	UPOL 000L26	RSA	DQ181054	DQ181128	DQ180980	DQ181202	DQ181356
Taphini	*Protaphes* sp.	UPOL A00525	Laos	KT752195	KT752356	KT752025	KT751707	–
Taphini	*Protaphes* sp.	UPOL A00527	Sumatra	KT752197	KT752358	KT752026	KT751709	–
Taphini	*Protaphes* sp.	UPOL A00531	Malaysia	KT752201	KT752362	KT752030	KT751713	KT751868
Taphini	*Protaphes* sp.	UPOL A00535	Sumatra	KT752204	KT752366	KT752034	KT751717	KT751872
Taphini	*Protaphes* sp.	UPOL A00543	Malaysia	KT752212	KT752374	KT752041	KT751722	KT751878
Taphini	*Protaphes* sp.	UPOL A00544	Malaysia	KT752213	KT752375	KT752042	KT751723	KT751879
Taphini	*Protaphes* sp.	UPOL A00573	Laos	KT752239	KT752404	KT752071	KT751748	KT751905
Taphini	*Taphes brevicollis*	UPOL A00526	Laos	KT752196	KT752357	–	KT751708	KT751864
Taphini	*Taphes brevicollis*	UPOL A00528	Laos	KT752198	KT752359	KT752027	KT751710	KT751865
Taphini	*Taphes brevicollis*	UPOL A00536	Sumatra	KT752205	KT752367	KT752035	KT751718	KT751873
Taphini	*Taphes brevicollis*	UPOL A00538	Sumatra	KT752207	KT752369	–	KT751719	KT751875
Taphini	*Taphes brevicollis*	UPOL 000812	Laos	DQ181098	DQ181172	DQ181024	DQ181246	DQ181400
Taphini	*Taphes* sp.	UPOL A00529	India	KT752199	KT752360	KT752028	KT751711	KT751866
Taphini	*Taphes* sp.	UPOL A00537	China	KT752206	KT752368	KT752036	–	KT751874
Taphini	*Taphes* sp.	UPOL A00539	Laos	KT752208	KT752370	KT752037	–	–
Thonalmini	*Thonalmus hubbardi*	UPOL 000595	Montserrat	DQ181094	DQ181168	DQ181020	DQ181242	DQ181396
Thonalmini	*Thonalmus sinuaticostis*	UPOL 000594	Montserrat	DQ181093	DQ181167	DQ181019	DQ181241	DQ181395
Thonalmini	*Thonalmus* sp.	UPOL A00592	Cuba	KT752258	KT752422	KT752090	KT751767	KT751924
Thonalmini	*Thonalmus* sp.	UPOL A00593	Cuba	KT752259	KT752423	KT752091	KT751768	KT751925
Thonalmini	*Thonalmus* sp.	UPOL A00595	Dominican Republic	KT752261	KT752425	KT752093	KT751769	KT751927

Table S2. Tribe-level taxa not included in the molecular analysis.

Tribe	Number of spp.	Distribution
Melanerotini Kazantsev, 2010	1	Pacific islands
Proterotaphini Kazantsev, 2012	1	Australia
Vikhreviini Kazantsev, 2013	1	Malay Peninsula
Mimolibnetinae Kazantsev, 2013	1	Afrotropical region
Dominopterini Kazantsev, 2013	1	Antilles
Electropterini Kazantsev, 2013	3	Antilles
Miniduliticolini Kazantsev, 2002	1	Borneo

Kazantsev SV (2002) A generic review of Duliticolinae, new subfamily (Coleoptera: Lycidae). Elytron, 16: 5–21.

Kazantsev SV (2009) New taxa of Lycidae from Samoa, Fiji and Tonga (Coleoptera: Lycidae). Russian Entomological Journal, 18: 191–195.

Kazantsev SV (2012) A review of Erotinae and Dictyopterinae (Coleoptera: Lycidae), with description of new taxa and a note on biogeography of the subfamilies. Russian Entomological Journal, 21: 395–414.

Kazantsev SV (2013) New and little known taxa of neotenic Lycidae (Coleoptera), with discussion of their phylogeny. Russian Entomological Journal, 22: 9–31.

Table S3. Primers used for PCR amplification.

Fragment	Code	Sequence (5’ > 3’)
18S rRNA	b5.0	TAA CCG CAA CAA CTT TAA T
	ai	CCT GAG AAA CGG CTA CCA CAT C
	bi	GAG TCT CGT TCG TTA TCG GA
	a2.0	ATG GTT GCA AAG CTG AAA C
28S rRNA	ff	TTA CAC ACT CCT TAG CGG AT
	dd	GGG ACC CGT CTT GAA ACA C
rrnL	16a	CGC CTG TTT AAC AAA AAC AT
mtDNA	ND1A	GGT CCC TTA CGA ATT TGA ATA TAT CCT
	ND1-2	ATC AAA AGG AGC TCG ATT AGT TTC
cox1	JerryM	CAA CAY YTA TTT TGR TTY TTT GG
mtDNA	MarcyM	TAR TTC RTA TGW RCA ATA YCA YTG RTG
	JerryN	CAA CAY YTA TTY TGA TTY TTY GG
	MarcyN	TTC RTA WGT TCA RTA TCA TTG RTG
nad5	OF1	CCT ACT CCT GTT TCT GCT TTA GTT CAT TC
mtDNA	R6	GAA ACG AAA AAT CGT ATT TAA TTT CGA CT
	R2M	AAT TGA ASC CAA AAA GAG GTA TAT CAC TG

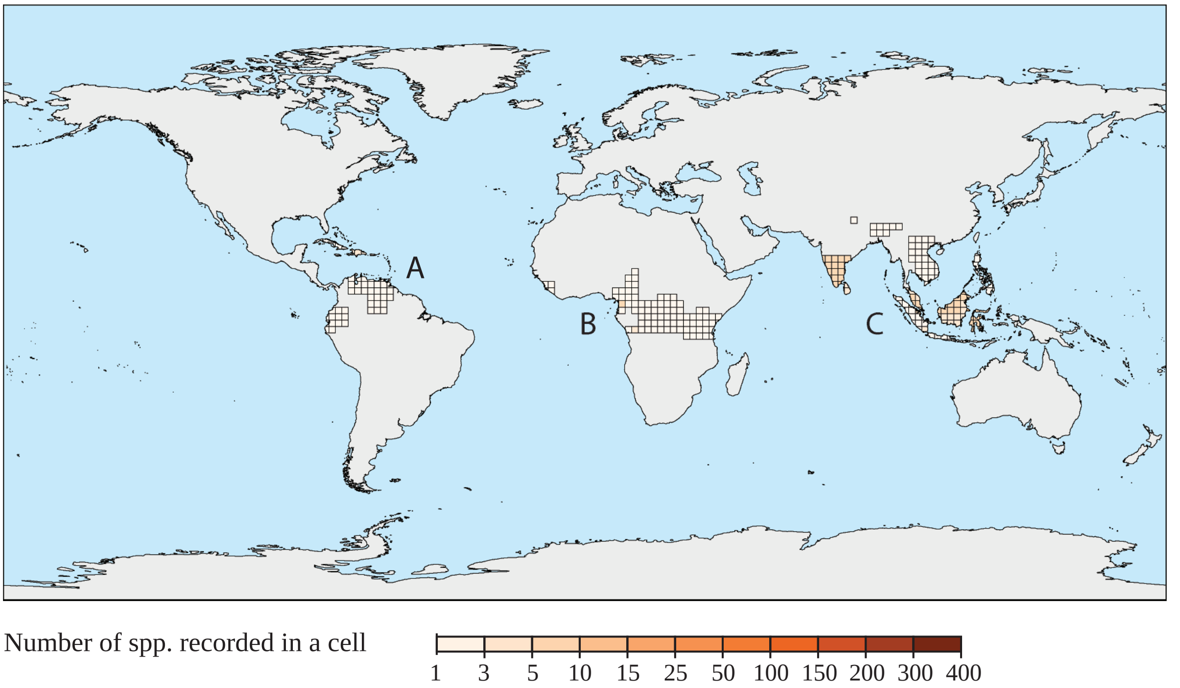


Figure S1. Distribution and species diversity of the tribes Leptolycini, Dexorini and Lyropaeini. A Leptolycini, B Dexorini, C Lyropaeini.

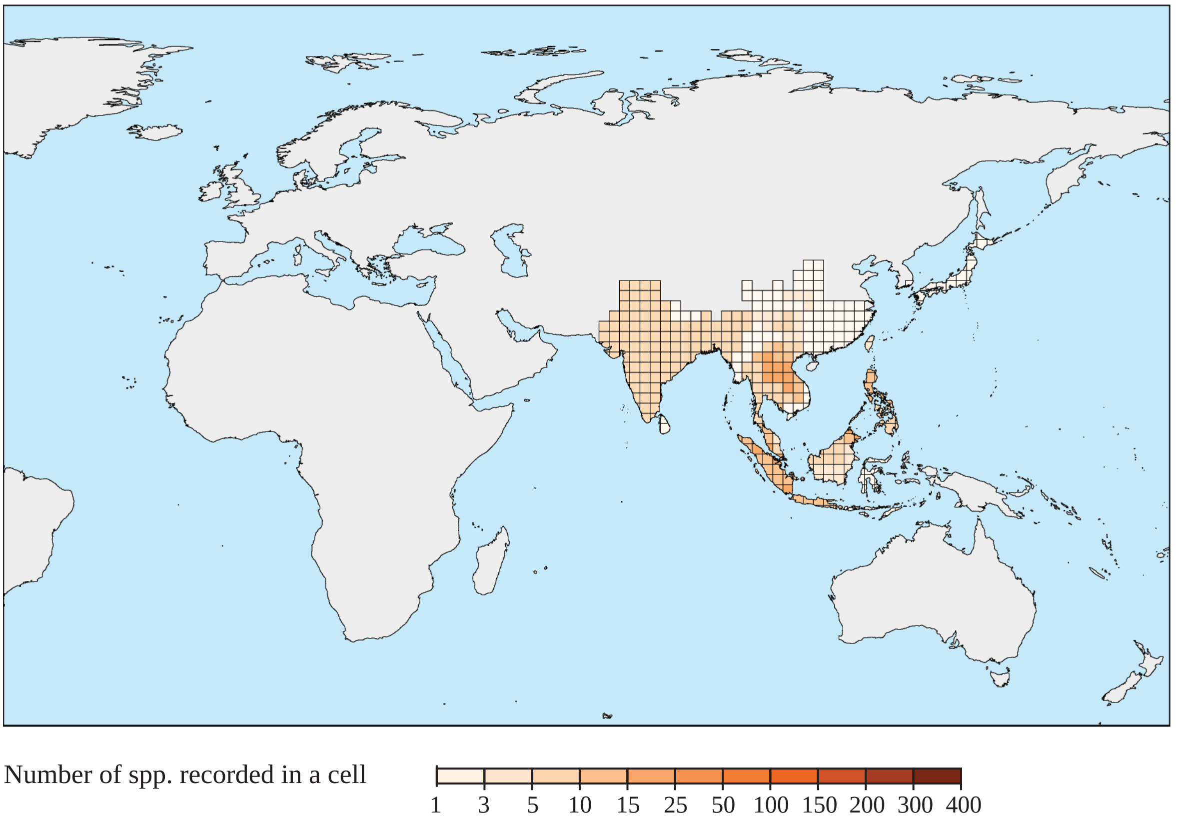


Figure S2. Distribution and species diversity of the subfamily Libnetinae.

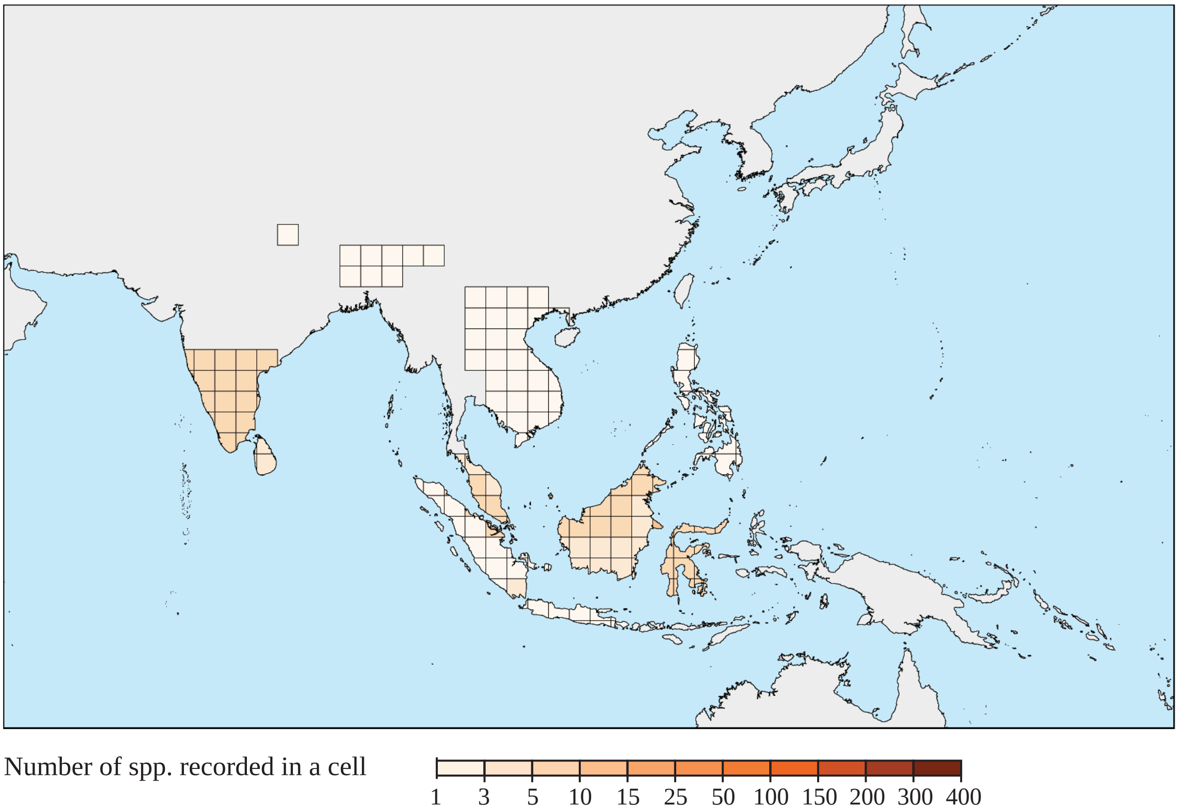


Figure S3. Distribution and species diversity of the tribe Lyropaeini.

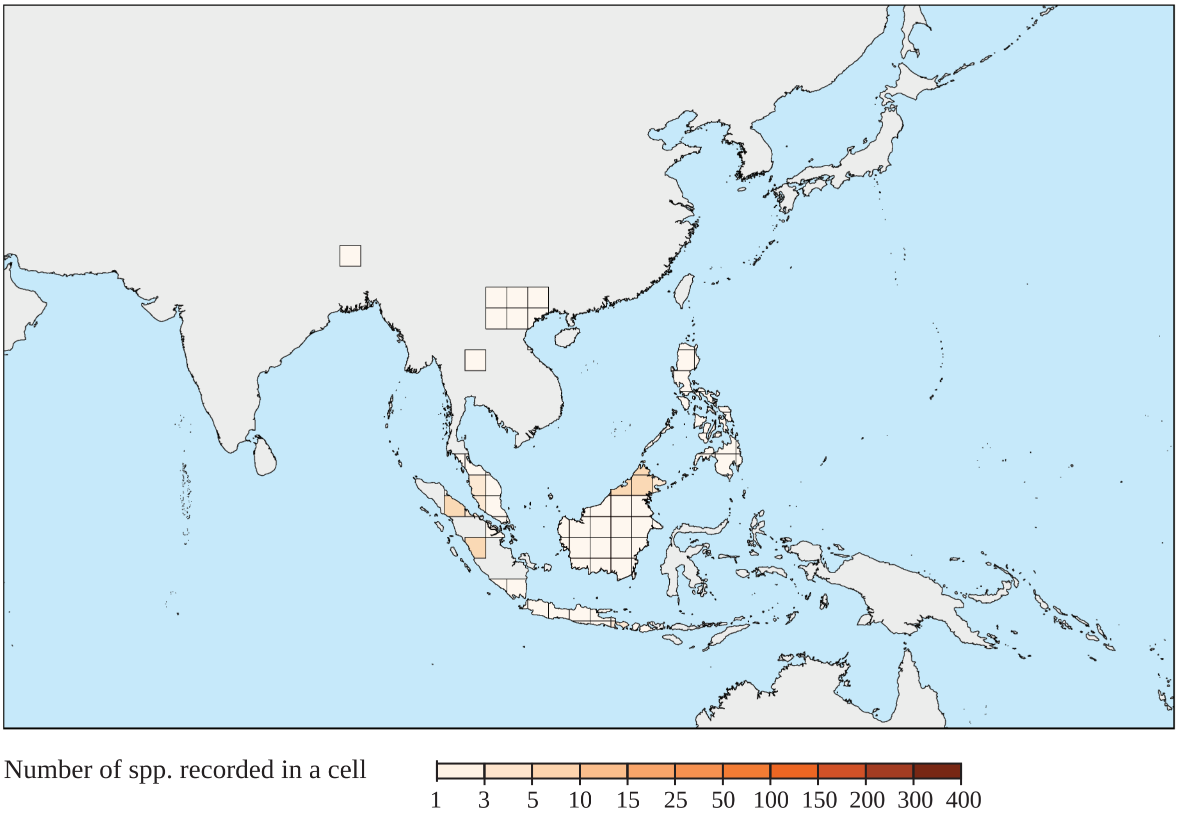


Figure S4. Distribution and species diversity of the tribe Platerodrilini.

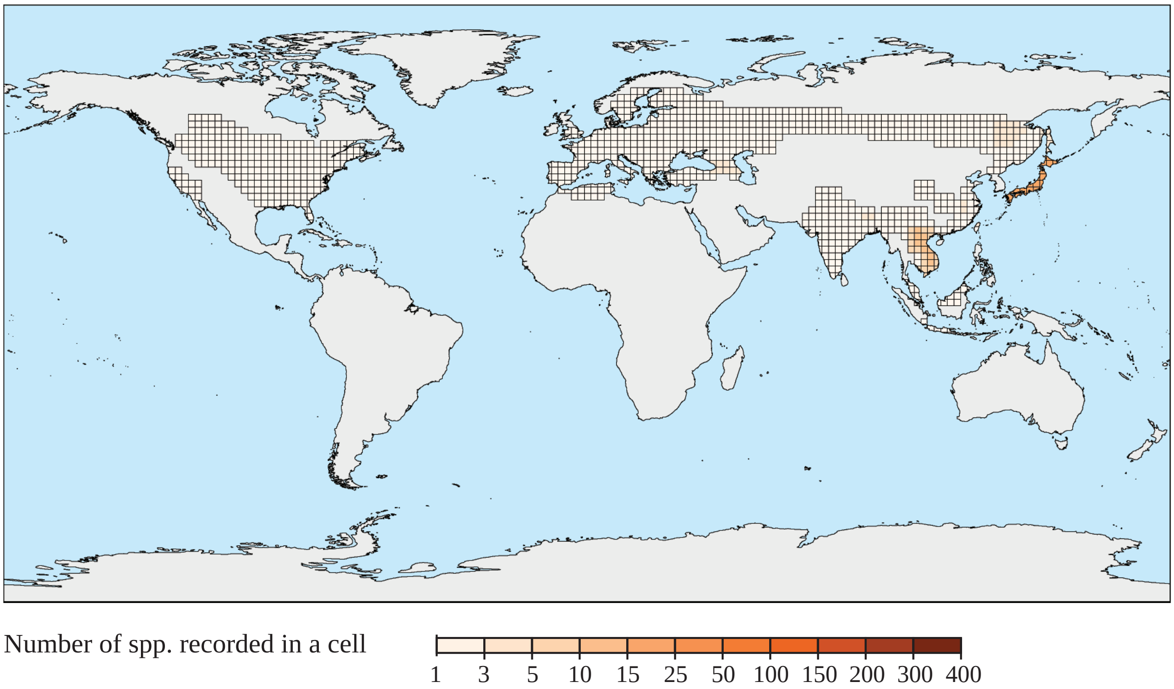


Figure S5. Distribution and species diversity of the tribe Dictyopterini.

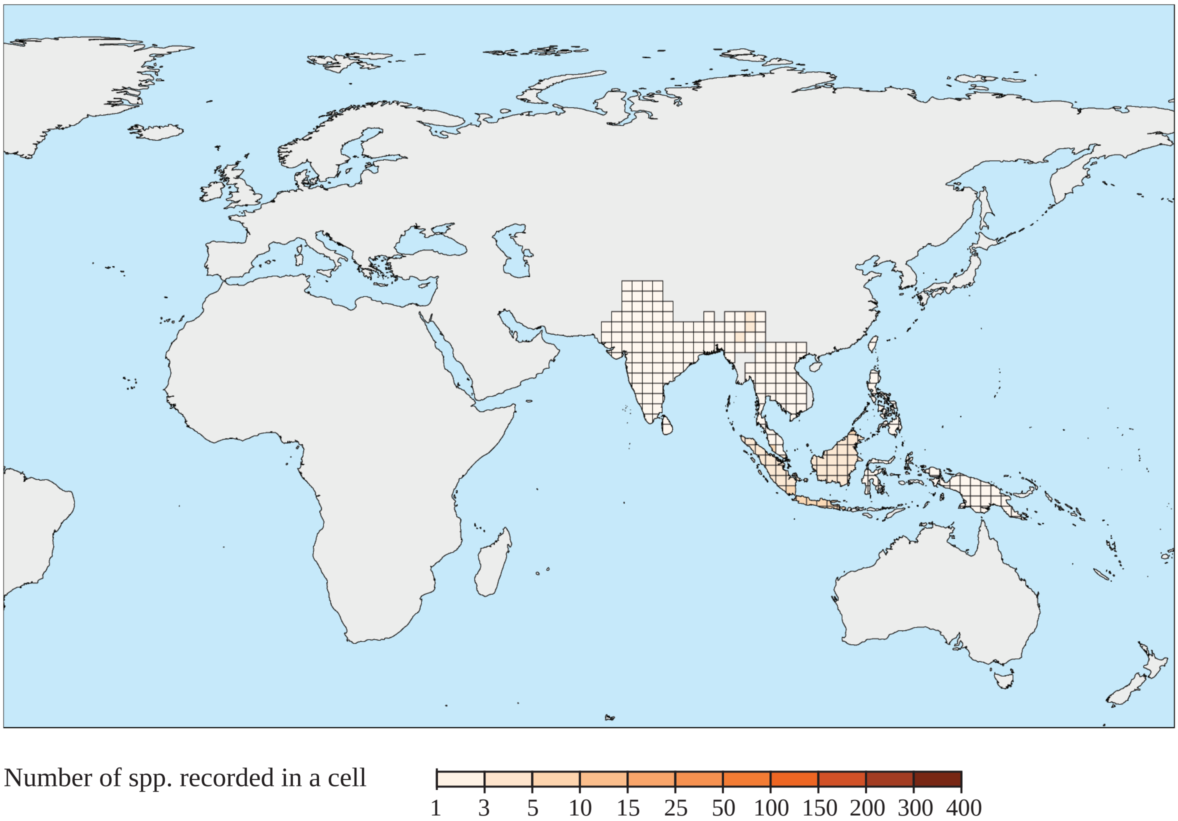


Figure S6. Distribution and species diversity of the tribe Taphini.

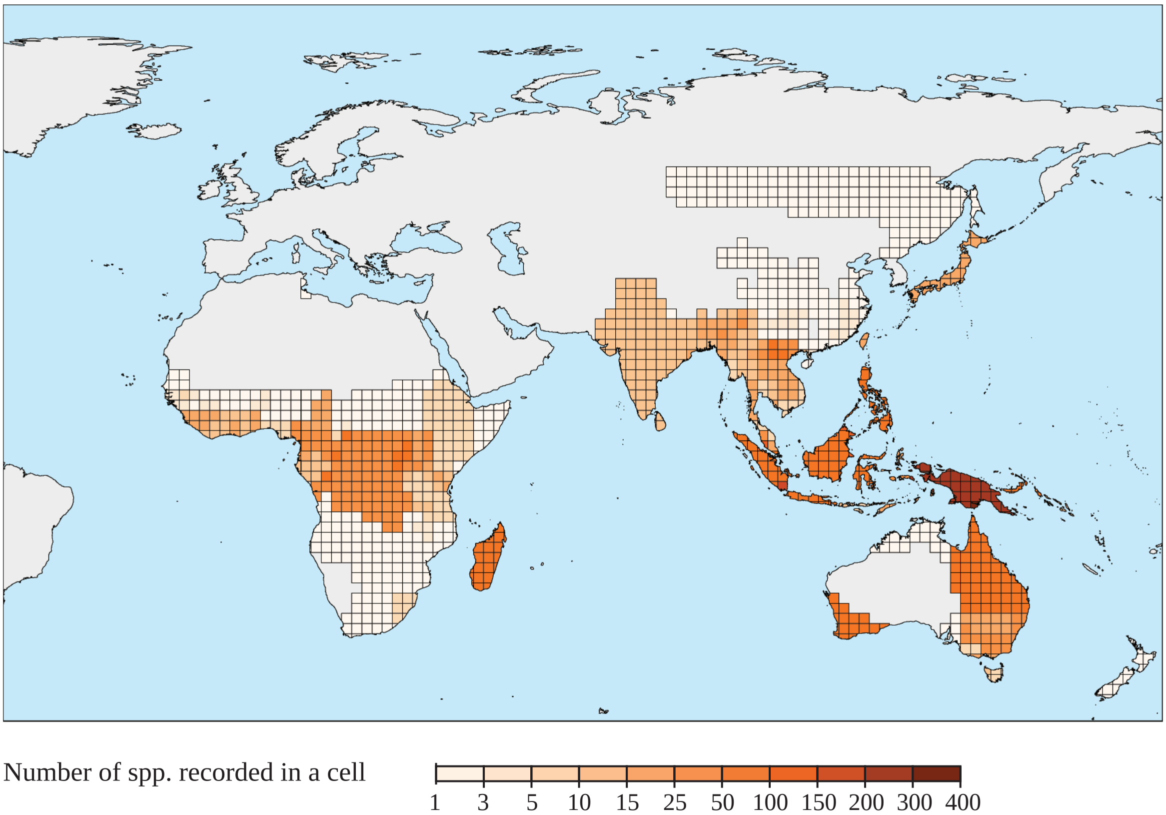


Figure S7. Distribution and species diversity of the tribe Metriorrhynchini.

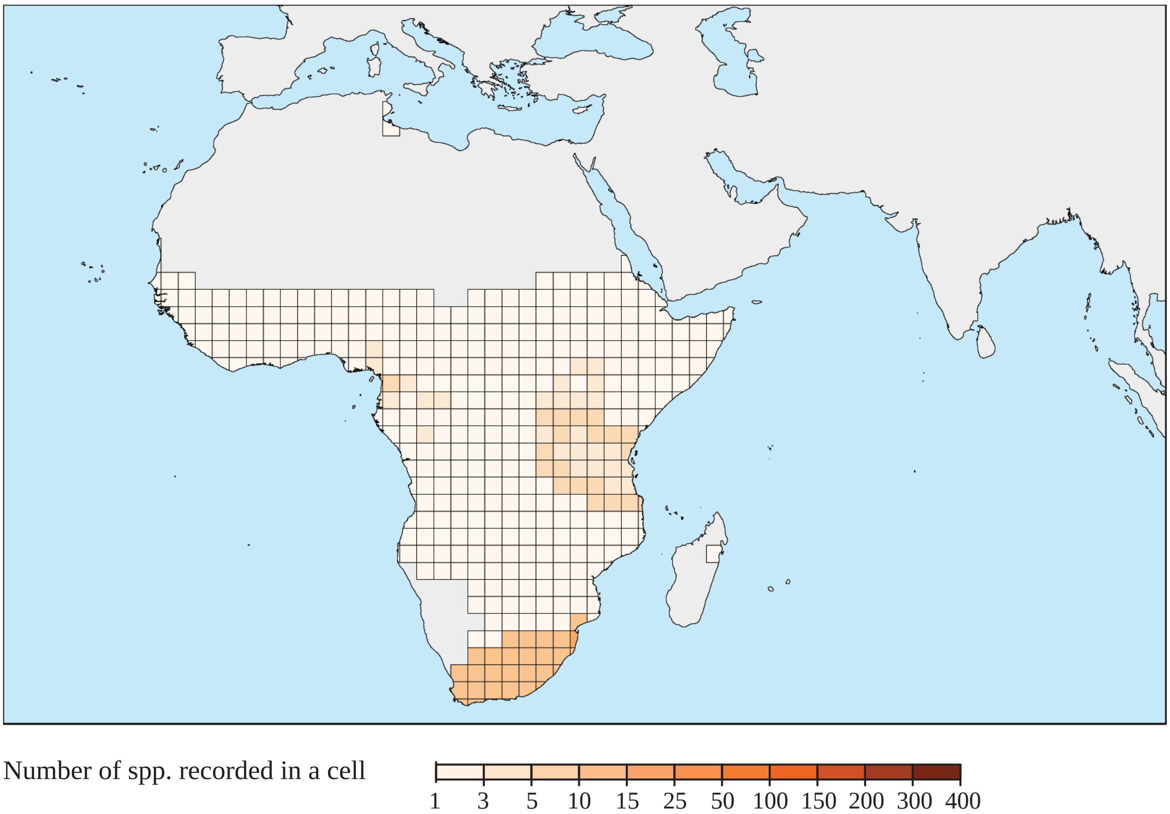


Figure S8. Distribution and species diversity of the tribe Slipinskiini.

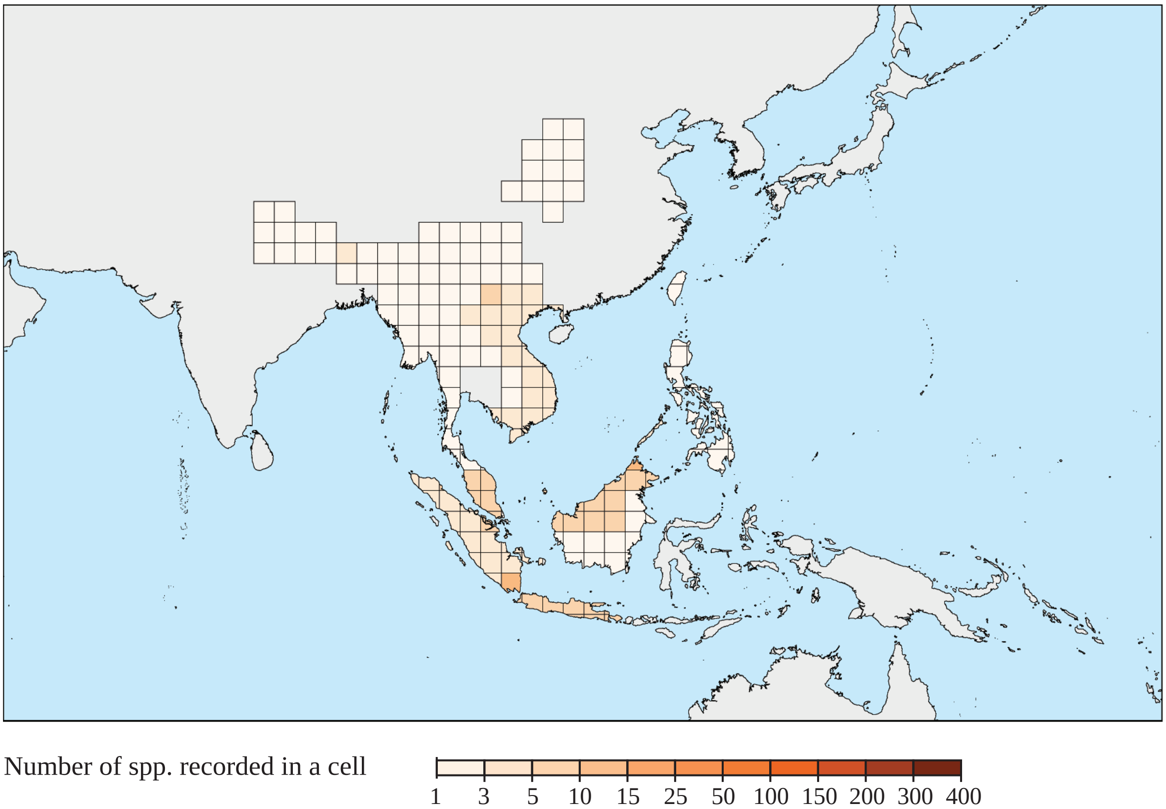


Figure S9. Distribution and species diversity of the tribe Dihammatini.

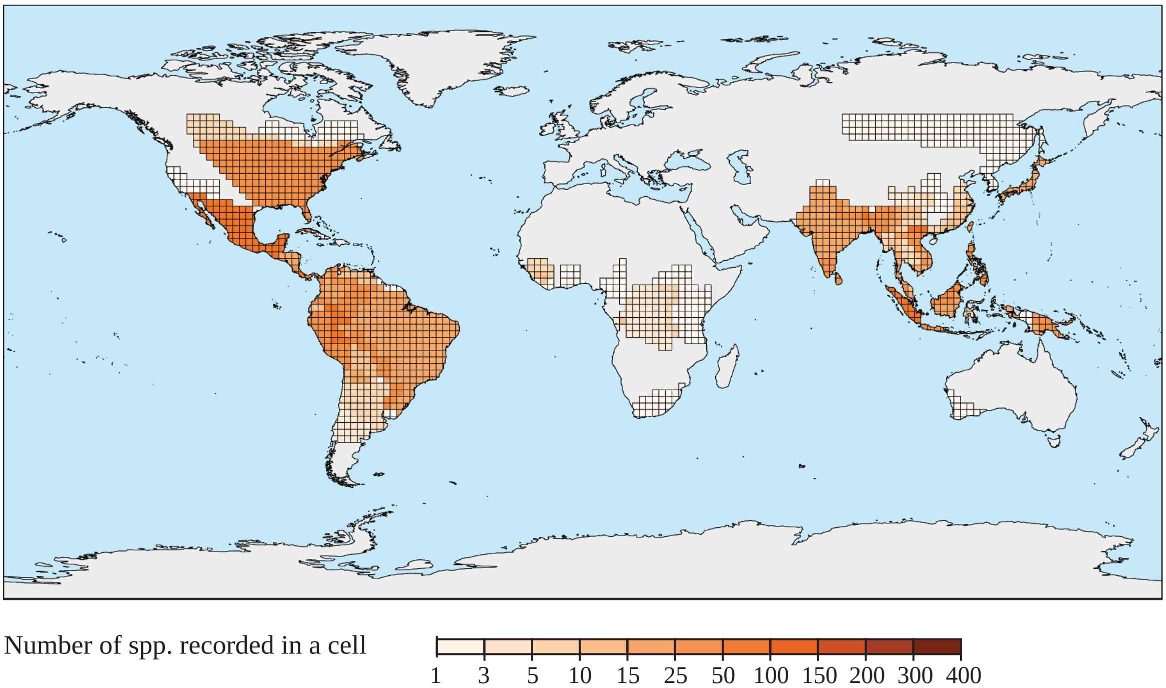


Figure S10. Distribution and species diversity of the tribe Platerodini.

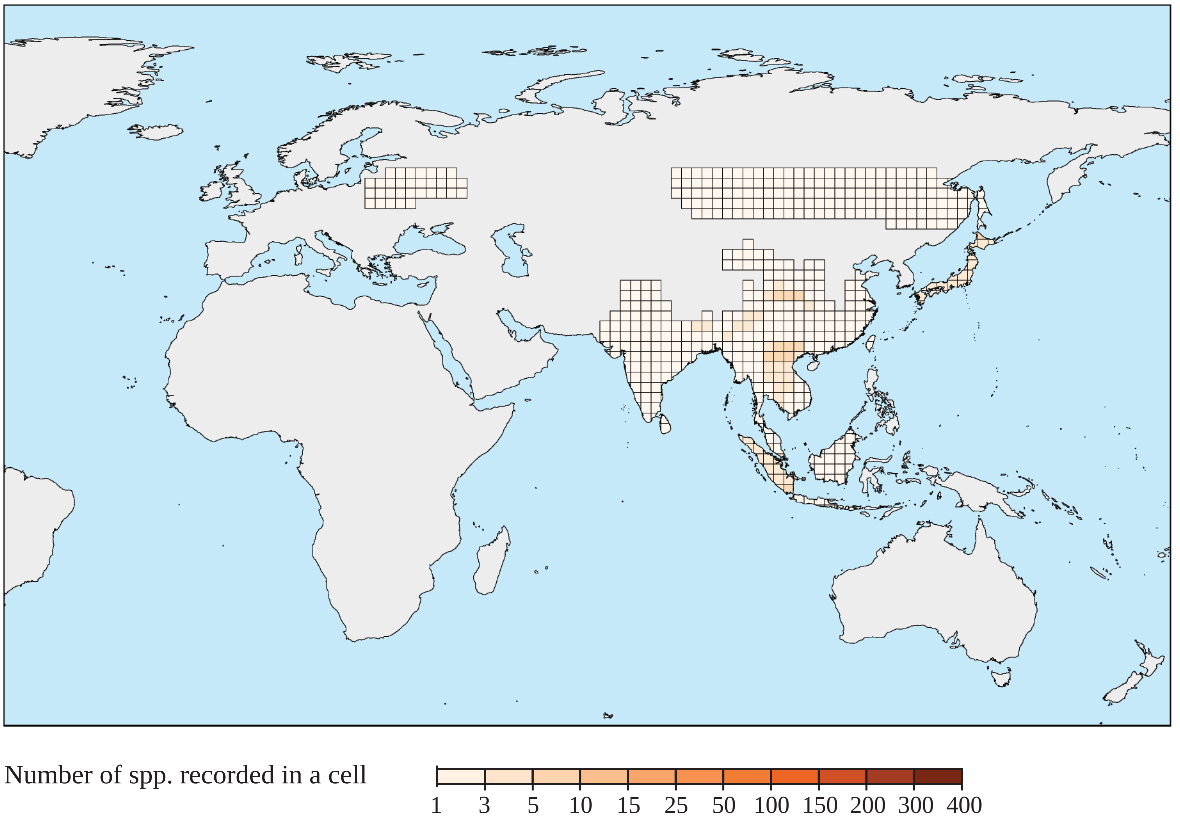


Figure S11. Distribution and species diversity of the tribe Conderini.

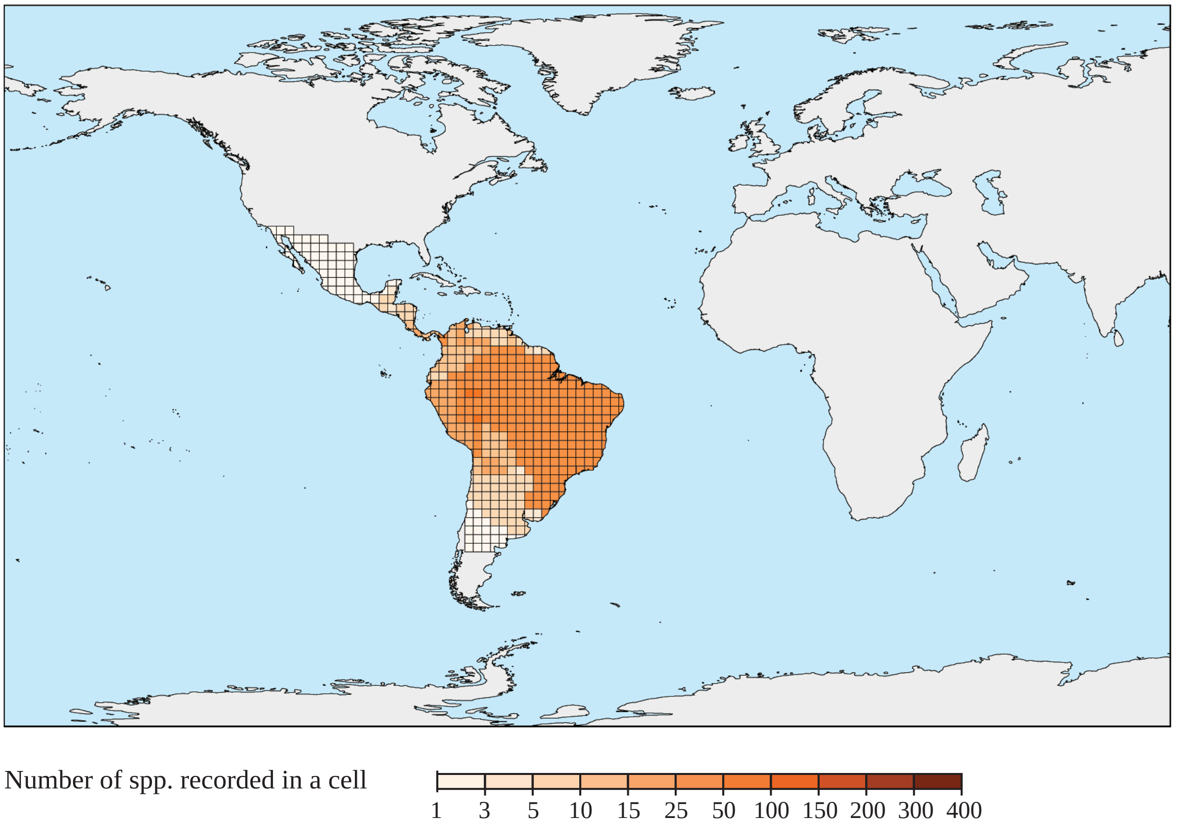


Figure S12. Distribution and species diversity of the tribe Eurhacini.

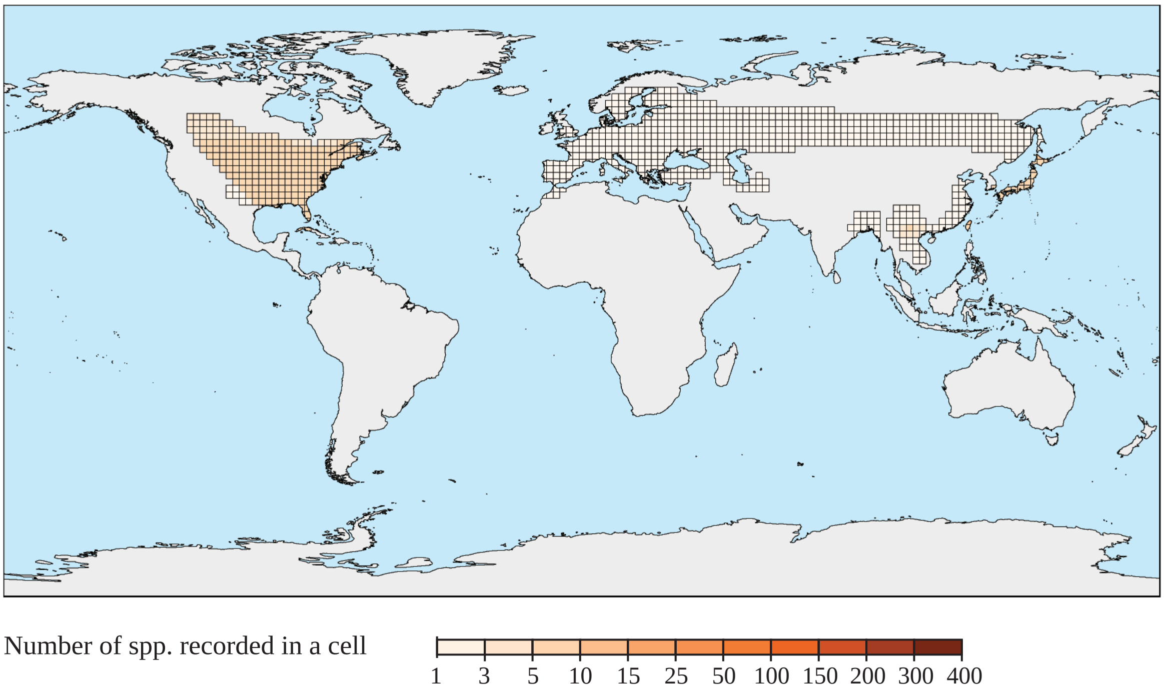


Figure S13. Distribution and species diversity of the tribe Erotini.

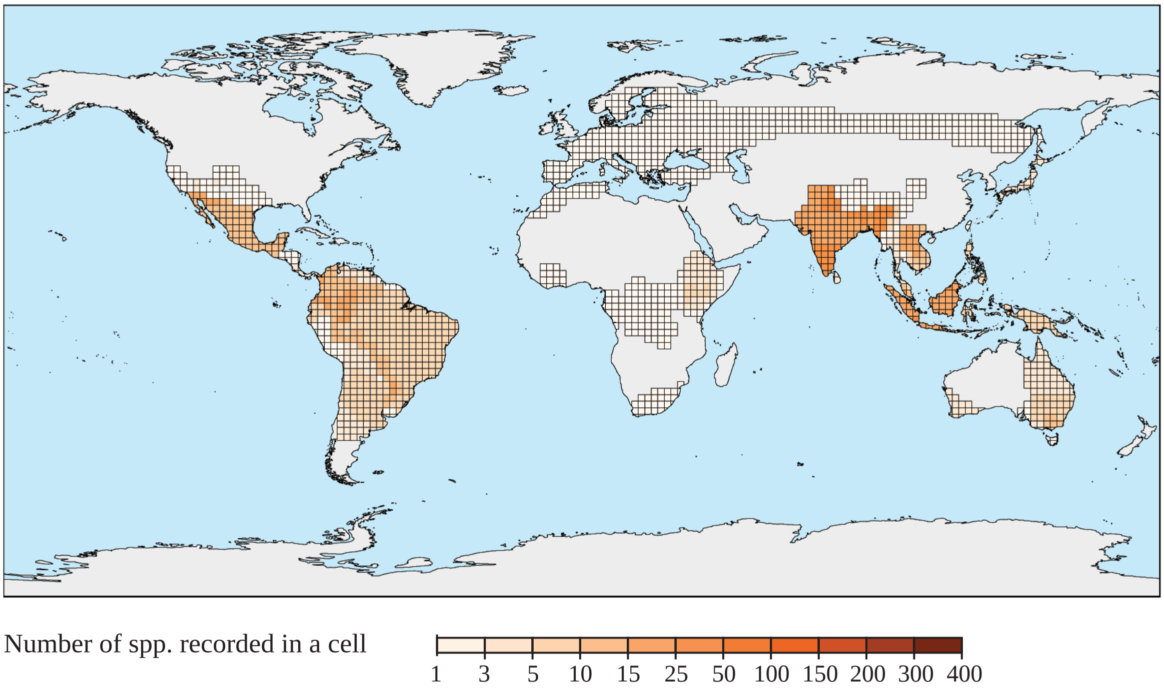


Figure S14. Distribution and species diversity of the tribe Calochromini.

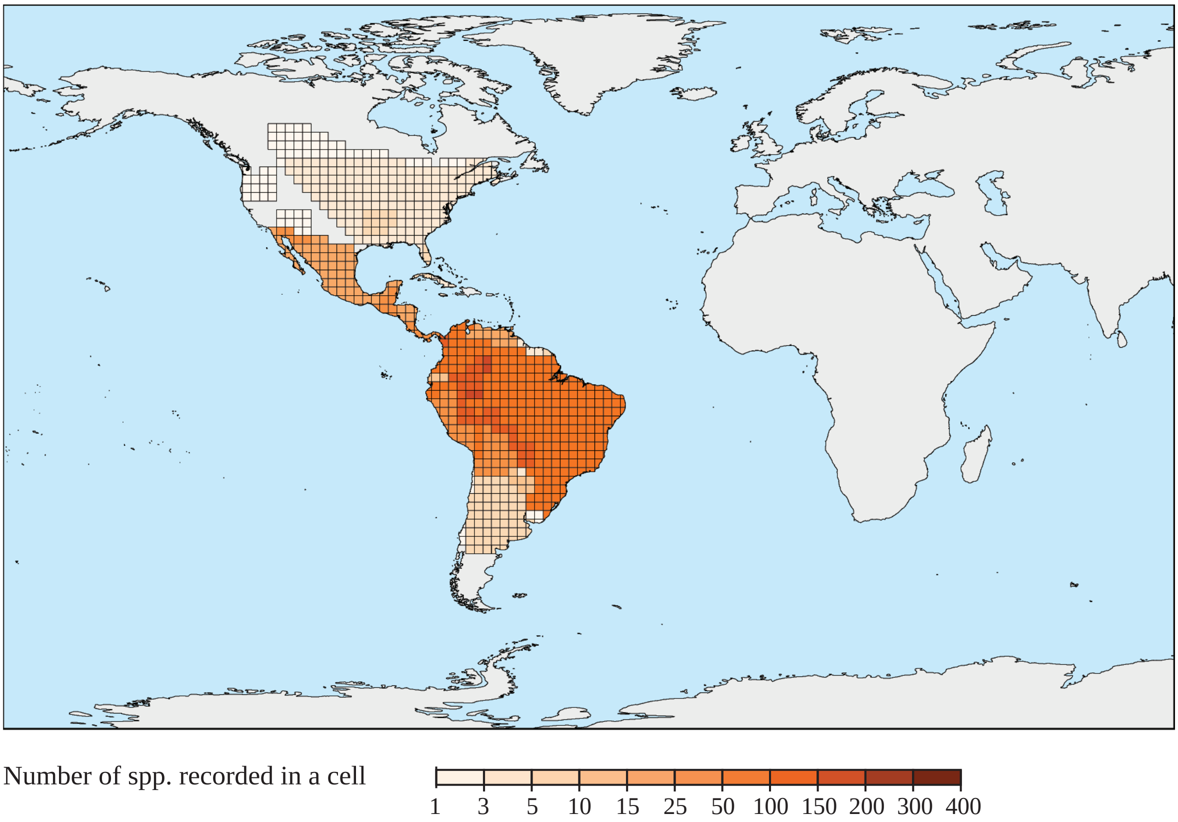


Figure S15. Distribution and species diversity of the tribe Calopterini.

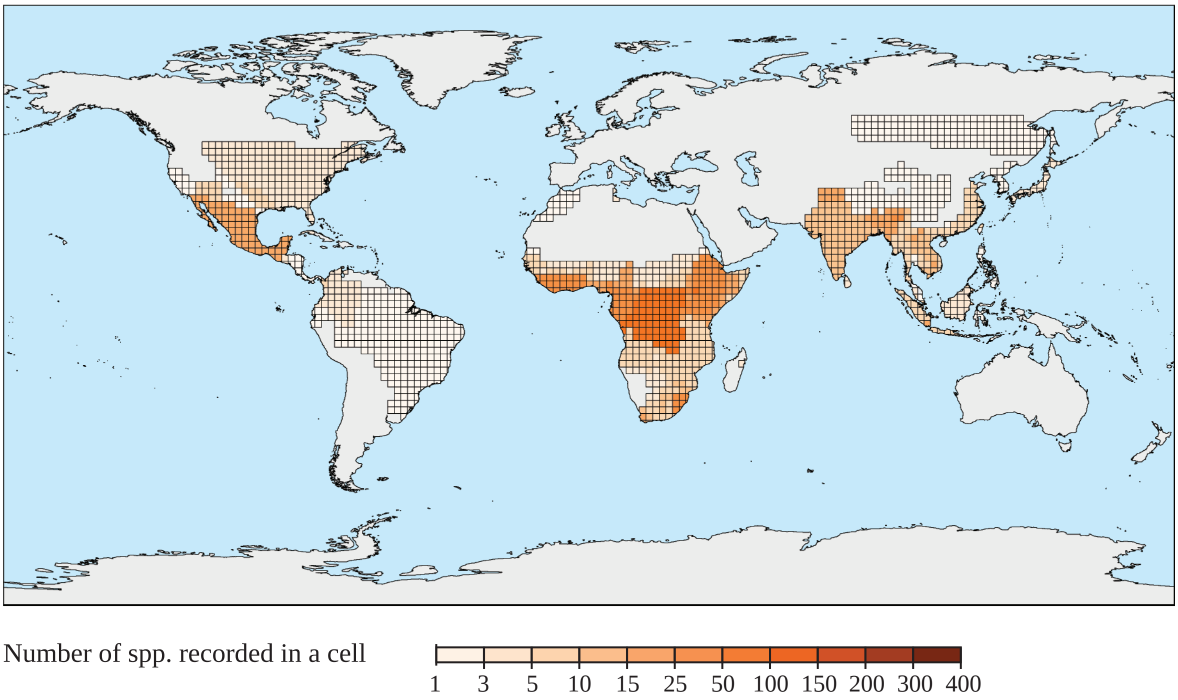


Figure S16. Distribution and species diversity of the tribe Lycini.

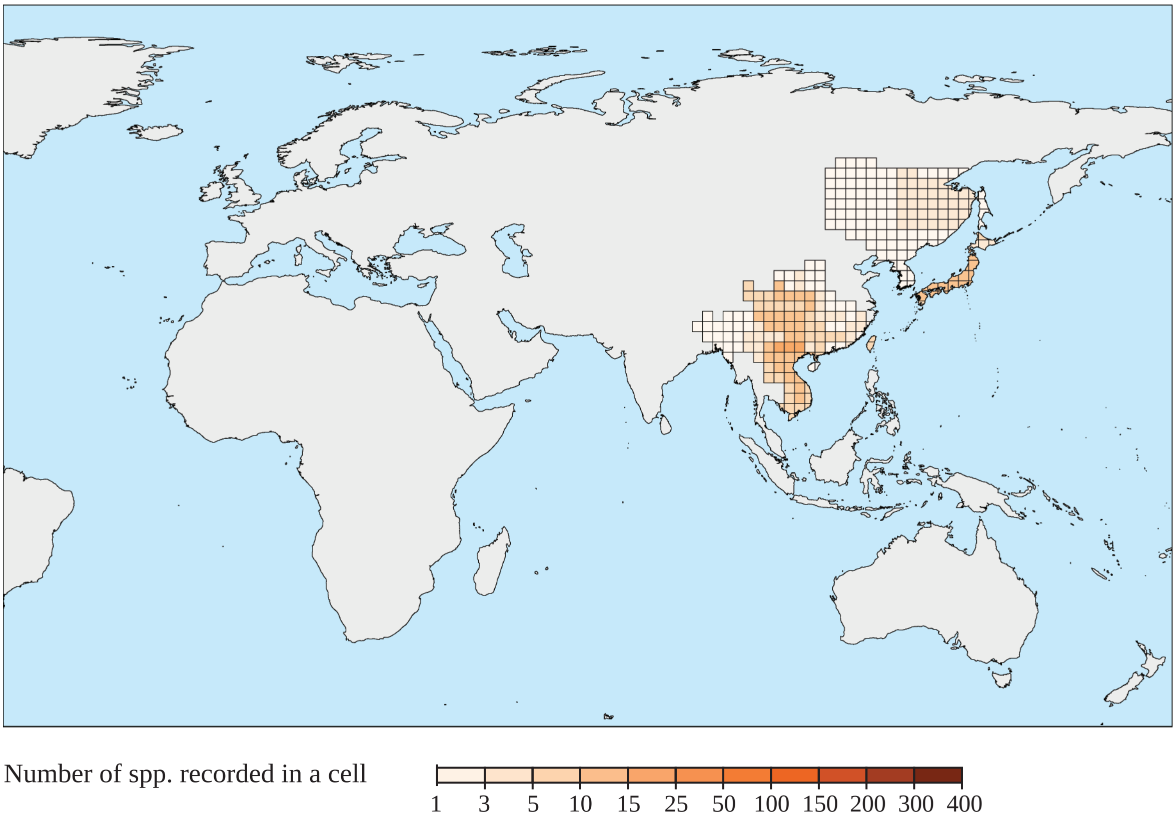


Figure S17. Distribution and species diversity of the tribe Macrolycini.

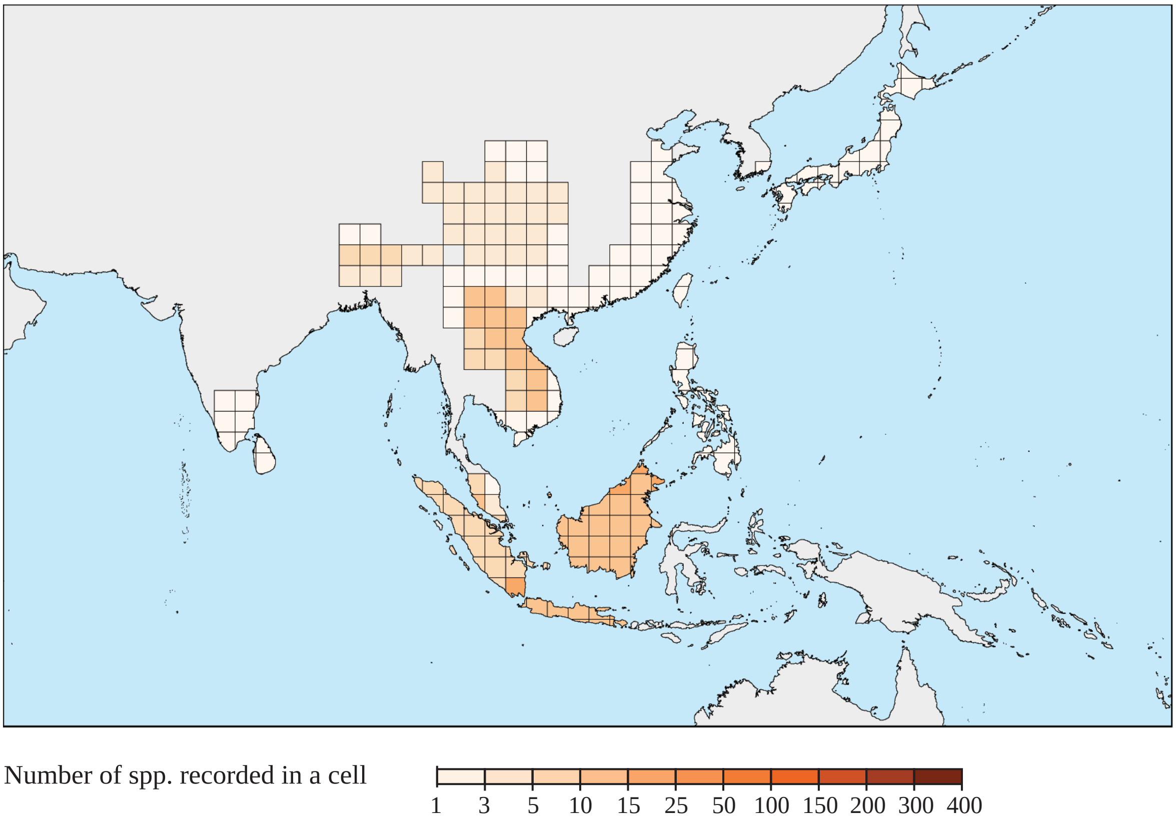


Figure S18. Distribution and species diversity of the tribe Dilophotini.

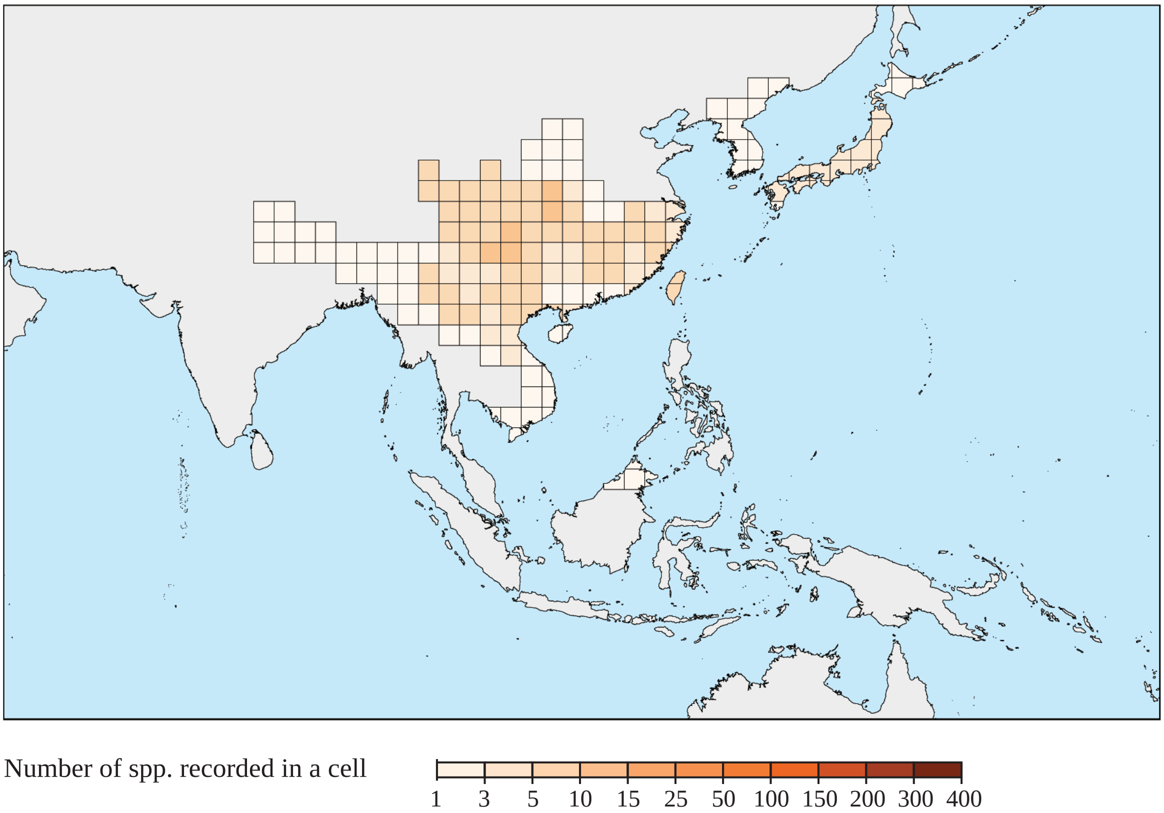


Figure S19. Distribution and species diversity of the tribe Lyponiini.

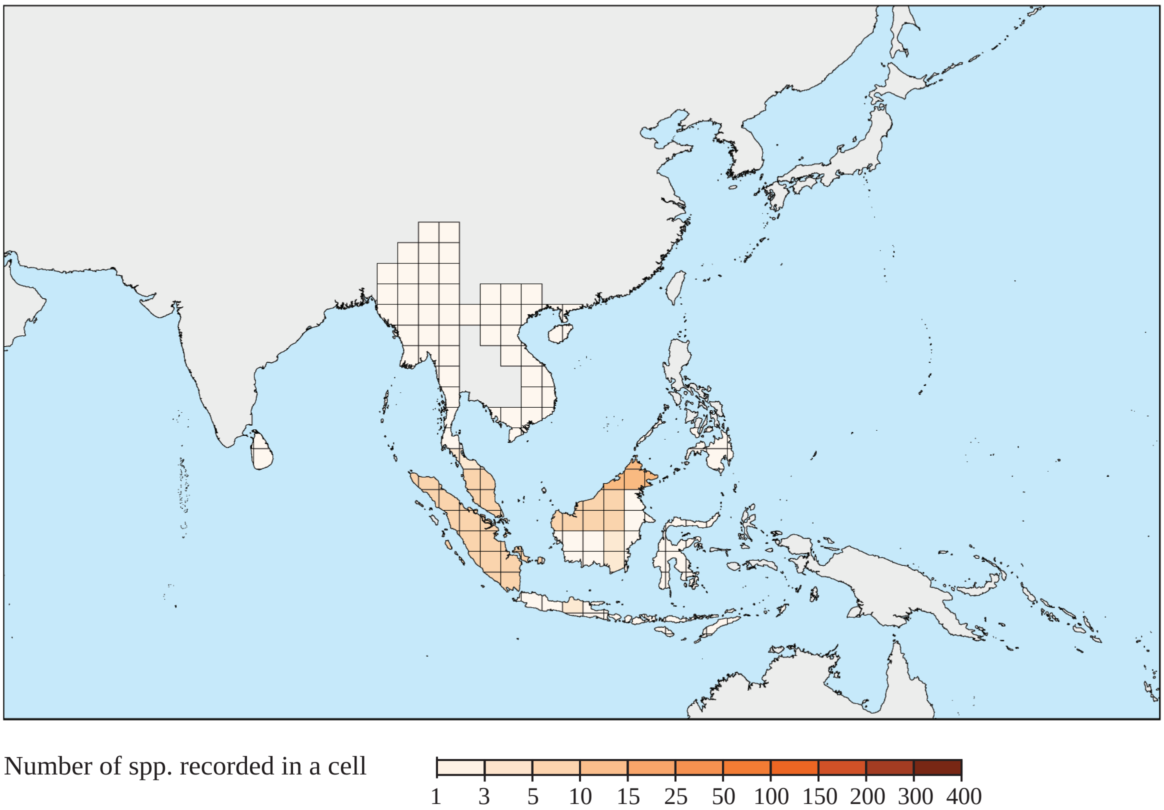


Figure S20. Distribution and species diversity of the tribe Ateliini.

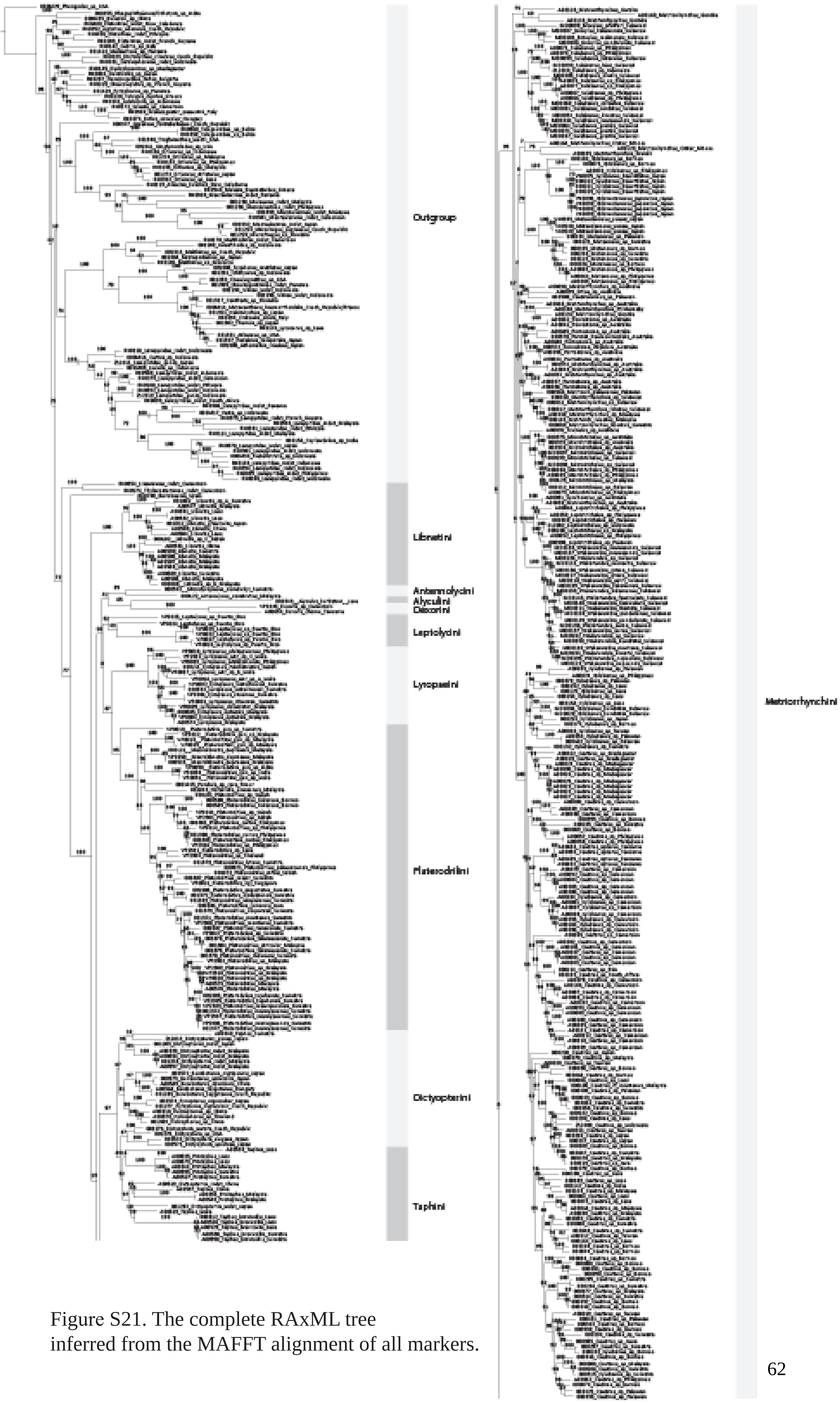
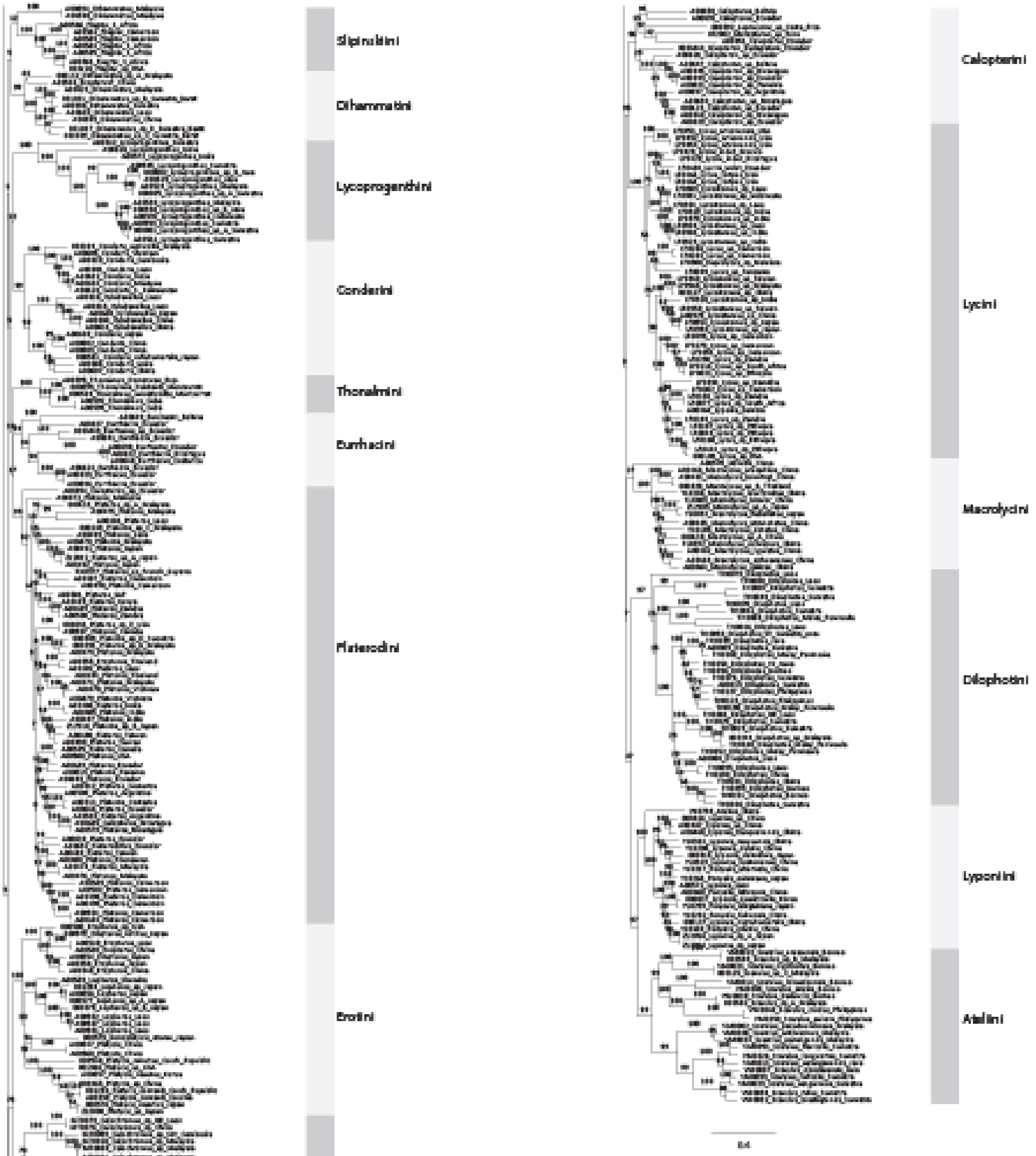


Figure S21. The complete RAxML tree inferred from the MAFFT alignment of all markers.


Slipinskiini
Dihammatini
Lycoprogenthini
Conderini
Thonalmini
Eurrhacini
Platerodini
Erotini
Calochromini
Calopterini
Lycini
Macrolycini
Dilophotini
Lyponiini
Ateliini

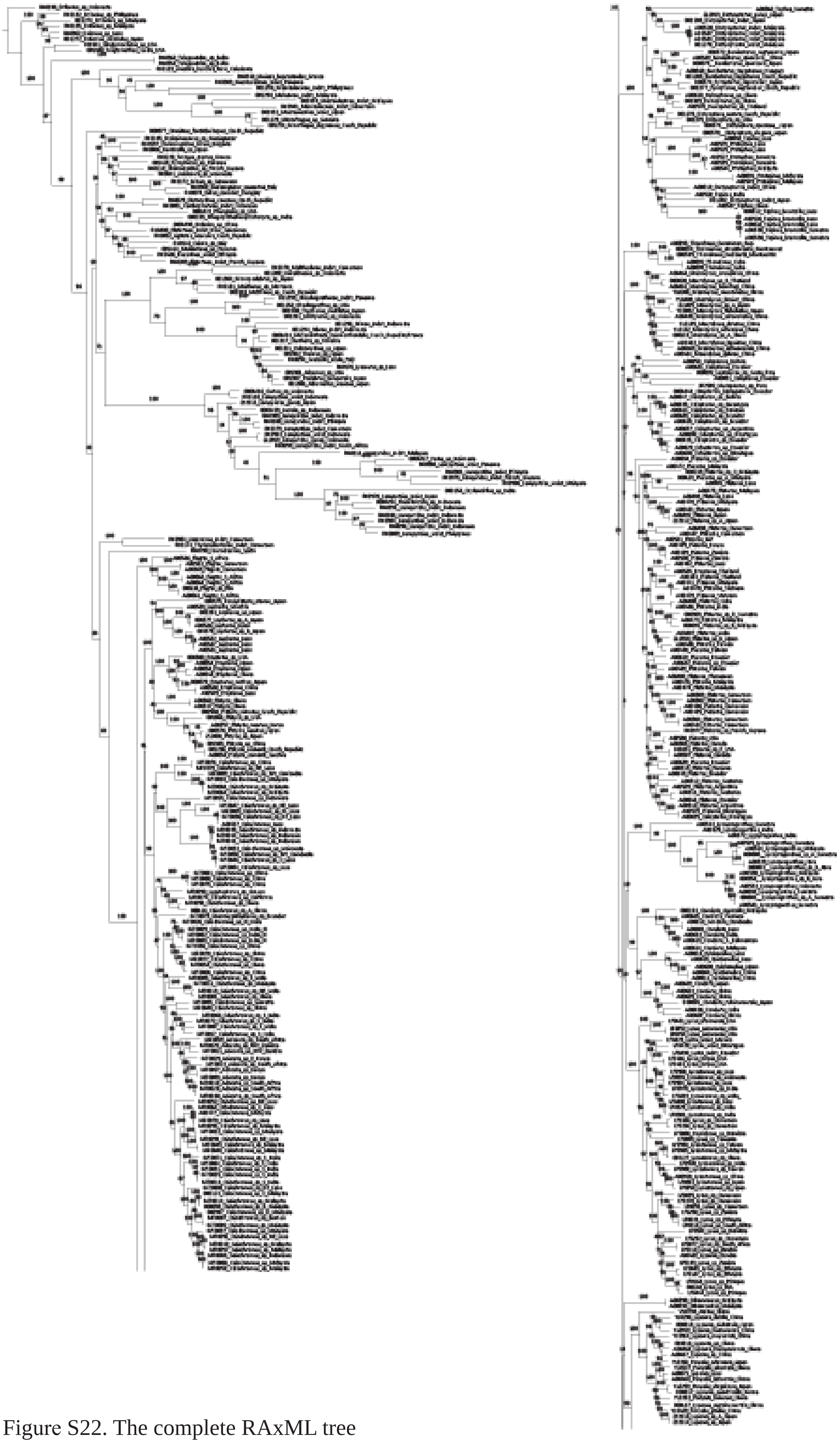


Figure S22. The complete RAxML tree
inferred from the BlastAligned dataset of all markers.

Part 2

Molecular phylogeny and zoogeography of net-winged beetles (Coleoptera: Lycidae)

Michal Masek

(published articles)

Publications

(WOS impact factors stated)

Bocak L, Grebennikov VV, Masek M (2013) A new species of Dexoris (Coleoptera: Lycidae) and parallel evolution of brachyptery in the soft-bodied elateroid beetles. Zootaxa, 3721 (5): 495–500. (IF = 1.06; 73/153).

Masek M, Ivie M, Palata V, Bocak L (2014) Molecular phylogeny and classification of Lyropaeini (Coleoptera: Lycidae) with description of larvae and new species of Lyropaeus). Raffles Bulletin of Zoology, 62: 136–145. (IF = 1.047; 77/154).

Masek M, Bocak L (2014) The taxonomy and diversity of Platerodrilus. ZooKeys, 426: 29–63. (IF = 0.933; 86/154).

Masek M, Palata V, Bray TC, Bocak L (2015) Molecular Phylogeny Reveals High Diversity, Geographic Structure and Limited Ranges in Neotenic Net-Winged Beetles Platerodrilus (Coleoptera: Lycidae). PLoS One, 10(4): e0123855. (IF = 3.057; 11/63).

Motyka M, Masek M, Bocak L (in press) Congruence between morphology and molecular phylogeny: the reclassification of Calochromini (Coleoptera: Lycidae) and their dispersal history. Zoological Journal of the Linnean Society. (IF = 2.316; 16/161).

Prohlášení

Mgr. Michal Mášek se v rámci studia podílel na výzkumném programu laboratoře a je prvním autorem tří publikací v časopisech registrovaných v databázi WOS. Na dalších dvou publikacích se podílel jako jeden ze spoluautorů.

V následujícím přehledu je uveden podíl spoluautorů. Jsou přiložena prohlášení jednotlivých spoluautorů potvrzujících jejich podíl. Podíl školitele je uveden v tomto prohlášení.

Seznam publikací:

Bocak L, Grebennikov VV, Masek M (2013) A new species of *Dexoris* (Coleoptera: Lycidae) and parallel evolution of brachyptery in the soft-bodied elateroid beetles, Zootaxa 3721 (5): 495–500. (IF = 1.06; 73/153).

L. Bocak 50% draft publikace, korespondující autor
V. V. Grebennikov 10% unikátní materiál z Tanzánie, komentář k draftu
M. Masek 40% disekce materiálu, hodnocení znaků, příprava ilustrací, komentář draftu

Masek M, Ivie MA, Palata V, Bocak L (2014) Molecular phylogeny and classification of *Lyropaeini* (Coleoptera: Lycidae) with description of larvae and new species of *Lyropaeus*), Raffles Bulletin Of Zoology 62: 136–145. (IF = 1.047; 77/154).

M. Masek 60% disekce materiálu, sekvenování cca 50% datového souboru, fylogenetické analýzy, hodnocení znaků, příprava ilustrací, příprava draftu
V. Palata 10% poskytnutí sekvencí pro fylogenetickou analýzu, cca 30% datového souboru, komentáře k draftu rukopisu
M.A. Ivie 10% unikátní materiál z Indie, komentář k draftu
L. Bocak 20% design projektu, vedení studie, podíl na draftu publikace, korespondující autor

Masek M, Bocak L (2014) The taxonomy and diversity of *Platerodrilus*, ZooKeys 426: 29–63. (IF = 0.933; 86/154).

M. Masek 80% disekce materiálu, sekvenování cca 80% datového souboru, fylogenetické analýzy, hodnocení znaků, příprava ilustrací, příprava draftu
L. Bocak 20% design projektu, vedení studie, podíl na draftu publikace, korespondující autor

Masek M, Palata V, Bray TC, Bocak L (2015) Molecular Phylogeny Reveals High Diversity, Geographic Structure and Limited Ranges in Neotenic Net-Winged Beetles *Platerodrilus* (Coleoptera: Lycidae), PLoS ONE 10(4): DOI:10.1371/journal.pone.0123855 (IF = 3.057; 11/63).

M. Masek 60% disekce materiálu, sekvenování cca 60% datového souboru, fylogenetické analýzy, hodnocení znaků, příprava ilustrací, příprava draftu
V. Palata 15% poskytnutí sekvencí pro fylogenetickou analýzu, cca 40% datového souboru, komentáře k draftu rukopisu
T. C. Bray 5% konzultace, komentář k draftu
L. Bocak 20% design projektu, vedení studie, podíl na draftu publikace, korespondující autor

Motyka M, Masek M, Bocak L (in press) Congruence between morphology and molecular phylogeny: the reclassification of *Calochromini* (Coleoptera: Lycidae) and their dispersal history, Zoological Journal of the Linnean Society (IF = 2.316; 16/161).

M. Motyka 60% disekce materiálu, sekvenování cca 90% datového souboru, fylogenetické analýzy, hodnocení znaků, příprava ilustrací, příprava draftu
M. Masek 20% zpracování zoogeografických informací, komentáře k draftu rukopisu
L. Bocak 20% design projektu, vedení studie, podíl na draftu publikace, korespondující autor

V Olomouci 17.2. 2017

Prof. Ing. Ladislav Bocak, Ph D
školitel

Věc: Spoluautorský podíl

Prohlašuji, že na následujících publikacích jsem se podílel v uvedeném rozsahu:

Masek M, Ivie AV, Palata V, Bocak L (2014) Molecular phylogeny and classification of *Lyropaeini* (Coleoptera: Lycidae) with description of larvae and new species of *Lyropaeus*), Raffles Bulletin Of Zoology 62: 136–145.

- poskytnutí sekvencí pro fylogenetickou analýzu, cca 30% datového souboru, komentáře k draftu rukopisu, autorský podíl 10%

Masek M, Palata V, Bray TC, Bocak L (2015) Molecular Phylogeny Reveals High Diversity, Geographic Structure and Limited Ranges in Neotenic Net-Winged Beetles *Platerodrilus* (Coleoptera: Lycidae), Plos ONE 10(4): DOI:10.1371/journal.pone.0123855

- poskytnutí sekvencí pro fylogenetickou analýzu, cca 40% datového souboru, komentáře k draftu rukopisu, autorský podíl 15%

V Novém Jičíně dne 15. 2. 2017

Mgr. Václav Palata

Canadian Food Inspection Agency	Agence canadienne d'inspection des aliments

Dr. Vasily V. Grebennikov
Research Scientist / Chercheur Scientifique
Ottawa Plant Laboratory / Laboratoire des plantes d'Ottawa
(613) 759-7519 | Vasily.Grebennikov@inspection.gc.ca | Facsimile / Télécopieur: (613) 759-6938
Canadian Food Inspection Agency / Agence canadienne d'inspection des aliments
Room 4068-D, K.W.Neatby Bldg. / Pièce 4068-D, édif. K.W. Neatby
960 Carling Avenue / 960 avenue Carling
Ottawa, Ontario K1A 0C6
CANADA

February 15, 2017
Ottawa, Canada

To whom it may concern

Subject: Statement of author contribution

Hereby, I declare the extent of my contribution as a co-author:

Bocak L, Grebenikov VV, Masek M (2013) A new species of *Dexoris* (Coleoptera: Lycidae) and parallel evolution of brachyptery in the soft-bodied elateroid beetles. Zootaxa 3721 (5): 495–500.

I provided unique material from Tanzania, commented on the draft of the manuscript, contribution 10%.

Sincerely Yours,

Vasily V. Grebennikov, PhD
Head, Entomology Research Laboratory, CFIA

Василий В. Гребенников

Canada

February 15th 2017
To whom it may concern

Hereby, I declare the extent of my contribution as a co-author:

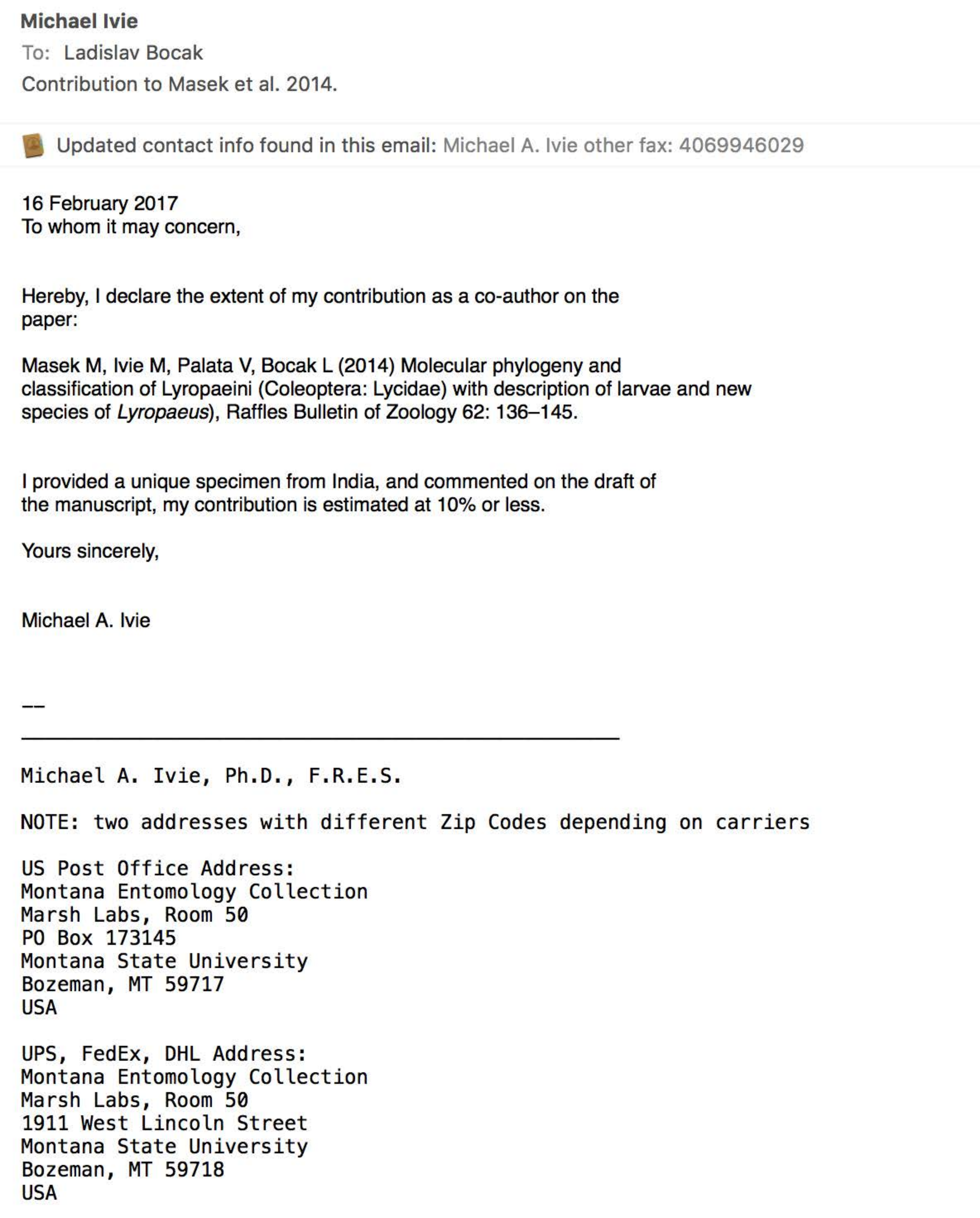
Masek M, Palata V, Bray TC, Bocak L (2015) Molecular Phylogeny Reveals High Diversity, Geographic Structure and Limited Ranges in Neotenic Net-Winged Beetles *Platerodrilus* (Coleoptera: Lycidae), PLoS One 10(4): DOI:10.1371/journal.pone.0123855

Advice during analyses, comments on the draft of the manuscript, contribution 5%.

Yours sincerely,

Tim Bray.

T. C. Bray



Michael Ivie

To: Ladislav Bocak

Contribution to Masek et al. 2014.

Updated contact info found in this email: Michael A. Ivie other fax: 4069946029

16 February 2017
To whom it may concern,

Hereby, I declare the extent of my contribution as a co-author on the paper:

Masek M, Ivie M, Palata V, Bocak L (2014) Molecular phylogeny and classification of Lyropaeini (Coleoptera: Lycidae) with description of larvae and new species of *Lyropaeus*), Raffles Bulletin of Zoology 62: 136–145.

I provided a unique specimen from India, and commented on the draft of the manuscript, my contribution is estimated at 10% or less.

Yours sincerely,

Michael A. Ivie

--

Michael A. Ivie, Ph.D., F.R.E.S.

NOTE: two addresses with different Zip Codes depending on carriers

US Post Office Address:
Montana Entomology Collection
Marsh Labs, Room 50
PO Box 173145
Montana State University
Bozeman, MT 59717
USA

UPS, FedEx, DHL Address:
Montana Entomology Collection
Marsh Labs, Room 50
1911 West Lincoln Street
Montana State University
Bozeman, MT 59718
USA

Prohlášení

Prohlašuji, že na následující publikaci jsem se podílel v uvedeném prozsahu:

Motyka M, Masek M, Bocak L (in press) Congruence between morphology and molecular phylogeny: the reclassification of *Calochromini* (Coleoptera: Lycidae) and their dispersal history, Zoological Journal of the Linnean Society (IF = 2.316; 16/161).

M. Motyka 60% disekce materialu, sekvenování cca 90% datového souboru, fylogenetické analýzy, hodnocení znaků, příprava ilustrací, příprava draftu

V Olomouci 17.2. 2017

Mgr. Michal Motyka

RAFFLES BULLETIN OF ZOOLOGY **62**: 136–145
Date of publication: 27 March 2014
http://zoobank.org/urn:lsid:zoobank.org:pub:6EFBCE81-9C2C-44C6-82C8-4AEBDCA885EF

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

Michal Masek[1*], Michael A. Ivie[2], Vaclav Palata[1] & Ladislav Bocak[1]

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

---

[1] Department of Zoology, Faculty of Science, Palacký University, Olomouc, Czech Republic; Email: michal.masek@upol.cz (*corresponding author MM); vaclav.palata@upol.cz (VP); ladislav.bocak@upol.cz (LB)

[2] Montana Entomology Collection, Montana State University, Bozeman, USA; Email: mivie@montana.edu

ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

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

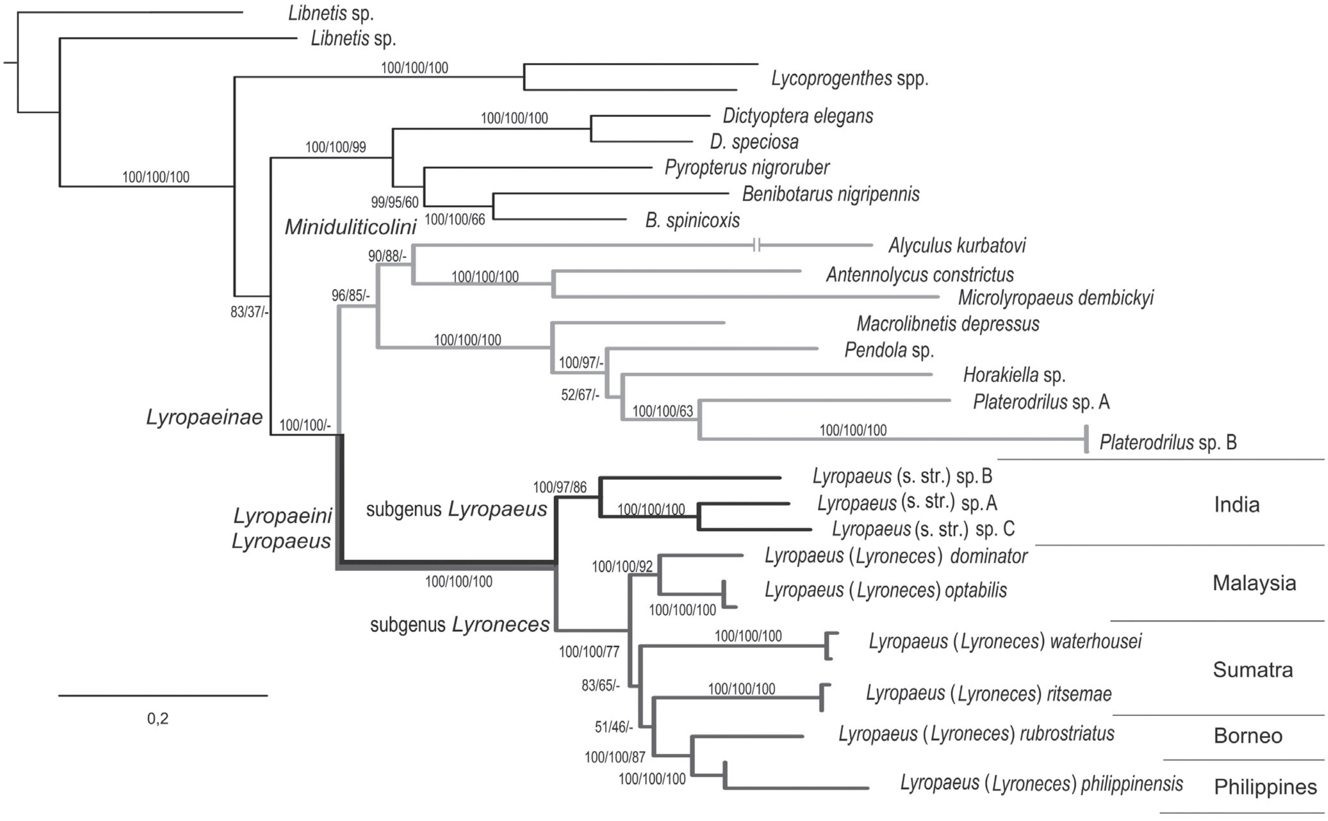


Fig. 1. Phylogenetic hypothesis for *Lyropaeus* Waterhouse, 1878 based on a maximum likelihood analysis of five fragments 18S and 28S rDNA, cox1, nad5 and rrnl mtDNA. Numbers at the branches are Bayesian frequencies and likelihood and parsimony bootstrap values.

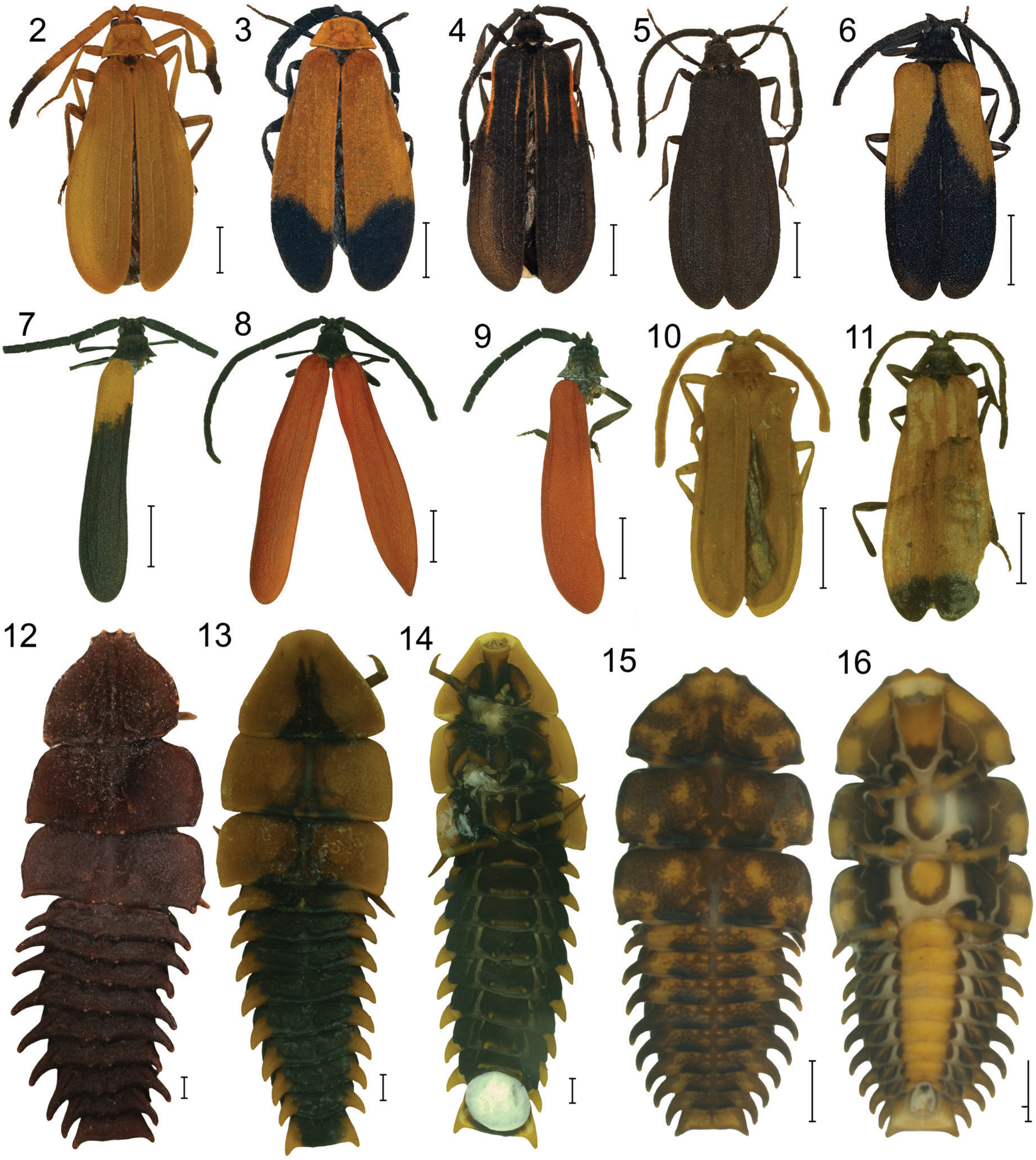
a digital camera attached to a stereoscopic microscope and line illustrations were derived from adjusted photographs. Morphometric data from adult males were measured with an ocular grid on an Olympus SZX-12 binocular dissecting microscope. The following measurements were taken: BL – body length; HW –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)

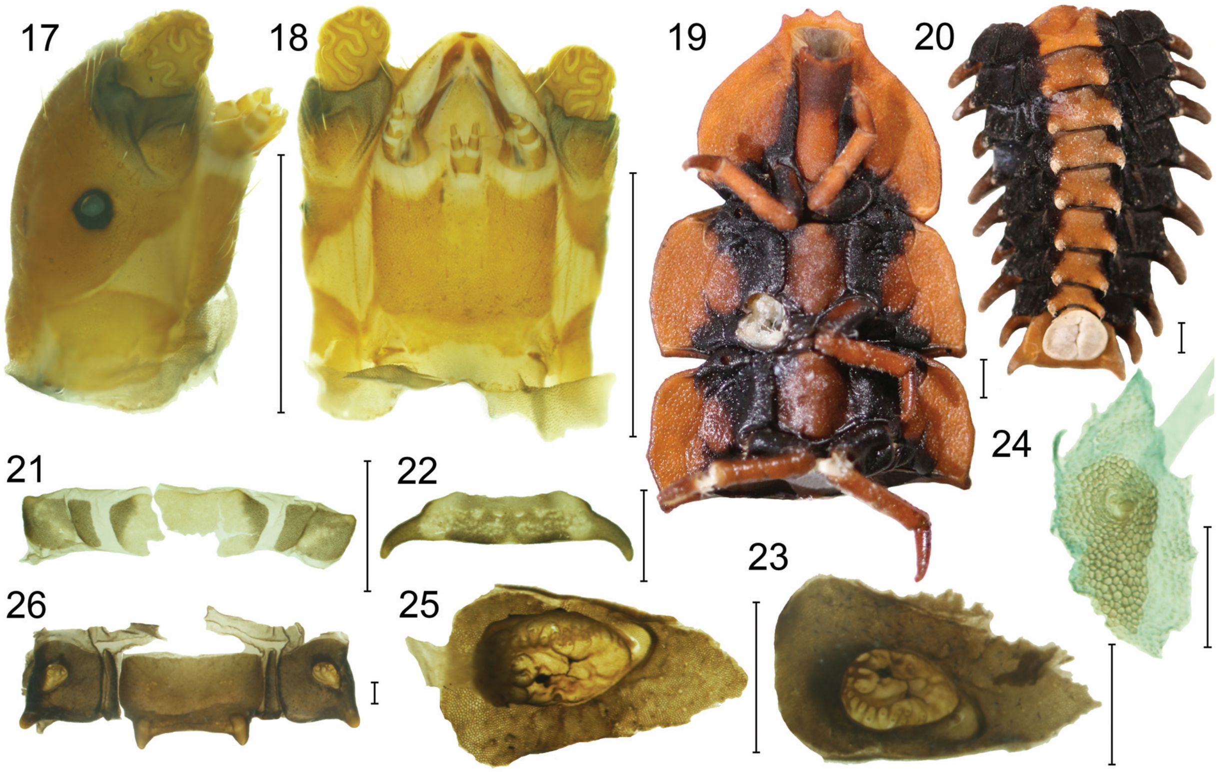
Adult. Differential diagnosis. Antennae 10-segmented, head hypognathous, mouthparts reduced and with merged basal palpomeres, pronotum without carinae, elytra with weak longitudinal costae, transverse costae absent. Only males winged (Figs. 2–11), females completely larviform (Figs. 12–24).

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).

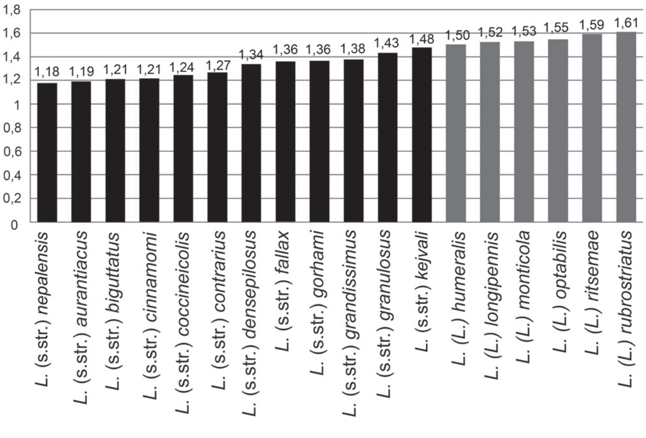


Fig. 27. Ratio between width at humeri and width of pronotum at basal margin in selected species of *Lyropaeus* (s. str.) (black bars) and *Lyropaeus* (*Lyroneces*) (gray bars).

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).

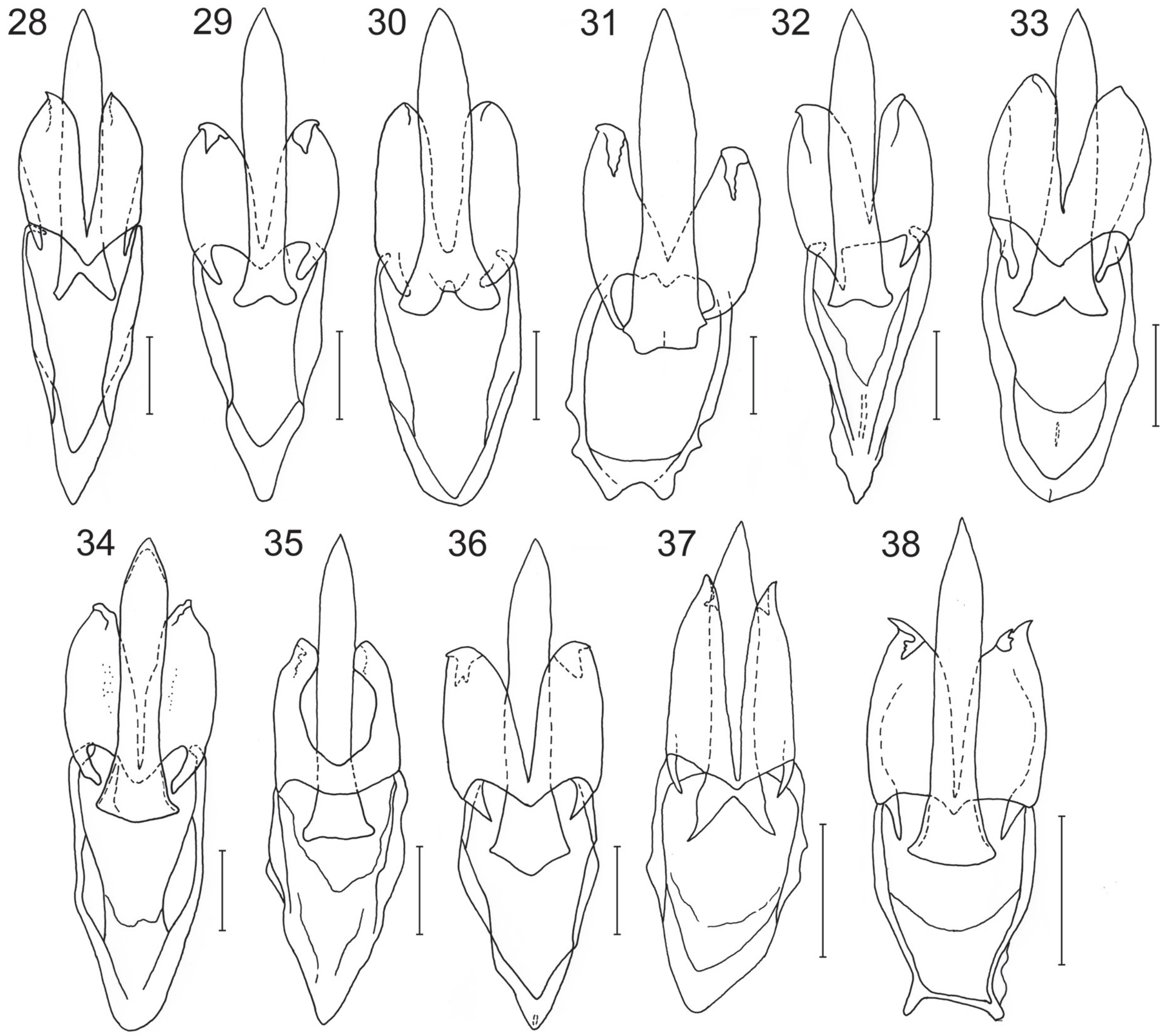
Gravely (1915) described a pupa of *Lyropaeus* which developed from a smaller larvae. We are not able to discriminate at the moment the male larvae from early instar female larvae and we can only say that the large bodied larvae (Voucher UPOLVP0016–7) must be females. We have only small-bodied specimens 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.

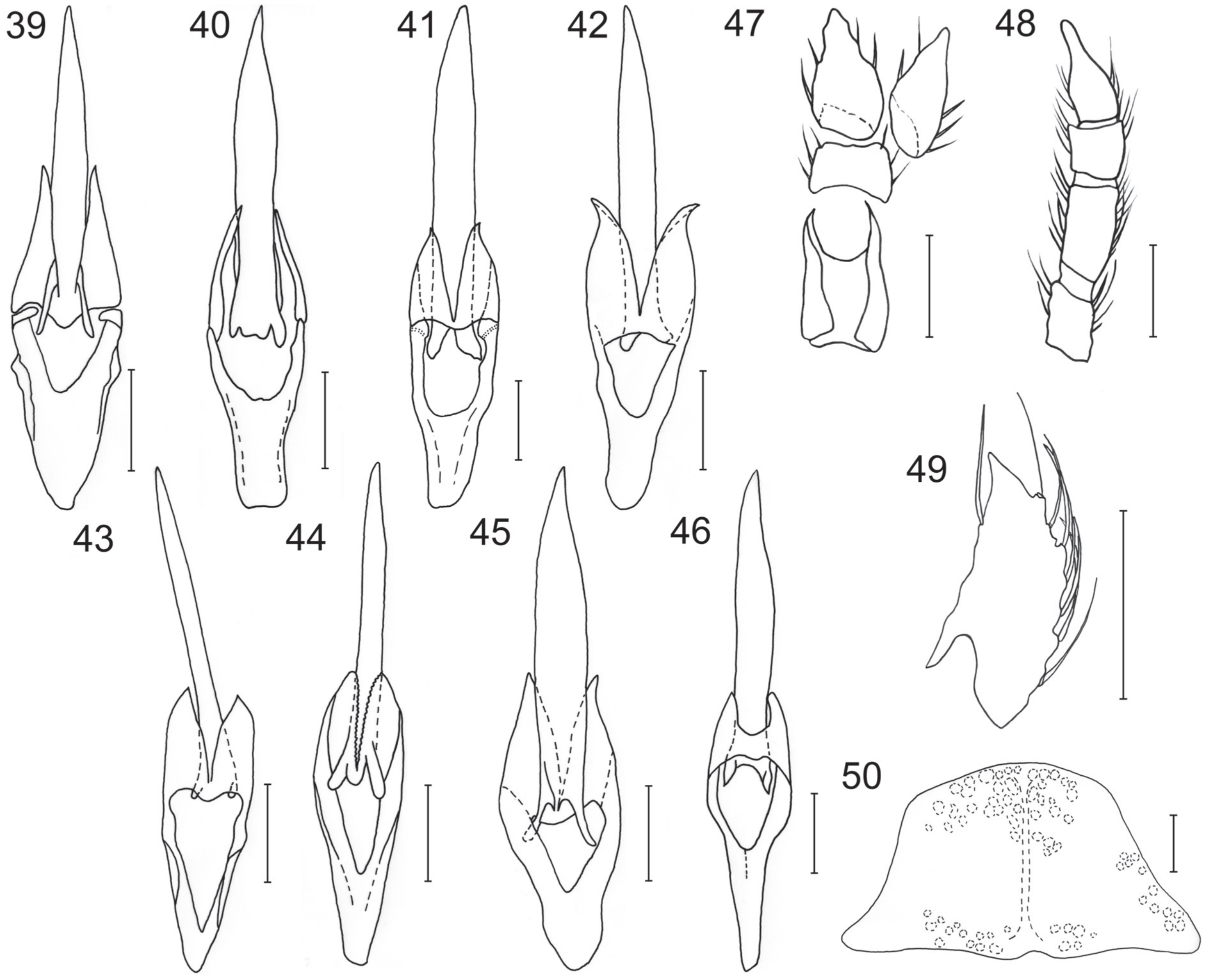
Etymology. The specific epithet refers to the type locality of the holotype.

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).

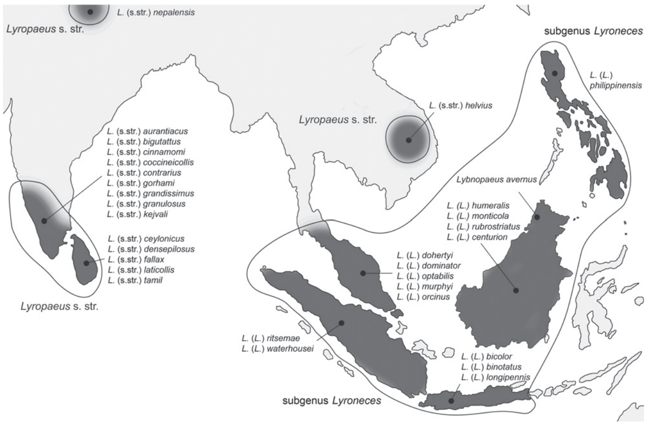


Fig. 51. Geographical distribution of Lyropaeini.

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.

ACKNOWLEDGEMENTS

We are deeply obliged to curators who enabled us to study the material in their care: Maxwell L. V. Barclay (The Natural History Museum, London), Thierry Deuve (Muséum National d'histoire naturelle, Paris), and Wioletta Tomaszewska (Museum and Institute of Zoology, Warszawa). The study was supported by grants to L. B. from the Czech Grant Agency (P506/11/1757) and Internal Grant of the Palacky University. MAI was supported by NSF-0531768 Beetle Tree of Life Project. Thanks to Ian Foley, Vincent Martinson, Prathapan K. Divakaran, and Kumar Ghorpade for their help. This is a contribution of the Montana Agricultural Experiment Station.

LITERATURE CITED

Bocak L, Bocakova M, Hunt T & Vogler AP (2008) Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. Proceedings of the Royal Society B, 275: 2015–2023.

Bocak L & Bocakova M (1989) New tribe Lyropaeini, with a description of a new species of *Lyropaeus* (Coleoptera, Lycidae). Polskie Pismo Entomologiczne, 58: 717–723.

Bocak L & Matsuda K (2003) Review of the immature stages of the family Lycidae (Insecta: Coleoptera). Journal of Natural History, 37: 1463–1507.

Bocakova M (2006) Review of the tribe Lyropaeini (Coleoptera: Lycidae). European Journal of Entomology, 103: 127–136.

Candèze EM (1861) Histoire des métamorphoses de quelques Coleopteres exotiques. Mémoires de la Société Royale des Sciences, Liège, 16: 358, 403–404.

Goloboff P, Farris S & Nixon K (2003) TNT (tree analysis using new technology). Cladistics, 20: 84.

Gorham HS (1882) New species of Lycidae, Lampyridae and Telephoridae from Sumatra. Notes from the Leyden Museum, 4: 93–126.

Gravely FH (1915) The larvae and pupae of some beetles from Cochin. Records of the Indian Museum, 11: 354–366.

Hall R (2011) Australia-SE Asia collision: plate tectonics and crustal flow. In: Hall R, Cottam MA & Wilson MEJ (eds.) The SE Asian Gateway: History and Tectonics of the Australia-Asia Collision. Geological Society Special Publications, London, 355: 75–109.

Huelsenbeck JP (2000) MrBayes: Bayesian inference of phylogeny version 3.1.2. Department of Biology, University of Rochester, New York.

Jiang H, Ji J, Gao LG, Tang Z & Ding Z (2008) Cooling-driven climate change at 12–11 Ma: multiproxy records from a long fluviolacustrine sequence at Guyuan, Ningxia, China. Palaeogeography, Palaeoclimatology, Palaeoecology, 265: 148–158.

Kazantsev SV (1998) Two new oriental genera of the tribe Lyropaeini (Coleoptera: Lycidae). Elytron, 12: 15–22.

Kazantsev SV (2002) A generic review of Duliticolinae, new subfamily (Coleoptera: Lycidae). Elytron 16: 5–21.

Kleine R (1926) Die Lyciden der Philippinen-Inseln. Philippine Journal of Science, 31: 33–114.

Kleine R (1933) Lycidae. Pars 128. In: Junk W & Schenkling S (eds.), Coleopterorum Catalogus. W. Junk, Berlin, 145 pp.

Levkanicova Z & Bocak L (2009) Identification of net-winged beetle larvae (Coleoptera: Lycidae) using three mtDNA fragments: a comparison of their utility. Systematic Entomology, 34: 210–221.

Malohlava V & Bocak L (2010) Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. Molecular Ecology, 19(21): 4800–4811.

Medvedev LN & Kazantsev SV (1992) A new subfamily and a new genus of Lycidae from Southeast Asia. In: Medvedev LN (ed.) Systematics and Ecology of Insects of Vietnam. Nauka, Moscow. Pp. 55–60. [In Russian], pp. 55–60.

Mjöberg E (1925) The mystery of the so called "Trilobite" or "Perty's larvae" definitely solved. Psyche, 22: 119–153.

Pic M (1911) Contribution a l'etude du genre *Lyropaeus* Wat. Mélanges Exotico-Entomologiques, 1: 14–16.

Pic M (1921) Nouveautes diverses. Mélanges Exotico-Entomologiques, 33: 12–13.

Pic M (1926) Malacodermes exotique. L'Echange, 42: 34.

Pic M (1938) Divers Coléoptères nouveaux de la présqu'ile malaise (IV). Journal of the Federated Malay States Museum, 18: 280–281.

Posada D (2008) JMODELTEST: phylogenetic model averaging. Molecular Biology and Evolution, 25: 1253–1256.

Rambaut A & Drummond AJ (2007) Tracer version 1.5. Institute of Evolutionary Biology University of Edinburgh, Edinburgh.

Stamatakis A, Ludwig T & Meier H (2005) RAxML-III: a fast program for maximum likelihood-based inference of large phylogenetic trees. Bioinformatics, 21: 456–463.

Thompson J, Higgins D & Gibson T (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignments through sequence weighting, position specific gap penalties and weight matrix choice. Nucleic Acids Research, 22: 4673–4680.

Waterhouse CO (1878) On the different forms occurring in the Coleopterous family Lycidae, with description of new genera and species. Transactions of the Entomological Society London, 1878: 95–118.

Waterhouse CO (1880) New species of Coleoptera belonging to the families Lycidae, Zophosinae, Leptinae, and Glaucitinae. Annals and Magazine of Natural History, 5(5): 213–214.

Womersley H (1944) Australian Acarina, families Alycidae and Nanorchestidae. Transactions of the Royal Society of South Australia, 68: 133–143.

Wong ATC (1996) A new species of neotenous beetle, *Duliticola hoiseni* (Insecta: Coleoptera: Cantharoidea: Lycidae) from peninsular Malaysia and Singapore. Raffles Bulletin of Zoology, 44: 173–187.

ZooKeys 426: 29–63 (2014)
doi: 10.3897/zookeys.426.7398
www.zookeys.org

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

The taxonomy and diversity of *Platerodrilus* (Coleoptera, Lycidae) inferred from molecular data and morphology of adults and larvae

Michal Masek[1], Ladislav Bocak[1]

[1] *Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 771 46 Olomouc, Czech Republic*

Corresponding author: *Ladislav Bocak* (ladislav.bocak@upol.cz)

Academic editor: *L. Penev* | Received 28 February 2014 | Accepted 3 July 2014 | Published 17 July 2014

http://zoobank.org/97E141BB-9073-4FB5-8CF3-BAD4179DEF07

Citation: Masek M, Bocak L (2014) The taxonomy and diversity of *Platerodrilus* (Coleoptera, Lycidae) inferred from molecular data and morphology of adults and larvae. ZooKeys 426: 29–63. doi: 10.3897/zookeys.426.7398

Abstract

The Oriental neotenic net-winged beetles attracted attention of biologists due to conspicuous large-bodied females; nevertheless phylogenetic relationships remain contentious and only a few species are known in both the fully metamorphosed males and neotenic females. The phylogenetic analyses and morphology of larvae and adults provide data for investigation of relationships and species delineation. *Platrilus* Kazantsev, 2009, *Platerodriloplesius* Wittmer, 1944, and *Falsocalochromus* Pic, 1942 are synonymized to *Platerodrilus* Pic, 1921. *Platrilus hirtus* (Wittmer, 1938) and *Pl. crassicornis* (Pic, 1923) are transferred to *Platerodrilus* Pic, 1921. *Platerodrilus hoiseni* Wong, 1996 is proposed as a junior subjective synonym of *Falsocalochromus ruficollis* Pic, 1942. *Platerodrilus* is divided in three species-groups: *P. paradoxus*, *P. major*, and *P. sinuatus* groups defined based on the shape of genitalia and molecular phylogeny. The following species are described: *Platerodrilus foliaceus* **sp. n.**, *P. wongi* **sp. n.** (*P. paradoxus* group); *P. ngi* **sp. n.**, *P. wittmeri* (*P. major* group), *P. ijenensis* **sp. n.**, *P. luteus* **sp. n.**, *P. maninjauensis* **sp. n.**, *P. montanus* **sp. n.**, *P. palawanensis* **sp. n.**, *P. ranauensis* **sp. n.**, *P. sibayakensis* **sp. n.**, *P. sinabungensis* **sp. n.**, *P. talamauensis* **sp. n.**, and *P. tujuhensis* **sp. n.** (*P. sinuatus* group). *P. korinchiana robinsoni* Blair, 1928 is elevated to the species rank as *P. robinsoni* Blair, 1928, **stat. n.** The conspecific semaphoronts are identified using molecular phylogeny for *P. foliaceus* **sp. n.**, *P. tujuhensis* **sp. n.**, *P. montanus* **sp. n.**, *P. maninjauensis* **sp. n.**; additional female larvae are assigned to the species-groups. Diagnostic characters are illustrated and keys are provided for *P. paradoxus* and *P. major* groups.

Keywords

Oriental Region, net-winged beetles, morphology, molecular phylogeny, taxonomy

Introduction

The platerodriline net-winged beetles are one of elateroid lineages with modified female morphology (Wong 1996, Bocak et al. 2008, Masek et al. 2014). The adult males are fully metamorphosed (Figs 4–17). In contrast, females do not pupate and the sexually mature females remain larviform ("trilobite larvae", Figs 2–3, 32–43, Mjöberg 1925, Wong 1996, Bocak and Matsuda 2003). The taxonomic situation is complicated by the fact that *Platerodrilus* males and females have been observed in copula only twice (Mjöberg 1925, Wong 1996).

The taxonomy of the neotenic lineages has quite short history despite the fact that the trilobite larvae were first time described in the 19th century (Perty 1831, Candèze 1861). *Platerodrilus* Pic, 1921 was proposed for five species and although compared with *Plateros* Bourgeois, 1879 (Lycidae), the new taxon was placed in the distantly related Drilidae (now Drilini in Elateridae; Kundrata and Bocak 2011). Mjöberg (1925) erected *Duliticola*, described both sexes of *D. paradoxa* Mjöberg, 1925 and discussed the possibility to establish Duliticolinae in Lycidae. Only recently the trilobite larvae attracted further students. Wong (1996) reported another case of a male and a female observed in copula and studied most M. Pic's types deposited in the Paris Museum, but his work remained unpublished (Wong 1998). Kazantsev (2002) described the subfamily Duliticolinae, but the name is unavailable and replaced by Miniduliticolinae (Kazantsev 2005). Kazantsev (2002) designated the type species of *Platerodrilus*, considered *Duliticola* as its junior synonym and later described a new genus *Platrilus* Kazantsev, 2009 which corresponds to *Platerodrilus* sensu Wong (1998). The subgenus *Platerodriloplesius* Wittmer, 1941 was elevated to the genus rank by Kazantsev (2002). These taxa are based on flabellate antennae (*Platerodriloplesius*) or the unique shape of male genitalia (*Platrilus*) and their relationships have remained contentious.

The DNA data represent an independent source of information for species delineation (Vuataz et al. 2011) and for identification of the conspecific semaphoronts (Ahrens et al. 2007). We present the molecular phylogeny of *Platerodrilus* and compare the results with morphology of adults and larvae to solve taxonomy of *Platerodrilus*. As a result, we describe new species and discuss their relationships.

Methods

Morphological taxonomy

Adult males and female larvae were used for morphological descriptions. A part of specimens used for morphological study was sequenced and labelled with the GenBank voucher numbers in the format UPOL + six-letter/number code and the status of all type specimens were designated with red labels (ICZN 1999). The codes are listed in examined material (Table 1). A. T. C. Wong studied many species in mid 1990's, but the types have not yet been returned to the Paris museum. Therefore,

Table 1. Taxonomic coverage, locality data and GenBank accession numbers.

Species	Voucher UPOL+	Local. data	*rrnL*
Outgroup			
Benibotarus nigripennis	000572	Japan	DQ181001
B. spinicoxis	000573	Japan	DQ181002
Dictyoptera elegans	000570	Japan	DQ181375
Dictyoptera speciosa	000571	Japan	DQ181000
Libnetis granicollis	001012	Japan	DQ181033
Libnetis sp.	001002	Sumatra	DQ181030
Libnetis sp.	001008	Malaysia	DQ181031
Libnetis sp.	000L02	Sabah	DQ180964
Lycoprogenthes sp.	000801	Sumatra	DQ181021
Lycoprogenthes sp.	000802	Java	DQ181022
Lycoprogenthes sp.	000805	Sumatra	DQ181023
Lycoprogenthes sp.	000358	Java	DQ180996
Pyropt. nigroruber	000574	Japan	DQ181003
Lyropaeus sp.	VP0016	India	KC736885
Lyropaeus sp.	VP0017	India	KC736886
Lyropaeus sp.	VP2312	India	KC736887
L. dominator	VP0003	Malaysia	KC736882
L. optabilis	VP0004	Malaysia	KC736883
L. optabilis	000585	Malaysia	DQ181014
L. ritsemae	VP0001	Sumatra	KC736880
L. ritsemae	VP0006	Sumatra	KC736884
L. rubrostriatus	000L11	Malaysia	DQ180968
L. waterhousei	VP0002	Sumatra	KC736881
L. waterhousei	000584	Sumatra	DQ181013
Ingroup			
Horakiella emasensis	001043	Malaysia	DQ181036
Macrolibnetis depressus	VP0050	Malaysia	KF802467
M. depressus	000L21	Malaysia	DQ180976
Pendola sp.	000M45	Java	DQ180984
Platerodrilini gen. sp.	VP0009	Malaysia	KF802457
Platerodrilini gen. sp.	VP0010	Sumatra	KF802480
Platerodrilini gen. sp.	VP0012	Malaysia	KF802458
Platerodrilini gen. sp.	VP0030	India	KF802462
Platerodrilini gen. sp.	VP0031	India	KF802463
Platerodrilini gen. sp.	VP0034	India	KF802464
Platerodrilus curtus	001380	Mindanao	KF625997
P. curtus	001381	Mindanao	KF626073
P. curtus	001383	Mindanao	KF626074
P. curtus	VP0014	Mindanao	KF802459
P. curtus	VP2316	Mindanao	KF802479
P. angustatus	001388	Sumatra	KF626001
P. corporaali	001373	Sumatra	KF625991
P. foliaceus	000588	Borneo	DQ181017

Species	Voucher UPOL+	Local. data	*rrnL*
P. foliaceus	000589	Borneo	EF143214
P. ijenensis	000586	Java	DQ181015
P. luteus	001379	Sumatra	KF625996
P. major	001387	Sumatra	KF626000
P. maninjauensis	001374	Sumatra	KF625992
P. maninjauensis	001377	Sumatra	KF625994
P. maninjauensis	001386	Sumatra	KF626075
P. maninjauensis	VP2303	Sumatra	KF802470
P. maninjauensis	VP2306	Sumatra	KF802473
P. montanus	001371	Sumatra	KF625989
P. montanus	VP2308	Sumatra	KF802475
P. ngi	VP0021	Singapore	KF802461
P. ranauensis	000587	Sumatra	DQ181016
P. robinsoni	001378	Sumatra	KF625995
P. sibayakensis	001372	Sumatra	KF625990
P. sibayakensis	001389	Sumatra	KF802552
Platerodrilus sp.	000L01	Sabah	DQ180963
Platerodrilus sp.	VP0044	Sabah	KF802465
Platerodrilus sp.	VP2301	Sabah	KF802468
Platerodrilus sp.	VP0020	Malaysia	KF802460
Platerodrilus sp.	VP0047	Sumatra	KF802466
Platerodrilus sp.	VP2302	Malaysia	KF802469
Platerodrilus sp.	VP2304	Thailand	KF802471
Platerodrilus sp.	VP2307	Sumatra	KF802474
Platerodrilus sp.	VP2309	Malaysia	KF802476
Platerodrilus sp.	VP2310	Malaysia	KF802477
Platerodrilus sp.	VP2311	Laos	KF802478
Platerodrilus sp.	MB1382	Palawan	EF625998
P. talamauensis	001375	Sumatra	KF626072
P. talamauensis	001376	Sumatra	KF625993
P. tujuhensis	001385	Sumatra	KF625999
P. tujuhensis	VP2305	Sumatra	KF802472

we redescribe only species, which are currently available in the types or are described as new. Other species were redescribed by Wong (1998) and Kazantsev (2009). All morphological measurements were taken using the ocular grid of an Olympus SZX-16 binocular microscope.

Abbreviations and depositories. Descriptions: BL–length of body; WH–width at humeri; PL–length of pronotum; PW–width of pronotum; Ediam–maximum eye diameter; Edist–minimum interocular distance in frontal part of cranium. Depositories: LMBC–Voucher collection of the Laboratory of Molecular Systematics, Faculty of Science UP, Olomouc; BMNH–Natural History Museum, London; MNHP–Museum d'histoire naturelle, Paris; ZRCS–Zoological Reference Collection, Raffles Museum of Biodiversity Research, NUS; KMTC–Kiyoshi Matsuda Collection, Takarazuka.

Laboratory methods and phylogenetic analyses

Total DNA was extracted using Wizard SV96 kit (Promega Inc.) and primers 16a (5'-CGCCTGTTTAACAAAAACAT-3'), 16b (5'-CCGGTCTGAACTCAGATCATGT-3') and ND1A (5'-GGTCCCTTACGAATTTGAATATATCCT-3') were used for PCR amplification of the 530–810 base pairs of *rrnL*, which showed the best results in identification of immature stages (Levkanicova and Bocak 2009). The setting of PCR reaction were described by Sklenarova et al. (2013). Purified PCR products were sequenced by an ABI 3130 automated sequencer using the Big Dye Terminator Cycle Sequencing Kit 1.1.

Sequence handling and phylogenetic analyses

Sequences were edited using the Sequencher 4.8 software package (Gene Codes Corp.). The *rrnL* mtDNA fragment was aligned using ClustalW 1.83 (Thompson et al. 1994), BlastAlign 1.2 (Belshaw and Katzourakis 2005) under default parameters, and Muscle 3.6 (Edgar 2004) under the gap opening parameter 2600 and gap extension parameter 240. The phylogenetic analyses were carried out under the maximum likelihood criterion using the RAxML 7.2.3 (Stamatakis et al. 2005) and the bootstrap support of branches (BS) assessed by analyzing 100 pseudoreplicates. All genes and codon positions in the protein coding fragments were partitioned. The model was proposed by jModelTest 2.1.2 (Posada 2008). The dataset was additionally analyzed using MrBayes 3.2.2 (Huelsenbeck 2000). The MCMC was set for independent variability of parameters in individual coding and non-coding genes under the GTR+I+G model. Two runs, each with four chains ran simultaneously for 40×10^6 generations, with trees being sampled every 1000th generation, all fragments were partitioned and unlinked. The first $6–9\times10^6$ trees were discarded as burn-in and posterior probabilities (PP) at nodes were determined from the remaining trees.

The ultrametric tree was produced from the tree depicted in Fig. 1 using r8s software (Sanderson 2002) and the GMYC method as implemented in SPLITS (http://www.rforge.r-project.org/projects/splits/) was applied to the ultrametric tree.

Results

Sequence variation and phylogeny

The DNA sequences of *rrnL* were produced for 73 specimens. The dataset of aligned *rrnL* sequences contained 530–723 homologous positions depending on the applied alignment procedure; 253–267 characters were parsimony informative. The topologies produced from BlastAlign, Muscle and Clustal alignments analyzed under maximum likelihood method and Bayesian inference identified the same strongly supported principal clades of Lyropaeinae and although topologies differed somewhat with respect to the deeper nodes of Miniduliticolini, all analyses recovered *Pendola*, *Macrolibnetis*, *Horakiella* and related taxa as deeper splits of Miniduliticolini and *Platerodrilus* as a terminal lineage (Fig. 1). One terminal, *Platerodrilus* sp. 000L01 was recovered outside Lyropaeinae and we consider its position as an artefact of the single marker analysis. The species was found in relationships to another *Platerodrilus* in the six-gene analysis of Lycidae (Bocak et al. 2008). Therefore this taxon is not considered in the further discussion.

The *P. paradoxus* and *P. major* clades were well supported in all analyses except by analysis of the Clustal alignment (BS 100%, PP 52–100% and BS 97–99%, PP 52–100%, respectively). The *P. sinuatus* group (including the nested *P. major* group) obtained much lower support (BS 46–56%, PP < 89%). The species level clusters and relationships of closely related species were regularly well supported (Fig. 1).

The GMYC analysis of the normalized tree was used as an independent test for morphology based delineation of species. The analysis suggested the clusters designated as *P. tujuhensis* and *P. maninjauensis* (uncorrected genetic distance 1.4%) as separate species and these are well supported also by morphological differences (see Taxonomy). Similarly, two separate species were inferred for two specimens of *P. sibayakensis* (uncorrected genetic distance 0.8%) and these do not differ in any morphological character and were collected in the same region.

DNA identification of immature stages

The origin of large-bodied neotenic larvae was recovered in three unrelated lineages: *Lyropaeus*, *Macrolibnetis depressus* + unidentified species from India and *Platerodrilus* (Fig. 1). Males and female larvae of four species, i.e. *P. foliaceus*, *P. maninjauensis*, *P. montanus* and *P. tujuhensis* clustered with conspecific males in clades with very high bootstrap support. Additionally, a number of larvae was assigned to the species groups in relationships to the previously described species (Fig. 1). We found that the species of the *P. paradoxus* clade share pronotum without glabrous prominent tubercles (Figs 1, 34, 40). Similarly, the species of the *P. sinuatus* group from continental Asia (Fig. 1) have smooth terga (VP2304, VP2311). The glabrous tubercles in the discs of the thoracic terga are present only in the lineage of Sumatran and Malay species of the *P. sinuatus* group (Fig. 1; terminals VP2308, VP2302, VP2307, VP0047 etc.). The robust, vermiform larva (Fig. 43) clustered with species of the *P. major* clade (Fig. 1).

Discussion

Supergeneric classification of *Platerodrilus* and related genera.

The results confirm that Lyropaeini (i.e., *Lyropaeus* Waterhouse, 1878 *sensu lato*) is an independent lineage with the large-bodied neotenic females and *Platerodrilus* belong to

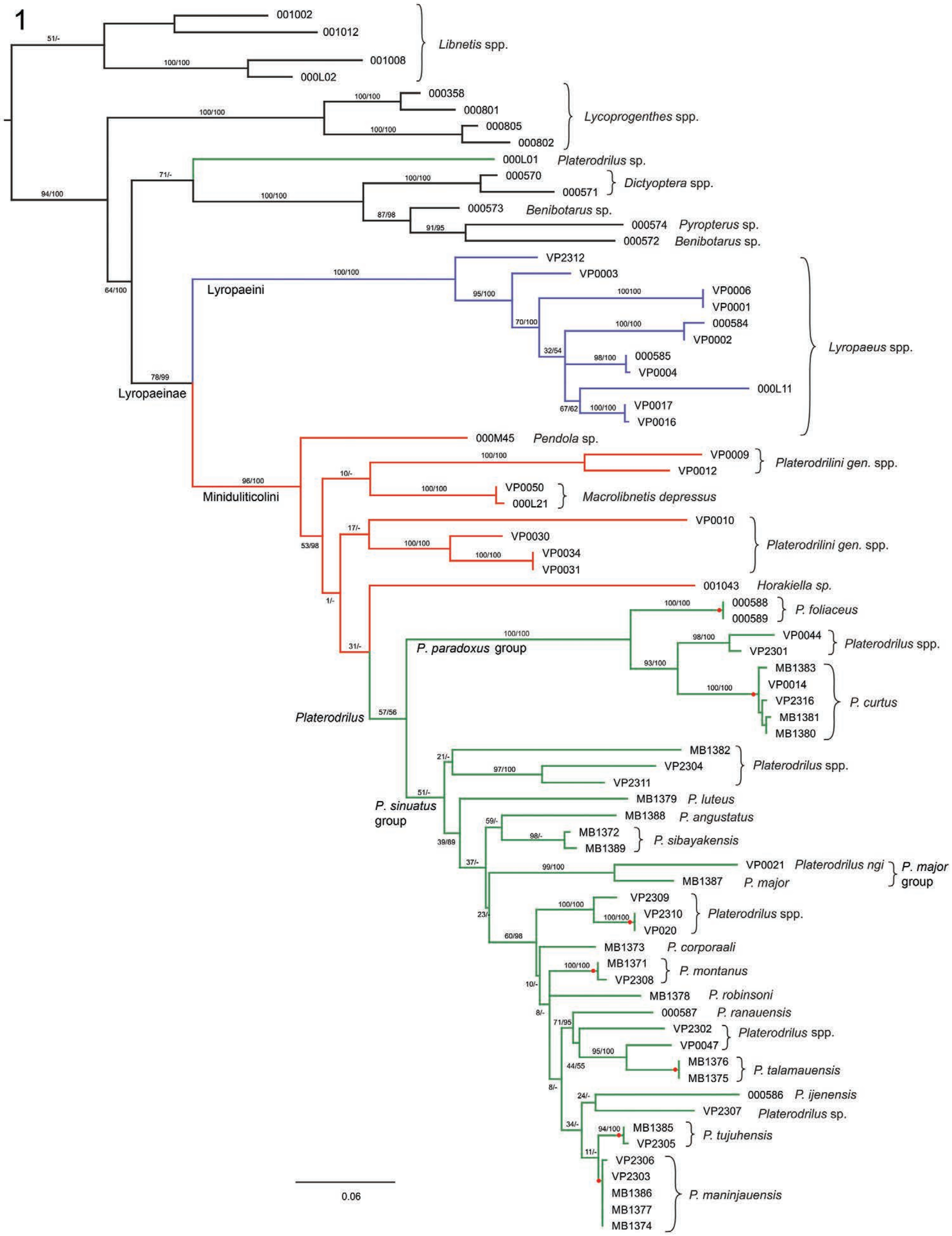


Figure 1. Phylogenetic hypothesis for *Platerodrilus* Pic, 1921 based on a maximum likelihood analysis of the Muscle alignment. Numbers at the branches are maximum likelihood bootstrap values and Bayesian posterior probabilities. The red dots designate GMYC species clusters.

a sister-clade of Lyropaeini along with *Macrolibnetis*, *Horakiella*, and *Pendola* (Fig. 1). Most of these genera are also known only from males but no large bodied female has been assigned to them and their females are probably larviform but similar in body size to males. The only miniduliticoline taxon with the large-bodied female except *Platerodrilus* is *Macrolibnetis* (Levkanicova and Bocak 2009).

The subfamiliar and tribal classification of *Platerodrilus* and related genera has been ambiguous. Mjöberg (1925) used the name Duliticolinae, but stated that the formal description should be postponed. Therefore, Duliticolinae Mjöberg, 1925 is an unavailable name. Kazantsev (2002) erected subfamily Duliticolinae without any description and with type genus *Platerodrilus* as a single genus classified in the new tribe, when he considered *Duliticola* as a junior synonym. According to the articles 13.1 and Articles 11.7.1.1 and 64 (ICZN 1999) the name Duliticolinae Kazantsev, 2002 is unavailable. Kazantsev (2002) further proposed the name Miniduliticolini for *Miniduliticola* Kazantsev 2002, but the description is uninformative: "The hypothesized apomorphies of the genus *Miniduliticola* gen. n., particularly glabrous elytra with no trace of longitudinal costae or tubercles support the erection of a new tribe". The single type specimen of *Miniduliticola* is damaged and there is no information available on male genitalia. The name Miniduliticolini Kazantsev, 2002 became the oldest available name for a clade which is recovered as a sister clade to Lyropaeini Bocak and Bocakova, 1989 (Fig. 1).

Kazantsev (2005) proposed Platerodrilini to replace Duliticolini Kazantsev, 2002. In this case, he provided description of the new taxon: "The Platerodrilini tr. n. is tentatively included in Miniduliticolinae. The hypothesized apomorphy of the new tribe distinguishing it from Miniduliticolini is the reticulated elytra." (Kazantsev 2005). Therefore, we have two available names for supergeneric taxa, one based on a single damaged specimen bearing characters correlated with small body (i.e. simplified structures, Bocak et al. 2014) and the second name without any delineation, based on *Platerodrilus*, which represents a crown branch in the current molecular phylogeny. As the position of Miniduliticolini was considered tentative in Duliticolinae sensu Kazantsev (2002) and also Platerodrilini were tentatively placed in Miniduliticolini (Kazantsev 2002), the names are not connected to any phylogenetic hypothesis to define their limits and relationships of *Miniduliticola* remain unknown. Therefore, we propose to use Miniduliticolini for designation of the whole clade in a sister position to Lyropaeini including *Platerodrilus*, *Pendola*, *Horakiella* and *Macrolibnetis* (Fig. 1). If Miniduliticolini belong to any other lineage, the sister-group to Lyropaeini would be designated as Platerodrilini.

Generic delineation of *Platerodrilus* and related genera.

Platerodrilus Pic, 1921, *Duliticola* Mjöberg, 1925, *Macrolibnetis* Pic, 1938, *Platerodriloplesius* Wittmer, 1941, *Falsocalochromus* Pic, 1942 and *Platrilus* Kazantsev, 2009 are available genus-group names referring to the platerodriline net-winged beetles with large-bodied neotenic females occurring in South East Asia (Fig. 2). The current results confirm that *Macrolibnetis* Pic, 1938 represents a distant lineage and does not belong to the *Platerodrilus* clade [considered as a synonym of *Platerodrilus* by Bocakova (2001) and Kazantsev (2002), reinstated by Bocak and Bocakova (2008)].

Figures 2–3. 2 Female larvae of *Platerodrilus.* **3** *Platerodrilus* sp. from Gn. Sinabung, Sumatra, ditto from Gn. Apo, Mindanao.

The other Miniduliticolini with large-bodied neotenic females form a clade designated as *Platerodrilus* in Fig. 1. The deepest split of *Platerodrilus* consists of a clade of *P. curtus*, *P. foliaceus* and several unidentified larvae (Figs 37–38). Their male genitalia (Figs 44–47) resemble those of *P. paradoxus* (see Kazantsev 2009) and the larvae do not have glabrous tubercles in the disc of the pronotum. These characters place *P. paradoxus* (type species of *Duliticola*) in the clade designated as *P. paradoxus* group in Fig. 1. Further, based on morphology, two species *P. svetae* and *P. wongi* (Fig. 5) are placed here. This group is a monophyletic lineage in Fig. 1, but we do not reinstate the name *Duliticola* Mjöberg, 1925 as the present sampling is limited and the genus cannot be recognized using external characters.

The sister clade to the *P. paradoxus* clade contains *Platerodrilus* species with two types of male genitalia: (a) the phallus with short, densely pubescent parameres (Figs 48–51) and (b) the phallus slender, curved, parameres with long membranous apical process (Figs 52–72). We designate these groups as *P. major* and *P. sinuatus* groups (Fig. 1). The *P. major* group (Figs 1, 17, 30, 48–51) contains species placed in *Platrilus* by Kazantsev (2009). This lineage represents a crown clade within *P. sinuatus* group (Fig. 1). This assemblage was designated as *Platerodrilus* sensu Wong (1998), when *P. major* Pic, 1921 was proposed as a type genus of *Platerodrilus* and *D. paradoxa* Mjöberg, 1925 for *Duliticola* to keep both names valid (invalid designations in the unpublished manuscript by Wong 1998). Kazantsev (2002) designated *P. sinuatus* Pic, 1921 as a type species of *Platerodrilus* and considered as *Duliticola* a junior synonym of *Platerodrilus*. Subsequently, he erected a separate genus *Platrilus* Kazantsev, 2009. As a subordinate lineage, *Platrilus* cannot be accepted in classification and is proposed to be a junior synonym of *Platerodrilus*.

The *P. sinuatus* group contains species from continental Asia, which form a deep split (terminals VP2304, VP2311) and further a group of species from the Sundaland and Palawan (Fig. 1). Larvae from continental Asia do not have any tubercles in the thoracic terga, similarly to the *P. paradoxus* and *P. major* group, only the species from Sumatra, Java and Malay Peninsula have the glabrous tubercles both in the disc and posterior margins of thoracic terga (Figs 32–33, 39). The males of these species can be assigned to continental or Sundaland lineages only with DNA data. Therefore, we propose to group them in the *P. sinuatus* group despite paraphyly of the assemblage.

Further two genus-group names were proposed for species now placed in *Platerodrilus*. *Platerodriloplesius* was erected for taxa with flabellate male antennae (Wittmer 1944). The male genitalia of *Platerodrilus bicolor* (Wittmer, 1941) (type species of *Platerodriloplesius*) resemble those of *P. paradoxus*. In contrast, genitalia of *P. palawanensis* sp. n. (Figs 69–70) and *P. borneensis* (Wittmer, 1966) (both species having the flabellate antennae) indicate their relationships to *P. sinuatus* group (Figs 52–72). Morphology of genitalia indicate that the species classified in *Platerodriloplesius* belong to different clades and *Platerodriloplesius* in Kazantsev's sense is a polyphyletic typological assemblage based on a highly variable morphology of male antennae, which might be used for pheromone communication, and therefore their surface is expanded by lamellae to house a higher number of olfactory sensors. As the type species of *Platerodriloplesius* belongs to the *P. paradoxus* group, *Platerodriloplesius* is a junior synonym of *Duliticola* and *Platerodrilus*.

Pic (1942) described *Falsocalochromus* in the supposed relationships to *Calochromus* Guérin-Méneville, 1833. The described species *Falsocalochromus ruficollis* Pic, 1942 is conspecific with *Duliticola hoiseni* Wong, 1996 from the *P. sinuatus* group and the *Falsocalochromus* is a junior synonym of *Platerodrilus.*

To sum up, we propose to consider *Duliticola*, *Platerodriloplesius*, *Platrilus* and *Falsocalochromus* to be junior synonyms of *Platerodrilus*. *Platerodriloplesius* represents a polyphyletic assemblage and *Platrilus* is a terminal branch supported by unique apomorphies rendering *Platerodrilus* in a paraphylum. As these taxa cannot be assigned to species groups without dissection of male genitalia, the proposed generic classification results in a definition of an easily recognisable monophyletic assemblage.

Rapid morphological divergence in male genitalia is widespread and results largely from sexual selection (Eberhard 2010). Therefore, delineations based on highly divergent genital morphology can lead to proposal of genus-rank taxa when the group of species sharing divergent genitalia represents only a terminal subclade. The molecular phylogeny revealed such pattern in broadly defined *Platerodrilus*, where three types of male genitalia are encountered. On the other hand, we can see low divergence in genitalia within *Platerodrilus* subclades, e.g., the *P. sinuatus* group. The diverging populations of *Platerodrilus* are in allopatry and the reinforcement of the reproductive barriers cannot take place. Probably as a result, the male genitalia are similar within species groups consisting of allopatrically distributed species (Wong 1998).

Taxonomy

***Platerodrilus* Pic, 1921**

Platerodrilus Pic, 1921: 13.

Type species: *Platerodrilus sinuatus* Pic, 1921 (subsequent designation by Kazantsev 2002: 6).

= *Duliticola* Mjöberg, 1925: 133; Kazantsev 2002: 6.
Type species: *Duliticola paradoxa* Mjöberg, 1925 (by monotypy).
= *Platerodriloplesius* Wittmer, 1941: 196 (as a subgenus of *Platerodrilus* Pic, 1921); Kazantsev 2009 (genus rank); syn. n.
Type species: *Platerodriloplesius bicolor* Wittmer, 1966 (by monotypy).
= *Falsocalochromus* Pic, 1942: 3, syn. n.
Type species: *Falsocalochromus ruficollis* Pic, 1942: 4 (by monotypy).
= *Platrilus* Kazantsev, 2009: 61, syn. n.
Type species: *Platerodrilus hirtus* Wittmer, 1938 (by original designation).

Adult male. Diagnosis. *Platerodrilus* differs from most Miniduliticolini in the stout body (6–11 mm) and characteristic types of male genitalia (Figs 44–72). The morphologically similar *Pendola* has genitalia resembling those of *Lyropaeus* (Bocak 2002). *Lyropaeus* differs in 10-segmented antennae and absent transverse costae on elytra.

Description. Male. Body 5.8–10.8 mm, flat, slightly widened posteriorly, densely pubescent. Pronotum and elytra bicoloured, uniformly yellow or black (Figs 4–17).

Head small, prognathous to slightly hypognathous, partly retracted in pronotum. Eyes hemispherically prominent, frontal interocular distance longer than maximum eye diameter. Labrum sclerotized, transverse, separated from clypeus, mandibles slender, long, slightly curved, incisor margin simple, without teeth, maxilla tiny, with setose mala, stipes plate-like, cardo vestigial, palpifer short, maxillary palpi 4-segmented, palpomere 1 shortest, about twice longer than palpifer, palpomere 2 longest, slender, palpomere 3 slightly longer than wide, apical palpomere slender, drop-like, with slender apical part. Labium reduced, mentum plate-like, formed by single sclerite, ligula absent, palpi 3-segmented, basal palpomeres subequal, rectangular to slightly longer than wide, apical palpomere twice longer than wide at base, pointed to apex.

Antennal tubercles present, usually strongly prominent. Antennae 11-segmented, slightly surpassing middle of elytral length, dark coloured, never with apical antennomeres pale, antennae usually weakly serrate, a few species with flabellate antennae. Scapus pear-like, robust, pedicel and antennomere 3 subequal in length, antennomeres of serrate antennae flattened, from antennomere 4 gradually slenderer, apical antennomere long, parallel-sided. Flabellate antennae with lamellae of antennomeres 3–10 longer than body of antennomere; whole antennae with dense erected pubescence.

Pronotum transverse with prominent to obtuse anterior angles (Figs 18–31), without carinae. Lateral margins elevated, straight to widely rounded, frontal angles sometimes inconspicuous, posterior angles mostly sharp, posterior margin bisinuate. Pronotum with deep depression along lateral margins, with sparse, long, erected pubescence. Scutellum longer than wide, triangular, simply rounded at apex. Elytra flat, slightly widened posteriorly, with well marked humeri; elytral costae inconspicuous, only costa 2 and 4 traceable in whole elytra, costa 4 forming humeral edge, other costae apparent at humeri, undefined in rest of elytral length. Two rows of inconspicuous, irregular cells traceable between costae, giving appearance of secondary costa in some parts of elytra. Elytra with dense, long pubescence. Wings fully developed. Legs slender, coxae long, movable, trochanters very slender, femora flat, robust, tibiae slenderer than femora, tarsi slender, 5-segmented, tarsomeres 3–4 with small pads, tarsomere 5 long, slender, claws simple. Male abdomen slender, shorter and narrower than elytra, 8 segmented, tergum 8 simply rounded at apex, sternum 8 with strengthened lateral margins at base and membranous window basally. Male genitalia trilobate, variable in relative length of phallus and parameres, phallus stout, almost straight and sometimes laterally compressed or phallus long, very slender, sickle like (Figs 52–72); parameres reaching to half or four fifths of phallic length, with fine spines along internal margin, fully sclerotized (Figs 44–47) or considerably shorter, apically with membranous process, phallobase short, emarginate basally (Figs 48–51).

Female mature larva. Diagnosis. Body shape characteristic ("trilobite larva" Figs 32–43). Two body types are present: the flat, wide (Figs 32–42) and robust, vermiform (Fig. 43). Although different in general appearance these larvae share common diagnostic characters: the fossa antennalis closed, separated from the mouth-parts by pleurostoma (the pleurostoma absent from other lycids); slender, longitudinal sclerite present ventrally of pleurostoma; mala sclerotized. The apical antennomere with several peg-like processes. The complex, oval meso- and metathoracic spiracles are cribriform, the sieve plate with multiple openings. They are situated in large depressions. Similar larvae of *Lyropaeus* differ in the shape of the apical antennomere and both *Macrolibnetis* and *Lyropaeus* do not have spiracular cavities in abdominal segments (Masek et al. 2014).

Description. Body wide, considerably flattened due to extensively projected lateral plates (Figs 32–41) or slender with postero-lateral processes (Fig. 43), usually dark brown, cryptically coloured, some species aposematically coloured with brightly coloured patches. Head prolonged, rounded anteriorly; epicranium consists of dorsal and pleural plates, membranous between plates. Complete fossa antennalis dorsally limited by epicranium, ventrally by sclerotized pleurostoma. Longitudinal sclerite situated ventrally of pleurostoma. Basal antennomere very short, apical antennomere with several peg-like processes ventrally and more extensive, sclerotized area dorsally. Mala sclerotized, with peg-like process. Cervical membrane extensive, with pigmented patches postero-ventrally. Pronotum trapezoid, terga with considerably widened lateral plates and sometimes with tubercles at posterior margin. Prosternum prolonged, episterna extensive, attached to prosternum. Extensive spiracular plates with spiracular openings at margin and bottom of extensive cavity in both, meso- and metathorax. Legs slender, relatively long, trochanters divided in two parts. Abdomen with large lateral processes, spiracular openings on margin and bottom of cavities in segments A1–A8. Sterna A1–A8 with slender postero-lateral processes, upper pleurites extensive, with similar process at outer posterior angle. Lower pleurites very small, with short process only in segments A3–A8. Segment A9 widest at apex, with short, fixed urogomphi (Figs 35–40, 43).

Remark. Sexually mature larviform females observed only by Mjöberg (1925) and Wong (1996) were not available to us. The collected larvae did not pass the final ecdysis and their maturity is supposed on the basis of their body length. Only several lower instar larvae were collected and they differ from later instars in shorter and partly missing processes and absence of spiracular cavities.

Biology. The information on biology was given by Wong (1996) and Bocak and Matsuda (2003).

List of species

Species group *Platerodrilus paradoxus* Mjöberg, 1925

Diagnosis. The species group *P. paradoxus* was recovered as a monophyletic assemblage representing one of principal *Platerodrilus* lineages. The species of this group share male genitalia with long, slender and completely sclerotized parameres (Figs 44–47). Known females do not have any glabrous tubercles in the middle of thoracic terga (Figs 34–38, 40), one species from Mt. Kinabalu has tubercles only at posterior margins of thoracic terga (Fig. 40). The following species are classified here: *P. bicolor* Wittmer, 1941, *P. curtus* Pic, 1931, *P. foliaceus* sp. n., *P. paradoxus* Mjöberg, 1925, *P. piceicollis* Pic, 1943, *P. strbai* Kazantsev, 2009, *P. svetae* Kazantsev, 2009, *P. wongi* sp. n.

Distribution. Most species are known from Borneo and the Philippines, only *P. wongi* sp. n. occurs in Sumatra.

Remark. As only *P. curtus*, *P. foliaceus* and several unidentified female larvae were available for DNA isolation, the monophyly of this lineage needs further support before validity of the name *Duliticola* Mjöberg, 1925 can be reconsidered.

Platerodrilus paradoxus (Mjöberg, 1925)

Duliticola paradoxa Mjöberg, 1925: 134.
Platerodrilus paradoxus: Kazantsev 2002: 6.

Material examined. Syntype. Male (BMNH), Borneo. Syntype. Female (BMNH), Lundu, Sarawak, G. E. Bryant, 6. 1. 14.

Diagnosis. *P. paradoxus* belongs to a group of Bornean species with robust and long parameres. The male of *P. paradoxus* resembles *P. foliaceus* but differs in the slender apex of parameres. Additionally these species differ in larval morphology (Figs 34, 40).

Redescription. Male. Body 7 mm, dark brown, only humeri and elytral suture slightly lighter. Head small, with hemispherically prominent eyes, head with eyes wider than frontal margin of pronotum, eye diameter 1.9 times frontal interocular distance. Antennae compressed, covered with long, erected, dense pubescence. Pronotum flat, without carinae, 1.8 times wider than long at midline, frontal margin widely rounded anteriorly, frontal angles obtuse, lateral margins almost straight, posterior margin bisinuate. Elytra flat, parallel-sided, elytral costae inconspicuous, elytra 2.6 times longer than width at humeri. Legs slender, compressed, densely pubescent. Male genitalia with robust parameres, phallus slightly curved with bulbous tip. Parameres stout with hooked tip, apical half of ventral edge serrate. Phallobase wide, deeply emarginate.

Female larva. Body flat and wide (Fig. 34), pronotum parallel-sided at base, then gradually tapering to front, triangular, without any glabrous tubercles in disc, only small tubercles in middle part of posterior margins of thoracic segments, in middle of anterior pronotal margin four subequal tubercles; mesothorax strongly transverse, with rounded lateral margins and straight posterior margin, posterior angles obtuse, metathorax similar in shape with more acutely projected posterior angles. Abdomen with short, robust lateral processes.

Measurements. Male. BL 6.9 mm, PL 1.0 mm, PW 1.9 mm, HW 2.0 mm, Edist 0.85 mm, Ediam 0.44 mm. Larva. BL 53.0 mm, PL 8.7 mm, PW 13.4 mm.

Distribution. Malaysia: Sarawak. Known only from the type locality.

Platerodrilus foliaceus **sp. n.**

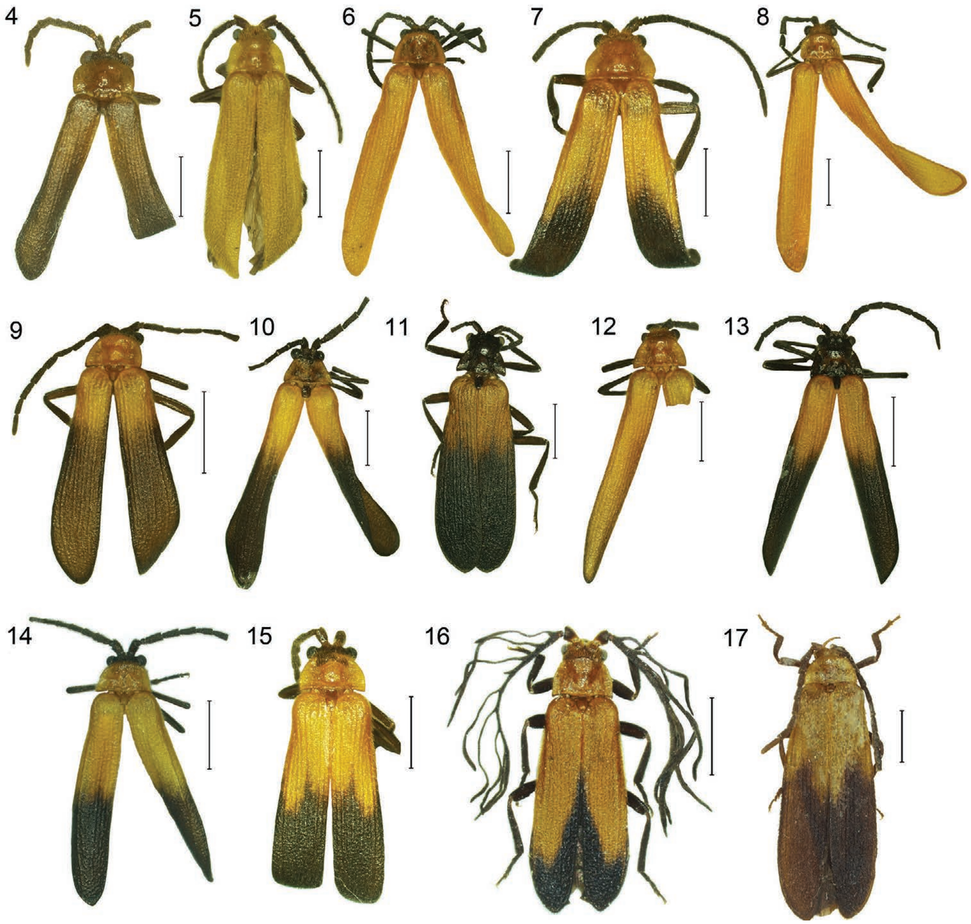
http://zoobank.org/53AA2216-605A-4A64-A10B-C58AEF0B8E31

Figs 4, 22, 40, 46–47

Material examined. Holotype. Male (LMBC, UPOL 000589), Borneo, Central Kalimantan Prov., 60 km SE Muara Teweh, 1°20'25"S, 115°20'16"E, 24.–28. Jun. 2001, 150 m. Paratypes. 12 females, same locality data (LMBC, UPOL 000588).

Diagnosis. *P. foliaceus* belongs to the *P. paradoxus* group and the male resembles *P. paradoxus* in general appearance. *P. foliaceus* differs in the rounded apex of parameres (Figs 46–47). The female larvae of *P. foliaceus* are very flat and have much slenderer lateral processes of abdominal segments than *P. paradoxus* (Figs 34, 40).

Description. Male. Body small-sized, brown, head, antennae, legs except bases of femora and apical three fifths of elytra dark brown (Fig. 4). Head small, with hemispherically prominent eyes, head with eyes slightly wider than frontal margin of pronotum, eye diameter 1.7 times frontal interocular distance. Antennae compressed, covered with long, erected, dense pubescence, length of antennomere 3 0.7 times antennomere 2. Pronotum flat, without carinae, 1.7 times wider than long at midline, frontal margin slightly projected anteriorly, frontal angles obtuse, but apparent, lateral margins rounded, posterior margin slightly bisinuate (Fig. 22). Elytra flat, parallel-sided, elytral costae inconspicuous, elytra 2.9 times longer than width at humeri. Legs slender, compressed, densely pubescent. Male genitalia with robust parameres, phallus slightly curved with bulbous tip. Parameres stout with hooked tip, apical half of ventral edge serrate. Phallobase wide, deeply emarginate (Figs 46–47).



Figures 4–17. Adult male, general appearance: **4** *P. foliaceus* **5** *P. wongi* **6** *P. robinsoni* **7** *P. maninjauensis* **8** *P. luteus* **9** *P. ranauensis* **10** *P. sibayakensis* **11** *P. sinabungensis* **12** *P. tujuhensis* **13** *P. montanus* **14** *P. ijenensis* **15** *P. talamauensis* **16** *P. palawanensis* **17** *P. wittmeri*. Scales 2 mm.

Female larva. Body extremely flat and wide (Fig. 40), pronotum triangular, without any glabrous tubercles, in middle of anterior margin four subequal tubercles; mesothorax strongly transverse, with rounded lateral margins and moderately projected posterior angles, metathorax similar in shape with more acutely projected posterior margins. Abdomen with very slender and long lateral processes.

Measurements. Male. BL 6.0 mm, PL 0.9 mm, PW 1.5 mm, HW 1.7 mm, Edist 0.78 mm, Ediam 0.46 mm. Larva. BL 19.3 mm, PL 5.1 mm, PW 11.2 mm.

Distribution. Indonesia: Kalimantan. Known only from the type locality.

Etymology. The specific epithet refers to the flat body shape of the female larva.

Remark. The males and female larvae were identified as conspecific on the basis of highly similar sequences of *rrnL* (Fig. 1).

Platerodrilus wongi sp. n.

http://zoobank.org/67F26E3D-C5E3-4E35-A630-B6A636DB969D
Figs 5, 28, 44–45

Material examined. Holotype. Male (LMBC), Sumatra Utara, Brastagi, Gn. Sibayak, 19–23. Feb. 1998, 700–2000 m.

Diagnosis. *P. wongi* is a single species of the *P. paradoxus* group occurring in Sumatra. It resembles *P. curtus* from the Philippines in the uniformly yellow elytra, but has relatively shorter parameres (Figs 44–45).

Description. Body brown, head, pronotum, mesoscutellum and elytra yellow (Fig. 5). Head small, with eyes is slightly wider than frontal margin of pronotum, antennal tubercles deeply separated. Eyes hemispherically prominent, frontal interocular distance 2.4 times eye diameter. Antennae slender, compressed, reaching two thirds of elytra length, antennomere 3 1.1 times antennomere 2. Head and antennae covered with short dense pubescence. Pronotum transverse, 1.6 wider than length at midline. Anterior margin only slightly projected, anterior angles well marked, lateral margins almost straight, posterior margin shallowly bisinuate (Fig. 28). Elytra parallel-sided, with inconspicuous carinae. Elytra 3.0 times longer than width at humeri, elytra widest in apical sixth. Legs compressed, densely pubescent. Male genitalia with laterally compressed, slightly curved phallus with bulbous tip, parameres stout, long, with hooked tip, apical half of ventral edge serrated, phallobase wide, deeply emarginate (Figs 44–45).

Measurements. BL 7.4 mm, PL 1.0 mm, PW 1.6 mm, HW 1.9 mm, Edist 0.91 mm, Ediam 0.38 mm.

Distribution. Indonesia: Northern Sumatra.

Etymology. The specific epithet is a patronym in honour of Alvin T. C. Wong.

The key to identification of males from the *P. paradoxus* species group

1 Parameres short, reaching slightly over half of phallic length .... ***P. strbai*** **Kazantsev**
– Parameres reaching almost to the apex of the phallus **2**
2 Male antennae flabellate .... ***P. bicolor*** **Wittmer**
– Male antennae serrate **3**
3 Whole elytra yellow (Fig. 5) **4**
– Elytra dark brown or light brown with dark coloured apical part **5**
4 Parameres reaching to five sixths of the phallic length .... ***P. curtus*** **Pic**
– Parameres reaching to three fourths of the phallic length .... ***P. wongi*** **sp. n.**
5 Only apical part of elytra dark coloured, pronotum black .... ***P. piceicollis*** **Pic and** ***P. svetae*** **Kazantsev***
– Whole elytra dark brown, at most the narrow humeral part slightly lighter brown **6**

6 Body slender, inner margin of parameres serrate only in its apical half .... ***P. foliaceus* sp. n.**
– Body robust, inner margin of parameres serrate in three quarter of their length ....***P. paradoxus* (Mjöberg)**

* We failed to find any distinguishing character between *P. svetae* and *P. piceicollis*. The type of *P. svetae* is deposited in a private collection and unavailable for study.

Species group *Platerodrilus major* Pic, 1921

Diagnosis. The species group *P. major* is a monophyletic assemblage representing a terminal branch, which includes the species placed in *Platrilus* Kazantsev, 2009 and it is represented in the current analysis by *P. major* and *P. ngi* (Fig. 1). The group is characterized by the short and setose parameres without long membranous apical processes (Figs 48–51). The following species are placed here: *P. atronotatus* Pic, 1943, *P. crassicornis* Pic, 1923, *P. hirtus* Wittmer, 1938, *P. major* Pic, 1921, *P. ngi* sp. n. and *P. wittmeri* sp. n. The species described by M. Pic were redescribed by Wong (1998).

Platerodrilus ngi sp. n.

http://zoobank.org/638DD7A0-68EC-499D-A6BA-16560A6D2808
Fig. 43

Material examined. Holotype. Male (LMBC), Singapore, Bukit Timah and Central Water Catchment, 19.–22. May 2013, 50–100 m, E. Jendek and O. Šauša leg. Paratypes. Female larvae, 6 spec., Malaysia, Pahang, Tioman, Kg. Tekek–Juara trail, 50–300 m, 2°49'10"N, 104°10'21"E, 29. Mar.–2. Apr. 2013, same locality data, 4.–16. Mar. 1998, L. Dembicky and P. Pacholatko (LMBC); 1 spec., Singapore, Sime Road swamp, 30. Oct. 2008 (ZRCS);1 spec., Singapore, Bukit Timah Nature Reserve, A. T. C. Wong 1993 (ZRCS); 1 spec., Singapore, Sime Road, C. Lee (ZRCS, #6.20969, 1993.7277, 1993.7278).

Diagnosis. *P. ngi* is the only representative of the *P. major* group known from Singapore and Tioman. It differs in dark red colouration of the pronotum and humeral two thirds of elytra from *P. atronotatus* from the Malay Peninsula. *P. atronotatus* has the black pronotum. Additionally, the phallus of *P. atronotatus* is slender and antennomeres 3 and 4 short and much wider.

Description. Male. Body small, dark brown to black, head, prothorax, mesoscutellum and basal two thirds of elytra dark red; whole body with dense, short, pubescence. Head small, including eyes slightly wider than frontal margin of pronotum. Eyes hemispherically prominent, frontal interocular distance 1.8 times eye diameter. Antennae robust at base, compressed, reaching two thirds of elytral length, antennomere 3 0.6 times antennomere 2, antennomere 3 as long as wide at apex. Pronotum flat, 1.7 times wider than long at midline. Anterior margin almost straight, anterior angles sharply marked, posterior margin bisinuate. Elytra slightly wider posteriorly, elytra 2.8 times longer than width at humeri; only slightly widened posteriorly, elytral costae conspicuous. Legs compressed, densely pubescent. Male genitalia with straight phallus and setose parameres, short phallobase slightly shorter than parameres.

Female larva. Body slender, parallel-sided (Fig. 43), pronotum triangular, with two basal, dark coloured, glabrous tubercles; mesothorax slightly transverse, without projected posterior angles, metathorax similar in shape. Abdomen with robust, short lateral processes and fixed urogomphi.

Measurements. Male. BL 6.9 mm, PL 0.9 mm, PW 1.6 mm, HW 2.1 mm, Edist 0.86 mm, Ediam 0.48 mm. Larva. BL 30.2 mm, PL 5.7 mm, PW 5.6 mm.

Distribution. Singapore, Malaysia: Pahang. Biology and female specimens collected in Singapore were reported by Lok (2008).

Etymology. The species name is a patronym in honour of Peter Ng.

Platerodrilus wittmeri sp. n.

http://zoobank.org/F646300B-C3B4-48BA-98B2-9BB9571C762B

Figs 17, 30, 50–51

Material examined. Holotype. Male (LMBC), Java, K. O. Blawan, Ijen Plateau, Jul. 1940, 900–1500 m, H. Lucht coll.

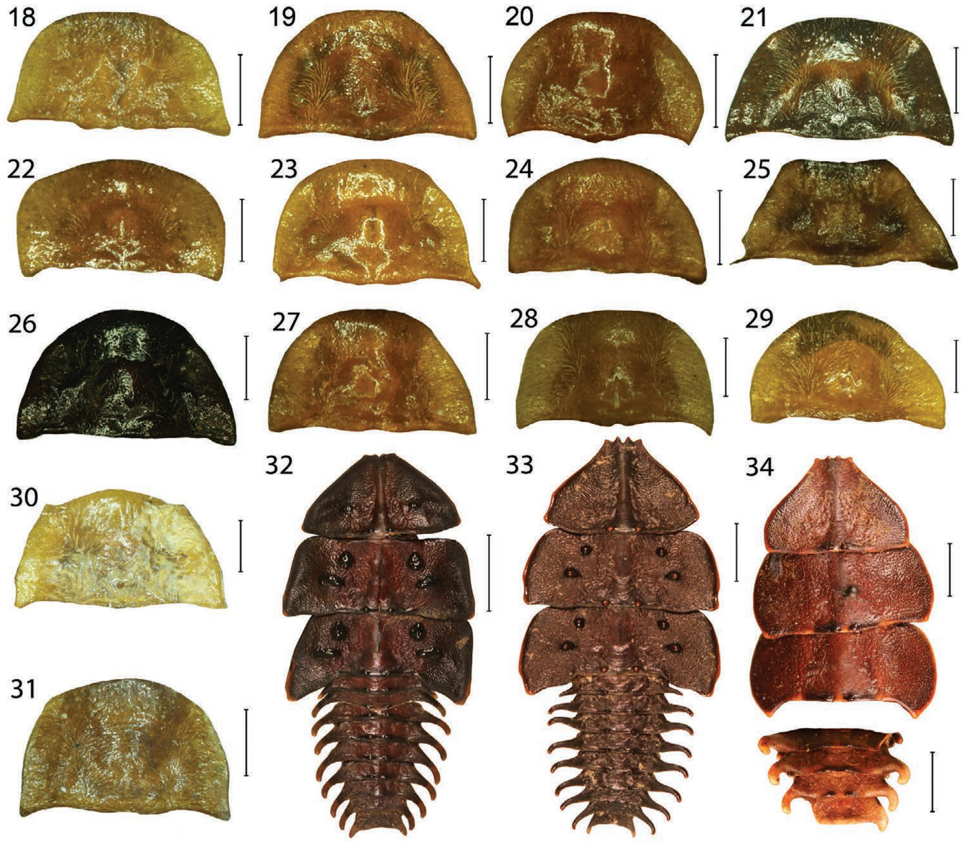
Diagnosis. *P. wittmeri* is the only bicoloured species from the *P. major* group in Java. It resembles *P. major* from Northern Sumatra in colouration but differs in the shorter phallobase (Figs 48–49, 50–51).

Description. Male. Body medium-sized, dark brown, head, prothorax, mesoscutellum and basal half of elytra testaceous; antennae, legs, apical half of elytra dark brown to black (Fig. 17). Head small, including eyes slightly wider than frontal margin of pronotum. Eyes hemispherically prominent, frontal interocular distance 1.9 times eye diameter. Antennae slender, compressed, reaching two thirds of elytral length, antennomere 3 0.7 times antennomere 2. Head and antennae with dense, short, pubescence. Pronotum flat, 1.9 times wider than long at midline. Anterior margin slightly projected anteriorly, anterior angles sharply marked, prominent, posterior margin bisinuate (Fig. 30). Elytra almost parallel-sided, 3.5 times longer than width at humeri; only slightly widened posteriorly, elytral costae inconspicuous. Legs compressed, densely pubescent. Male genitalia with straight phallus and setose parameres, short phallobase slightly shorter than parameres (Figs 50–51).

Measurements. BL 10.1 mm, PL 1.1 mm, PW 2.0 mm, HW 2.6 mm, Edist 0.95 mm, Ediam 0.49 mm.

Distribution. Indonesia: Java.

Etymology. The specific epithet is a patronym in honour of the late W. Wittmer, who donated the specimen to the senior author in 1992.



Figures 18–34. Male pronotum of *Platerodrilus*. **18** *P. ijenensis* **19** *P. robinsoni* **20** *P. maninjauensis* **21** *P. montanus* **22** *P. foliaceus* **23** *P. luteus* **24** *P. ranauensis* **25** *P. sibayakensis* **26** *P. sinabungensis* **27** *P. tujuhensis* **28** *P. wongi* **29** *P. talamauensis* **30** *P. wittmeri* **31** *P. palawanensis*. Larva, general appearance: **32** *P. maninjauensis* **33** *P. montanus* **34** *P. paradoxus*. Scales 0.5 mm (Figs **18–31**); Scales 5 mm (**32–34**).

The key to identification of males from the *P. major* species group

1 Metathorax orange brown .... ***P. crassicornis* Pic**

– Metathorax dark brown to black **2**

2 Phallobase shorter than parameres (≤ 0.95 times length of parameres) .... ***P. wittmeri* sp. n.**

– Phallobase longer than parameres (≥ 1.05 times length of parameres **3**

3 Phallus short and stout, about 0.90 the combined length of parameres and phallobase, pronotum similar in colour to humeral part of elytra **4**

– Phallus long and slenderer, about as long as the combined length of parameres and phallobase, pronotum blac .... ***P. atronotatus* Pic**

4 Antennomere 4 wide, about as long as wide at apex .... ***P. ngi* sp. n.**

– Antennomere 4 at least 1.25 times longer than wide at apex **5**

5 The expanded base of phallus in lateral view mostly hidden by parameres, phallobase deeply emarginate basally, elytra black apically......... ***P. major*** **Pic**

– The expanded base of phallus in lateral view exposed, considerably widened, phallobase shallowly emarginate basally, elytra testaceous..***P. hirtus*** **Wittmer**

Species group *Platerodrilus sinuatus* Pic, 1921

Diagnosis. The group *P. sinuatus* is a paraphyletic assemblage consisting of *P. luteus*, the Indo-Burmese species (represented in the analyzed dataset by female larvae VP2304, VP2311), *P. palawanensis* from Palawan, *P. indicus* from Assam and Nepal and the terminal lineage of *Platerodrilus* from Sundaland (Figs 1–2). All species have a long, slender, considerably curved phallus and short parameres with the membranous apical process (Figs 52–72). The following species are placed in this species group: *P. angustatus* Pic, 1921*, P. apicalis* Pic, 1936*, P. atricolor* Pic, 1938*, P. corporaali* Pic, 1921, *P. grootaerti* Kazantsev, 2009, *P. holynskae* Kazantsev, 2009, *P. inapicalis* Pic, 1937*, P. indicus* Wittmer, 1966, *P. luteus* sp. n., *P. maninjauensis* sp. n., *P. montanus* sp. n., *P. palawanensis* sp. n., *P. ranauensis* sp. n., *P. reductus* Pic, 1926, *P. rotundicollis* Wittmer, 1938, *P. ruficollis* Pic, 1942, *P. rufus* Pic, 1924, *P. sinuatus* Pic, 1921, *P. talamauensis* sp. n., *P. tujuhensis* sp. n., *P. sibayakensis* sp. n. and *P. sinabungensis* sp. n. The female larvae of species occurring in continental Asia north of the Isthmus of Kra have terga without glabrous tubercles similarly to the species of the *P. paradoxus* clade. The group of species from the Malay Peninsula, Sumatra and Java are characterized by larvae with glabrous tubercles in thoracic terga (Figs 1, 32–33, 39, 41). The male genitalia are similar in the shape of the basal part of the phallus and phallobase. The minute differences are difficult to describe in a form of the identification key and the DNA data were used for confirmation of the species delineation in several cases.

Platerodrilus ijenensis sp. n.

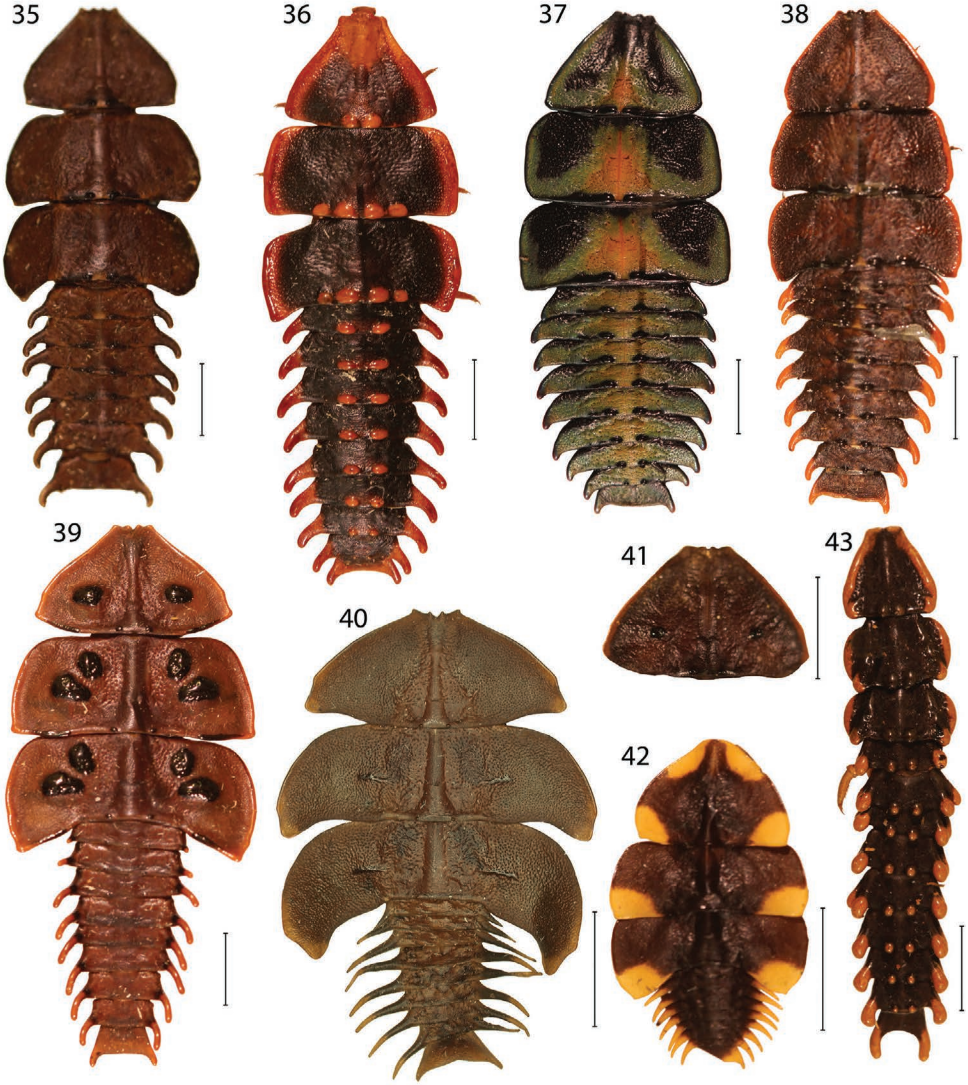
http://zoobank.org/21013FB1-3B9C-42F2-879D-A1CAC5AF4EED

Figs 14, 18, 64–65

Material examined. Holotype. Male (LMBC, 000586), Java, Ijen N. P., 12 km W of Sodora, 3–5. May 2001, 1000 m.

Diagnosis. *P. ijenensis* is the only Javanese species of *P. sinuatus* group with bicoloured elytra. It resembles in colour pattern the Sumatran species *P. corporaali*, which differs in the reddish coloured head and basal antennomeres, and the very short antennomere 3.

Description. Body and head dark brown to black, pronotum, mesoscutellum and elytra in humeral half orange, apical part of elytra dark brown to black (Fig. 14). Head small, including eyes narrower than pronotum at posterior angles, antennal tubercles slightly prominent. Eyes hemispherically prominent, eye diameter 1.8 times frontal interocular distance. Antennae slender, compressed, length of antennomere 3 1.2 times



Figures 35–43. Larvae of *Platerodrilus* and *Macrolibnetis*: **35–38** *Platerodrilus* spp. **39** *Platerodrilus ruficollis* **40** *P. foliaceus* **41** *P. tujuhensis* **42** *Macrolibnetis depressus* **43** *Platerodrilus ngi*. Scales 5 mm.

antennomere 2. Pronotum transverse, 1.8 wider than long at midline, anterior margin slightly projected forward, anterior angles marked, lateral margins almost straight, posterior margin bisinuate (Fig. 18). Elytra 3.3 times longer than width at humeri, elytra parallel-sided, elytral costae inconspicuous. Legs slender, compressed, densely pubescent. Male genitalia with slender, curved phallus and small rounded parameres bearing slender membranous process, phallobase wide, narrowly and deeply emarginate (Figs 64–65).

Measurements. BL 7.2 mm, PL 0.9 mm, PW 1.6 mm, HW 1.8 mm Edist 0.70 mm, Ediam 0.40 mm.

Distribution. Indonesia: Java.

Etymology. The specific name refers to the type locality.

Platerodrilus korinchianus (Blair, 1928)

Duliticola korinchiana Blair, 1928: 181.
Platerodrilus korinchianus (Blair, 1928): Kazantsev 2009.

Material examined. Lectotype (hereby designated). Male (BMNH), Sumatra, Korinchi, 4500 ft, N. 1914, K. G. Blair. Paralectotype. Female (BMNH), same locality data.

Diagnosis. The male genitalia are missing. Therefore, only information on external morphology can be compared. The orange pronotum and humeral part of elytra resemble *P. corporaali* or *P. maninjauensis*, but no similar species is known from the Kerinci massif.

Redescription. *Male.* Body black, head dark brown, pronotum and basal quarter of elytra orange; antennae, and legs dark brown to black. Head small, antennal tubercles weak, eyes hemispherically prominent, frontal interocular distance 2.3 times maximum eye diameter. Antennae slender, compressed, densely pubescent, antennomere 3 as long as antennomere 2. Pronotum transverse, 1.5 times wider than long, anterior margin almost straight, frontal angles conspicuous, lateral margins almost straight, posterior angles acute, surface mat at margins, slightly glabrous in middle. Elytra parallel-sided, elytral costae weak, covered with dense pubescence. Male genitalia missing.

Measurements. PL 1.3 mm, PW 1.9 mm, HW 2.6 mm, Edist 0.84 mm, Ediam 0.36 mm.

Distribution. Indonesia: Sumatra, Jambi, Kerinci massif.

Remark. The lectotype is damaged (the apical half of elytra and abdomen are missing). *P. korinchianus* differs in the shape of pronotum and colouration of elytra from *P. tujuhensis* and *P. robinsoni*. The paralectotype, a female larva, is very similar to the female larva of *P. tujuhensis* from the same locality and might not be conspecific with the male specimen. As larvae are generally difficult to identify without DNA data, we prefer to designate a lectotype to keep status and preserve the validity of the name. The species can be misidentified as high diversity of neotenic net-winged beetles in the region was documented (Malohlava and Bocak 2010) and further species of *Platerodrilus* can occur in this locality.

Platerodrilus luteus sp. n.

http://zoobank.org/6BE29EC6-3F39-4775-83EC-7BAB16828345
Figs 8, 23, 67–68

Material examined. Holotype. Male (LMBC, UPOL 001379), Sumatra, Jambi Kersik Tua, Gn. Kerinci, 19.–22. Jan. 2005, 1600–2200 m.

Diagnosis. *P. luteus* resembles in general appearance the syntopically occurring *P. robinsoni*, but these species are distantly related according to the recovered molecular

Figures 44–55. Male genitalia of *Platerodrilus*: **44–45** *P. wongi* **46–47** *P. foliaceus* **48–49** *P. major* **50–51** *P. wittmeri* **52–53** *P. talamauensis* **54–55** *P. ranauensis*. Scales 0.25 mm.

phylogeny (Fig. 1). The male of *P. luteus* differs from similarly coloured Sumatran *Platerodrilus* in the very wide and broadly emarginate phallobase (Fig. 67).

Description. Body black, head dark brown, pronotum and elytra orange; antennae, and legs dark brown to black (Fig. 8). Head small, antennal tubercles weak, eyes hemispherically prominent, frontal interocular distance 2.8 times maximum eye diameter. Antennae slender, compressed, densely pubescent, antennomere 3 1.5 times longer than antennomere 2. Pronotum transverse, 1.7 times wider than long, frontal angles inconspicuous, lateral margins slightly convex, posterior angles acute (Fig. 23). Elytra parallel-sided, 3.7 times longer than width at humeri, elytral costae weak, covered with dense pubescence. Male genitalia with curved phallus; parameres short, rounded, with slender membranous processes; phallobase wide, deeply emarginate (Fig. 67–68).

Measurements. BL 10.1 mm, PL 1.1 mm, PW 1.8 mm, HW 2.3 mm, Edist 0.83 mm, Ediam 0.45 mm.

Distribution. Indonesia: Sumatra.

Etymology. The specific epithet refers to yellow colouration of the body.

Platerodrilus maninjauensis **sp. n.**

http://zoobank.org/6F62649B-E974-4BF7-BD30-BF13FD3A8681

Figs 7, 20, 32, 60–61

Material examined. Holotype. Male (LMBC, UPOL 001386), Sumatra, Barat Lake Maninjau, E coast, 12.–23. Jan. 2005, 800 m. Paratype. Male (LMBC, UPOL 001374), Sumatra, Barat Lake Maninjau, E coast, 12.–23. Jan. 2005, 800 m. Paratypes. Male, 2 females (LMBC, UPOL 001377), Sumatra, Barat, Pasaman, Gn. Talamau, 14.–15. Jan. 2005, 1000 m; female larva (LMBC, UPOL VP2303), Sumatra, Barat Lake Maninjau, E coast, 12.–23. Jan. 2005, 800 m.

Diagnosis. *P. maninjauensis* is a sister species to *P. tujuhensis* from Northern Sumatra. These species differ in the colouration (Figs 7, 12) and the shape of the phallus and phallobase (Figs 56–57, 60–61). The female larvae of both species are similar and differ only in the relative size of the mesonotal tubercles, which are smaller in *P. tujuhensis* (Figs 32, 41).

Description. Male. Body medium-sized, dark brown; head, prothorax, mesoscutellum and basal three fifths of elytra orange; antennae, legs, apical two fifths of elytra dark brown to black (Fig. 7). Head small, including eyes narrower than frontal margin of pronotum. Eyes hemispherically prominent, eye diameter 2.2 times frontal interocular distance. Antennae slender, compressed, reaching two thirds of elytral length, antennomere 3 0.9 times antennomere 2. Head and antennae with dense, short, pubescence. Pronotum flat, 1.1 times wider than long at midline. Anterior margin widely rounded, anterior angles inconspicuous, posterior margin bisinuate (Fig. 20). Elytra almost parallel-sided, 3.5 times longer than width at humeri; slightly widened posteriorly, widest at apical fourth. Elytral costae inconspicuous. Legs compressed, densely pubescent. Male genitalia with short rounded parameres bearing slender membranous process. Phallus curved, phallobase wide, widely emarginate (Figs 60–61).

Female larva. Body flat, wide (Fig. 32), pronotum triangular, with two glabrous rounded tubercles postero-laterally, another two tubercles in middle of anterior margin; mesothorax strongly transverse, with rounded lateral margins and weakly projected posterior angles, laterally with four tubercles, upper rounded, lower transverse, metathorax similar in shape with more acutely projected posterior margins. Abdominal segments with slender and long lateral processes.

Measurements. BL 7.0 mm, PL 0.9 mm, PW 1.6 mm, HW 1.7 mm, Edist 0.84 mm, Ediam 0.38 mm. Larva. BL 24.1 mm, PL 5.4 mm, PW 10.3 mm.

Figures 56–66. Male genitalia of *Platerodrilus*: **56–57** *P. tujuhensis* **58–59** *P. sinabungensis* **60–61** *P. maninjauensis* **62–63** *P. robinsoni* **64–65** *P. ijenensis* **66** *P. montanus*. Scales 0.25 mm.

Distribution. Indonesia: Sumatra.

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

Platerodrilus montanus sp. n.

http://zoobank.org/A434CA37-4D6B-4055-92F6-A16A1D3CA9B5

Figs 13, 21, 33, 66

Material examined. Holotype. Male (LMBC, UPOL 001371), Sumatra Utara, Brastagi, Gn. Sibayak, 26. Jan.–1. Feb. 2005, 1600–2200 m. Paratype. Female larva

(LMBC, UPOL VP2308), Sumatra Utara, Brastagi, Gn. Sinabung, 29.–30. Jan. 2005, 1400–2000 m.

Diagnosis. *P. montanus* and *P. sinabungensis* are the only Sumatran species with the dark coloured pronotum. These species differ in the shape of the phallobase, when *P. montanus* has the narrowly emarginate base (Figs 58–59, 66). The larva of *P. montanus* has pronotum without any glabrous tubercles in the disc (Fig. 33).

Description. Body medium-sized, dark brown to black, only basal half of elytra orange and pronotum with irregular light coloured patches in disc (Fig. 13). Head small, including eyes slightly narrower than frontal margin of pronotum. Eyes hemispherically prominent, eye diameter 2.4 times frontal interocular distance. Antennae compressed, length of antennomere 3 1.1 times antennomere 2. Head and antennae with dense, short, pubescence. Pronotum transverse, 1.9 times wider than long at midline; anterior margin slightly projected, lateral margins almost straight, anterior angles weakly marked, posterior margin of pronotum slightly bisinuate (Fig. 21). Elytra almost parallel-sided, elytra 3.5 times longer than width at humeri; slightly widened posteriorly, widest at apical fourth, elytral costae inconspicuous. Legs compressed, with dense pubescence. Male genitalia with short rounded parameres bearing slender membranous processes. Phallus curved, phallobase wide, deeply emarginate (Fig. 66).

Female larva. Body flat, wide (Fig. 33), pronotum triangular, without glabrous tubercles except two tubercles in middle of posterior margin; mesothorax strongly transverse, with rounded lateral margins and weakly projected posterior angles, laterally with four tubercles, upper rounded, lower only slightly transverse, metathorax similar in shape with more acutely projected posterior margins. Abdominal segments with slender and long lateral processes.

Measurements. BL 8.2 mm, PL 0.9 mm, PW 1.8 mm, HW 2.1 mm, Edist 0.94 mm, Ediam 0.39 mm. Larva. BL 32.3 mm, PL 7.7 mm, PW 13.0 mm.

Distribution. Indonesia: Sumatra, North Sumatra Province, Gn. Sibayak.

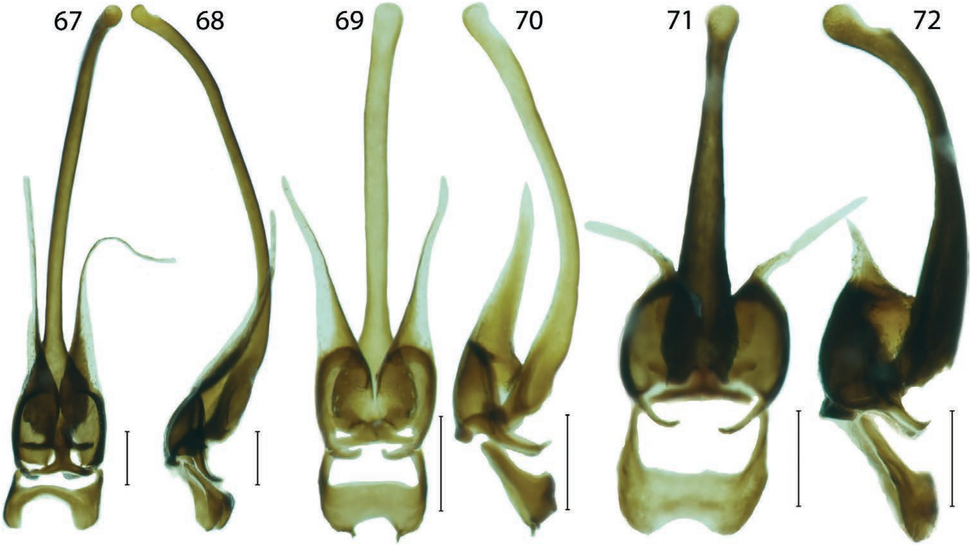
Etymology. The specific epithet is derived from the Latin adjective *montanus* (mountainous) referring to the habitat of the species.

Platerodrilus palawanensis sp. n.

http://zoobank.org/F7FBBEE1-3910-4258-AEE4-E819747B834C

Figs 16, 31, 69–70

Material examined. Holotype. Male (LMBC, UPOL 001382), Philippines, Palawan, Tanabak river, 150 m, 10°02'49"N, 118°58'31"E, 2.–5. Jan. 2007, Bolm lgt. Paratypes, 8 males (LMBC), same locality data, 22. Dec. 1991; 3 paratypes. Males (KMTC), Philippines, Palawan, Brooke's point, 8. Dec. 2002, leg. F. A. Dacasin. Paratype. Male (KMTC), Philippines, Palawan, Brooke's point, 18. May 2003, leg. F. A. Dacasin. Paratype. Male (KMTC), Philippines, Palawan, Brooke's point, 15. Jan. 2005, leg. F. A. Dacasin.



Figures 67–72. Male genitalia of *Platerodrilus*: **67–68** *P. luteus* **69–70** *P. palawanensis* **71–72** *P. sibayakensis*. Scales 0.25 mm.

Diagnosis. *P. palawanensis* sp. n. resembles *P. borneensis* in flabellate antennae and these species differ in colouration. *P. borneensis* is dark brown and *P. palawanensis* bicoloured (Fig. 16). Additionally *P. palawanensis* has the very short pronotum and straight frontal pronotal margin (Fig. 31).

Description. Body medium-sized, dark brown to black, only pronotum, mesoscutellum and humeral two thirds of elytra orange; apical third of elytra and two thirds of elytral suture dark brown to black. Head small, including eyes apparently narrower than frontal margin of pronotum, antennal tubercles robust, deeply separated. Eyes hemispherically prominent, eye diameter 1.9 times frontal interocular distance. Antennae flabellate, antennomere 3 with long process, pubescent, length of antennomere 3 1.6 times antennomere 2. Pronotum strongly transverse, 1.5 times wider than long at midline, anterior margin straight, with prominent anterior angles, lateral margins almost straight, posterior margin bisinuate, surface of disc mat, finely punctuate, with dense short pubescence. Elytra 2.9 times longer than width at humeri, elytra almost parallel-sided; slightly widened posteriorly, widest at apical fourth, elytral costae inconspicuous. Legs compressed, with dense pubescence. Male genitalia with curved phallus, short rounded parameres bearing slender membranous processes; phallobase wide, deeply emarginate (Figs 69–70).

Measurements. BL 7.1 mm, PL 1.0 mm, PW 1.6 mm, HW 1.9 mm, Edist 0.66 mm, Ediam 0.34 mm.

Distribution. Philippines: Palawan.

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

Platerodrilus ranauensis sp. n.

http://zoobank.org/F09DE9AF-6800-4A06-AF7D-B82F3207217E

Figs 9, 24, 54–55

Material examined. Holotype. Male (LMBC, UPOL 000587), Sumatra, SW coast of Ranau Lake, 1–4. Jun. 2001, 1200 m.

Diagnosis. *P. ranauensis* was found as a sister species to *P. talamauensis* (Fig. 1) and these species differ in the extent and shape of the orange part of elytra and in the shape of the posterior margin of phallobase (Figs 54–55).

Description. Body medium-sized, dark brown to black, only pronotum testaceous to brown and basal quarter of elytra orange (Fig. 9). Head small, including eyes slightly narrower than frontal margin of pronotum, antennal tubercles small. Eyes hemispherically prominent, eye diameter 2.3 times frontal interocular distance. Antennae compressed, pubescent, length of antennomere 3 1.1 times antennomere 2. Pronotum transverse, 1.7 times wider than long at midline, anterior margin widely rounded, semicircular, without prominent anterior angles, posterior margin of pronotum bisinuate, surface of disc glabrous, with sparse long pubescence (Fig. 24). Elytra almost parallel-sided, 3.0 times longer than width at humeri; slightly widened posteriorly, widest at apical fourth. Elytral costae inconspicuous. Legs compressed, with dense pubescence. Male genitalia with short rounded parameres bearing slender membranous processes; phallus curved, phallobase wide, deeply emarginate (Figs 54–55).

Measurements. BL 6.0 mm, PL 0.8 mm, PW 1.3 mm, HW 1.7 mm, Edist 0.79 mm, Ediam 0.35 mm.

Distribution. Indonesia: Sumatra.

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

Platerodrilus sibayakensis sp. n.

http://zoobank.org/3A4F0BBB-BA23-498D-8C1E-E39CA46F1D84

Figs 10, 25, 71–72

Material examined. Holotype. Male (LMBC, UPOL 001389), Sumatra Utara, Brastagi, Gn. Sibayak, 26. Jan.–1. Feb. 2005, 1600–2200 m. Paratypes. 2 males (LBMC), Sumatra, SW of Brastagi, Gn. Sinabung, 22. Feb. 1991, 1300–1800 m. Paratype. Male (LBMC), Sumatra, SW of Brastagi, Gn. Sinabung, 19.–23. Feb. 1991, 1300–1800 m. Paratype. Male (LBMC, UPOL 001372), Sumatra, Utara, Brastagi, Gn. Sibayak, 26. Jan.–1. Feb. 2005, 1600–2200 m. Paratype. Male (LBMC), Sumatra, Sinabung, Mar. 1998.

Diagnosis. *P. sibayakensis* and *P. angustatus* were recovered as sister species (Fig. 1) and they share the pronotum with acutely projected posterior angles. *P. sibayakensis* differs in the 4.1 times longer antennomere 4 than its width in the middle and the more robust phallus tapering gradually from the base to apex (Figs 71–72).

Description. Body medium-sized, dark brown to black, pronotum testaceous to brown and basal third of elytra orange (Fig. 10). Head small, including eyes slightly narrower than frontal margin of pronotum, antennal tubercles small. Eyes hemispherically prominent, eye diameter 1.7 times frontal interocular distance. Antennae compressed, pubescent, length of antennomere 3 0.7 times antennomere 2. Pronotum transverse, 1.9 times wider than long at midline, anterior margin almost straight, with marked anterior angles, lateral margins straight, posterior margin of pronotum bisinuate, posterior angles acutely projected, surface of disc weakly glabrous, finely punctuate, with long pubescence (Fig. 25). Elytra almost parallel-sided, elytra 3.5 times longer than width at humeri; slightly widened posteriorly, widest at apical fourth, elytral costae inconspicuous. Legs compressed, with dense pubescence. Male genitalia with short rounded parameres bearing slender membranous processes; phallus curved, phallobase wide, deeply emarginate (Figs 71–72).

Measurements. BL 8.5 mm, PL 0.9 mm, PW 1.8 mm, HW 2.0 mm, Edist 0.73 mm, Ediam 0.44 mm.

Distribution. Indonesia: Sumatra.

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

Platerodrilus sinabungensis **sp. n.**

http://zoobank.org/4275B855-5901-45B6-BD6A-CF6EB0BFB430

Figs 11, 26, 58–59

Material examined. Holotype. Male (LMBC), Sumatra, SW of Brastagi, Gn. Sinabung, 22. Feb. 1991, 1300–1500 m. Paratypes. 2 males (LBMC), Sumatra, SW of Brastagi, Gn. Sinabung, 22. Feb. 1991, 1400–1900 m.

Diagnosis. *P. sinabungensis* resembles *P. montanus* in the dark coloured pronotum. These species differ in the shape of the phallobase (Figs 58–59, 66).

Description. Body medium-sized, dark brown to black, only basal two fifths of elytra orange testaceous (Fig. 11). Head including eyes slightly wider than frontal margin of pronotum. Eye hemispherically prominent, their diameter 2.3 times frontal interocular distance. Antennae compressed, antennomere 3 as long as antennomere 2. Head and antennae with short dense pubescence. Pronotum transverse, 1.7 wider than long at midline, anterior and lateral margins weakly rounded, posterior margin of pronotum simply rounded to straight in middle, disc bare in middle, pubescent along lateral margins (Fig. 26). Elytra with inconspicuous carinae. Elytra 3.4 times longer than width at humeri, elytra widest posteriorly. Legs compressed with dense pubescence. Male genitalia with curved phallus and short rounded parameres bearing slender membranous processes with basal part serrate; phallobase wide, widely emarginate (Figs 58–59).

Measurements. BL 8.9 mm, PL 1.0 mm, PW 1.7 mm, HW 2.1 mm, Edist 0.89 mm, Ediam 0.4 mm.

Distribution. Indonesia: Sumatra.

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

Platerodrilus talamauensis **sp. n.**

http://zoobank.org/FB6FE156-5B2D-4232-897F-62EC10EFFB1F
Figs 15, 29, 52–53

Material examined. Holotype. Male (LMBC, UPOL 001376), Sumatra Barat, Pasaman, Gn. Talamau, 14.–15. Jan. 2005, 1000 m. Paratype. Male (LMBC, UPOL 001375), Sumatra Barat, Pasaman, Gn. Talamau, 14.–15. Jan. 2005, 1000 m.

Diagnosis. *P. talamauensis* and *P. ranauensis* are closely related (Fig. 1) and they differ in the extent and shape of the orange part of the elytra (Figs 9, 15) and in the shape of posterior margin of phallobase (Figs 52–55).

Description. Male. Body medium-sized, dark brown to black, only pronotum, mesoscutellum and basal three fifths of elytra orange (Fig. 15). Head small, with eyes slightly wider than frontal margin of pronotum. Eyes hemispherically prominent, eye diameter 2.4 times frontal interocular distance. Antennae compressed, reaching two thirds of elytral length, antennomere 3 0.9 times antennomere 2. Head and antennae densely pubescent. Pronotum transverse, 1.2 wider than long at midline. Anterior margin of pronotum rounded, anterior angles inconspicuous, posterior margin bisinuate (Fig. 29). Elytra with inconspicuous carinae, parallel-sided, 2.9 times longer than width at humeri, widest posteriorly. Legs compressed with dense pubescence. Male genitalia with curved phallus, phallus twice longer than apical processes of parameres, phallobase widely emarginate. (Fig. 52–53).

Measurements. BL 6.5 mm, PL 1.0 mm, PW 1.6 mm, HW 1.9 mm, Edist 0.88 mm, Ediam 0.36 mm.

Distribution. Indonesia: Sumatra.

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

Platerodrilus tujuhensis **sp. n.**

http://zoobank.org/52952DAE-6457-4DF0-B57C-E4A7F0989063
Figs 12, 27, 41, 56–57

Material examined. Holotype. Male (LMBC, UPOL 001385), Sumatra, Jambi Kersik Tua, Gn. Kerinci, 19–22. Jan. 2005, 1600–2200 m. Paratype. Female (LMBC, VP2305), Sumatra, Jambi prov. Kerinci Seblat N. P., 7 km E Kayuaro, Mt. Tujuh, 1°45'S, 101°25'E, 25. Feb.–2. Mar. 2003, 1750 ± 250 m.

Diagnosis. *P. tujuhensis* resembles in the uniformly light coloured head, pronotum and elytra *P. robinsoni*, which differs in the more robust basal part of the phallus. The molecular phylogeny suggests the sister relationships of *P. maninjauensis* and *P. tujuhensis*. These species differ in colouration (Figs 7, 12) and the shape of the phallus and phallobase (Figs 56–57, 60–61). The female larvae of both species are similar and differ only in the relative size of mesonotal tubercles, which are smaller in *P. tujuhensis*.

Description. Body dark brown to black; head, pronotum and elytra yellow to orange, apical margins of elytra infuscate (Fig. 12). Head including eyes narrower than pronotum, antennal tubercles slightly prominent. Eyes hemispherically prominent, frontal interocular distance 2.6 times eye diameter. Antennae compressed, slender, length of antennomere 3 0.9 times antennomere 2. Pronotum transverse, 1.8 wider than long at midline, anterior margin widely rounded, anterior angles inconspicuous, posterior margin bisinuate (Fig. 27). Elytra 3.7 times longer than width at humeri, widest posteriorly, elytral costae inconspicuous. Legs slender, compressed with dense pubescence. Male genitalia with slender, curved phallus and small rounded parameres bearing slender membranous processes, phallobase wide, narrowly and deeply emarginate (Figs 56–57).

Female larva. Body flat, wide, dark brown, only margins of tergites lighter, pronotum triangular (Fig. 41), with two glabrous rounded tubercles postero-laterally, another two tubercles in middle of anterior margin; mesothorax strongly transverse, with rounded lateral margins and weakly projected posterior angles, laterally with four tubercles, upper rounded, lower transverse, metathorax similar in shape with more acutely projected posterior margins. Abdominal segments with slender and long lateral processes.

Measurements. BL 8.1 mm, PL 0.9 mm, PW 1.6 mm, HW 1.9 mm, Edist 0.81 mm, Ediam 0.31 mm. Larva. BL 32.7 mm, PL 6.6 mm, PW 10.2 mm.

Distribution. Indonesia: Sumatra.

Etymology. The specific epithet refers to the locality of the paratype.

Platerodrilus robinsoni Blair, 1928

Figs 6, 19, 62–63

Platerodrilus korinchiana robinsoni Blair 1928: 182.
Platerodrilus robinsoni Blair, 1928, stat. n.

Material examined. Holotype. Sumatra, Sungei Kumbang, Korinchi, 4500 ft, Apr. 1914 (BMNH). Other material examined. Male (LMBC, UPOL 001378), Sumatra, Jambi Kersik Tua, Gn. Kerinci, 19.–22. Jan. 2005, 1600–2200 m.

Diagnosis. *P. robinsoni* resembles *P. luteus* in general appearance, but differs in the shape of the phallobase and phallus (Figs 62–63, 67–68).

Redescription. Body black; head and mesoscutellum dark brown, pronotum and elytra orange yellow; antennae, and legs dark brown to black (Fig. 6). Head small, antennal tubercles separated by deep groove. Eyes hemispherically prominent, frontal interocular distance 2.1 times maximum eye diameter. Antennae slender, compressed, densely pubescent, antennomere 3 1.1 times longer than antennomere 2. Pronotum transverse, 1.6 times wider than long, anterior margin rounded, frontal angles obtuse, lateral margins slightly convex, posterior angles approximately rectangular (Fig. 19). Elytra parallel-sided, elytra 3.3 times longer than width at humeri, elytral costae weak, covered with dense pubescence. Male genitalia with curved phallus; parameres short, rounded, with slender membranous process; phallobase wide, deeply emarginate (Figs 62–63).

Measurements. BL 7.8 mm, PL 1.0 mm, PW 1.6 mm, HW 2.0 mm, Edist 0.85 mm, Ediam 0.40 mm.

Distribution. Indonesia: Sumatra.

Remark. *P. robinsoni* differs from *P. korinchianus* in the colouration; but both species are syntopic. Therefore, the species rank is proposed for *P. robinsoni* stat. n.

Platerodrilus ruficollis Pic, 1942, comb. n.

Fig. 39

Falsocalochromus ruficollis Pic, 1942
Duliticola hoiseni Wong, 1996: 175, syn. n.

Material examined. Holotype, male, Presqu'ile Malaise (MNHP).

Remark. Wong (1996) described and illustrated *Duliticola hoiseni*. During the recent search in the Paris Museum we found that Pic (1942) described the same species as *Falsocalochromus ruficollis* and placed in the relationships with *Calochromus* despite that fact that the species perfectly fits in his own concept of *Platerodrilus*. Therefore, we propose *D. hoiseni* as a junior subjective synonym of *P. ruficollis*.

Species incertae sedis

Platerodrilus testaceicollis Pic, 1921: 14.

Remark. *P. testaceicollis* was placed in *Platerodrilus* by Kazantsev, 2009, but the abdomen of the type is missing and the species cannot be placed in any species group unless further specimen is available. The redescription was given by Wong (1998).

Duliticola javanica Kemner, 1928: 136.

Remark. The type series contains just female larvae judging from the illustrations might include two species. The adult is unknown.

Acknowledgements

We are obliged to P. Ng and A. Wong for providing as with the manuscript of A. Wong's Master Thesis and for permission to publish all information. The authors are grateful to R. Bilkova for technical assistance, to M. Barclay for providing an access to the BMNH collection and to K. Matsuda for an access to additional material. The study was funded by the Grant Agency of the Czech Republic (P506/11/1757) and IGA Project from UP Olomouc. Additionally, this research received support from the Synthesys Project, which is financed by EC Research Infrastructure Action.

References

Ahrens D, Monaghan MT, Vogler AP (2007) DNA-based taxonomy for associating adults and larvae in multi-species assemblages of chafers (Coleoptera: Scarabaeidae). Molecular Phylogenetic and Evolution 44: 436–449. doi: 10.1016/j.ympev.2007.02.024

Belshaw R, Katzourakis A (2005) BlastAlign: a program that uses blast to align problematic nucleotide sequences. Bioinformatics 21: 122–123. doi: 10.1093/bioinformatics/bth459

Bocak L (2002) Pendola, a new lycid genus (Coleoptera, Lycidae) from the Australian Region. Biologia 57: 557–561.

Bocak L, Bocakova M, Hunt T, Vogler AP (2008) Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. Proceedings of the Royal Society B 275: 2015–2023. doi: 10.1098/rspb.2008.0476

Bocak L, Bocakova M (1989) New tribe Lyropaeini, with a description of a new species of *Lyropaeus* (Coleoptera, Lycidae). Polskie Pismo Entomologiczne 58: 717–723.

Bocak L, Bocakova M (2008) Phylogeny and classification of the family Lycidae (Insecta: Coleoptera). Annales Zoologici 58(4): 695–720. doi: 10.3161/000345408X396639

Bocak L, Grebennikov VV, Sklenarova K (2014) *Cautires apterus*, a new species and the first record of wingless male Lycidae (Coleoptera) discovered in the North Pare Mountains, Tanzania. Annales Zoologici 64: 1–7. doi: 10.3161/000345414X680500

Bocak L, Matsuda K (2003) Review of the immature stages of the family Lycidae (Insecta: Coleoptera). Journal of Natural History 37: 1463–1507. doi: 10.1080/00222930210125362

Bocakova M (2001) Revision and phylogenetic analysis of the subfamily Platerodinae (Coleoptera: Lycidae). European Journal of Entomology 98: 53–85. doi: 10.14411/eje.2001.010

Bourgeois J (1879) Lycides recueillis au Brésil par C. Van Volxem. Annales de la Société entomologique de Belgique 22: 15–19.

Candèze EM (1861) Histoire des métamorphoses de quelques Coléoptères exotiques. Memoires de la Société Royale des Sciences, Liège 16: 358, 403–404.

Eberhard WG (2010) Evolution of genitalia: theories, evidence, and new directions. Genetica 138: 5–18. doi: 10.1007/s10709-009-9358-y

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792–1797. doi: 10.1093/nar/gkh340

Huelsenbeck JP (2000) MrBayes: Bayesian inference of phylogeny version 3.1.2. Department of Biology, University of Rochester, NY.

ICZN [International Committee for Zoological Nomenclature] (1999) International Code of Zoological Nomencalture. International Trust for Zoological Nomenclature, London, 305 pp.

Kazantsev S (2002) A generic review of Duliticolinae, new subfamily (Coleoptera: Lycidae). Elytron 16: 5–21.

Kazantsev S (2005) Morphology of Lycidae with some considerations on evolution of the Coleoptera. Elytron 17: 73–248.

Kazantsev S (2009) New taxa of Platerodrilini. Russian Entomological Journal 18: 55–62.

Kundrata R, Bocak L (2011) The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? Zoologica Scripta 40: 364–378. doi: 10.1111/j.1463-6409.2011.00476.x

Levkanicova Z, Bocak L (2009) Identification of net-winged beetle larvae (Coleoptera: Lycidae) using three mtDNA fragments: a comparison of their utility. Systematic Entomology 34: 210–221. doi: 10.1111/j.1365-3113.2008.00457.x

Lok AFSL (2008) A Singapore trilobite larva, *Duliticola* species. Nature in Singapore 1: 175–178.

Malohlava V, Bocak L (2010) Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. Molecular Ecology 19: 4800–4811. doi: 10.1111/j.1365-294X.2010.04850.x

Masek M, Ivie MA, Palata V, Bocak L (2014) Molecular phylogeny and classification of Lyropaeini (Coleoptera: Lycidae) with description of larvae and new species of *Lyropaeus*. Raffles Bulletin of Zoology 62: 136–145.

Mjöberg E (1925) The mystery of the so called "Trilobite" or "Perty's larvae" definitely solved. Psyche 22: 119–153. doi: 10.1155/1925/19784

Perty M (1831) Observationes Nonnullae in Coleoptera Indiae Orientalis. Lindauer 1831: 33–44.

Pic M (1921) Nouveautes diverses. Mélanges exotico-entomologiques 33: 12–13.

Pic M (1942) *Falsocalochromus ruficollis* Pic, 1942. L'Echange, Numero spéciale [1940–44] (Opuscula martialis VII), 101 pp.

Posada D (2008) JMODELTEST: phylogenetic model averaging. Molecular Biology and Evolution 25: 1253–1256. doi: 10.1093/molbev/msn083

Sanderson MJ (2002) Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. Molecular Biology and Evolution 19:101–109. doi: 10.1093/oxfordjournals.molbev.a003974

Sklenarova K, Chesters D, Bocak L (2013) Phylogeography of Poorly Dispersing Net-Winged Beetles: A Role of Drifting India in the Origin of Afrotropical and Oriental Fauna. PLoS ONE 8(6): e67957. doi: 10.1371/journal.pone.0067957

Stamatakis A, Ludwig T, Meier H (2005) RAxML-III: a fast program for maximum likelihood–based inference of large phylogenetic trees. Bioinformatics 21: 456–463. doi: 10.1093/bioinformatics/bti191

Thompson J, Higgins D, Gibson T (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignments through sequence weighting, position specific gap penalties and weight matrix choice. Nucleic Acids Research 22: 4673–4680. doi: 10.1093/nar/22.22.4673

Vuataz L, Sartori M, Wagner A, Monaghan MT (2011) Toward a DNA Taxonomy of Alpine Rhithrogena (Ephemeroptera: Heptageniidae) Using a Mixed Yule-Coalescent Analysis of Mitochondrial and Nuclear DNA. PLoS ONE 6(5): e19728. doi: 10.1371/journal.pone.0019728

Wittmer W (1938) Neue Drilidae (Coleoptera/Malacodermata) aus Java. Entomologische Berichten 221: 36–40.

Wittmer W (1941) Malacodermata von den Philippinen aus der Samlung des Zoologischen Museums in Amsterdam. The Philippine Journal of Science 74: 195–228.

Wittmer W (1944) Catalogue des Drilidae E. Oliv. (Coleoptera–Malacodermata). Revista de la Sociedad Entomológica Argentina 12: 203–221.

Wong ATC (1996) A new species of neotenous beetle, *Duliticola hoiseni* (Insecta: Coleoptera: Cantharoidea: Lycidae) from peninsular Malaysia and Singapore. Raffles Bulletin of Zoology 44: 173–187.

Wong ATC (1998) A revision of the neotenous 'trilobite larvae' of the genera *Duliticola* and *Platerodrilus* (Coleoptera: Cantharoidea: Lycidae). MSc Thesis, National University of Singapore, Singapore.

RESEARCH ARTICLE

Molecular Phylogeny Reveals High Diversity, Geographic Structure and Limited Ranges in Neotenic Net-Winged Beetles *Platerodrilus* (Coleoptera: Lycidae)

Michal Masek, Vaclav Palata, Timothy C. Bray, Ladislav Bocak*

Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 771 46, Olomouc, Czech Republic

* ladislav.bocak@upol.cz

Citation: Masek M, Palata V, Bray TC, Bocak L (2015) Molecular Phylogeny Reveals High Diversity, Geographic Structure and Limited Ranges in Neotenic Net-Winged Beetles *Platerodrilus* (Coleoptera: Lycidae). PLoS ONE 10(4): e0123855. doi:10.1371/journal.pone.0123855

Academic Editor: Alex Córdoba-Aguilar, Universidad Nacional Autonoma de Mexico, MEXICO

Received: October 20, 2014

Accepted: February 23, 2015

Published: April 28, 2015

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: The study was funded by the Grant Agency of the Czech Republic (P506/11/1757). MM and VP were additionally supported by the Internal Grant of the Palacky University (IGA_PrF_2014013) and TB was supported by the grant POST-UP funded by the European Science Foundation and the Ministry of Education of the Czech Republic (CZ.1.07/2.3.00/30.0004). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Abstract

The neotenic *Platerodrilus* net-winged beetles have strongly modified development where females do not pupate and retain larval morphology when sexually mature. As a result, dispersal propensity of females is extremely low and the lineage can be used for reconstruction of ancient dispersal and vicariance patterns and identification of centres of diversity. We identified three deep lineages in *Platerodrilus* occurring predominantly in (1) Borneo and the Philippines, (2) continental Asia, and (3) Sumatra, the Malay Peninsula and Java. We document limited ranges of all species of *Platerodrilus* and complete species level turnover between the Sunda Islands and even between individual mountain regions in Sumatra. Few dispersal events were recovered among the major geographical regions despite long evolutionary history of occurrence; all of them were dated at the early phase of *Platerodrilus* diversification up to the end of Miocene and no exchange of island faunas was identified during the Pliocene and Pleistocene despite the frequently exposed Sunda Shelf as sea levels fluctuated with each glacial cycle. We observed high diversity in the regions with persisting humid tropical forests during cool periods. The origins of multiple species were inferred in Sumatra soon after the island emerged and the mountain range uplifted 15 million years ago with the speciation rate lower since then. We suppose that the extremely low dispersal propensity makes *Platerodrilus* a valuable indicator of uninterrupted persistence of rainforests over a long time span. Additionally, if the diversity of these neotenic lineages is to be protected, a high dense system of protected areas would be necessary.

Introduction

The lyropaeine net-winged beetles (Lycidae) are a rare example of developmental modifications between sexes [1, 2]. The males undergo complete metamorphosis, passing through the pupal stage, to become fully winged adults, with body length varying from 1.3–10 mm [3]. In

Competing Interests: The authors have declared that no competing interests exist.

contrast, the females remain larviform when sexually mature and differ from larvae only in the structure of cuticle and opened sexual tract (Fig 1) [4, 5]. The neotenic development of females has several macroevolutionary consequences. First of all, the winglessness results in the very limited dispersal propensity of all net-winged beetles with larviform females. Males, although winged, fly only in short distances within the lowest strata of the tropical rainforests, when searching for females (personal observation). Further some lyropaeine beetles have very large bodied females unknown in non-neotenic lineages of net-winged beetles ("trilobite larvae", body length 30–70 mm, Fig 1). These females live for several years in the larval stage and produce a relatively low number of large eggs from which hatch larvae comparable in size to adult males [5]. Such a reproductive strategy is energetically costly and was hypothesized as a case of K-strategy [1]. The high female investment in offspring has also been similarly predicted also for other neotenics [6]. Unlike females, the conspecific males often have a very small body (6–10 mm in *Platerodrilus*, but slightly over 1 mm in *Alyculus*), live only shortly in the adult stage [5], and invest a minimum energy in offspring compared to females. Apparently, the different selective regime affects the males and results in very disparate adult morphology. Although information on these beetles remains incomplete and females are unknown for most species and genera, the significant morphological differences among large-bodied females were proved in *Platerodrilus* [4, 5], *Macrolibnetis* [7] and *Lyropaeus* [2] and the previous studies support the parallel origins of extremely large females.

Forty-two species of *Platerodrilus* are known and their ranges are limited to three major biodiversity hotspots [8]: Indo-Burma, Sundaland and the Philippines including Palawan [3].

Fig 1. Female larvae, late instars. A-C *Platerodrilus*, Bornean clade; A—from Borneo, Sabah, Mt. Kinabalu, B—Borneo, Sabah, Poring, C—Mindanao, New Bataan; D—*Macrolibnetis*, Malaysia, Pahang, Cameron Highlands.

doi:10.1371/journal.pone.0123855.g001

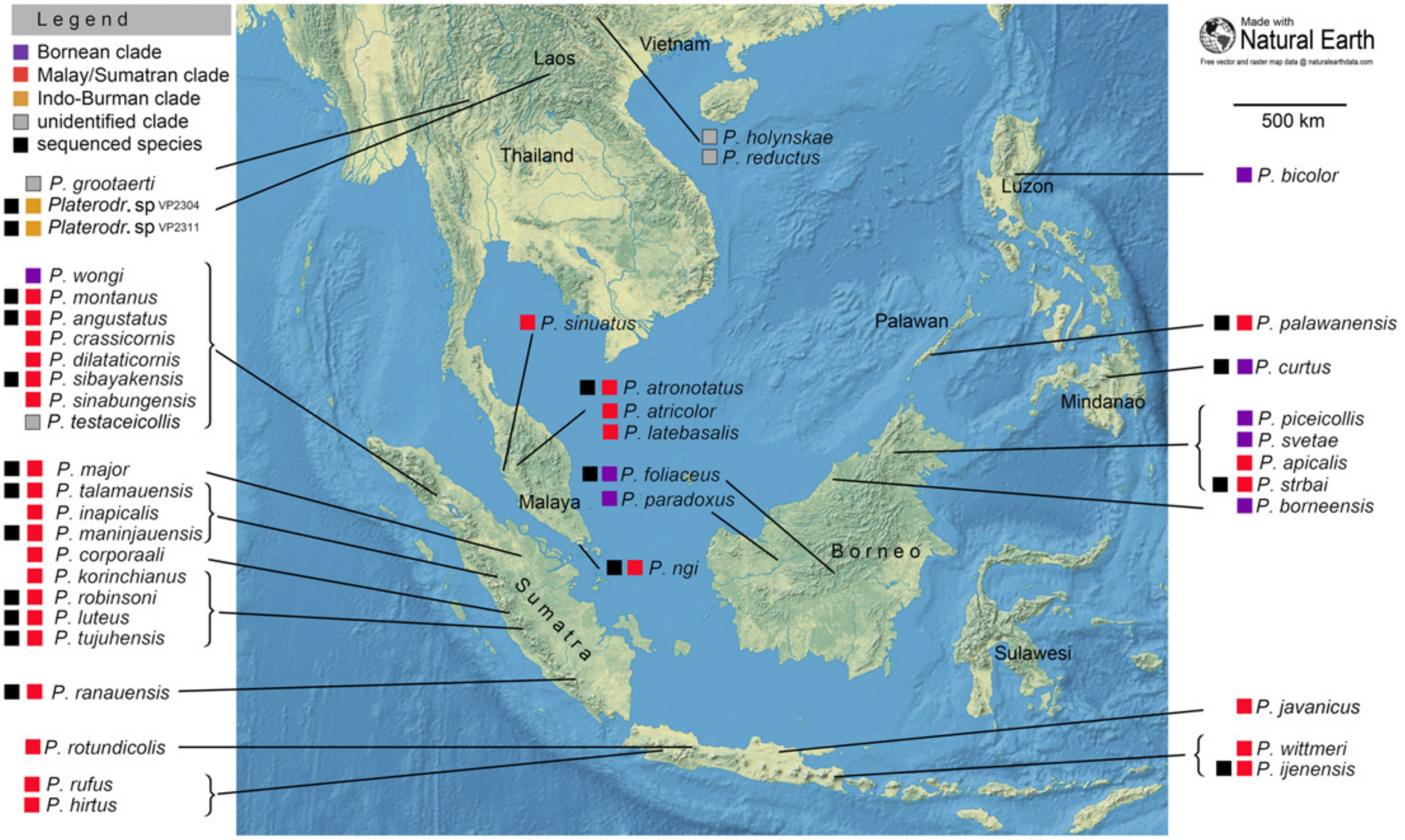


Fig 2. Distribution of *Platerodrilus*. The taxa were assigned to clades by the phylogenetic analysis and/or morphological similarity. *P*. *testaceicollis* Pic, 1921 is known in a damaged holotype and no diagnostic characters are available to evaluate its relationships.

doi:10.1371/journal.pone.0123855.g002

Platerodrilus do not occur in continental China (except the southernmost part of Yunnan along Lao and Burman borders) or in the southern part of the Indian subcontinent (Fig 2).

The majority of elateroid beetles are winged and quite effective at dispersal. On the other hand, there are multiple lineages within Elateroidea with wingless to larviform females. These lineages, e.g. Omethidae: Telegeusinae, multiple lineages of Lampyridae, all Omalisidae and Plastoceridae, Elateridae: Cebrioninae, Agrypninae: Drilini and others, usually share with their close relatives the biology and differ only in an incomplete metamorphosis. The lycid neotenic females remain completely larviform, their dispersal ability is extremely low and they heavily depend on humid rainforests as their larvae need constant access to liquid food and even the winged males do not fly effectively. Additionally, they are relatively species rich and previous studies have suggested their persistence in stable habitats [3, 5]. Therefore, these neotenic beetles can be used as a model group for evolutionary and zoogeographical studies and their presence and *in situ* diversification can identify regions with uninterrupted persistence of the rainforests during climatic fluctuations. Herein, we present the multi-marker molecular phylogeny of *Platerodrilus* and reconstruct the ancestral range and dispersal routes of *Platerodrilus* in the Oriental region. The aim of this study is to recover the diversification history of *Platerodrilus* and define ranges with occurrence of ancient lineages of the neotenic beetles in South East Asia. We suggest that these are biodiverse regions worthy of protection and whose constituent species would be in danger of extinction should the habitats be destroyed.

Material and Methods

The specimens were preserved in 96% ethanol in the field and stored in a freezer until DNA was isolated. The sampled localities included the Kinabalu and Emas National Parks (Access Licence JMK/MBS.1000-2/2(110) issued by the Sabah Biodiversity Council, and Permit Penyelidikan No TS/PTD/5/4Jld48(41) by Lembaga Pemegang Amanah Taman-Taman). Other material was collected outside protected areas and species included in the research are not protected by international or national laws. The sequenced specimens are deposited in the voucher collection of the Laboratory of Molecular Systematics, Faculty of Science, Olomouc, Czech Republic, only the voucher specimen of *P. ngi* is deposited the Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore. The voucher numbers provide access to all sequenced DNA fragments deposited in GenBank (S1 Table).

Laboratory methods and phylogenetic analyses

DNA was extracted following the standard protocol with Wizard SV96 kit (Promega) from the flight muscles and larval thoracic segments. Extraction yield was measured using a NanoDrop-1000 Spectrophotometer. PCR was performed in a 50 μl reaction volume with 0.5 U Taq polymerase, 1 mM $MgCl_2$, 50 mM of dNTPs, 0.2 mM of each primer, and typically 30 ng of template. Cycle conditions were generally 2 min at 94°C, 30–60 sec at 94°C, 30–60 sec at 45–52°C, 1–2 min at 72°C (repeated steps 2–4 for 35–40 cycles), and 10 min at 72°C. Two nuclear DNA markers were included in the study: the complete 18S rRNA (~1900 bp), the D2 region of the 28S rRNA (630 bp). Three fragments of the mitochondrial genome were sequenced: the 800 bp *cox1* 3′ region of *cox1*, the 1200 bp fragment of *nad5* and adjacent *tRNA-Phe*, *tRNA-Glu*, *tRNA-Ser* (the whole fragment referred as *nad5* further), and a fragment of *rrnL* (530 bp). The used primers are listed in S3 Table. PCR products were purified using PCRu96 Plates (Millipore Inc.) and sequenced by an ABI 3130 automated sequencer using the Big Dye Terminator Cycle Sequencing Kit 1.1.

Sequence handling and phylogenetic analyses

Sequences were edited using the Sequencher 4.8 software package (Gene Codes Corp.). The protein-coding markers, *i.e.*, *nad5* and *cox1* were aligned by ClustalW 1.83 [9] under default settings. Length variable fragments, *i.e.*, 18S, 28S rRNA, *rrnL*, and tRNA mtDNA fragments, were separately aligned using ClustalW 1.83, BlastAlign 1.2 [10] under default parameters, and Muscle 3.6 [11] under the gap opening parameter 2600 and gap extension parameter 240. All DNA fragments were concatenated for final analyses. Multiple alignment methods were chosen to test the impact of various procedures on the tree topology. Phylogenetic analyses were carried out under the likelihood criterion (ML) using RAxML 7.2.3 [12] and bootstrap support of branches (BS) were assessed by analyzing 100 pseudoreplicates. All genes and codon positions in the protein coding fragments were partitioned under the models proposed by jModelTest 0.1.1 [13]. The dataset was additionally analyzed using the Bayesian inference (BI) implemented in MrBayes 3.2.2 [14]. The Markov Chain Monte Carlo (MCMC) was set for independent variability of parameters in individual coding and non-coding genes under the GTR+I+G model. Two runs, each with four chains ran simultaneously for 40×10^6 generations, with trees being sampled every 1000th generation, all fragments were partitioned and unlinked. The results were evaluated in Tracer 1.6 [15]. The first 2×10^6 trees of the first run and 16×10^6 trees of the second run were discarded as burn-in and posterior probabilities (PP) at nodes were determined from the remaining trees in the analysis of the Muscle alignment, 5×10^6 and 5×10^6 generations were discarded as burn-in in analysis of the BlastAlign matrix and 21×10^6 and 12×10^6 generations in the analysis of the Clustal alignment. The convergence of all parameters was assessed when runs were combined and the effective sample size (ESS) was over 1000 in all analyses. We used the MP-based statistical dispersal-vicariance analysis implemented in RASP 2.1 [16] for an ancestral range reconstruction on the best ML tree inferred from the Muscle alignment. We coded six geographical regions: (1) Continental Asia north of Isthmus Kra represented by Lao and Thai species (2) Peninsular Malaysia, (3) Sumatra, (4) Java, (5) Borneo and (6) the Philippines. Two regions were simultaneously allowed at node during optimization.

The relative age of nodes was estimated using penalized likelihood and cross-validation analysis as implemented in r8s 1.71 [17]. The age of the in-group was arbitrary set to 100 as no fossils are available for calibration. We used previously inferred age of *Platerodrilus* [1] for an approximate estimation of the absolute age of critical dispersal events and speciation in Sumatra. Branch lengths were optimized on the preferred tree topology and a wide range of smoothing parameters were tested before final analysis. Sampling intervals for inferred divergences were obtained from 100 bootstrap pseudoreplicates as described in the r8s manual. The lineage-through-time (ltt) plot for *Platerodrilus* was constructed from the inferred normalized tree using the Phytools package 0.4–05 in R ([18]; http://r-forge.r-project.org/projects/splits/).

Additionally, we estimated the time to the most recent common ancestor for *Platerodrilus* using a Bayesian approach implemented in Beast 1.8.1 [19]. The analysis was performed using the Muscle alignment and a GTR+I+G model as given by the AICc criterion in jModelTest 3.7 [13], a relaxed molecular clock and an uncorrelated lognormal model of rate variation among branches. The *Platerodrilus* clade was fixed to have an age of 1.0 and subsequently calibrated with previously hypothesized age [1]. The data were partitioned according to the genes and codon positions in the protein coding genes, with each partition allowed independent parameters. Altogether 5 x 10^7 generations were run, trees sampled every 10,000 generations and 5 x 10^6 generations were erased as pre-stationary stage. Convergence and ESS were assessed in Tracer 1.5 [15].

There are no fossils available for more accurate dating of the tree and we depend on the previous estimation of origin of major net-winged beetle lineages [1]. Therefore, we specifically ask about the origin of the Philippine fauna (ancient colonization in the Oligocene / Lower Miocene 20–35 mya versus recent dispersal history during low sea stands in the Upper Pliocene and Pleistocene) and putative accelerated speciation in Sumatra when it was established in the present form about 15 mya [20].

Results

Sequence variation

We concatenated the DNA sequences of five fragments: 18S rRNA (78 specimens), 28S rRNA (74 spec.), *rrnL* (75 spec., published by Masek and Bocak [3]), *cox1* (60 spec.) and *nad5* mtDNA (61 spec.). Amplification problems were commonly encountered when tissue was taken from larvae and as a result only 78.6% of markers were available for *Platerodrilus*. The complete dataset of aligned 18S, 28S, *rrnL*, *cox1*, and *nad5* DNA fragments contained 5086–5274 homologous positions depending on the applied alignment procedure (Table 1); 1727–1816 characters were parsimony informative. The aligned 18S fragment contained 1873–1883 positions, (7.6% of the parsimony informative characters), 28S 637–641 positions (3.8%), *rrnL* 530–723 positions (14.5%), *cox1* 790 positions (24.7%), and *nad5* 1237–1284 positions (47.0%).

Phylogeny and distribution

The topologies produced from BlastAlign, Muscle and Clustal alignments analyzed under maximum likelihood method (ML) and Bayesian inference (BI) were similar (Fig 3, S1A–S1C Fig).

Table 1. The length of DNA fragments and the numbers of informative characters in datasets (gaps considered as the 5th character).

Datasets		All data	18S rRNA	28S rRNA	*rrnL*	*cox1*	*nad5-tRNAs*
	# of spec.	83	78	74	75	60	61
ClustalW	# of char.	5087	1875	637	530	790	1255
	parsimony informative	1816	138	67	267	447	897
BlastAlign	# of char.	5274	1883	641	723	790	1237
	parsimony informative	1727	134	73	253	447	820
Muscle	# of char.	5116	1873	638	531	790	1284
	parsimony informative	1789	142	67	264	447	869

doi:10.1371/journal.pone.0123855.t001

The Platerodrilini were regularly inferred as monophyletic group with robust support (BS 96%, PP 98%). Only the ML analysis of the Muscle alignment did not recover Platerodini, when *Alyculus* + *Microlyropaeus* + *Antennolycus* were found as a sister to remaining Lyropaeinae. *Macrolibnetis*, *Horakiella*, *Pendola* and related genera represented the basal grade within Platerodrilini (Fig 3) and *Platerodrilus* clade was consistently recovered as a subordinate branch within Platerodrilini (BS and PP 100%). *Platerodrilus* split in a Bornean clade (BS and PP 100%), Indo-Burman clade and (BS and PP 100%) and Malay/Sumatran clade (Fig 1; BS 87%, PP 100%). The alternative topologies were recovered in the terminal clades: the relationships among Bornean species (*P. curtus* and two unidentified spp.) was unstable, the sister species of *P. palawanensis* were either *P. strbai* or *P. ngi* (Fig 3, S1 Fig) and variable relationships were recovered for *P. robinsoni* and *P. ijenensis* within the Malay/Sumatran clade (Fig 3, S1 Fig). The ancestral ranges were inferred using parsimony and the phylogenetic hypothesis produced by the ML analysis of the Muscle alignment (Fig 3). We identified Sumatra and Borneo as an ancestral range of *Platerodrilus* with available distributional data (Fig 4). Borneo was identified as an ancestral range of the *P. foliaceus* and related species from Borneo and Mindanao (i.e., *P. foliaceus*, *P. curtus* and three unidentified species). This lineage is designated as the Bornean clade in Figs 3, 5, 6 and S1 Fig). Further the basal lineage known from Laos and Thailand in two unidentified female larvae (VP2304, 2311) is designated as the Indo-Burman clade. Most species of *Platerodrilus* are known from Sumatra and we identified the Malay Peninsula and Sumatra as ancestral range for twenty species of *Platerodrilus*. The clade is designated as the Malay/Sumatran in Fig 3 and only two species of this clade are known from Borneo and a single species from Palawan.

Altogether 29 species of 42 formally described were available for DNA analyses and we assign species, which could not be sequenced, to three principal clades using morphology. Accordingly, eight species are assigned to the Bornean clade (five of them sequenced, Fig 3): five from Borneo, two from the Philippines, and one from Sumatra (Fig 2). The Indo-Burman clade (Figs 2, 4 and 5A, voucher numbers VP2304, 2311) is known only in larvae and without adults we cannot confirm the association of the sequenced larvae with any of the previously described three species from the region, therefore these are placed in the clade only tentatively. The Malay/Sumatran clade is represented by 17 spp. in Sumatra, 6 spp. in Java, 4 spp. in Peninsular Malaysia, 2 spp. in Borneo and a single species in Palawan (Figs 2, 3 and 5A). Some species were represented in the sequenced material only by female larvae and could not be identified to the species level. As we suppose, that at least some of them are conspecific with Sumatran and Malay species described in males, we do not list them in Fig 2.

As no fossils are available for calibration, the approximate estimation of absolute time was derived from the previous analysis, which dealt with whole family [1] and dated the basal split of *Platerodrilus* to 47 mya. The relatively ancient origin of Platerodini and *Platerodrilus* is

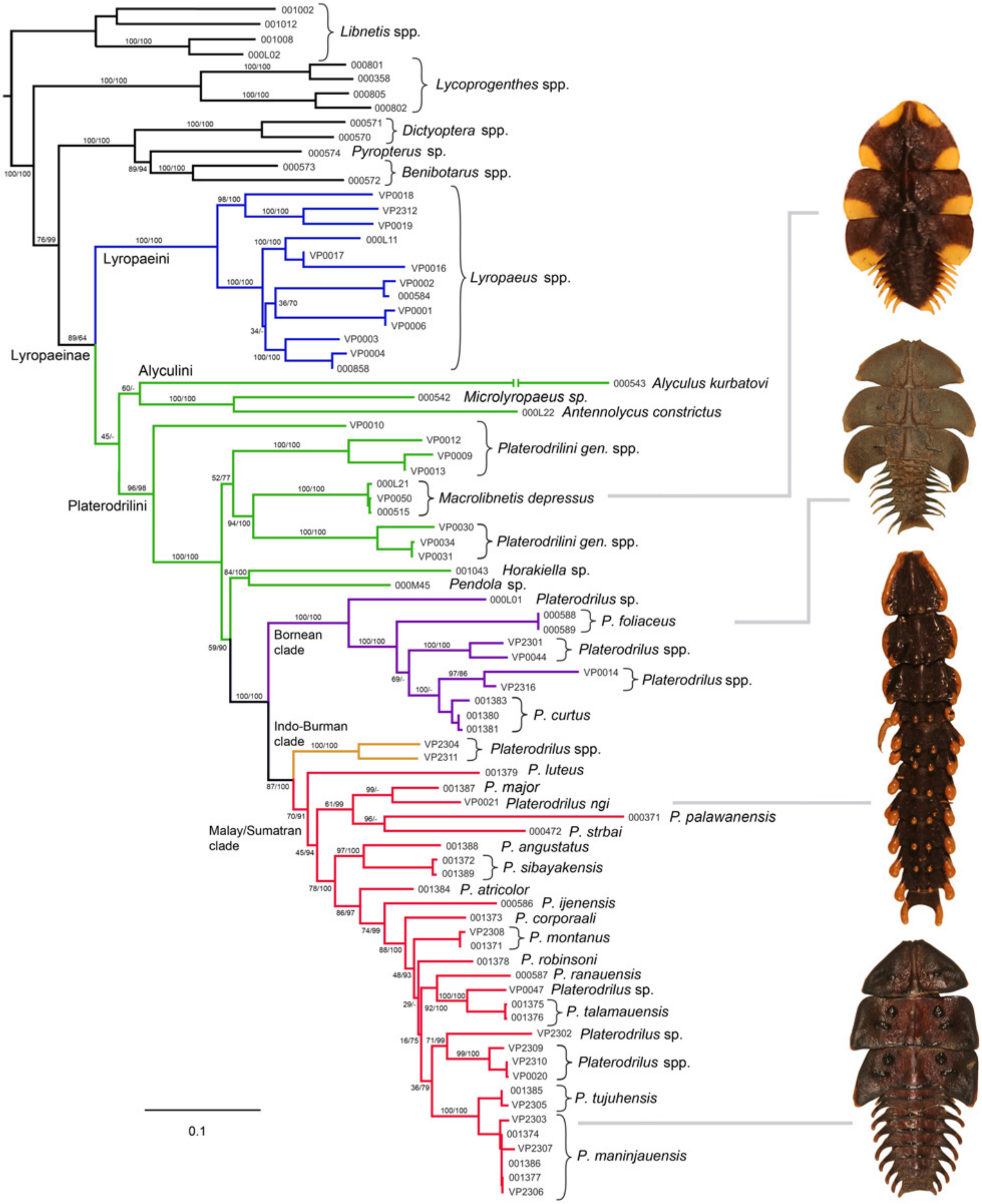


Fig 3. Phylogenetic hypothesis for *Platerodrilus* Pic, 1921 based on a maximum likelihood analysis of the Muscle alignment. Numbers at the branches are maximum likelihood bootstrap values and Bayesian posterior probabilities.

doi:10.1371/journal.pone.0123855.g003

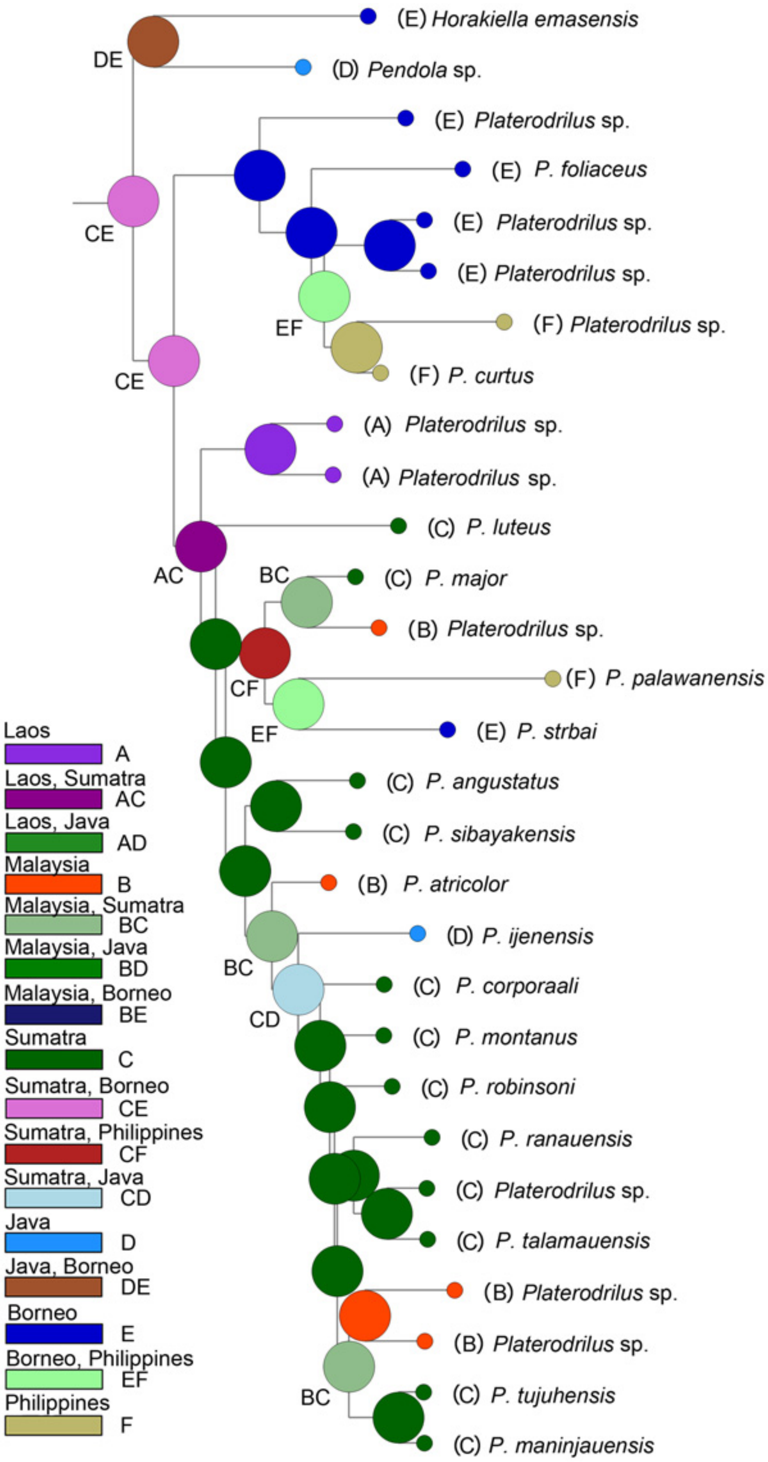


Fig 4. Reconstruction of ancestral ranges using statistical parsimony.

doi:10.1371/journal.pone.0123855.g004

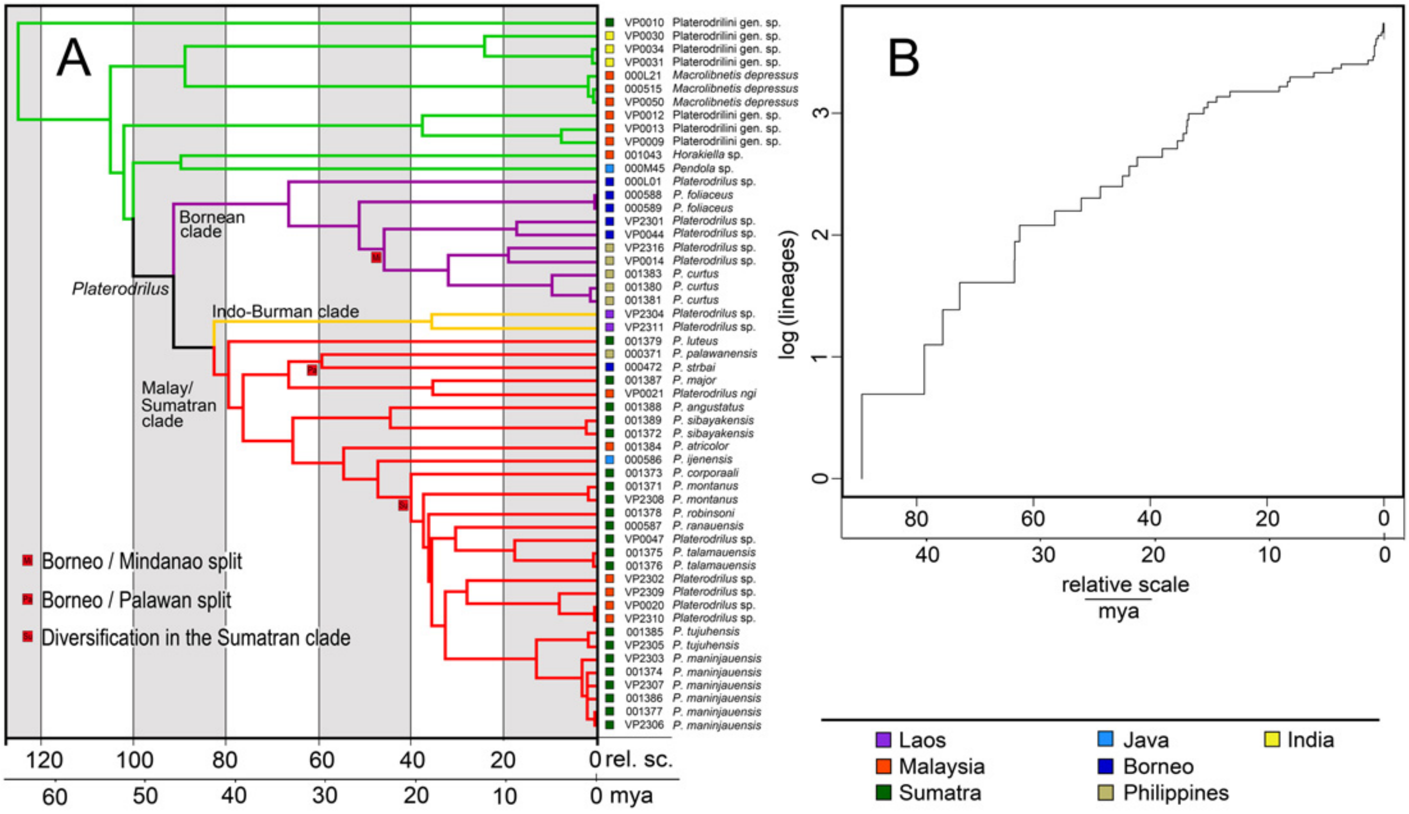


Fig 5. A—Relative age of nodes estimated using penalized likelihood. The age of *Platerodrilus* was arbitrarily set to 100. The lower axes show ageestimation in mya derived from the age of *Platerodrilus* inferred at 47 mya by Bocak *et al*. (2008). B—Lineage-through-time pot for *Platerodrilus*, the time axis is calibrated as in Fig 5A.

doi:10.1371/journal.pone.0123855.g005

supported by the fact that they represent one of the deep lineages in the phylogeny of net-winged beetles and that they are a morphologically very distinct group [1].

The age estimation of principal splits using penalized likelihood shows that *Platerodrilus* originated early in evolution of the Platerodrilini (Fig 5A) and the principal clades within *Platerodrilus* were established soon thereafter (Fig 5A). With the basal split in *Platerodrilus* dated to 47 mya, the principal clades separated ~40 mya, the species from Borneo and Palawan or Mindanao split ~25 mya and the multiple splits giving origins of Sumatran clades are dated at ~17 mya. The ltt plot (Fig 5B) suggests increased diversification rate at the beginning of *Platerodrilus* evolution and at ~17 mya. The diversification slowed down since ~12 mya to present.

Alternative dating using the Bayesian approach provided similar, only slightly shallower time estimation for important splits in *Platerodrilus* (Fig 6). The analysis was affected by the missing fragments and the 95% confidence intervals were large. Nevertheless, we can conclude that basal splits between lineages from Indo-Burma, Borneo and the Malay Peninsula are ancient and dated to ~35 mya, the splits Palawan or Mindanao species are dated to ~20 mya and the beginning of the radiation in the Sumatran clade to ~15 mya. There were not identified any dispersal events between major geographic regions during the Pliocene and Pleistocene low sea stands in the last 3 million years even when the uncertainty of the dating is considered (Figs 3 and 5A).

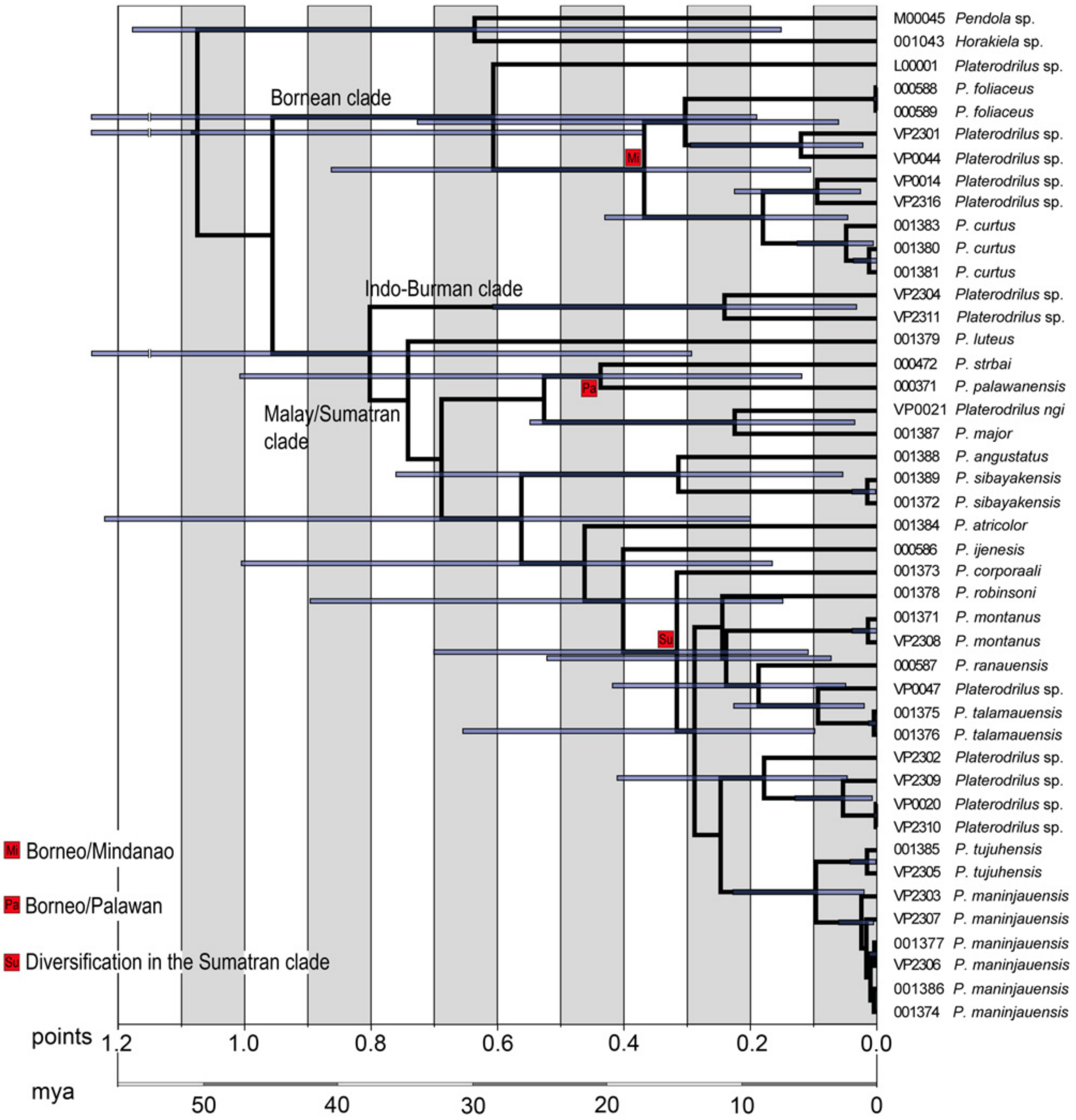


Fig 6. Timing of the *Platerodrilus* radiation. Estimated ages of nodes are based on Bayesian analysis of all fragments and Muscle alignment. The bars depict 95% confidence intervals.

doi:10.1371/journal.pone.0123855.g006

Discussion

The current dataset presented here provides more data for study of relationships of neotenic net-winged beetle lineages than the previous study, which included only four individuals [1]. The phylogenetic analyses confirm that Lyropaeinae represent a monophylum, which consists of Lyropaeini, Alyculini and Platerodrilini, all of them with confirmed or previously proposed neotenic development of females. Further, all inferred topologies indicate that the large-bodied larviform females evolved independently in both lineages: in *Lyropaeus* Waterhouse, 1878 (*sensu* Masek *et al.* [2]) in Lyropaeini and in *Platerodrilus* and *Macrolibnetis* (Platerodrilini). The first larviform platerodriline females are reported from Northeastern India and they represent a sister clade to *Macrolibnetis depressus* Pic, 1938 from Peninsular Malaysia in the present analyses. The available taxa from India are known only in the female larvae (terminals VP0030, 31, 34, Fig 3) and further information is needed before their placement in *Macrolibnetis* is confirmed. The adults of further genera, *i.e.*, *Horakiella*, *Pendola*, *Microlyropaeus*, *Antennolycus*, and several undescribed taxa (Fig 1), are exclusively known in adult males, when about two hundred specimens are currently available in collections. Both the larvae and adult females of these genera remain unknown and their neoteny has been only inferred from the absence of females in collected samples, morphology of males (all males are small bodied, with reduced mouthparts and often with light coloured and weakly sclerotized apexes of antennae) and proven presence of neotenic females in related genera (Fig 3). Field research in South East Asia yielded several dozen large-bodied larvae, all morphologically distinct samples were sequenced and all of them represent various species of *Platerodrilus* and *Macrolibnetis*. Neotenic female development has already been reported for a few species of these genera: *Platerodrilus paradoxus* [4], *P. ruficollis* (Pic, 1942) (= *Duliticola hoiseni* Wong, 1996) and *Macrolibnetis depressus* Pic, 1928 [4, 5, 7]. Therefore, considering the high number of identified males and females exclusively in *Platerodrilus*, we suppose that the adult larviform females of other genera are of a similar body size to males and that given their small size they have been overlooked until now.

Phylogeography and diversification of *Platerodrilus*

The distribution of *Platerodrilus* is limited to the eastern part of the Oriental region (Fig 2). The highest diversity of *Platerodrilus* is known from Sumatra (18 spp.), Borneo (7 spp.) and Peninsular Malaysia (5 spp.). Only a few species have been reported from Vietnam, Laos, Thailand and southernmost China ([21] and unpublished records from Hainan and Yunnan; Yun Li, pers. comm.). A similarly limited number of species is known from the Philippines (Fig 2). Despite presumed ancient origin of *Platerodrilus* supported by morphological and genetic divergence [1], the range of these neotenic beetles is limited to regions with stable occurrence of humid tropical forests and they are not able to readily expand their ranges during periods with favourable climatic conditions. Although other lycid lineages dispersed from the Oriental region to northern China and Japan in a high number of species, *e.g.*, Metriorrhynchini [22], *Platerodrilus* have their northernmost limits in Hainan and southern and south-western Yunnan.

The phylogeographic analysis suggests Borneo and Sumatra as an ancestral range of *Platerodrilus* (Fig 3); *P. foliaceus* and its relatives identified on the basis of similar robust parameres occur predominantly in Borneo and *P. sinuatus* and its relatives, characterized by the slender curved phallus and slender parameres, in Sumatra and continental Asia [3]. Three principal splits in the phylogeny of *Platerodrilus* were designated as the Bornean (+Philippines), Malay/Sumatran (+ Java, Borneo, Palawan) and Indo-Burman clades (Figs 1 and 3). The ranges and centres of diversity of these clades differ.

The Bornean clade contains five Bornean, two Philippine species and only a single species of the clade occurs in Sumatra (*P. wongi* from Northern Sumatra, not available for DNA analysis and assigned to the clade using morphology). The Philippine species represent a terminal lineage and a single colonization event to the Philippines was recovered in an early phase of diversification of the clade. The dating must be viewed as preliminary, nevertheless the approximate estimation of their age points to a similar age as recovered in Philippine *Scarelus* by Malohlava and Bocak [23], when mutation rate was used for dating in this distantly related lineage. The inferred age of ~25 my is close to the glacial maximum in the early Oligocene [24] and tectonic activity of the Sulu-Cagayan Arc [20]. The neotenics are not able to disperse across the sea and the indication of Oligocene colonization of the terrains forming the present day Philippines suggest a dry-land connection with Borneo. The dependence on a land connection for dispersal is supported by the fact that neither *Scarelus* nor *Platerodrilus* were able to disperse to the Philippines in the Pleistocene when most of the shelf was subaerial and the overseas distances lower than now [25]. Similarly, other neotenics are missing even in close regions if these are isolated by sea (*e.g.*, the absence of neotenic leptolycines in Jamaica and other Caribbean islands [26]).

The Malay/Sumatran clade was represented in the current molecular analysis by 17 species. The ancestral range was identified in Sumatra (Fig 4) and most species never dispersed outside of the eastern part of the Sunda Shelf, *i.e.*, Sumatra, Java and Malaya. Only *P. borneensis* Wittmer, 1966 (unavailable for DNA isolation), *P. strbai* Kazantsev, 2009 and *P. palawanensis* Masek et Bocak, 2014 (Fig 3) occur in Borneo and Palawan. The molecular phylogeny supports an early origin of *P. palawanensis* (30 mya and 20 mya in penalized likelihood and Bayesian analyses, respectively) and no exchange between faunas of Borneo, Malaya and Sumatra during Pliocene and Pleistocene low sea levels [27, 28]. The geographically close, repeatedly connected terrains of Sumatra and the Malay Peninsula also hold different fauna at the species level and the number of dispersal between them is limited. The single dispersal from Sumatra to the Malay Peninsula was dated to ~18 or ~12 mya according to available analyses (Figs 5A and 6). The other identified species pairs occurring in these regions had split in the Upper Oligocene and Lower Miocene (*Platerodrilus ngi* and *P. major*, 17mya), *P. luteus* represents an ancient lineage in the Malay/Sumatran clade and *P. angustatus* + *P. sibayakensis* clade separated from their relatives ~33 or 26 mya (Figs 5A and 6). We did not recover any more recent dispersal events (Figs 5A and 6). The fauna of Java was represented by a single species *P. ijenensis* Masek et Bocak, 2014 and this species was recovered as a sister to the diversified crown clade of Sumatran and Malay species. The Sumatran fauna is the only one, which is represented by a sufficient number of lineages to estimate the dynamics of their diversification. The ltt plot (Fig 5B) shows the increased diversification rate in *Platerodrilus* at ~17 mya and subsequent slow down till present. Alternatively, this sequence of splits was dated to 15 mya using the Bayesian inference (Fig 6). We suppose that the emergence of Sumatra 15 mya [20] and formation of the Barisan mountain range triggered diversification of *Platerodrilus*. The stable rainforest conditions in those areas isolated during glacial minima resulted in populations with lower diversification rates in the last 10 my. Dense sampling of species and populations is needed for a comprehensive analysis of speciation rates and these results must be viewed as preliminary.

The low dispersal propensity favours in situ diversification and very limited exchange between major geographical regions. No *Platerodrilus* species has been found in more than a single island and/or a mountain region. The long-term sequence of connection and isolation periods in Southeast Asia during the last 2.7 my [29] provided favourable conditions for multiple dispersal events at least in the last several million years, but no dispersal events were identified in *Platerodrilus*. The reasons for observed patterns include the above mentioned low dispersal propensity, but also the climatic conditions in the subaerial Sunda Shelf. The rainforests in South East Asia depend on the monsoon system, which developed after the uplift of the Himalayas, but these rich habitats covered a variable part of the shelf depending on climatic fluctuations. The cool periods resulted in aridisation of the interior of the shelf [30] and the savannah regions might have prevented the exchange between centres of diversity in eastern and western mountain ranges, which obtained a higher amount of rainfall and house very diverse fauna of neotenics. Similarly, decreased diversity of termites was reported in previously arid regions by Gathorne-Hardy *et al.* [31], but the preserved distribution patterns evolved in the described case during recent Pleistocene periods of climatic fluctuations. In contrast, the faunas of *Platerodrilus* remained isolated in the ancestral ranges over much longer time span and we identified only several dispersal events and/or vicariance between these centres of diversity in the Miocene or earlier.

The low dispersal propensity of neotenic net-winged beetles also affects diversification within individual islands. We found the complete turn over with no species overlap between mountain ranges in Sumatra (Fig 2), from where the higher density of sampling was available. Altogether 18 species occur in Sumatra and most are closely related and belong to the terminal lineage designated as the Malay/Sumatran clade (Fig 5A). The individual mountain systems house completely distinct faunas and no species was collected in two or more distant localities. The stability of the tropical forests since the uplift of the island is postulated to be a necessary condition for *in situ* evolution and long-term persistence of *Platerodrilus* in Sumatra. Additionally, the extremely low dispersal propensity of larviform females contributes to the observed small ranges and the whole-year humid mountain forests in the Sumatran mountain massifs represent separate "islands" where populations of *Platerodrilus* diversified in isolation. The protection of major forest complexes like the Leuser National Park is important, but our findings suggest that only a fragment of genetic diversity is housed even in such a large national park. If diversity of the organisms with limited dispersal propensity is to be protected, the preservation of rainforest habitats is needed in a form of an extensive network covering most of the mountain ranges in South East Asia.

Supporting Information

S1 Fig. The Bayesian phylogenetic trees of *Platerodrilus* inferred from the dataset aligned using (A) BlastAlign, (B) Clustal and (C) Muscle.
(TIF)

S1 Table. Taxonomic coverage, geographic origin, and GenBank accession numbers.
(PDF)

S2 Table. The locality data for *Platerodrilus* samples.
(PDF)

S3 Table. Primers used for PCR amplifications.
(PDF)

Acknowledgments

The authors are grateful to R. Bilkova for technical assistance, to A. F. S. L. Lok, E. Jendek, L. Dembicky and P. Pacholatko for donation of specimens, and to N. Gunter for comments on the manuscript and proofreading.

Author Contributions

Conceived and designed the experiments: LB. Performed the experiments: MM VP. Analyzed the data: MM VP LB. Contributed reagents/materials/analysis tools: LB. Wrote the paper: MM TB LB.

References

1. Bocak L, Bocakova M, Hunt T, Vogler AP. Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. Proc R Soc B. 2008; 275: 2015–2023. doi: 10.1098/rspb.2008.0476 PMID: 18477542

2. Masek M, Ivie MA, Palata V, Bocak L. Molecular phylogeny and classification of Lyropaeini (Coleoptera: Lycidae) with description of larvae and new species of Lyropaeus. Raffl Bull Zool. 2014; 62: 136–145.
3. Masek M, Bocak L. The taxonomy and diversity of *Platerodrilus* (Coleoptera: Lycidae) inferred from molecular data and morphology of adults and larvae. ZooKeys 2014; 426: 29–63. doi: 10.3897/zookeys.426.7398 PMID: 25147457
4. Mjöberg E. The mystery of the so called "Trilobite" or "Perty's larvae" definitely solved. Psyche. 1925; 32: 119–154, pl. 3–4.
5. Wong ATC. A new species of neotenous beetle, *Duliticola hoiseni* (Insecta: Coleoptera: Cantharoidea: Lycidae) from Peninsular Malaysia and Singapore. Raffl Bull Zool. 1996; 44: 173–187.
6. Gould SJ. Ontogeny and phylogeny. Cambridge, MA: Harvard University Press; 1977
7. Levkanicova Z, Bocak L. Identification of net-winged beetle larvae (Coleoptera: Lycidae) using three mtDNA fragments: a comparison of their utility. Syst Ent. 2009; 34: 210–221.
8. Myers N, Mittermeier RA, Mittermeier C, da Fonseca GAB, Kent J. Biodiversity hotspots for conservation priorities. Nature. 2000; 403: 853–858. PMID: 10706275
9. Thompson J, Higgins D, Gibson T. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignments through sequence weighting, position specific gap penalties and weight matrix choice. Nucl Ac Res. 1994; 22: 4673–4680. PMID: 7984417
10. Belshaw R, Katzourakis A. BlastAlign: a program that uses blast to align problematic nucleotide sequences. Bioinformatics. 2005; 21: 122–123. PMID: 15310559
11. Edgar RC. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucl Ac Res. 2004; 32: 1792–1797. PMID: 15034147
12. Stamatakis A, Ludwig T, Meier H. RAxML-III: a fast program for maximum likelihood-based inference of large phylogenetic trees. Bioinformatics. 2005; 21: 456–463. PMID: 15608047
13. Posada D. JMODELTEST: phylogenetic model averaging. Mol Biol Evol. 2008; 25: 1253–1256. doi: 10.1093/molbev/msn083 PMID: 18397919
14. Huelsenbeck JP, Ronquist F. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 2001; 17: 754–755. doi: 10.1093/bioinformatics/17.8.754 PMID: 11524383
15. Rambaut A, Suchard MA, Xie D, Drummond AJ. Tracer version 1.6. 2014. Available: http://beast.bio.ed.ac.uk/Tracer.
16. Yu Y, Harris AJ, He XJ. RASP (Reconstruct Ancestral State in Phylogenies) 2.1b. 2012. Available: http://mnh.scu.edu.cn/soft/blog/RASP.
17. Sanderson MJ. Estimation absolute rates of molecular evolution and divergence times: a penalized likelihood approach. Mol Biol Evol. 2002; 19: 101–109. PMID: 11752195
18. Revell LJ. Phytools: An R package for phylogenetic comparative biology (and other things). Meth Ecol Evol. 2012; 3: 217–223.
19. Drummond AJ, Rambaut A. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol Biol. 2007; 7: 214. PMID: 17996036
20. Hall R. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. J Asian Earth Sci. 2002; 20: 353–431.
21. Kazantsev SV. New taxa of Platerodrilini. Russ Ent J. 2009; 18: 55–62.
22. Sklenarova K, Chesters D, Bocak L. Phylogeography of Poorly Dispersing Net-Winged Beetles: A Role of Drifting India in the Origin of Afrotropical and Oriental Fauna. PLoS One. 2013; 8(6): e67957. doi: 10.1371/journal.pone.0067957 PMID: 23840793
23. Malohlava V, Bocak L. Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. Mol Ecol. 2010; 19: 4800–4811. doi: 10.1111/j.1365-294X.2010.04850.x PMID: 20958816
24. Zachos J, Pagani M, Sloan L, Thomas E, Billups K. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science. 2001; 292: 686–693. PMID: 11326091
25. Voris HK. Maps of Pleistocene sea levels in south-east Asia: shorelines, river systems and time duration. J Biogeogr. 2000; 27: 1153–1167.
26. Bocak L, Bocakova M. Phylogeny and classification of the family Lycidae (Insecta: Coleoptera). Ann Zool. 2008; 58: 695–720.
27. Dwyer GS, Chandler MA. Mid-Pliocene sea level and continental ice volume based on coupled benthic Mg/Ca palaeotemperatures and oxygen isotopes. Phil Trans R Soc A. 2009; 367: 157–168. doi: 10.1098/rsta.2008.0222 PMID: 18854304
28. Hanebuth T, Stattegger K, Grootes PM. Rapid flooding of the Sunda Shelf: a Late glacial sea-level record. Science. 2000; 288: 1033e1035. PMID: 10807570

29. Woodruff DS. Biogeography and conservation in Southeast Asia: how 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. Biodiv Cons. 2010; 19: 919–941.

30. Ray N, Adams JM. A GIS-based vegetation map of the World at the last Glacial Maximum (25,000–15,000 BP). Intern Arch. 2001; 11: 1–44.

31. Gathorne-Hardy FJ, Syaukani, Davies RG, Eggleton F, Jones DT. Quaternary rainforest refugia in south-east Asia: using termites (Isoptera) as indicators. Biol J Linn Soc. 2002; 75: 453–466.

Zootaxa 3721 (5): 495–500
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.3721.5.5
http://zoobank.org/urn:lsid:zoobank.org:pub:6C1AC403-7BBC-4B00-9DCE-AD0C717AABB2

A new species of *Dexoris* (Coleoptera: Lycidae) and parallel evolution of brachyptery in the soft-bodied elateroid beetles

LADISLAV BOCAK[1, 3], VASILY V. GREBENNIKOV[2] & MICHAL MASEK[1]

[1]*Department of Zoology, Faculty of Science, Palacky University, 771 46 Olomouc, Czech Republic*
[2]*Canadian Food Inspection Agency, Ottawa Plant Laboratory, KW Neatby Bldg, 960 Carling Ave, Ottawa, ON K1A 0C6, Canada. E-mail: Vasily.Grebennikov@inspection.gc.ca*
[3]*Corresponding author. E-mail: ladislav.bocak@upol.cz*

Abstract

Dexoris chome **sp. nov.** is described from South Pare mountains, Tanzania, based on a male specimen. This is the only *Dexoris* with shortened elytra, rudimentary hind wings and large, larviform abdomen. Unlike males of other species in the genus, *D. chome* **sp. nov.** has a modified number of palpomeres and remarkably short, robust legs and antennae. Such modifications are similar to those in the neotenic female of *Omalisus fontisbellaquei* Fourcroy, 1785 (Omalisidae), suggesting analogous morphological changes in unrelated lineages supposedly caused by similar modifications of their metamorphosis. The distribution of all 11 known species of African *Dexoris* closely overlap with the location of the hypothesized centres for evolution of new species in the Afrotropical region.

Key words: Net-winged beetles, neoteny, metamorphosis, Afrotropical region, distribution, new species

Introduction

Dexoris Waterhouse, 1878 is a peculiar net-winged beetle genus with 10 known species from humid regions of Sub-Saharan Africa (Kleine 1942, Bocak & Bocakova 1988, Kazantsev 2000). Here we describe the unique case of fore-wing brachelytry and hind-wing microptery among net-winged beetle males. Although cases of brachelytry have been described in *Alyculus* Kazantsev, 1999 (Palata & Bocak 2012, Lyropaeinae: Alyculini) and *Cautires* Waterhouse, 1879 (Bocak *et al*., in press, Lycinae: Metriorrhynchini), the hind wings were either fully developed or absent in these taxa. The insect wings are considered a key innovation responsible for evolutionary success, but many insects have given up their ability to fly in order to save energy for propagation (Guerra 2011) or to avoid being blown away from their preferred habitat (Medeiros & Gillespie 2011). The loss of flight in soft-bodied Elateriformia beetles, however, might have different biological connotations. The lycid flightless neotenics have limited distributions, are species-poor and their flightlessness cannot be correlated with any evolutionary adaptation. Probably it is merely not penalized in stable environments (Bocak *et al*. 2008). When conditions fluctuate, such flightless and humidity-dependent species are endangered. The knowledge of neotenic beetle species is limited mainly due to their poor representation in collections. Up to now, only three neotenic genera, *Platerodrilus* Pic, 1921 *Macrolibnetis* Pic, 1938 and *Lyropaeus* Waterhouse, 1878, are known in both sexes (Wong 1996, Levkanicova & Bocak 2009, Masek *et al.* in press). Several other genera, *e.g. Scarelus* Waterhouse, 1879 and *Leptolycus* Leng et Mutchler, 1922, are known from a large number of winged males, while the neotenic development of their still unknown females is only hypothesized. Unlike closely related Lampyridae, the known neotenic lycid females remain completely larviform, and brachelytry is seldom observed in males.

Accepted by C. Majka: 26 Sept. 2013; published: 17 Oct. 2013

Material and methods

The description is based on a single adult male specimen. In order to study its genitalia, the apical part of abdomen was briefly placed in hot 10% KOH to macerate the muscles and fat bodies. Photographs of diagnostic characters and measurements were taken using an Olympus SZX-16 microscope.

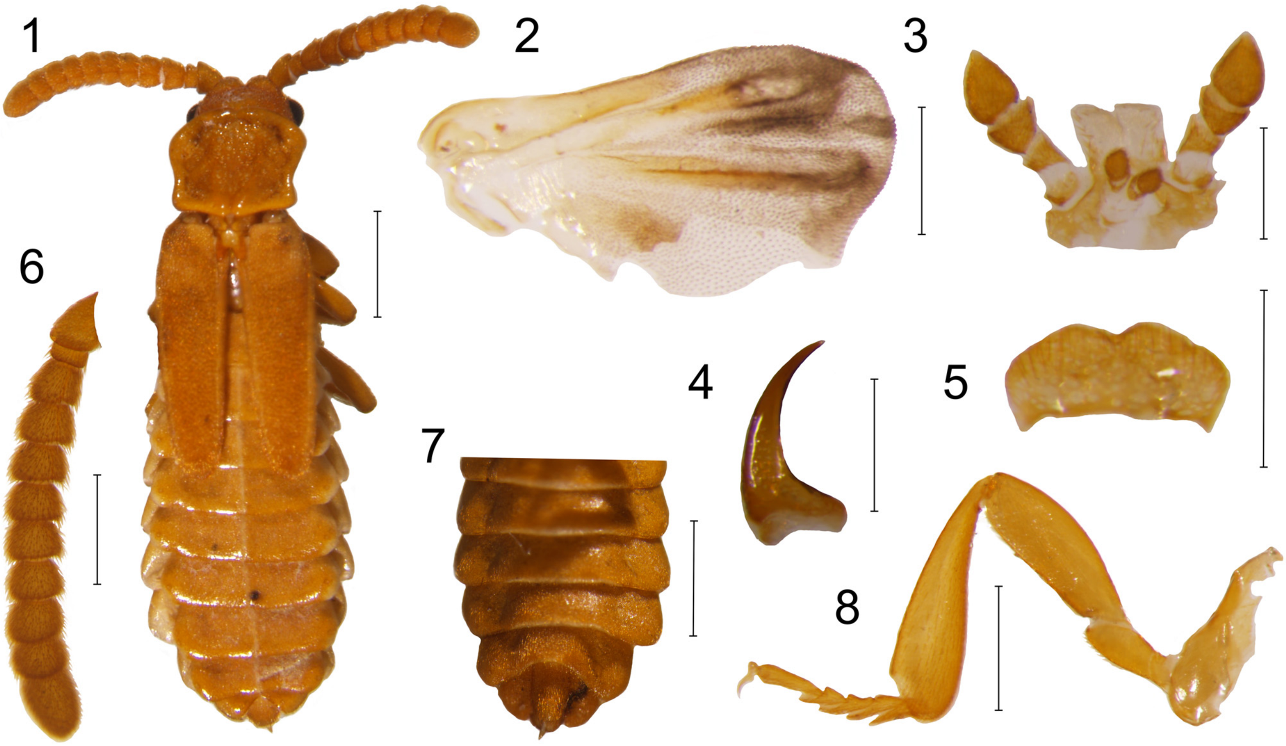
Dexoris **(s. str.)** ***chome*** **sp. nov.**

(Figs 1–8, 10–13)

Type material. Holotype. Male, "Tanzania, South Pare Mts., Chome For., S4.27064° E37.92595°, 2159 m, 3.i.2013, sift38, V. Grebennikov leg." The holotype is deposited in the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa.

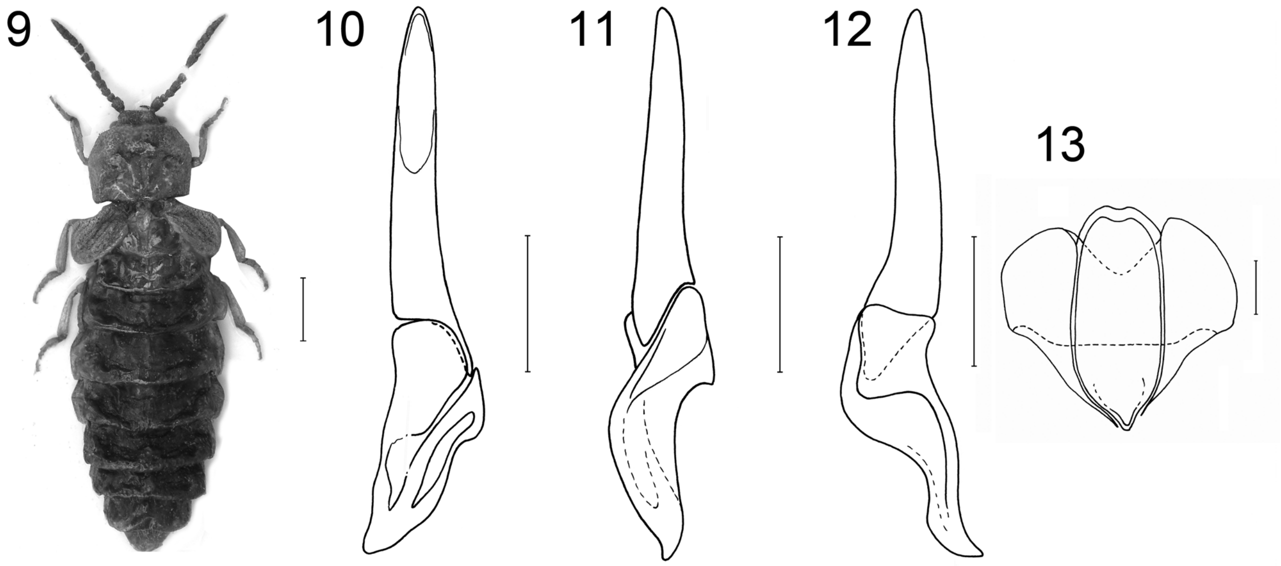
Type locality. Tanzania, South Pare, Chome Forest, S4.27064° E37.92595°, 2159 m.

Diagnosis. *Dexoris chome* **sp. nov.** is the only species in the genus with a brachelytrous male. The only known male of the new species differs from other fully winged *Dexoris* males in having shorter elytra, nonfunctional and vestigial hind wings, short robust antennae and the pronotum widest in the anterior third (Fig. 1). Additionally, *D. chome* **sp. nov.** differs in having 3-segmented maxillary palpi (4-segmented in other *Dexoris*) and 2-segmented labial palpi (a single free palpomere in other *Dexoris* species). Male genitalia have a well sclerotized asymmetrical phallobase, unlike other *Dexoris* (Figs 10–12).



FIGURES 1–8. *Dexoris chome* **sp. nov.** 1 general appearance, 2 hind wing, 3 maxillae and labium, 4 mandible, 5 labrum, 6 antenna, 7 abdomen, 8 hind leg. Scales 1 mm (Figs 1, 7), 0.5 mm (Figs 6, 8), 0.25 mm (Figs 2–5).

Description. Male. Body small, light testaceous, wings partly infuscate, eyes black (Figs 1–2). Head small, hypognathous, partly covered by pronotum; cranium with slightly prominent frontal part, surface roughly punctured, very sparsely pubescent. Antennae 11-segmented, inserted fronto-laterally, below frontal tubercles, short, reaching slightly behind posterior angles of pronotum, rounded in cross section; scapus robust and pear-like, pedicel small and slightly shorter than wide, antennomere 3 1.5x longer than antennomere 2, subsequent antennomeres gradually shorter, antennomere 11 parallel-sided and long, all antennomeres with short dense pubescence (Fig. 6). Eyes small, hemispherically prominent, eye diameter 0.29x interocular distance. Mouthparts with slender and short mandibles (Fig. 4). Labrum transverse, with shallowly emarginate apex (Fig. 5). Hypopharynx forming simple oblong plate, much narrower than labrum. Maxillae with plate-like stipes, cardo inconspicuous and partly membranous; mala reduced and with sparse setae; maxillary palpi 3-segmented, basal palpomere short, transverse, ring-like, palpomere 2 twice longer, palpomere 3 robust, apex pointed. Labium small, single weakly sclerotized plate present, ligula inconspicuous, palpi 2-segmented, basal palpomere short, apical palpomere 3 times longer (Fig. 3). Pronotum slightly wider than long, parallel-sided at base, widening anterad, basal angles slightly obtuse, not prominent, frontal angles obtuse, anterior margin almost straight, deeply and narrowly emarginate in middle; pronotum with robust longitudinal carinae forming well marked areola attached to posterior margin, middle of longitudinal carinae with attached vestiges of lateral keels, surface with deep irregular punctures (Fig. 1), disc covered with sparse pubescence. Scutellum bilobed apically, distal processes slender (Fig. 1). Elytra shortened, tapering towards apex, without longitudinal or transverse costae, with small papillae each bearing single tiny seta (Fig. 1), elytra completely covered with dense microsetae. Wings vestigial, about 0.4x elytral length, longitudinal costae present, transverse costae absent, fused costal veins at base of wing robust, radia and media inconspicuous at base, gradually becoming visible distad, other longitudinal veins absent (Fig. 2). Legs short, robust, femora with emarginate posterior part, basal interconnecting membrane reaching in posterior part to middle of femoral length, tarsomeres slender, similar in width (Fig. 8). Abdomen wide, terminal sternite parallel-sided, shallowly emarginate at apex (Figs 7, 13). Male genitalia with phallus and asymmetrical phallobase, parameres absent. Phallus about 7.5x longer than wide in middle, gradually tapering and pointed apically, internal sac membranous, without sclerotized structures (Figs 10–12).



FIGURES 9–13. 9 *Omalisus fontisbellaquaei*, general appearance; 10–12 *Dexoris chome* **sp. nov.**, male genitalia; 13 ditto, terminal abdominal segments. Scale 1 mm (Fig. 9), 0.2 mm (Figs 10–13).

Measurements. Body length 6.15 mm, pronotal length at midline 1.0 mm, maximum pronotal width 1.25 mm, length of elytra 2.18 mm, length of hind wings 0.94 mm, length of abdomen (ventrally) 3.88 mm, maximum width of abdomen 1.88 mm, minimum frontal distance between eyes 0.83 mm, maximum eye diameter in the lateral view 0.24 mm.

Distribution. *Dexoris chome* **sp. nov.** is known only from the type locality. It is the only *Dexoris* recorded from Tanzania. The distribution of all 11 known *Dexoris* species (Fig. 14) closely corresponds to the hypothesized distribution of the stable forests during the arid periods (Fjeldså & Lovett 1997), also currently matching the diversity hotspots in Africa (Myers *et al.* 2000). The very limited dispersal capacity of *Dexoris* species, all having wingless females, limits these beetles to regions with uninterrupted, relatively wet forest.

Etymology. The specific epithet refers to the Chome Forest in the North Pare mountains in Tanzania, the geographic origin of the holotype; noun in apposition.

Biology. A single male was extracted using a Winkler funnel, from the fine fraction of the forest floor leaf litter sifted through a seven millimetre mesh in almost undisturbed mountain rainforest. Females of the species remain unknown and we hypothesise them to be completely larviform and resembling in this respect other neotenics Lycidae (Wong 1996). Detecting only a single specimen of the new species is rather remarkable considering that a relatively large sifting effort has been conducted.

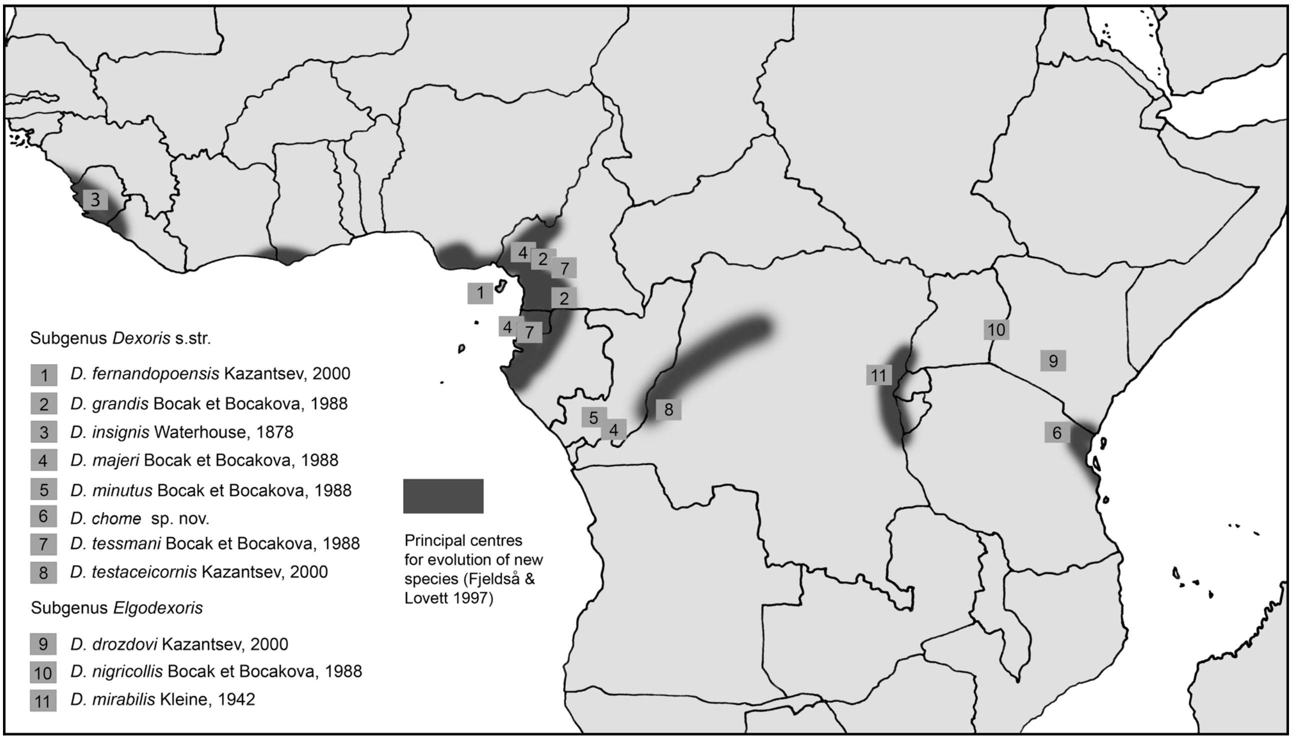


FIGURE 14. The distribution of *Dexoris* and centres for evolution of new species defined by Fjeldså & Lovett (1997).

Discussion

Classification. *D. chome* **sp. nov.** is classified in the *Dexoris* s. str. on the basis of the shape of the pronotal carinae, the phallus and the structure of the elytra and wide pronotum. Several characters listed in the differential diagnosis help to identify the species, even though they supposedly relate to the incomplete metamorphosis and are, therefore, likely subjected to parallel development in various unrelated neotenic lineages. The reduction of mouthparts is common in neotenic net-winged beetles since the males are short-lived and probably do not take any food (*e.g. Lyropaeus*; Bocak & Bocakova 2008). Shortened elytra and appendages were observed in various neotenics species across unrelated soft-bodied Elateroidea (*e.g. Omalisus*; Fig. 9; Bocak & Brlik 2008). Therefore, although *D. chome* **sp. nov.** differs morphologically from other species of the genus, it does not deserve a higher monotypic taxon to accommodate it.

Diversity of morphological modifications in Elateroidea. The Elateroidea contains both the well-sclerotized (Artematopodidae, Eucnemidae, Throscidae, Cerophytidae and Elateridae), as well as soft-bodied families (Lycidae, Cantharidae, Lampyridae, Phengodidae etc.; Bocakova *et al*. 2007, Kundrata & Bocak 2011). The degree of female neotenic modifications varies greatly among them. Relatively minor modifications are observed in *Omalisus* (Omalisidae) with the females being adult-like and having shortened elytra, lacking hind wings and shortened appendages (Fig. 9). A more advanced stage of neoteny is observed in Lampyridae, such as females of *Lampyris noctiluca* (Linnaeus, 1767) and *Phosphaenus hemipterus* (Geoffroy, 1762) having neither elytra nor hind wings, while females of *Lamprorhiza splendidula* (Linnaeus, 1767) have vestigial elytra and no hind wings (Branham 2010). The females of *Drilus* spp. (Elateridae: Agrypninae: Drilini) have a larviform body and adult-like head (Kundrata & Bocak 2011). In these examples males are occasionally modified as well; however, no strict correlation between morphological modifications in both sexes has been observed.

Some net-winged beetles, such as *Platerodrilus* and *Lyropaeus* have completely larviform females (Wong 1996), while their males are fully winged. The shortened elytra in males were reported in two genera: *Alyculus* with four species (Palata & Bocak 2012) and *Cautires* (Bocak *et al*. in press). *Dexoris chome* **sp. nov.** is the third known case of such modification. The male of *D. chome* **sp. nov.** has shortened elytra and vestigial hind wings and in this respect resembles females of *Omalisus fontisbellaquei*. All lycid lineages with shortened elytra belong to three various subfamilies: Lyropaeinae (*Alyculus*), Lycinae: Metriorrhynchini (*Cautires*) and Dexorinae (*Dexoris*) (Bocak *et al*. 2008), which suggests parallel evolution of neotenic modifications across elateroid lineages with very similar changes occurring in males and females.

Acknowledgements

The study was funded by the Grant Agency of the Czech Republic (LB, P506/11/1757) and the Internal Grant of Palacky University (MM, PrF2013-018). Karen McLachlan Hamilton (Ottawa, Canada) critically read the MS prior to its submission.

References

Bocak, L. & Bocakova, M. (1988) Revision of the genus *Dexoris* C. O. Waterhouse (Coleoptera, Lycidae). *Acta Entomologica Bohemoslovaca*, 85, 194–204.

Bocak, L. & Bocakova, M. (2008) Phylogeny and classification of the family Lycidae (Insecta: Coleoptera). *Annales Zoologici*, 58, 695–720.
http://dx.doi.org/10.3161/000345408x396639

Bocak, L., Bocakova, M., Hunt, T. & Vogler, A.P. (2008) Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. *Proceedings of the Royal Society B*, 275, 2015–2023.
http://dx.doi.org/10.1098/rspb.2008.0476

Bocak, L. & Brlik, M. (2008) Revision of the family Omalisidae (Coleoptera, Elateroidea). *Insect Systematics & Evolution*, 39, 189–212.

Bocak, L., Grebennikov, V. & Sklenarova, K. (in press) *Cautires apterus*, a new species and the first record of wingless male Lycidae (Coleoptera) discovered in the North Pare Mountains, Tanzania. *Annales Zoologici*.

Bocak, L. & Matsuda, K. (2003) Review of the immature stages of the family Lycidae (Insecta: Coleoptera). *Journal of Natural History*, 37, 1463–1507.
http://dx.doi.org/10.1080/00222930210125362

Bocakova, M., Bocak, L., Hunt, T., Terävainen, M. & Vogler, A.P. (2007) Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics*, 23, 477–496.
http://dx.doi.org/10.1111/j.1096-0031.2007.00164.x

Branham, M.A. (2010) Lampyridae Latreille, 1817. *In:* Leschen, R.A.B. & Beutel, R.G. (Eds.), *Handbook of Zoology. Part 38, Vol. 2. Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujoidea)*. Walter de Gruyter, Berlin, New York, pp. 141–149.

Fjeldså, J. & Lovett, J.C. (1997) Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodiversity and Conservation*, 6, 325–346.

Guerra, P.A. (2011) Evaluating the life-history trade-off between dispersal capability and reproduction in wing dimorphic insects: a meta-analysis. *Biological Reviews*, 86, 813–835.
http://dx.doi.org/10.1111/j.1469-185x.2010.00172.x

Kazantsev, S.V. (2000) New and little known African lycids (Coleoptera: Lycidae). *Russian Entomological Journal*, 9, 241–248.

Kleine, R. (1942) Brenthidae und Lycidae (Addendum). *Exploration du Parc National Albert, Mission G.F. de Witte (1933-1935)*, 8, 1–9.

Kundrata, R. & Bocak, L. (2011) The phylogeny and limits of Elateridae (Insecta, Coleoptera): is there a common tendency of click beetles to soft-bodiedness and neoteny? *Zoologica Scripta*, 40, 364–378.
http://dx.doi.org/10.1111/j.1463-6409.2011.00476.x

Levkanicova, Z. & Bocak, L. (2009) Identification of net-winged beetle larvae (Coleoptera: Lycidae) using three mtDNA fragments: a comparison of their utility. *Systematic Entomology*, 34, 210–221.
http://dx.doi.org/10.1111/j.1365-3113.2008.00457.x

Malohlava, V. & Bocak, L. (2010) Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. *Molecular Ecology*, 19, 4800–4811.
http://dx.doi.org/10.1111/j.1365-294x.2010.04850.x

Masek, M., Ivie, M.A., Palata, V. & Bocak, L. (2013) Molecular phylogeny and classification of Lyropaeini (Coleoptera: Lycidae) with description of larvae and new species of *Lyropaeus*. *Raffles Bulletin of Zoology*. [in press]

Medeiros, M.J. & Gillespie, R.G. (2011) Biogeography and the evolution of flightlessness in a radiation of Hawaiian moths (Xyloryctidae: Thyrocopa). *Journal of Biogeography*, 38, 101–111.
http://dx.doi.org/10.1111/j.1365-2699.2010.02402.x

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.
http://dx.doi.org/10.1038/35002501

Palata, V. & Bocak, L. (2012) Revision of *Alyculus* Kazantsev, 1999 (Coleoptera: Lycidae). *Zootaxa*, 3564, 61–67.

Waterhouse, C.O. (1878) On the different forms occurring in the Coleopterous family Lycidae, with description of new genera and species. *Transactions of the Entomological Society London*, 1878, 95–118.
http://dx.doi.org/10.1111/j.1365-2311.1878.tb01944.x

Wong, A.T.C. (1996) A new species of neotenous beetle, *Duliticola hoiseni* (Insecta: Coleoptera: Cantharoidea: Lycidae) from peninsular Malaysia and Singapore. *Raffles Bulletin of Zoology*, 44, 173–187.

Zoological Journal of the Linnean Society, 2016. With 5 figures

Congruence between morphology and molecular phylogeny: the reclassification of Calochromini (Coleoptera: Lycidae) and their dispersal history

MICHAL MOTYKA, MICHAL MASEK and LADISLAV BOCAK*

Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 771 46 Olomouc, Czech Republic

Received 25 February 2016; revised 7 July 2016; accepted for publication 13 August 2016

Calochromini is a tribe of net-winged beetles (Elateroidea: Lycidae) with 284 described species, which have a global distribution. Historically, the species have been placed in eight genera, although the morphological boundaries between genera have been poorly defined. We assembled a five-marker DNA dataset (18S and 28S rRNA, and *rrnL*, *nad5* and *cox1* mtDNA) with 89 terminals, representing 61 calochromine species from eight genera and from all geographical regions. The analyses recovered a well-resolved phylogeny of Calochromini and identified major lineages, which were tested by detailed evaluation of adult morphology. The inferred topology is in conflict with the traditional morphology-based concepts of genera and highlights that historically used diagnostic characters such as the prolonged rostrum are homoplastic. New morphological diagnostic characters that are congruent with the molecular phylogeny are defined mainly from male genitalia. We delimit the genera *Calochromus* Guérin-Méneville, 1833 (incl. the subgenera *Flabellochromus* Pic, 1925 and ***Paracalochromus* subgen. nov.**), *Micronychus* Motschoulsky, 1861, *Macrolygistopterus* Pic, 1929, *Lucaina* Dugès, 1879, *Lygistopterus* Mulsant, 1838, ***Parantis* gen. nov.** and *Caloptognatha* Green, 1954. *Micronychus* Motschoulsky, 1861 is removed from synonymy with *Calochromus* Guérin-Méneville, 1833 and ***Adoceta*** Bourgeois, 1882 **syn. nov.** is proposed as a junior synonym of *Lygistopterus* Mulsant, 1838. These changes in the generic classification result in 147 new combinations. Additionally, we estimate divergence dates and dispersal history of the tribe. Calochromini originated in continental Southeast Asia in the Palaeocene (56 Mya), dispersed twice to the New World, in the Early Eocene (51 Mya, *Lucaina* and *Macrolygistopterus*) and in the Late Oligocene (28 Mya, *Lygistopterus*). Our results indicate that the Western Palearctic region was colonized by extant *Lygistopterus* (28 Mya), and the Afrotropical region by *Micronychus* (29 Mya). Dispersal routes are discussed in the context of the tectonic and palaeoclimatic history. The highest phylogenetic diversity is identified in southern China and Indo-Burma where most principal lineages occur. Conversely, the highest alpha diversity is identified in the semi-arid areas of southern India.

doi: 10.1111/zoj.12497

ADDITIONAL KEYWORDS: ancestral areas – divergence dating – Net-winged beetles – taxonomy – zoogeography.

INTRODUCTION

The classification of biological life is often affected by the earlier applied typological approach and the absence of modern taxonomic revisions. Historical generic concepts based on a limited number of species became poorly defined when hundreds of species were described. Calochromini are no exception and more than half of calochromine species, often morphologically diverse, have been placed in a single genus *Calochromus* Guérin-Méneville, 1833 (Kleine, 1933). Therefore, the classification has not provided any support for evolutionary and zoogeographical studies. Here, we present the first genus-level molecular phylogeny of Calochromini to revise this classification.

Calochromini are one of the principal lineages of the net-winged beetles (Elateroidea: Lycidae; Bocak

---

*Corresponding author. E-mail: ladislav.bocak@upol.cz

& Bocakova, 2008) and they were the first group with subfamilial status (as Calochrominae Lacordaire, 1857). This lineage is morphologically well defined by the very obtuse pronotal carinae, weak longitudinal and absent transverse costae in elytra, characteristic asymmetrical phallobase and very long and slender ovipositor. Recently, Bocak & Bocakova (2008) rejected the idea that absent pronotal carinae and elytral costae are ancestral traits and lowered Calochrominae to the tribal rank in Lycinae. The taxonomy of Calochromini has been based only on historical studies (Guérin-Méneville, 1833; Mulsant, 1838; Waterhouse, 1879; Bourgeois, 1882; Pic, 1929; Kleine, 1933, 1941; Green, 1950, 1954) and the concepts of genera have not been revised. Altogether, eight genus-group names have been available in Calochromini: *Calochromus* Guérin-Méneville, 1833 with *Flabellochromus* Pic, 1925 considered as a subgenus or a synonym of *Calochromus*, *Micronychus* Motschoulsky, 1861 (a synonym of *Calochromus*), *Macrolygistopterus* Pic, 1929, *Lucaina* Dugès, 1879, *Lygistopterus* Mulsant, 1838, *Adoceta* Bourgeois, 1882 and *Caloptognatha* Green, 1954 (Kleine, 1933; Green, 1954). Previous studies removed some genera earlier placed in Calochromini: *Falsocalochromus* Pic, 1942 was transferred to Lyropaeinae: Platerodrilini, *Dumbrellia* Lea, 1909 was transferred to Lycinae: Platerodini and *Lycoprogenthes* Pic, 1915 was transferred to Dictyopterinae: Lycoprogenthini (Bocak, 2002; Bocak & Bocakova, 2008; Masek & Bocak, 2014; Motyka & Bocak, 2015). The generic classification produced by 19th century authors and later summarized by Kleine (1933, 1941) was typological and has been based on external morphological characters such as the shape of antennae, body-size, the presence and the length of the rostrum or pubescence on elytra. Green (1954) attempted to provide a generic classification with a clear set of characters. Unfortunately, his study was restricted to the USA where only a few genera occur.

Most studies on alpha-taxonomic diversity are isolated descriptions in geographically restricted reports dealing with Lycidae (e.g. Pic, 1925, 1930, 1931; Kleine, 1926). Further chaos at the alpha-taxonomical level resulted from the taxonomic works of Maurice Pic whose descriptions were anecdotal and sometimes uninformative (e.g. Pic, 1913, 1923, 1925). Due to unclear generic concepts, altogether 159 species were placed in the apparently polyphyletic genus *Calochromus* (56% of the tribal diversity) and conflicting classifications were proposed for 42 species of Neotropical Calochromini (Pic, 1929; Kleine, 1933; Ferreira, 2016). The few taxonomic revisions published after World War II were geographically restricted (Bocakova, 1992; Motyka & Bocak, 2015; Ferreira, 2016) or limited to descriptions of a few new species (Papp, 1952; Nakane, 1969; Ramsdale, 2007).

Most ecological traits of Calochromini are shared with other lycid lineages. Lycids depend strongly on forest and shrub habitats; their larvae live in moist decaying organic material and suck up liquids rich in microbial life (Bocak & Matsuda, 2003). Therefore, the highest diversity of Lycidae is found in tropical rain forests (Bocak & Bocakova, 2008) where desiccation does not represent an acute threat. Unlike most relatives, Calochromini are not as common in humid tropics and they tolerate semi-dry habitats where their larvae develop in decaying roots in soil or their development is limited to the rainy season (field observation). Among Lycidae, Calochromini have greater dispersal capability and, in contrast to most net-winged beetles, their adults visit flowers, probably using nectar as an alternative source of water (field observation). They fly in open situations and are able to cross barriers that prevent dispersal of other groups (Sklenarova, Chesters & Bocak, 2013). One further factor affecting lycid ecology and dispersal propensity is their unpalatability to predators (Moore & Brown, 1981; Eisner *et al.*, 2008). Typically, members of each mimetic complex share the similar shape and size of the body and aposematic colour pattern. The distribution of the mimetic complexes is regularly restricted to clearly limited ranges and we can suppose that adaptation to the local mimetic pattern limits their ability to disperse outside the area where predators have experience to avoid them (Bocak & Yagi, 2010). Although species of Calochromini are regularly involved in mimetic complexes, they do not display a large number of mimetic patterns and they have wide distributional ranges.

There is a need for classification of Calochromini to be based on a robust phylogenetic hypothesis and here we use molecular data, which are not affected by adult ecology, to construct the first phylogeny of Calochromini (Vuataz *et al.*, 2011). Congruence between our phylogenetic hypothesis and morphological characters was extensively evaluated using material from major museum collections. The aim of this study is to propose a generic classification of Calochromini based on a combination of molecular and morphological data, although a formal dataset of morphological characters was not assembled for phylogenetic inference due to their limited number. Using our molecular phylogeny, distributional data of sequenced species and information gathered from museum collections, we propose a hypothesis on the dispersal history of Calochromini and infer their ancestral distribution.

MATERIAL AND METHODS

Material, laboratory procedures and phylogenetic analyses

The ingroup contained 89 Calochromini specimens representing 61 species from all geographical regions and from all genera except *Caloptognatha* (Table S1, Supporting Information). The outgroup was represented by 11 Lycinae taxa reported in a previous study (Bocak *et al.*, 2008). Multiple tribes were included in the outgroup as the sister group of Calochromini has not been conclusively identified (Bocak & Bocakova, 2008). DNA was extracted using the Wizard SV96 kit (Promega) from thoracic muscles. Five gene fragments, i.e. 18S rRNA (~1850 bp), 28S rRNA (~630 bp), *rrnL* (~800 bp), *cox1* (~1000 bp) and *nad5* mtDNA (~1200 bp), were amplified using the primers listed in the Supporting Information (Table S2, Supporting Information). A voucher number was assigned to each specimen in the format UPOL XX1236 (Table S1, Supporting Information, Fig. 1A). The PCR settings and sequencing procedures followed those described by Sklenarova *et al.* (2013). The sequences were submitted to GenBank and the accession numbers KU495936–6215 are listed for individual samples in Table S1 (Supporting Information).

Chromatograms were edited using the Sequencher 4.8 software package (Gene Codes Corp.). Length-invariable protein coding sequences were aligned using ClustalX 1.83 in Geneious R7.1.7 (Biomatters Inc.) with default settings (Thompson, Higgins & Gibson, 1994); the rRNA fragments were aligned using Mafft 7.017 (Katoh & Standley, 2013) and MUSCLE in Geneious R7.1.7 (Drummond *et al.*, 2014). The concatenated supermatrix was partitioned by the genes and the codon positions in protein coding genes and analysed using the maximum-likelihood (ML) criterion and Bayesian inference. The ML analyses were performed in RAxML 7.2.3 (Stamatakis, 2006) with GTRCAT model and bootstrap supports (BS) computed from 500 pseudoreplicates; the model was identified by jModeltest 2.1.8 (Darriba *et al.*, 2012). The Bayesian inference was run under the GTR+I+G model for 50 million generations. The first 9×10^6 trees were discarded as burn-in and posterior probabilities (PP) were calculated from post-burn-in trees. The convergence of runs, stationary phase and the effective sample size for all parameters were identified with TRACER 1.5 (Drummond & Rambaut, 2007).

Divergence dating

The Bayesian tree reconstruction and divergence time of the Calochromini tribe were estimated using a Bayesian relaxed-clock method implemented in BEAST 1.8.0 (Drummond *et al.*, 2012) using an uncorrelated lognormal relaxed clock model, HKY+I+G nucleotide substitution model and birth–death process tree prior. The model was identified with jModeltest as above; the analysis using GTR+I+G model was unable to reach the stationary phase and repeated analyses did not converge. Therefore, the model with the second highest Akaike criterion was applied. The analysis ran for 60 million generations and was partitioned by genes; the convergence was tested by the second independent run of the same length. All runs were computed on the CIPRES cluster (Miller, Pfeiffer & Schwartz, 2010). Only a single fossilized *Lygistopterus* is known from Mid-Eocene Baltic amber (Spahr, 1981). Therefore, we relied on a variety of molecular rates inferred for various beetle lineages and various mitochondrial genes (Table 1) to calibrate the dated molecular tree. We ran separate analyses using the *cox1* dataset and the rates 0.0115 mutations per lineage per million years (m/l/Myr) and 0.0177 m/l/Myr, the *rrnL* dataset and the rate 0.054 m/l/Myr, and the *nad5* dataset and the rate 0.012 m/l/Myr. Furthermore, we used a combined dataset of *cox1* and *rrnL* fragments with the rates 0.0177 and 0.054 m/l/Myr for the respective fragments. These rates were proposed by Brower (1994) and Papadopoulou, Anastasiou & Vogler (2010) and their application in the analyses of net-winged beetles has been satisfactory in previous studies (Malohlava & Bocak, 2010; Sklenarova *et al.*, 2013).

Distribution and phylogeographical analysis

Distributional data were obtained from the world catalogue of Lycidae (Kleine, 1933), Zoological records database, primary descriptions and from the collections deposited in the institutions listed below. The World map was downloaded from http://www.naturalearthdata.com and the range polygons were created using QGIS 2.6.1 software. Species richness was visualized using a 2.5 degree grid.

The ancestral areas were identified using the discrete phylogeographical model implemented in BEAST 2.2.1 (Bouckaert *et al.*, 2014) with the model as above. The geographical origins of the samples were coded to the zoogeographical realms (Holt *et al.*, 2013). The analysis was set to 50 million generations, applying the uniform arbitrary rate 1.0, the coalescent process with the constant population size as recommended in the BEAST 2 tutorial. The first 30% of trees were then discarded as burn-in after Tracer 1.5 (Rambaut & Drummond, 2007) evaluation and the maximum credibility tree was calculated using TreeAnnotator 2.2.1 (Drummond & Rambaut, 2007) from post burn-in trees and visualized in

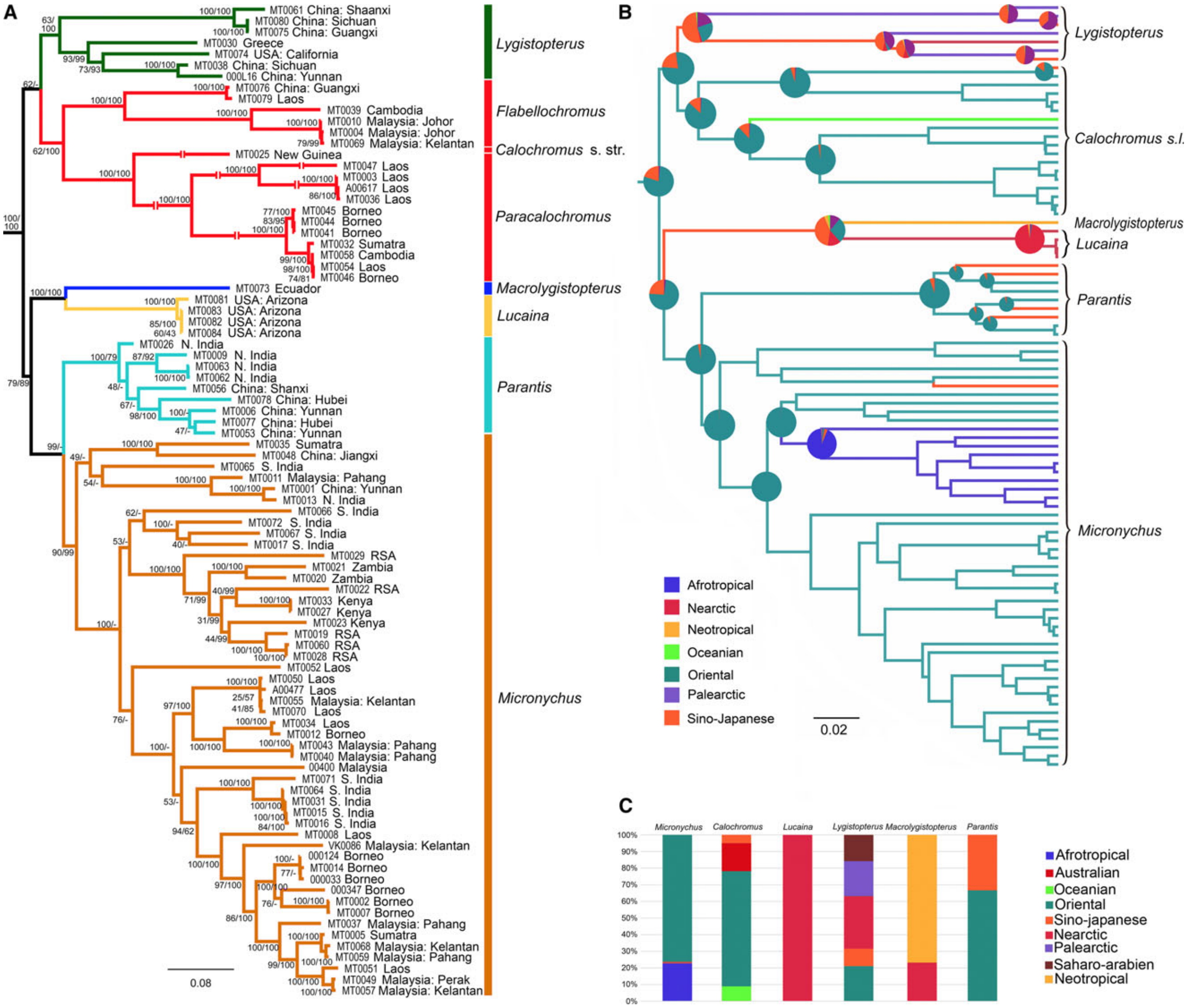


Figure 1. A, phylogenetic hypothesis for Calochromini based on the maximum-likelihood analysis of the MUSCLE alignment. Numbers at the branches are maximum-likelihood bootstrap values and Bayesian posterior probabilities. The complete tree with outgroups and full-branch lengths is shown in Fig. S8 (Supporting Information). B, discrete phylogeography reconstruction using a Bayesian approach as implemented in BEAST 2.1; pie charts represent posterior probabilities of biogeographical origins. C, geographical distribution chart of the Calochromini genera.

FigTree 1.4.2 (Rambaut, 2014). Ancestral areas and routes of distribution were visualized with SPREAD 1.0.6 (Bielejec *et al.*, 2011) and redrawn in a graphics software program.

MORPHOLOGY AND TAXONOMY

The morphological part of the study is based on adult semaphoronts, primarily males as female morphology provides less information. The genitalia of all males used for DNA isolation were dissected after treatment in a hot 10% aqueous solution of potassium hydroxide. Photographs were taken by a camera mounted on a microscope and measures were taken using an ocular grid in an eyepiece. The taxonomical authorities, years of publication and the list of taxonomic references for Calochromini species are listed in the Supporting Information.

Type material was studied from the following institutions: BMNH, Natural History Museum London; MHNP, Museum national d'Histoire naturelle, Paris; MIZW, Museum and Institute of Zoology PAN, Warszawa; ZMMU, Zoological Museum of the Moscow University, Moscow; AMNH, American Museum of Natural History, New York. The sequenced specimens are deposited in the voucher collection of the

Table 1. Estimated dates of the principal splits inferred from the BEAST analysis using various mtDNA fragments and previously published mutation rates. The numbers in parentheses designate 95% probability intervals.

Marker (mtDNA)	*cox1*	*rrnL*	*cox1*	*cox1+rrnL*	*nad5*
Rate (mutatiuons/lineage/my)	0.0115*	0.054†	0.0177†	0.0177/0.054†	0.012†
Origin of Calochromini	56.8 (44–70)	54.4 (36–75)	38.7 (31–48)	36.9 (30–44)	76.0 (58–92)
Separation between *Lygistopterus* and *Calochromus* s. l.	55.1 (43–67)	48.4 (33–71)	37.5 (30–47)	35.6 (28–42)	73.6 (56–89)
Split between *Calochromus* s. str. and *Flabellochromus*	53.4 (34–59)	45.5 (27–63)	36.3 (28–44)	34.8 (28–41)	67.1 (52–83)
Origin of *Macrolygistopterus* and *Lucaina* clade	51.6 (40–53)	39.6 (26–56)	35.2 (27–43)	32.9 (26–39)	67.7 (56–88)
Split between *Macrolygistopterus* and *Lucaina*	45.7 (31–59)	19.6 (5–36)	31.2 (22–41)	27.8 (19–36)	48.7 (27–71)
Split between *Parantis* and *Micronychus*	49.3 (39–60)	29.3 (19–39)	33.5 (26–41)	29.1 (23–34)	59.3 (47–73)
Origin of Afrotropical *Micronychus*	38.8 (22–38)	19.1 (9–22)	26.3 (15–25)	23.1 (12–20)	39.5 (18–34)

*Brower (1994), †Papadopoulou *et al.* (2010).

Laboratory of Molecular Systematics, UP Olomouc. We studied all type species of the Calochromini genera except *Caloptognatha* which was unavailable and additionally the types or identified specimens representing about 75% of the alpha-taxonomic diversity.

RESULTS

The DNA dataset contained the 18S and 28S rRNA sequences (~1800 bp, 44 samples, and 629 bp, 47 samples, respectively), and mitochondrial fragments *rrnL-nad1* (802 bp, 90 samples), *cox1-tRNA-Leu-cox2* (1063 bp, 95 samples) and *nad5* and adjacent *tRNAs* (1216 bp, 90 samples). Depending on the algorithm, the aligned dataset contained 5584–5601 homologous positions, 1637–1640 of them parsimony-informative.

The recovered limits of genera were similar across various alignments and optimality criteria applied in the phylogenetic analyses (Fig. 1A, Figs S1–S4, Supporting Information). The results confirmed monophyly of the tribe Calochromini with bootstrap support (BS) and PP 100% (Fig. 1A). Six principal lineages corresponding to redefined genera were identified with relatively robust support (BS 63–99%, PP 79–100%, Fig. 1A). The basal split is formed by the *Lygistopterus* + *Calochromus s.l.*, and the *Macrolygistopterus* + *Lucaina* + *Parantis* + *Micronychus* clades; the position of *Macrolygistopterus* + *Lucaina* was not recovered from the MUSCLE alignment (Fig. S4, Supporting Information). The monophyletic *Lygistopterus* (BS 63%, PP 100%) clade contains the type species *L. sanguineus* from Greece and a number of species from China and the USA and was recovered as a sister to *Calochromus s.l.* *Calochromus* (BS 62%, PP 100%) split into three subclades: *Flabellochromus* (BS and PP 100%) from the Oriental region, *Paracalochromus* subgen. nov. (BS and PP 100%) from the Eastern Palaearctic and Oriental regions, and *Calochromus s.s.* (BS and PP 100%) from New Guinea. The type species of the genus, *C. glaucopterus*, is sister to the rest of *Calochromus s.l.* species with non-flabellate antennae. *Macrolygistopterus* sp. from Ecuador and *Lucaina* spp. from Arizona form a clade (BS and PP 100%) in a sister position to *Parantis* gen. nov. and *Micronychus* (BS 90%, PP 99%). The *Parantis* clade (BS 100%, PP 79%) contains species from southern China and northern India and is sister to the *Micronychus* clade (BS 90%, PP 99%). The latter contains species from Afrotropical and Oriental regions.

DIVERSITY, DIVERGENCE DATING AND ANCESTRAL AREA RECONSTRUCTION

The reconstruction of dispersal routes, worldwide distribution of genera and alpha-taxonomic diversity are displayed in Figs 2, 3 and S6–S11 (Supporting Information). The highest number of genera was recorded in the transitional zone between Palearctic and Oriental regions, i.e. southern China and Indo-Burma where four genera were recorded (Figs S7, S10, S11, Supporting Information). Conversely the highest alpha-taxonomic diversity was identified in India where only the genera *Micronychus* and *Parantis* gen.

nov. occur. The Australian fauna is represented solely by *Calochromus* (Fig. S7, Supporting Information). Similarly, poor phylogenetic diversity was identified in the Afrotropical and Neotropical regions where only *Micronychus* and *Macrolygistopterus* have been respectively collected (Figs S8, S10, Supporting Information). The Nearctic fauna is represented by two endemic New World genera, *Macrolygistopterus* and *Lucaina*, which represent deep lineages in the Calochromini phylogeny. Additionally, only a single Nearctic species of *Lygistopterus* was included in the dataset, which represents a terminal lineage within the *Lygistopterus* clade (Fig. 1A). Nearctic *Lygistopterus* species, for which no sequence data current exist, were identified using morphological characters.

The dating analyses used two rates for *cox1* and a single rate for *rrnL* and *nad5* mtDNA. The inferred dates for selected splits are listed in Table 1 and the origins of Calochromini vary widely between 36.9 and 75.9 Mya. The origins of the Calochromini genera are mostly dated to the Eocene.

The geographical origin of Calochromini is hypothesized to lie in the southern part of Eurasia, i.e. present-day China and Indo-Burma (Fig. 3). All basal lineages were identified in this region, except the Nearctic and Neotropic endemic genera *Lucaina* and *Macrolygistopterus* which represent relatively deep branches (Fig. 1A). Palaearctic and Neotropical *Lygistopterus* split 28 Mya. Papuan *Calochromus s.s.* stands as an early split lineage within the clade represented by Oriental and East Palaearctic species. The genera *Parantis* gen. nov. and *Micronychus* originated in the southern margin of the Asian continent, i.e. China, Indo-Burma and northern India, where the majority of species still occur. Only a single lineage of *Micronychus* gave rise to all Afrotropical species about 29 Mya (Fig. 1A, B).

TAXONOMY

CALOCHROMINI LACORDAIRE, 1857

Calochromines Lacordaire, 1857: 301 (Type genus: *Calochromus* Guérin-Méneville, 1833).
Calochrominae: Kleine, 1928: 222.
Calochromini: Kleine, 1933: 102; Bocak & Bocakova, 2008: 715.
= Lygistopteri Leconte, 1881: 27; Bocak & Bocakova, 1990: 653 (Type genus: *Lygistopterus* Mulsant, 1838).
= Lygistopterini: Kleine, 1933: 102.

Diagnosis: Adult. Small to large bodied, 5–24 mm, dorso-ventrally flattened, parallel-sided to slightly widened posteriorly (*Macrolygistopterus*); regularly brightly aposematically coloured with red and yellow elytra, seldom uniformly black, dark coloured body parts often with blue metallic shine (*Calochromus* and *Macrolygistopterus*). Pronotum and elytra without pubescence (metallic coloured *Calochromus* and *Macrolygistopterus*), with erected setae (*Lucaina*, *Caloptognatha*) or densely shortly pubescent (other genera).

Head prognathous to slightly hypognathous, movable if rostrate (Fig. 4A, B), partly covered by pronotum if not rostrate, prolonged rostrum long in *Macrolygistopterus* and *Lucaina*; variable in length in *Lygistopterus* and *Micronychus* or rostrum absent in other genera. Antennae 11-segmented, scapus pear-shaped, pedicel and antennomere 3 short (*Parantis* gen. nov.) or twice as long as pedicel (other genera), antennae filiform (*Parantis* gen. nov.), serrate in other genera, seldom flabellate male antennae (*Flabellochromus*), reaching between half and two-thirds of elytral length. Mouthparts miniaturized if head rostrate, *Parantis* gen. nov. with miniaturized mandibles and absent rostrum.

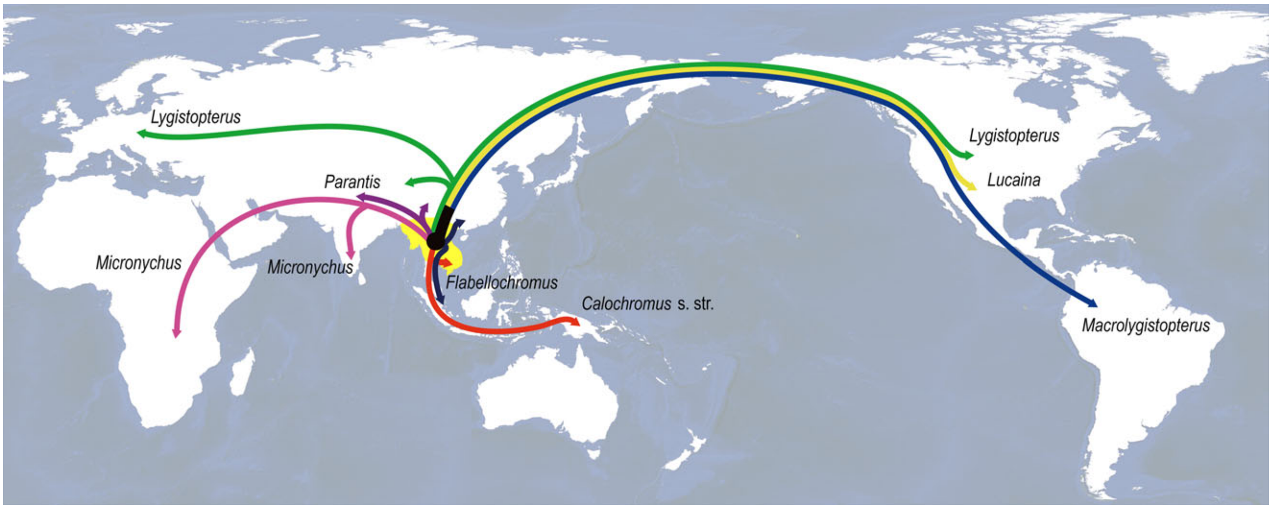


Figure 2. The ancestral areas and dispersal routes.

Pronotal shape variable, mostly quadrate to prolonged, parallel-sided (*Lygistopterus*, some *Calochromus*, *Lucaina*, some *Micronychus*), triangular (in some *Macrolygistopterus*, *Micronychus* and *Calochromus*) or with concave lateral margins (some *Macrolygistopterus*). Pronotum without any sharp carinae, with two longitudinal boulders; lateral margins widely rounded (*Calochromus*) or sharp edge present (other genera). Elytra parallel-sided, fully developed, each elytron with four weak costae, sometimes shortened apically, transverse costae absent in small-bodied species or weak, irregular, resembling leaf nerves in large-bodied species, humeri rounded, never with sharp edge. Male genitalia trilobate, phallobase asymmetrical, parameres robust, about as long as phallus, phallus slender to triangular, internal sac membranous in most genera, sclerotized in *Micronychus* and *Parantis* gen. nov. (Fig. 5I–O). Female genitalia slender, long, with paraproctal baculi multiple times longer than coxites.

Larva (known for *Lygistopterus*, *Calochromus* and *Macrolygistopterus*). Body cylindrical. Antennal peg small, slender, mala sclerotized, dorsally attached to palpifer, thoracic terga incompletely divided into two parts by very narrow median longitudinal suture, terminal abdominal segment with two long, fixed urogomphi (Bocak & Matsuda, 2003; Costa & Vanin, 2012).

THE GENERIC CLASSIFICATION OF CALOCHROMINI

LYGISTOPTERUS MULSANT, 1838
(FIGS 4A–M, 5A, K, P)

Lygistopterus Mulsant, 1838: 79.

Type species: Lygistopterus sanguineus Linnaeus, 1758 (by monotypy).
Adoceta Bourgeois, 1882: 97, syn. nov.

Type species: Adoceta caroli Bourgeois, 1882 (by monotypy).

Differential diagnosis: Lygistopterus is widely distributed and differs from the Old World genera *Micronychus* and *Parantis* gen. nov. in the membranous internal sac (Fig. 5I, J) and from *Calochromus* by the presence of sharp pronotal lateral edges. This genus occurs sympatrically with *Lucaina* and *Caloptognatha* in the Nearctic region and differs in the absence of long erected setae in the elytra. Neotropical *Macrolygistopterus* differs in the shape of male genitalia (Fig. 5N). The length of the rostrum is variable in *Lygistopterus*; for example, *Lygistopterus sanguineus* has a well-developed rostrum, but the rostrum is absent in the closely related East Palearctic species or extremely short in the North African species.

Distribution: Palearctic, Nearctic, Oriental regions.

Remarks: Adoceta Bourgeois, 1882 is proposed as a junior synonym of *Lygistopterus* as *A. caroli* (type species) has a membranous internal sac and cannot be distinguished from *Lygistopterus*. All sequenced species from sub-Saharan Africa represent a distant clade. They have a sclerotized internal sac and form a subclade within *Micronychus*. Two North African species are placed in *Lygistopterus* and the Neotropical species of *Lygistopterus* Kleine, 1933 are transferred to *Macrolygistopterus* as earlier proposed by Pic (1929). See Appendix for details.

CALOCHROMUS GUÉRIN-MÉNEVILLE, 1833

Calochromus Guérin-Méneville, 1833: 158.

Type species: Calochromus glaucopterus Guérin-Méneville, 1833 (by monotypy).

Differential diagnosis: Calochromus differs from other genera in the widely rounded obtuse lateral edge of the pronotum, relatively long parameres (Fig. 5L) and the lateral process of the phallobase widely rounded (Fig. 5L), unlike in *Lygistopterus* where it is pointed. *Calochromus* has a compact cranium, unlike *Lucaina* and *Macrolygistopterus*, each of which has a long rostrum, or some *Lygistopterus* and *Micronychus* with a short rostrum. *Micronychus* and *Parantis* gen. nov., previously placed in *Calochromus*, have a sclerotized internal sac (Fig. 5I, J). We define three lineages in *Calochromus* with subgeneric rank: *Flabellochromus* Pic, 1925; *Calochromus s.s.* and *Paracalochromus* subgen. nov. (Fig. 5B–D, L–M).

SUBGENUS *CALOCHROMUS S.S*

Type species: Calochromus glaucopterus Guérin-Méneville, 1833 (by monotypy).
Figure 5B, L.

Differential diagnosis: Calochromus s.s. represents a morphologically uniform lineage of species from Wallacea and Papua with the elytra without pubescence and partly yellow or metallic blue coloured.

Distribution: All species are distributed east of the Wallace line and a single species reaches Fiji.

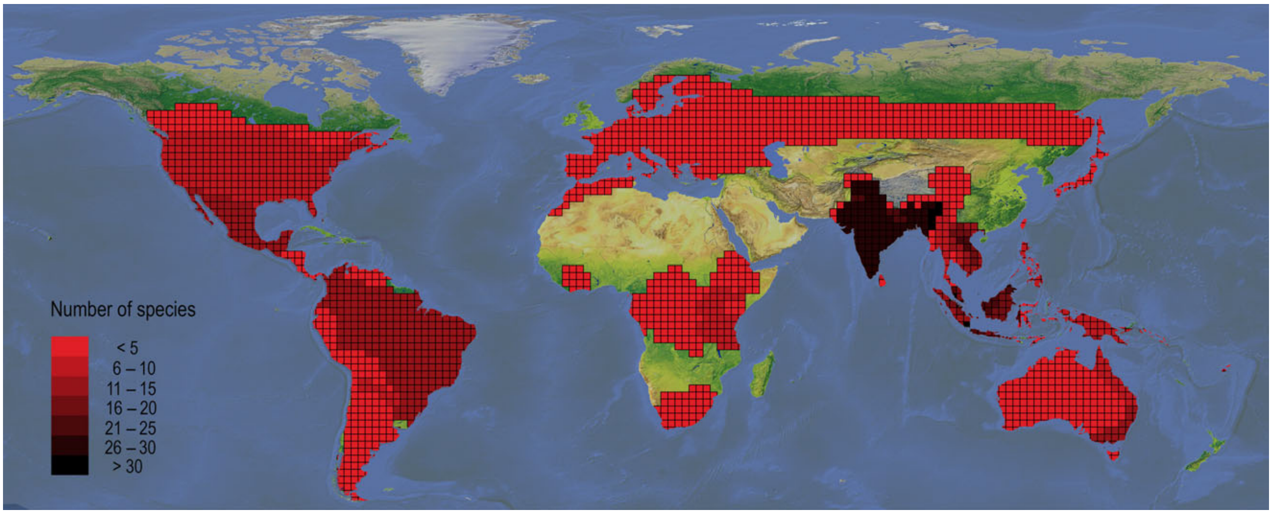


Figure 3. Distribution and species richness of the tribe Calochromini.

Subgenus *Flabellochromus* Pic, 1925

Type species: Calochromus pallidus Pic, 1925 (by monotypy).

Figure 5C, M.

Differential diagnosis: All males of *Flabellochromus* have flabellate antennae, unlike other Calochromine genera. *Flabellochromus* were recovered in a sister position to *Calochromus* (Fig. 1A).

Distribution: Himalayas, Indo-Burma and the Great Sundas.

Subgenus ***Paracalochromus*** **subgen. nov.**

Type species: Calochromus giganteus Pic, 1913 (hereby designated).

Figure 5D.

Differential diagnosis: All species of this subclade of *Calochromus* are characterized by densely pubescent elytra and they never have metallically coloured elytra.

Description: Male: Body large to medium-sized, 8–25 mm long, parallel-sided. Head small, only slightly retracted in pronotum, movable, prognathous, without rostrum. Eyes small, hemispherically prominent, frontal interocular distance four times as long as maximum eye diameter in lateral view. Labrum sclerotized, small, widely rounded apically; mandibles long, robust, curved almost in right angle apically; maxillary palpi slender, four-segmented, apical palpomere pointed. Antennal tubercles well developed, close to each other, separated by deep groove; antennae 11-segmented, surpassing half of elytral length, filiform to weakly serrate, never flabellate, scapus pear-like, robust, pedicel minute, antennomeres 4–11 gradually more slender to apex, apical antennomere slender, pointed. Pronotum transverse, without apparent sharp carinae, only with clear longitudinal median impression, oblique folds laterally, anterior and posterior angles rounded. Scutellum small, flat, subquadrate. Elytra flat, parallel-sided, humeri rounded, with four longitudinal elytral costae, transverse costae absent. Legs slender, compressed, tarsi five-segmented, tarsomeres 1–4 with membranous pads, tarsomeres 1 and 5 similar in length, tarsomeres 2–4 gradually shorter. Male genitalia trilobate, phallus and parameres similar in length, parameres parallel-sided, phallobase asymmetrical, internal sac membranous.

Female: Similar to male, usually with large body, without sexual polymorphism in antennae.

Distribution: Indo-Burma, China, Japan and Australia.

Etymology: The name *Paracalochromus* refers to the close relationship with *Calochromus s.s.* Gender: masculine.

Macrolygistopterus Pic, 1929

Macrolygistopterus Pic, 1929: 1.

Type species: Lycus succinetus Latreille, 1811 (by monotypy).

Figure 5F, N.

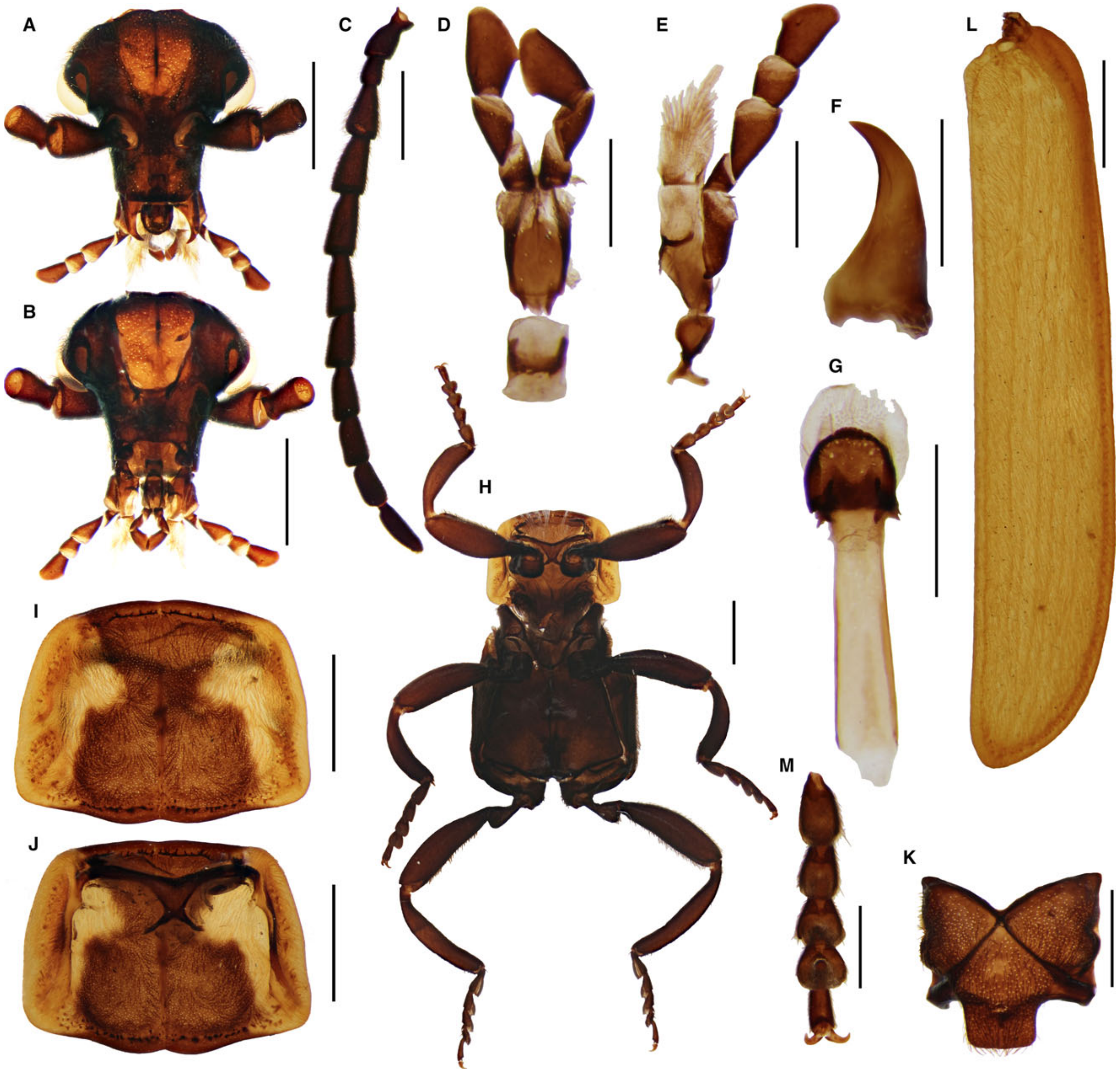


Figure 4. A–M, *Lygistopterus sanguineus*. A, head dorsal view; B, head ventral; C, antenna; D, labium; E, maxilla; F, mandible; G, labrum and hypopharynx; H, thorax ventrally; I, pronotum dorsally; J, pronotum ventrally; K, mesonotum; L, elytron; M, tarsus. Scale bars: A–C, I, J, L = 1 mm; D–H, K, M = 0.25 mm.

Differential diagnosis: Macrolygistopterus differs from other New World Calochromini genera in the slender basal part and widened apical third of parameres. *Lucaina* has the similar slender basal part of the parameres but the apex is characteristically modified (Fig. 5O) and this genus has, similar to *Caloptognatha*, long erect setae in the elytra. *Lygistopterus* is distantly related and differs by its wide, parallel-sided parameres (Fig. 5K, N).

Distribution: Mexico, Central America, South America.

LUCAINA DUGÈS, 1879

Lucaina Dugès, 1879: 180.

Type species: Lucaina schini Dugès, 1879 (by monotypy).

Figure 5E, O.

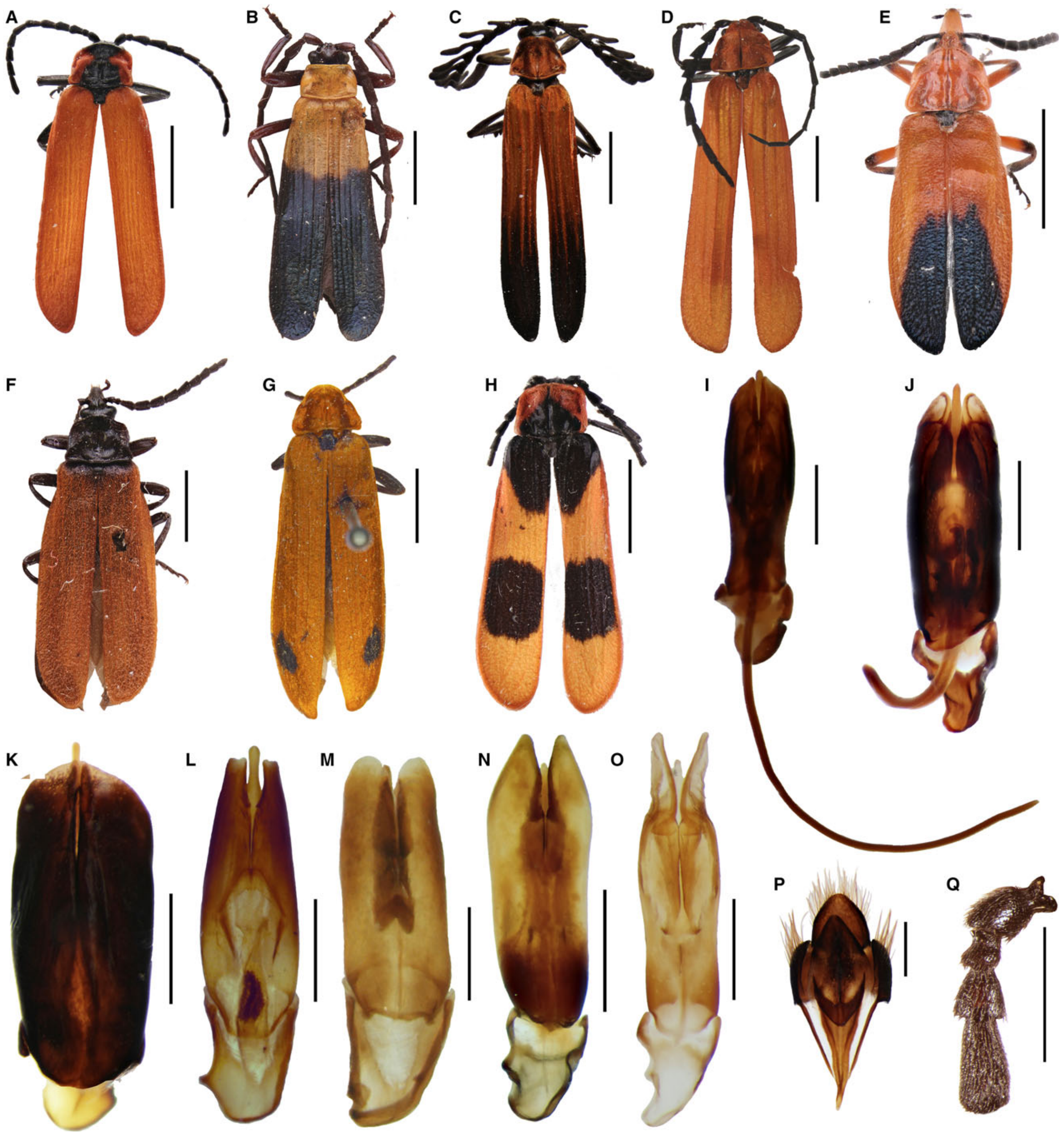


Figure 5. A–H, general appearance: A, *Lygistopterus sanguineus*; B, *Calochromus* (*s.s.*, *glaucopterus*; C, *C.* (*Flabellochromus*, *kelantanensis*; D, *C.* (*Paracalochromus*) *giganteus*; E, *Lucaina discoidalis*; F, *Macrolygistopterus rubripennis*; G, *Micronychus bimaculatus*; H, *Parantis triguttatus*. I–O, male genitalia, ventrally: I, *Micronychus bimaculatus*; J, *Parantis triguttatus*; K, *Lygistopterus sanguineus*; L, *Calochromus* (*s.s.*), *glaucopterus*; M, *C.* (*Flabellochromus*) *kelantanensis*; N, *Macrolygistopterus rubripennis*; O, *Lucaina schini*. P, *Lygistopterus sanguineus*, terminal abdominal sclerites, ventrally. Q, *Parantis triguttatus*, antenna, detail. Scale bars: A–H = 2.5 mm; I–Q = 0.25 mm.

Differential diagnosis: Lucaina and closely related *Macrolygistopterus* (Fig. 1A) share the rostrate head and they differ in the shape of the apical part of parameres (Fig. 5N–O) and the long erect setae in the elytra of *Lucaina*. These genera have a vicariant distribution (Figs S8, S9, Supporting Information). *Caloptognatha* has similar setae in the elytra, but does not have the prolonged rostrum and has long, slender mandibles (Green, 1954). *Lygistopterus* is another genus distributed in the Nearctic region and differs by its wide, parallel-sided parameres.

Distribution: USA: California, Arizona; Mexico.

MICRONYCHUS MOTSCHOULSKY, 1861

Micronychus Motschoulsky, 1861: 137.

Type species: Micronychus bimaculatus Motschoulsky, 1861 (by monotypy).
Figure 5G, I, Q.

Differential diagnosis: Micronychus and *Parantis* gen. nov. are characterized by the presence of a sclerotized internal sac (Fig. 5I, J). *Micronychus* differs by antennomere 3 being twice as long as the pedicel, well-developed mouthparts and sometimes in the rostrate head.

Distribution: Oriental and Afrotropical region.

Remarks: Kleine (1933) listed *Micronychus* as a junior synonym of *Calochromus*, but we found that these genera are distantly related. Here, we resurrect the name *Micronychus* for Oriental species previously classified in *Calochromus* and the Afrotropical species placed in *Adoceta* (Kleine, 1933).

CALOPTOGNATHA GREEN, 1954

Caloptognatha Green, 1954: 55.

Type species: Caloptognatha beameri Green, 1954: 56 (original designation).

Differential diagnosis: Caloptognatha differs from other genera in having densely pubescent elytral costae. Additionally, *Lygistopterus*, *Lucaina* and *Macrolygistopterus* occur in the New World and the latter two have a long rostrum while *Lygistopterus* is easily distinguishable by wide, parallel-sided parameres.

Distribution: USA: Arizona.

Remarks: Green (1954) noted that *Caloptognatha* is unique among the Nearctic genera due to sparse and unequally distributed elytral pubescence, but this character is shared with *Lucaina*. Unfortunately, *Caloptognatha*, despite its occurrence in western USA, has not been collected again. As the type was inaccessible, we provisionally classify *Caloptognatha* as related to *Lucaina* and its definitive position can be resolved with further material.

PARANTIS MOTYKA, MASEK & BOCAK **GEN. NOV.**

Type species: Calochromus triguttatus Kleine, 1929: 260 (hereby designated).
Figure 5H, J

Differential diagnosis: Parantis gen. nov. and *Micronychus* share a characteristic sclerotized internal sac (Fig. 5I, J). *Parantis* differs from the latter in the short antennomere 3 (Fig. 5Q), minute mouthparts and absent rostrum (Fig. 5H).

Description: Male: Body medium-sized, 9–18 mm long, parallel-sided, dorso-ventrally flattened. Head small, partly hidden by pronotum, non-rostrate, movable, prognathous to hypognathous. Eyes small, hemispherically prominent, frontal interocular distance three times as long as maximum eye diameter. Labrum sclerotized, transverse, with long setae at anterior margin; mandibles minute, curved in apical part, incisor margin simple; maxillary palpi four-segmented, slender, apical palpomere variable in shape, flat, more or less pointed apically. Antennal tubercles conspicuous, separated by narrow straight depression. Antennae 11-segmented, moderately long, surpassing humeral third of elytra, filiform, scapus pear-like, robust, pedicel small, antennomere 3 short, never more than twice as long as pedicel, antennomeres 4–10 approximately same length, gradually shorter to apex of antennae, antennomere 11 longest, slender, pointed at apex. Pronotum transverse to quadrate, parallel-sided, with deep median depression, anterior angles prominent, posterior ones slightly pointed to weakly rounded. Scutellum short, nearly quadrate, posterior margin simple, at most with shallow incision. Elytra flat, parallel-sided, humeri rounded, elytra with four straight longitudinal costae, costae are moderately robust at humeri, very weak apically, transverse costae absent. Legs slender, flattened, tarsi five-segmented, tarsomeres 1–4 with membranous pads, tarsomere 5 long, claws simple, slender. Male genitalia trilobate, phallus and parameres similar length, parameres slender apically, phallobase asymmetrical, internal sac sclerotized.

Female: Similar to male, without sexual polymorphism in the shape of antennae.

Distribution: India, China: Yunnan, Hubei (Fig. S11, Supporting Information).

Etymology: The name *Parantis* is a matronym in honour of Justinah Parantis, a biologist from the Sabah National Park Authority, Poring, Malaysia. Gender: masculine.

KEY TO THE CALOCHROMINI GENERA*

1. A. Male genitalia with sclerotized internal sac… 2
   B. Male genitalia with membranous internal sac… 3
2. A. Antennomere 3 no more than twice as long as pedicel, antennae slender, never flabellate or serrate… ***Parantis* gen. nov.**
   B. Antennomere 3 three or more times longer than pedicel, antennae mostly serrate, seldom slender… *Micronychus*
3. A. Head with long rostrum, apical part of parameres divergent, distributed in New World … 4
   B. Head without rostrum or only short rostrum present, distributed in Palearctic, Oriental, Australian, Nearctic regions… 5
4. A. Long erect setae on pronotum and elytra, egg-shaped elytra, distributed in the southern part of the Nearctic region… *Lucaina*
   B. Pronotum and elytra without long setae, often brightly or metallically coloured, most species distributed in the Neotropical region, several species in Mexico… *Macrolygistopterus*
5. A. Pronotum with sharp lateral edges, lateral process of phallobase acute… *Lygistopterus*
   B. Pronotum with obtuse lateral edges, lateral process of phallobase widely rounded… 6
6. A. Male antennae flabellate, pronotum and elytra dark red or black without metallic shine, covered with dense pubescence… *Flabellochromus*
   B. Male antennae filiform to serrate… 7
7. A. Pronotum and elytra brightly yellow or blue coloured with metallic shine, without pubescence… *Calochromus s.s.*
   B. Pronotum and elytra dark red or black, without metallic shine, covered with dense pubescence… ***Paracalochromus* subgen. nov.**

**Caloptognatha* is not included in the key. The genus is known only from the type and it was inaccessible (N. Penny, pers. comm.). *Caloptognatha beameri* is characterized by small eyes, non-rostrate head and short, non-overlapping, small, acute mandibles. The lateral elevations of the pronotum are parallel-sided and the elytral pubescence is sparse, confined mostly to the costae. The intercostal intervals are sub-glabrous (Green, 1954).

DISCUSSION

PHYLOGENY AND CLASSIFICATION

The tribe Calochromini represents a monophylum in agreement with earlier delimitations (e.g. Kleine, 1933; Bocak & Bocakova, 2008). Conversely, the generic classification previously based solely on morphology turned out to be widely inconsistent with the phylogeny recovered from the current DNA dataset. The previous concepts often merged unrelated lineages and we identified discrepancies between clades inferred from molecular data and morphology-based limits of genera.

Six principal lineages are identified as monophyla in the molecular phylogeny and they were given genus rank (Fig. 1A). We use the previously proposed names *Lygistopterus*, *Calochromus*, *Lucaina*, *Macrolygistopterus*, *Flabellochromus* (subgenus) and *Micronychus* and the newly proposed *Parantis* gen. nov. and *Paracalochromus* subgen. nov. for the formal taxonomic delimitation of genus-group taxa. All these taxa are morphologically diagnosed, but due to the morphological uniformity of the tribe, the number of reliable diagnostic characters is limited to the shape of antennae, pronotum and male genitalia (Figs 4, 5). These genera and *Caloptognatha* are proposed to be the only valid genera in Calochromini. *Caloptognatha* was not available for the study and the genus is based on the unique vestiture of the elytra reported by Green (1954). The similar male genitalia of *Caloptognatha* and *Macrolygistopterus* (Fig. 5N) and non-rostrate cranium are characters enabling diagnosis of the genus, but the modification of the cranium in the rostrum is variable in *Lygistopterus* and *Micronychus* as well as in other net-winged beetle lineages (Sklenarova, Kubecek & Bocak, 2014) and the distribution of this character suggests multiple origins and potential correlation with using flower nectar as a source of water in semi-arid regions. We assume that differences in the length of the mandibles described by Green (1950, 1954) are correlated with the presence of the rostrum and similarly cannot be used for the delimitation of genera.

Lygistopterus sanguineus from Europe is the type species of the genus *Lygistopterus*, which has historically been defined by the presence of a prolonged rostrum. *Lygistopterus* contained until now three west-Palaearctic species and 39 species from the Nearctic and Neotropical regions (Kleine, 1933; Ferreira, 2016). The *Lygistopterus* clade (Fig. 1A) is morphologically diagnosed by the simply rounded apex of the parameres (Fig. 5K) and by the shape of the pronotum (Fig. 5A). Both molecular data and morphology merged some non-rostrate East Asian *Calochromus* species, two *Adoceta* species from North Africa, the rostrate species from the western part of the Palaearctic region and six species from the Nearctic region. Conversely, we transfer from *Lygistopterus* to *Macrolygistopterus* all Neotropical species earlier included in *Lygistopterus* by Kleine (1933).

Further, we propose a new delimitation of *Calochromus*. The type species, *C. glaucopterus*, occurs in New Guinea along with a few other species (Bocakova, 1992). Until now, most Calochromini were classified in this genus and the range included the Oriental region, the eastern part of the

Palearctic region, Afrotropical and Nearctic region (Kleine, 1933; Green, 1950). No clear definition of the genus has been available and all species without a long rostrum have been included here by previous authors (Kleine, 1933). The molecular phylogeny suggests a much narrower concept of *Calochromus*. We place in *Calochromus* the species with characteristic male genitalia (Fig. 5L). The Nearctic species are transferred to *Lygistopterus* and the Afrotropical species to *Micronychus* and the range of *Calochromus* shrinks and now includes the Asian humid tropics, Wallacea, New Guinea and Australia (Fig. S7, Supporting Information). *Calochromus* consists of three lineages, *Calochromus s.s.*, *Paracalochromus* subgen. nov. and *Flabellochromus*, all sharing similar genitalia and having the variable shape of antennae and different pubescence of elytra (Fig. 5B–D). *Flabellochromus* was recently synonymized with *Calochromus* (Motyka & Bocak, 2015), but based on the current molecular phylogeny and above listed characters, we prefer to reinstate its subgeneric rank. Due to small morphological differences and difficult identification of females, we prefer the definition of subgenera.

The Nearctic and Neotropic fauna contains the endemic genera *Macrolygistopterus*, *Luciana* and *Caloptognatha*. The first two represent a deeply rooted independent branch (Fig. 1A). *Lygistopterus* was previously reported from the Neotropical region and represented by 25 species. This genus is now limited to only six species in the Nearctic region (Supporting text). *Macrolygistopterus* is redefined and all *Lygistopterus* from the Neotropical region are newly combined with *Macrolygistopterus* (59 species). *Macrolygistopterus* and *Lucaina* (three species from the Nearctic region) share a slender phallus in ventral view (Fig. 5N, O). *Macrolygistopterus* has a long rostrum and does not have erect elytral pubescence. *Lucaina* is undoubtedly closely related to *Macrolygistopterus* and their close relationship is supported by both molecular data (Fig. 1A) and morphological characters. Due to the rareness of *Macrolygistopterus*, only a single species was available for the molecular study and we are not able to find any synapomorphy supporting *Macrolygistopterus*. Therefore, further study is needed to reject the possible paraphyly of one of these genera.

Micronychus is reinstated here from the synonymy of *Calochromus* and numerous species previously placed in *Calochromus* and *Adoceta* are transferred to this genus. *Micronychus* is easily recognizable by the sclerotized ductus ejaculatoris (Fig. 5I). *Micronychus* contains species distributed from sub-Saharan Africa (these species were previously incorrectly placed in *Adoceta*), across southern India to eastern China, Indo-Burma, Malay Peninsula, the Sundas and the Philippines (Fig. S10, Supporting Information). *Parantis* gen. nov. was inferred as a sister-clade of *Micronychus* and differs from all Calochromini by the very short antennomere 3 (Fig. 5H). At present, 12 species from the Oriental region are placed in *Parantis* gen. nov.

BIOGEOGRAPHY AND DIVERGENCE DATING

The dated trees are based on various earlier estimated rates of molecular evolution and provided a relatively wide date range for the origin of Calochromini and their genera (Table 1). We prefer for further discussion the tree produced from the *cox1* dataset and 0.0115 m/l/Myr (Fig. S5, Supporting Information) which dates the origin of *Lygistopterus* in agreement with the presence of *Lygistopterus* in Baltic amber (44 Mya, Spahr, 1981). The fossil *Lygistopterus* represents a minimum age for the genus as *Lygistopterus* originated in East Asia and the extant European *Lygistopterus* represents a much younger dispersal event (26 Mya, Fig. S5, Supporting Information). The preferred dating is also supported by the inferred time of dispersal to the Afrotropical region via a forest belt along the southern coast of Asia in the Lower Miocene and through Beringia in the Early Eocene and Late Oligocene (Gheerbrant & Rage, 2006; Abbate *et al.*, 2014). The higher rate proposed for *cox1* (Papadopoulou *et al.*, 2010) provided much shallower dating (Table 1) which is falsified by fossils of *Lygistopterus* in Baltic amber (estimated age 44 Myr; Spahr, 1981). We also tested rates estimated for *rrnL* and *nad5* (both Papadopoulou *et al.*, 2010) and they provided shallower and deeper estimations, respectively. These estimations were in conflict with at least some information. We can compare the current results with the dated phylogeny of Lycidae, which recovered the first split within Calochromini at 49.8 Mya (Bocak *et al.*, 2008). The origin of Lycidae in that analysis is slightly shallower than the origin inferred from the combined analysis of complete mitochondrial genomes and RNA genes (Bocak *et al.*, 2016) and only slightly deeper than for the same clade dated by McKenna *et al.* (2015). We suggest that Calochromini originated early after the Cretaceous–Palaeocene crisis and has differentiated since then.

The phylogeny was used for reconstruction of the ancestral distribution of Calochromini and their dispersal routes. Despite the large ranges of most genera, we have identified only a limited number of over-sea dispersals across narrow sea passages and a single long-distance dispersal represented by the discovery of *Calochromus* in Fiji, about 1800 km from the nearest land with *Calochromus* occurrence (Ramsdale, 2007). Calochromini has not been recorded in Madagascar despite the Mozambique Strait being only 450 km wide and rich fauna being present in eastern Africa. Calochromini is absent from the British Isles despite the common occurrence of *Lygistopterus* in France and Scandinavia as well as on numerous islands of oceanic origin (Supporting text).

The area of origin of Calochromini was identified as Indo-Burma and southern China (Fig. 2). The eastern part of the Oriental region is known for tectonic and climatic stability (Scotese, Gahagan & Larson, 1988; Hall, 1998) and humid tropical to subtropical forests have been present in the region for tens of millions of years (Morley, 2000; Najman *et al.*, 2001). South East Asia also retains the highest phylogenetic diversity of Calochromini with four genera known from the region. In contrast to the phylogenetic diversity, the region with the highest number of species was identified as seasonally dry southern India where other lineages of Lycidae are relatively poorly represented (Fig. 2; Kleine, 1933; Bocak & Bocakova, 2008).

Two lineages, *Parantis* gen. nov. and *Flabellochromus*, remain restricted to the Oriental region and adjacent parts of the Palaearctic region. Further, we identified four dispersal routes used by Calochromini during the Tertiary (Fig. 2). The West Palaearctic fauna contains only five *Lygistopterus* species represented by *L. sanguineus* in the analysed dataset. This species is closely related to a species from Shaanxi and they split relatively recently at 23.56 Mya. These regions are connected by the temperate forest belt. At present, four species are endemic to the Mediterranean and only *L. sanguineus* is widely distributed from the Russian Far East to the western coast of Europe (Fig. S6, Supporting Information). Furthermore, a dispersal route brought Calochromini to India (*Micronychus* and *Parantis* gen. nov.), and only *Micronychus* used the route opened by higher precipitation in areas along the northern coast of the Tethys Sea since the Late Eocene, which was also used by plants and other animals (Kosuch *et al.*, 2001; Yu *et al.*, 2014). Unexpectedly, only a single lineage of *Micronychus* colonized the Afrotropical region and diversified into 14 described species. A significantly higher number of species can be expected in Africa considering poor knowledge of the Afrotropical fauna in general.

The clade of *Macrolygistopterus*, *Lucaina* and potentially *Caloptognatha* (unavailable for molecular analyses) is deeply rooted in Calochromini (Fig. 1A, B). Their common ancestor dispersed to the Nearctic region very early in Calochromini history. Due to limited sampling caused by the rarity of most New World Calochromini we cannot propose a detailed dispersal scenario for *Macrolygistopterus* + *Lucaina* and this dispersal event is provisionally dated to the Mid Eocene or Palaeocene about 51.6 Mya (95% confidence interval 40–53 Mya). Much later, the northwestern dispersal route was used by *Lygistopterus* (28 Mya with 95% highest posterior density 17–40 Mya) and this lineage reached the Nearctic region via the Bering Strait as did other beetle lineages (Sota, Bocak & Hayashi, 2008). *Lygistopterus* never reached the Neotropical region despite several million years of connection between these landmasses (Montes *et al.*, 2012) in contrast to *Macrolygistopterus* which dominates the extant Neotropical fauna (Fig. S8, Supporting Information). These lineages, although widely distributed in the New World, remain rare. Many species are known only from type specimens, such as *Caloptognatha* from California. Despite intensive field research *Macrolygistopterus* is seldom collected (Costa & Vanin, 2012; Ferreira, 2016).

Dispersal in the southern direction brought Calochromini to Wallacea, New Guinea and Australia. Only a single species was available in the molecular dataset from these regions south of the Asian continental margin. We identified a deep split between the Papuan *C. glaucopterus* and other *Calochromus* from the Sundas and Indo-Burma, in contrast to a quite recent contact between Asian and Australian cratons (Hall, 2002). Similar to other net-winged beetle lineages, other Asian lineages of Calochromini were unsuccessful in dispersal to the south. These include Metriorrhynchini reaching not farther than Sulawesi (Kubecek, Dvorak & Bocak, 2011), Taphini and Platerodini reaching only Papua and northernmost Australia (Bocakova, 1992; our unpubl. data). The Australian fauna is quite rich (16 spp.), only five species of *Calochromus* are known from Papua, two from the Solomon Islands and a single species, morphologically very similar to the Papuan species, reached Fiji (Ramsdale, 2007).

CONCLUSION

The combined approach using molecular data and comprehensive morphological evaluation produced a phylogenetic hypothesis elucidating the phylogeny of Calochromini. The genera *Calochromus* and *Lygistopterus* served as 'rubbish baskets' where most species have been described in respective regions and several previously used diagnostic characters (Mulsant, 1838; Pic, 1929; Green, 1954) are clearly homoplastic. Extensive study of the primary types enabled revision of the Calochromini taxonomy. The complete list of species and all taxonomic acts are available in the Appendix and Supporting Information. The clear delimitation of genera enables a fresh start to the taxonomic research in this group, especially considering a large part of Calochromini has not yet been formally described.

The zoogeographical analyses showed that the south-eastern margin of Eurasia was an area where the evolution of Calochromini started and that early in the diversification the Nearctic and later Neotropic and Afrotropical regions were colonized. A high diversity of net-winged beetles has been preserved in the eastern part of the Oriental region since that time. Although Calochromini are exceptional among net-winged beetles due to their tolerance to seasonal drought and ability to fly outside the forest canopy, the number of inferred dispersal events is low in comparison with many winged beetles (Balke *et al.*, 2009). This makes net-winged beetles a better model for phylogeographical studies than highly vagile groups (e.g. Cruaud *et al.*, 2011; Li *et al.*, 2015). The ranges of Calochromini species are relatively small, as documented by quite high turnover between the Sunda islands and between India and Indo-Burma. This finding is in contrast to their well-documented connectivity (Hall, 1998; Voris, 2000) and explains the high alpha-taxonomic diversity of the group.

ACKNOWLEDGEMENTS

We thank P. Cechovsky, L. Dembicky E. Jendek and P. Pacholatko who provided us with a part of the material for the present study and to W. Tomaszewska, A. Taghavian, T. Deuve, M. Barclay, M. Geiser, P. Hudson, P. Limbourg, N. B. Nikitsky and L. Herman for providing access to the collections in their care. We thank M. Bocakova for information on types in the Motschoulsky collection. The work was funded by the IGA project from the Palacky University, the Czech Science Foundation (P506/11/1757, LB) and SYNTHESYS Project http://www.synthesys.info/, which is financed by European Community Research Infrastructure Action under the FP7 Program.

REFERENCES

Abbate E, Bruni P, Ferretti MP, Delmer C, Laurenzi MA, Hagos M, Bedri O, Rook L, Sagri M, Libsekal Y. 2014. The East Africa Oligocene intertrappean beds: regional distribution, depositional environments and Afro/Arabian mammal dispersals. *Journal of African Earth Sciences* **99:** 463–489.

Balke M, Ribera I, Hendrich L, Miller AM, Sagata K, Posman A, Vogler AP, Meier R. 2009. New Guinea highland origin of a widespread arthropod supertramp. *Proceedings of the Royal Society B* **276:** 2359–2367.

Bielejec F, Rambaut A, Suchard MA, Lemey P. 2011. SPREAD: spatial phylogenetic reconstruction of evolutionary dynamics. *Bioinformatics* **27:** 2910–2912.

Bocak L. 2002. Revision and phylogenetic analysis of Metriorrhynchinae. *European Journal of Entomology* **99:** 315–351.

Bocak L, Bocakova M. 1990. Revision of the supergeneric classification of the family Lycidae (Coleoptera). *Polskie Pismo Entomologiczne* **59:** 623–676.

Bocak L, Bocakova M. 2008. Phylogeny and classification of the family Lycidae (Insecta: Coleoptera). *Annales Zoologici* **58:** 695–720.

Bocak L, Matsuda K. 2003. Review of immature stages of the family Lycidae (Insecta: Coleoptera). *Journal of Natural History* **37:** 1463–1507.

Bocak L, Yagi T. 2010. Evolution of mimicry patterns in *Metriorrhynchus* (Coleoptera: Lycidae): the history of dispersal and speciation in South East Asia. *Evolution* **64:** 39–52.

Bocak L, Bocakova M, Hunt T, Vogler AP. 2008. Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. *Proceedings of the Royal Society B* **275:** 2015–2023.

Bocak L, Kundrata R, Andújar Fernández C, Vogler AP. 2016. The discovery of Iberobaeniidae (Coleoptera: Elateroidea): a new family of beetles from Spain, with immatures detected by environmental DNA sequencing. *Proceedings of the Royal Society of London B-Biological Sciences* **283:** 20152350.

Bocakova M. 1992. Revision of the genus *Calochromus* Guérin-Méneville (Coleoptera, Lycidae) from New Guinea and adjacent islands. *Acta Entomologica Bohemoslovaca* **89:** 301–308.

Bouckaert R, Heled J, Kuhnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* **10:** e1003537.

Bourgeois J. 1882. Monographie des Lycides de l'ancien-monde. *L'Abeille: Journal d'Entomologie* **20:** 1–120.

Brower AVZ. 1994. Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial DNA evolution. *Proceedings of the National Academy of Science of the United States of America* **91:** 6491–6495.

Costa C, Vanin SA. 2012. Descriptions of *Macrolygistopterus subparallelus* Pic, 1930 immatures from south-eastern Brazil (Coleoptera, Lycidae, Lycinae, Calochromini). *Zootaxa* **3403:** 54–60.

Cruaud A, Jabbour-Zahab R, Genson G, Couloux A, Yan-Qiong P, Rong YD, Ubaidillah R, Pereira RAS, Kjellberg F, van Noort S, Kerdelhué C, Rasplus JY. 2011. Out of Australia and back again: the world-wide historical biogeography of non-pollinating fig wasps (Hymenoptera: Sycophaginae). *Journal of Biogeography* **38:** 209–225.

Darriba D, Taboada GL, Doallo R, Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9:** 772.

Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7:** 214.

Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* **29:** 1969–1973.

Drummond AJ, Ashton B, Buxton S, Cheung M, Cooper A, Duran C, Field M, Heled J, Kearse M, Markowitz S, Moir R, Stones-Havas S, Sturrock S, Thierer T, Wilson A. 2014. Geneious R7.1.7 http://www.geneious.com.

Dugès E. 1879. Descripcion de coleopteros indigenas. *La Naturaleza Mexicana* **4:** 167–188.

Eisner T, Schroeder FC, Snyder N, Grant JB, Aneshansley DJ, Utterback D, Meinwald J, Eisner M. 2008. Defensive chemistry of Lycid beetles and of mimetic Cerambycid beetles that feed on them. *Chemoecology* **18:** 109–119.

Ferreira VS. 2016. A revision of the genus *Macrolygistopterus* Pic, 1929 (Coleoptera, Lycidae, Calochromini). *Zootaxa* **4105:** 321–338.

Gheerbrant E, Rage JC. 2006. Paleobiogeography of Africa: how distinct from Gondwana and Laurasia? *Palaeogeography Palaeoclimatology Palaeoecology* **241:** 224–246.

Green JW. 1950. The Lycidae of the United States and Canada. II. The Tribe Lygistopterini (Coleoptera). *Transaction of the American Entomological Society* **76:** 13–25.

Green JW. 1954. An addition to the Lycid fauna of the United States (Coleoptera). *The Coleopterists' Bulletin* **8:** 55–57.

Guérin-Méneville FE. 1833. Memoire sur deux nouveaux genres de l'ordre des Coleopteres et description des espèces qui les composent. *Annales de la Socie̕te̕ entomologique de France* **2:** 155–160.

Hall R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. *Evolution* **10:** 99–131.

Hall R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences* **20:** 353–431.

Holt B, Lessard JP, Borregaard MK, Fritz SA, Araujo MB, Dimitrov D, Fabre PH, Graham CH, Graves GR, Jonsson KA, Nogues-Bravo D, Wang ZH, Whittaker RJ, Fjeldsa J, Rahbek C. 2013. An update of Wallace's zoogeographic regions of the world. *Science* **339:** 74–78.

Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30:** 772–780.

Kleine R. 1926. Die Lyciden der Philippinen-Inseln. *Philippine Journal of Science* **31:** 33–114.

Kleine R. 1928. Neue Indische Lyciden nebst faunistichen Bemerkungen. *Indian Forest Records* **13:** 221–268.

Kleine R. 1933. *Coleopterorum Catalogus auspiciis et auxilio W. Junk editus S. Schenkling*. Pars 128: Lycidae. Berlin: W. Junk.

Kleine R. 1941. Bestimmungstabelle der Gattung *Calochromus* Guer. (Col.). *Stettiner Entomologishe Zeitung* **102:** 206–241.

Kosuch J, Vences M, Dubois A, Ohler A, Bohme W. 2001. Out of Asia: mitochondrial DNA evidence for an oriental origin of tiger frogs, genus *Hoplobatrachus*. *Molecular Phylogenetics and Evolution* **21:** 398–407.

Kubecek V, Dvorak M, Bocak L. 2011. The phylogenetic structure of Metriorrhynchini fauna of Sulawesi, (Coleoptera: Lycidae) with description of a new genus. *Zoological Studies* **50:** 645–656.

Lacordaire JT. 1857. *Histoire Naturelle des Insectes. Genera des Coléopteres*, Vol. 4. Paris: Libraire Encyclopédique de Roret.

Leconte JL. 1881. Synopsis of the Lampyridae of the United States. *Transactions of the American Entomological Society* **9:** 15–72.

Li Y, Gunter N, Hong P, Bocak L. 2015. DNA-based species delimitation separates highly divergent populations within morphologically coherent clades of poorly dispersing beetles. *Zoological Journal of the Linnean Society* **175:** 59–72.

Malohlava V, Bocak L. 2010. Evidence of extreme habitat stability in a Southeast Asian biodiversity hotspot based on the evolutionary analysis of neotenic net-winged beetles. *Molecular Ecology* **19:** 4800–4811.

Masek M, Bocak L. 2014. The taxonomy and diversity of *Platerodrilus* (Coleoptera, Lycidae) inferred from molecular data and morphology of adults and larvae. *ZooKeys* **426:** 29–63.

McKenna DD, Wild AL, Kanda K, Bellamy CL, Beutel RG, Caterino MS, Farnum CW, Hawks DC, Ivie MA, Jameson ML, Leschen RAB, Marvaldi AE, Mchugh JV, Newton AF, Robertson JA, Thayer MK, Whiting MF, Lawrence JF, Slipinski A, Maddison DR, Farrell BD. 2015. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology* **40:** 835–880.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, LA, 1–8.

Montes C, Cardona A, McFadden R, Morón SE, Silva CA, Restrepo-Moreno S, Bayona GA. 2012. Evidence for middle Eocene and younger land emergence in central Panama: implications for Isthmus closure. *Geological Society of America Bulletin* **124:** 780–799.

Moore BP, Brown WV. 1981. Identification of warning odour components, bitter principles and antifeedants in an aposematic beetle: *Metriorrhynchus rhipidius* (Coleoptera: Lycidae). *Insect Biochemistry* **11:** 493–499.

Morley RJ. 2000. *Origin and evolution of tropical rain forests*. Chichester: John Wiley and Sons.

Motschoulsky V. 1861. D'un catalogue des insecten de l'ile Ceylon. *Bulletin of the Moscow Society of Naturalists* **34:** 95–155.

Motyka M, Bocak L. 2015. The classification of *Flabellochromus* and *Dumbrellia* (Coleoptera: Lycidae) with descriptions of two new species of *Calochromus* from the Sundaland Region. *Zootaxa* **3941:** 125–130.

Mulsant E. 1838. Tableaux synoptiques des Lycides ou des espèces du genre *Lycus*, qui se rencontrent dens les environs de Lyon. *Annales des Sciences physiques et Naturelles, d'Agriculture et d'Industrie* **1:** 77–81.

Najman Y, Pringle M, Godlin L, Oliver G. 2001. Dating of the oldest continental sediments from the Himalayan foreland basin. *Nature* **410:** 194–197.

Nakane T. 1969. *Fauna Japonica. Lycidae (Insecta: Coleoptera).* Tokyo: Academic Press of Japan.

Papadopoulou A, Anastasiou I, Vogler AP. 2010. Revisiting the insect mitochondrial molecular clock: the Mid-Aegean trench calibration. *Molecular Biology and Evolution* **27:** 1659–1672.

Papp CS. 1952. Eine neue *Calochromus*-Art und -Larve aus Indien (West-Bengal) und ein Catalog uber die bisher bekannten Arten (Coleoptera: Lycidae). *Arkiv for Zoologi Stockholm* **3:** 159–171.

Pic M. 1913. Notes diverses, descriptions et diagnoses. *L'Èchange, Revue Linnéenne* **348:** 185–187.

Pic M. 1923. Contribution à l'étude des Lycides. *L'Échange Revue Linnénne* **411–413:** 29–40.

Pic M. 1925. Malacodermes exotiques. *L'Echange* **419:** 5–8.

Pic M. 1929. Nouveautés diverses. *Mélanges Exotico-Entomologiques* **53:** 1–36.

Pic M. 1930. Coleópteres Nouveaux de La Republique Argentine. *Bulletin de La Sociéte Zoologique de France* **55:** 175–179.

Pic M. 1931. Coléoptères exotiques en partie nouveaux. *L'Échange, Revue Linnénne* **443:** 4.

Rambaut A. 2014. FIGTREE v. 1.4.2. Available at: http://tree.bio.ed.ac.uk/software/figtree/

Rambaut A, Drummond AJ. 2007. Tracer v1.5. Available at: http://beast.bio.ed.ac.uk/Tracer

Ramsdale AS. 2007. A new species of *Calochromus* Guérin-Méneville (Coleoptera: Lycidae) from Fiji. *Zootaxa* **1625:** 43–46.

Scotese CR, Gahagan LM, Larson RL. 1988. Plate tectonic reconstructions of the Cretaceous and Cenozoic ocean basins. *Tectonophysics* **155:** 27–48.

Sklenarova K, Chesters D, Bocak L. 2013. Phylogeography of poorly dispersing net-winged beetles: a role of drifting India in the origin of Afrotropical and Oriental fauna. *PLoS ONE* **8:** e67957.

Sklenarova K, Kubecek V, Bocak L. 2014. Subtribal classification of Metriorrhynchini (Insecta: Coleoptera: Lycidae): an integrative approach using molecular phylogeny and morphology of adults and larvae. *Arthropod Systematics & Phylogeny* **72:** 37–54.

Sota T, Bocak L, Hayashi M. 2008. Molecular phylogeny and historical biogeography of the Holarctic wetland leaf beetle of the genus *Plateumaris*. *Molecular Phylogenetics and Evolution* **46:** 183–192.

Spahr U. 1981. Bibliographie der Bernstein- und Kopal-Käfer (Coleoptera). *Stuttgarter Beiträge zur Naturkunde serie B* **72:** 1–21.

Stamatakis A. 2006. Phylogenetic models of rate heterogeneity: a high performance computing perspective. Greece. Proceedings of IPDPS 2006.

Thompson JD, Higgins DG, Gibson TJ. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research* **22:** 4673–4680.

Voris HK. 2000. Maps of Pleistocene sea levels in south-east Asia: shorelines, river systems and time duration. *Journal of Biogeography* **27:** 1153–1167.

Vuataz L, Sartori M, Wagner A, Monaghan MT. 2011. Toward a DNA taxonomy of Alpine *Rhithrogena* (Ephemeroptera: Heptageniidae) using a mixed Yule-coalescent analysis of mitochondrial and nuclear DNA. *PLoS ONE* **6:** e19728.

Waterhouse CO. 1879. *Illustration of the typical specimens of Coleoptera in the collection of the British Museum. Part I. - Lycidae*. London: British Museum.

Yu XQ, Maki M, Drew BT, Paton AJ, Li HW, Zhao JL, Conran JG, Li J. 2014. Phylogeny and historical biogeography of *Isodon* (Lamiaceae): rapid radiation in south-west China and Miocene overland dispersal into Africa. *Molecular Phylogenetics and Evolution* **77:** 183–194.

SUPPORTING INFORMATION

Additional supporting information may be found online in the supporting information tab for this article:

Table S1. The list of sequenced samples.
Table S2. Primers used for PCR amplification.
Text S1. The overview of current Calochromini classification.
Figure S1. The complete RAxML tree inferred from the MAFFT alignment of all markers.
Figure S2. The RAxML tree inferred from the MAFFT alignment of the set of nuclear genes.
Figure S3. The RAxML tree inferred from the MAFFT alignment of the set of mtDNA genes.
Figure S4. The complete RAxML tree inferred from the MUSCLE alignment of all markers.
Figure S5. Dated tree based on the BEAST analysis of the *cox1* dataset and rate of 0.0115 m/l/Myr.
Figure S6. Distribution and the species richness of *Lygistopterus*.
Figure S7. Distribution and the species richness of *Calochromus*.
Figure S8. Distribution and the species richness of *Macrolygistopterus*.
Figure S9. Distribution and the species richness of *Lucaina*.
Figure S10. Distribution and the species richness of *Micronychus*.
Figure S11. Distribution and the species richness of *Parantis* gen. nov.

APPENDIX

LIST OF TAXONOMIC ACTS

The overview of current Calochromini classification is available in the Supporting Information. The following taxonomic acts are proposed: ***Lygistopterus caroli*** (Bourgeois, 1882) **comb. nov.**, ***L. ignitus*** (Green, 1949) **comb. nov.** and ***L. monticolus*** (Kleine, 1930) **comb. nov.** are transferred from *Adoceta* Bourgeois, 1882 to *Lygistopterus* Mulsant, 1838. ***Lygistopterus ramicornis*** (Pic, 1928) **comb. nov.**, ***L. rubrovestitus*** (Nakane et Ohbayashi, 1955) **comb. nov.**, ***L. slevini*** (Van Dyke, 1918) **comb. nov.** and ***L. thibetanus*** (Pic, 1916) **comb. nov.** are transferred from *Calochromus* Guérin-Méneville, 1833 to *Lygistopterus* Mulsant, 1838.

Macrolygistopterus amabilis (Gorham, 1880) **comb. nov.**, ***M. bajacalifornicus*** (Zaragoza Caballero, 2003) **comb. nov.**, ***M. buqueti*** (Kirsch, 1865) **comb. nov.**, ***M. elegans*** (Bourgeois, 1880) **comb. nov.**, ***M. elegans*** (Bourgeois, 1880) **comb. nov.**, ***M. eximia*** (Bourgeois, 1877) **comb. nov.**, ***M. fastuosus*** (Bourgeois, 1899) **comb. nov.**, ***M. femoralis*** (Pic, 1924) **comb. nov.**, ***M. flammeus*** (Gorham, 1884) **comb. nov.**, ***M. gounellei*** (Bourgeois, 1886) **comb. nov.**, ***M. goyasensis*** (Pic, 1923) **comb. nov.**, ***M. goyasensis*** (Pic, 1923) **comb. nov.**, ***M. griseolineatus*** (Pic, 1929) **comb. nov.**, ***M. guerini*** (Kirsch, 1865) **comb. nov.**, ***M. guerrerensis*** (Zaragoza Caballero, 2003) **comb. nov.**, ***M. haemopterus*** (Gorham, 1880) **comb. nov.**, ***M. huautlaensis*** (Zaragoza Caballero, 2003) **comb. nov.**, ***M. humeralis*** (Buquet, 1842) **comb. nov.**, ***M. chamelensis*** (Zaragoza Caballero, 2003) **comb. nov.**, ***M. chiapensis*** (Zaragoza Caballero, 2003) **comb. nov.**, ***M. chihuahuensis*** (Zaragoza Caballero, 2003) **comb. nov.**, ***M. imperialis*** (Buquet, 1842) **comb. nov.**, ***M. jalisiensis*** (Zaragoza Caballero, 2003) **comb. nov.**, ***M. lacordairei*** (Kirsch, 1865) **comb. nov.**, ***M. laetus*** (Gorham, 1884) **comb. nov.**, ***M. lineicollis*** (Chevrolat, 1834) **comb. nov.**, ***M. mediorufus*** (Pic, 1923) **comb. nov.**, ***M. miles*** (Kirsch, 1865) **comb. nov.**, ***M. missionum*** (Berg., 1885) **comb. nov.**, ***M. morelensis*** (Zaragoza Caballero, 2003) **comb. nov.**, ***M. nevermanni*** (Kleine, 1942) **comb. nov.**, ***M. nobilis*** (Gorham, 1880) **comb. nov.**, ***M. oberthüri*** (Berg., 1899) **comb. nov.**, ***M. puniceus*** (Bourgeois, 1880) **comb. nov.**, ***M. quadricostatus*** (Buquet, 1842) **comb. nov.**, ***M. rubripennis*** (Leconte, 1875: 172) **comb. nov.**, ***M. ruficollis*** (Leconte, 1875) **comb. nov.**, ***M. sulcicollis*** (Gorham, 1880) **comb. nov.**, ***M. trifasciatus*** (Buquet, 1842) **comb. nov.** and ***Macrolygistopterus umanghi*** (Bourgeois, 1879: 18) **comb. nov.** are transferred from *Lygistopterus* Mulsant, 1838 to *Macrolygistopterus* Pic, 1921. ***Macrolygistopterus peruvianus*** (Kleine, 1951) **comb. nov.** is transferred from *Calochromus* Guérin-Méneville, 1833 to *Macrolygistopterus* Pic, 1921.

Micronychus alluaudi (Pic, 1925) **comb. nov.**, ***M. assiniensis*** (Bourgeois, 1889) **comb. nov.**, ***M. atricollis*** (Pic, 1925) **comb. nov.**, ***M. barkeri*** (Bourgeois, 1902) **comb. nov.**, ***M. dregei*** (Bourgeois, 1889) **comb. nov.**, ***M. feai*** (Pic, 1924) **comb. nov.**, ***M. hirsutulus*** (Bourgeois, 1908) **comb. nov.**, ***M. inapicalis*** (Pic, 1928) **comb. nov.**, ***M. jeaneli*** (Pic, 1925) **comb. nov.**, ***M. longipennis*** (Pic, 1953) **comb. nov.**, ***M. mitis*** (Bourgeois, 1908) **comb. nov.**, ***M. prescutellaris*** (Pic, 1924) **comb. nov.**, ***M. stabilis*** (Kleine, 1935) **comb. nov.**, ***M. suturalis*** (Pic, 1925) **comb. nov.**, ***M. turneri*** (Pic, 1934) **comb. nov.** and ***M. ugandanensis*** (Kleine, 1933) **comb. nov.** are transferred from *Adoceta* Bourgeois, 1882 to *Micronychus* Motschoulsky, 1861. ***Micronychus apicalis*** (Pic, 1922) **comb. nov.**, ***M. brevelineatus*** (Pic, 1922) **comb. nov.** and ***M. reductus*** (Pic, 1922) **comb. nov.** are transferred from *Lygistopterus* Mulsant, 1838 to *Micronychus* Motschoulsky, 1861. ***Micronychus aemulus*** (Waterhouse, 1877) **comb. nov.**, ***M. aeneicollis*** (Kirsch, 1875) **comb. nov.**, *M. andrewesi* (Kleine, 1930) **comb. nov.**, ***M. assamicus*** (Kleine, 1929) **comb. nov.**, ***M. atrosulcatus*** (Pic, 1916) **comb. nov.**, ***M. bifasciatus*** (Kleine, 1941) **comb. nov.**, ***M. bimaculatus*** (Motschoulsky, 1861) **comb. nov.**, ***M. bryanti*** (Kleine, 1939) **comb. nov.**, ***M. cerberus*** (Kleine, 1941) **comb. nov.**, ***M. conveniens*** (Kleine, 1926) **comb. nov.**, ***M. coomani*** (Pic, 1926) **comb. nov.**, ***M. costatipennis*** (Pic, 1916) **comb. nov.**, ***M. costatus*** (Pic, 1923) **comb. nov.**, ***M. crinitus*** (Kleine, 1929) **comb. nov.**, ***M. cyaneipes*** (Kleine, 1925) **comb. nov.**, ***M. cyanescens*** (Kleine, 1930) **comb. nov.**, ***M. dispar*** (Waterhouse, 1877) **comb. nov.**, ***M. diversicornis*** (Pic, 1916) **comb. nov.**, ***M. diversus*** (Kleine, 1925) **comb. nov.**, ***M. drescheri*** (Kleine, 1936) **comb. nov.**, ***M. elongatus*** (Pic, 1916) **comb. nov.**, ***M. fruhstorferi*** (Pic, 1913) **comb. nov.**, ***M. holtzi*** (Pic, 1914) **comb. nov.**, ***M. imitator*** (Kleine, 1926) **comb. nov.**, ***M. impressipennis*** (Pic, 1913) **comb. nov.**, ***M. impressipes*** (Pic, 1916) **comb. nov.**, ***M. indus*** (Kleine, 1935) **comb. nov.**, ***M. lepidus*** (Waterhouse, 1877) **comb. nov.**, ***M. luzonicus*** (Kleine, 1932) **comb. nov.**, ***M. macropalpis*** (Kleine, 1926) **comb. nov.**, ***M. malayensis*** (Kleine, 1932) **comb. nov.**, ***M. malignus*** (Kleine, 1936) **comb. nov.**, ***M. miniatus*** (Kleine, 1930) **comb. nov.**, ***M. monstratus*** (Kleine, 1926) **comb. nov.**, ***M. multifidus*** (Kleine, 1926) **comb. nov.**, ***M. mysticus*** (Kleine, 1926) **comb. nov.**, ***M. nanus*** (Kleine, 1930) **comb. nov.**, ***M. nigromarginatus*** (Bourgeois, 1906) **comb. nov.**, ***M. nigronotatus*** (Pic,

1913) **comb. nov.,** ***M. nilgirensis*** (Kleine, 1930) **comb. nov.**, ***M. pallidipennis*** (Kleine, 1926) **comb. nov.**, ***M. pallidulus*** (Kleine, 1926) **comb. nov.,** ***M. paradoxus*** (Kleine, 1939) **comb. nov.**, ***M. peculiaris*** (Kleine, 1930) **comb. nov.**, ***M. perakensis*** (Kleine, 1930) **comb. nov.,** ***M. postmaculatus*** (Kleine, 1939) **comb. nov.**, ***M. pyrochroides*** (Kleine, 1931) **comb. nov.**, ***M. reverens*** (Kleine, 1930) **comb. nov.**, ***M. ruber*** (Waterhouse, 1877) **comb. nov.**, ***M. rubrofasciatus*** (Kleine, 1928) **comb. nov.**, ***M. sanguinolentus*** (Kleine, 1930) **comb. nov.**, ***M. segregatus*** (Waterhouse, 1877) **comb. nov.,** ***M. sericeus*** (Bourgeois, 1883) **comb. nov.**, ***M. siamensis*** (Kleine, 1930) **comb. nov.**, ***M. simplicicornis*** (Pic, 1923) **comb. nov.**, ***M. singaporensis*** (Pic, 1925) **comb. nov.**, ***M. sondaicus*** (Kleine, 1926) **comb. nov.**, ***M. sororius*** (Kleine, 1926) **comb. nov.**, ***M. subparallelus*** (Pic, 1925) **comb. nov.**, ***M. substrictus*** (Kleine, 1930) **comb. nov.**, ***M. sumatrensis*** (Bourgeois, 1889) **comb. nov.**, ***M. teres*** (Kleine, 1932) **comb. nov.**, ***M. terminatus*** (Waterhouse, 1886) **comb. nov.**, ***M. thoracicus*** (Kleine, 1930) **comb. nov.**, ***M. timorensis*** (Kleine, 1930) **comb. nov.**, ***M. vesticollis*** (Gorham, 1895) **comb. nov.**, ***M. vestitus*** (Waterhouse, 1877) **comb. nov.** and ***M. viridicollis*** (Pic, 1913) **comb. nov.** are transferred from *Calochromus* Guérin-Méneville, 1833 to *Micronychus* Motschoulsky, 1861.

Parantis apicalis (Hope in Gray, 1831) **comb. nov.**, ***P. costulatus*** (Kleine, 1929) **comb. nov.**, ***P. darjeelinensis*** (Bourgeois, 1883) **comb. nov.**, ***P. densecostatus*** (Kleine, 1930) **comb. nov.**, ***P. fraterculus*** (Kleine, 1939) **comb. nov.**, ***P. kaschmirensis*** (Kleine, 1929) **comb. nov.**, ***P. nigrovittatus*** (Pic, 1925) **comb. nov.**, ***P. rugatus*** (Waterhouse, 1877) **comb. nov.**, ***P. triguttatus*** (Kleine, 1929) **comb. nov.** and ***P. velutinus*** (Waterhouse, 1877) **comb. nov.** are transferred from *Calochromus* Guérin-Méneville, 1833 to ***Parantis*** **gen. nov.**

UNIVERZITA PALACKÉHO V OLOMOUCI
PŘÍRODOVĚDECKÁ FAKULTA
KATEDRA ZOOLOGIE

Molecular phylogeny and zoogeography of net-winged beetles (Coleoptera: Lycidae)

AUTOREFERÁT DIZERTAČNÍ PRÁCE

Michal Mášek

P1527 – Biologie
Zoologie
prezenční studium

Olomouc 2017

Doktorská dizertační práce byla vypracována při prezenční formě studia doktorského studijního programu na Katedře zoologie Přírodovědecké fakulty Univerzity Palackého v Olomouci v období 2011–2017.

Autoreferát dizertační práce

Autor: Michal Mášek
Studijní program: P1527 Biologie
Studijní obor: Zoologie

Název práce: Molecular phylogeny and zoogeography of net-winged beetles (Coleoptera: Lycidae)
Školitel: Prof. Ing. Ladislav Bocák, Ph.D.

Obhajoba disertační práce se koná dne .... v .... hod. na učebně č. ………......

katedry zoologie PřF UP, 17. listopadu 50, Olomouc.

Obsah

Úvod

Ultimativním úkolem systematické biologie je postavit přirozenou klasifikaci na robustní fylogenezi zahrnující kompletní diversitu života. Tento cíl zůstává obtížně dosažitelný pro skupiny extrémně bohaté na druhy, vzhledem k omezeným kapacitám laboratoří a absenci materiálu vhodného pro izolaci DNA. Nicméně nedávné pokroky v molekulární fylogenetice posouvají možnosti zkoumání evoluce i velmi rozsáhlých skupin živočichů. Přitom se výrazně zvyšuje počet zkoumaných druhů i počet použitých znaků. Skupina dlouhoústcovitých brouků (Coleoptera: Elateriformia: Lycidae) je použitelná jako modelová skupina pro rozsáhlou fylogenetickou anlýzu. Ve své práci jsem se zaměřil především na příbuzenské vztahy, geografický původ hlavních linií, jejich druhovou diversitu a rekonstrukci jejich geografického rozšíření v průběhu času.

Disperzní schopnosti a ekologická adaptabilita jsou velmi proměnlivé faktory a podstatně ovlivňují současné rozšíření živočichů (Cruaud *et al*. 2011, Fabre *et al*. 2014, Gomez-Rodriguez *et al*. 2015). V důsledku toho je rekonstrukce oblastí vzniku starých evolučních linií velmi obtížná a pro skupiny živočichů s rychlou dispersí a rozmanitými životními strategiemi jsou oblasti jejich vzniku velmi často překryty opakovanými migracemi v dynamicky měnícím se prostředí. Naopak, skupiny charakteristické nízkou schopností šíření a ekologicky konzervativní skupiny, mohou sloužit jako vhodné modely pro rekonstrukci celosvětové historie vikariance a šíření v dlouhodobém časovém horizontu. Brouci čeledi Lycidae jsou známí, jako skupina s velmi omezeným potenciálem se šířit, a proto jsou vhodní pro zoogeografické studie (Sklenarova *et al*. 2014, Masek *et al*. 2015).

Skupiny obsahující tisíce druhů byly jen zřídka studovány fylogenetickým přístupem. Omezujícím faktorem je obtížnost alignmentu a pokrytí diversity jak z hlediska rovnoměrného zastoupení hlavních skupin, tak geografického původu. Ve své studii se zabývám fylogenezí několika set druhů čeledi Lycidae, jedné z hlavních čeledí v nadčeledi Elateroidea (Bocakova *et al*. 2007). Z celkového počtu 4224 popsaných druhů jsou nejvíce zastoupeny triby Metriorrhynchini, Platerodini, Lycini, Calopterini a Calochromini. Každý z vyjmenovaných tribů obsahuje alespoň několik set druhů (Bocak & Bocakova 2008).

Brouci čeledi Lycidae se vyskytují ve všech zoogeografických regionech, s výjimkou velkých pouští a polárních oblastí (Kleine 1933). Larvy žijí v horních vrstvách půdy bohatých na organický materiál, v zetlelých kořenech v hlubších půdních vrstvách, v rozkládajících se kmenech stromů nebo v odumřelých větvích v korunách stromů deštných lesů. Unikátní synapomorfií brouků čeledi Lycidae je podélně rozdělená mandibula (Cicero 1994, Bocak & Matsuda 2003), uzpůsobená pro příjem tekutin, které obsahují bohatý mikrobiální život. Tento specifický způsob získávání potravy omezuje geografické rozšíření brouků čeledi Lycidae do oblastí, ve kterých je k dispozici alespoň po určitou část roku vlhké zetlelé dřevo nebo jiný organický materiál (Bocak & Matsuda 2003). Lycidae patří mezi brouky s charakteristickým měkkým tělem (Crowson 1960, 1972). Tato stavba těla je důsledkem neúplné sklerotizace, potenciálně související s neúplnou metamorfózou (Bocak *et al*. 2008). Jemná nesklerotizovaná kutikula omezuje jejich odolnost vůči vysychání (Ahearn 1970, Bocak & Bocakova 2008) a současně měkký integument poskytuje nedostatečnou podporu pro metathorakální svalovinu ovládající křídla a kromě problému s vysycháním, omezuje jejich disperzní možnosti. Ačkoliv většina druhů je okřídlených, létají jen pomalu, na krátké vzdálenosti a obvykle se vyhýbají otevřeným větrným a slunečným místům. Nejčastěji se vyskytují v lesních porostech pod korunami stromů (Bocak & Bocakova 2008, pozorování v terénu).

Do fylogenetických analýz bylo zahrnuto 766 vzorků, reprezentujících přes 600 popsaných druhů. Přibližně 1900 sekvencí bylo použito z předchozích studií. Nově bylo vyprodukováno téměř 800 fragmetů, které tvoří přibližně 40% analyzovaného datasetu. Osekvenované vzorky obsahují zástupce ze všech hlavních linií čeledi Lycidae.

Pro izolaci DNA byla použita metathorakální svalovina a zadní pár nohou. Svalovina byla izolována pomocí kitu Wizard SV96 a koncentrace výsledného roztoku byla změřena pomocí spektrofotometru (nanodrop ND-1000). Následně byla provedena PCR amplifikace. Vyčištěný sekvenační produkt byl rozpuštěn ve formamidu a analyzován na sekvenátoru ABI 3130 (Bocak *et al*. 2008). Sekvence byly editované pomocí programu Sequencher 4.8 (Gene Codes Corp.). Protein kódující fragmenty (cox1, cox2 a nad5 mtDNA) byly alignovány pomocí programu ClustalW 1.83 (Thompson *et al*. 1994) a výsledná matice byla překontrolována na proteiny. Délkově variabilní části 18S rRNA, 28S rRNA, *rrnL* a tRNA mtDNA byly alignovány pomocí programů MAFFT 7 (Katoh & Standley 2013), BlastAlign 1.2 (Belshaw & Katzourakis 2005) a MUSCLE 3.6 (Edgar 2004). Všechny zalignované fragmenty byly sestaveny do výsledné supermatice pro následující fylogenetické analýzy. Fylogenetické stromy byly vyprodukovány metodou maximální pravděpodobnosti (Maximum likelihood) pomocí programu RAxML 7.2.5 (Stamatakis *et al*. 2005).

V rámci této práce bylo studováno také geografické rozšíření a místa vzniku druhů. Všechna dostupná data byla sestavena z posledního katalogu brouků čeledi Lycidae (Kleine 1933) a databáze zoologických záznamů obsahující informace do konce roku 2014 (Thomson Reuters Inc.). Kartografické nákresy celé čeledi a jejich jednotlivých podčeledí byly vyprodukovány pomocí podkladové mapy světa (http://www.naturalearthdata.com/downloads/10m-physical-vectors/). Zeměpisné souřadnice každého jedince byly editovány v textovém souboru csv a analyzovány na zeměpisné síti o 2° zeměpisné délky a 2° zeměpisné šířky. Výsledné nákresy byly vykresleny v open source programu QGIS Desktop 2.10.1 (https://www.qgis.org/en/site/forusers/download.html). Pro vyhodnocení druhové bohatosti jednotlivých zoogeografických oblastí byly použity oblasti definované v publikaci Holt *et al*. (2013). Oblasti vzniku druhů byly analyzovány pouze u linií s dostatečným zastoupením terminálních liní, pomocí programu BEAST 2.3.0 (Bouckaert *et al*. 2014). Oblasti vzniku a směry šíření jednotlivých linií byly vizualizovány programem SPREAD 1.0.6 (Bielejec *et al*. 2011).

Cíle práce

Cílem studie je analyzovat fylogenezi brouků čeledi Lycidae (Coleoptera: Elateroida) na základě velmi rozsáhlého datového souboru a diskutovat fylogenetické vztahy, které dosud nebyly identifikovány v předchozích studiích. Dále se zaměřuje na rozšíření hlavních linií čeledi Lycidae a na základě údajů o rozšíření a molekulární fylogeneze, vymezuje oblasti s vysokou fylogenetickou a alfa-taxonomickou diversitou. Tato studie obsahuje doposud taxonomicky nejrozsáhleji vytvořenou fylogenetickou analýzu brouků čeledi Lycidae, umožňující popsat efektivnost základních dispersních bariér.

Výsledky

Studie přináší novou fylogenetickou hypotézu založenou na dosud nejrozsáhlejším 5-markerovém datovém souboru obsahujícím přes 600 druhů ze všech zoogeografických oblastí, kompilaci dat o rozšíření všech dosud popsaných druhů. Přitom byly zohledněny informace o paleoklimatu a tektonice všech oblastí. Vzhledem k stavu taxonomie byla použita algoritmická delimitace druhů na základě GMYC (general mixed Yule coalescent model). Fylogenetická analýza identifikovala dobře podpořené klády na úrovni tribu v souladu s morfologickými informacemi, ale pouze ve velmi malém rozsahu podpořila příbuzenské vztahy na úrovni podčeledí a mezitribové příbuznosti. Ancestrální oblasti byly identifikovány pro robustně podpořené, obvykle tribální linie: 17 tribů vzniklo v silně propojené oblasti zahrnující východní část Orientální oblasti a Čínsko-Japonské oblasti, vznik dvou tribů byl určen v Panamské oblasti, dvou v Afrotropické oblasti, dvou v Neotropické oblasti a jednoho v jihovýchodní části Gondwany, t.j. v oblasti představované současnou Indií a Austrálií. Rozložení fylogenetické diversity podporuje hypotézu, že Lycidae vznikli v jižní části Eurasie a Amurie. Alpha-taxonomická diversita je v současnosti nejvyšší ve vlhkých tropických oblastech, především v současné Malesii. Tři skupiny Calochromini, Erotini a Dictyopterini kolonizovali Nearktickou oblast z východní Asie; Calochromini a pravděpodobně i Lycini kolonizovali Afrotropickou oblast šířením po severním pobřeží oceánu Tethys v miocénu, a Calochromini se dále rozšířili do Wallacei a Austrálie. Další linie (Metriorrhynchini, Calopterini, Slipinskiini a Dexorini) zůstaly izolované v oblasti Gondwany po jejím definitivním oddělení od severních kontinentů. Metriorrhynchini kolonizovali Afrotropickou a Orientalní oblast v době, kdy se vyskytovali na driftujícím Indickém subkontinentu, Dexorinae a Lycinae: Slipinskiini zůstali omezeni na Afrotropickou oblast nebo její malou část. Calopterini diversifikovali v Neotropické oblasti a kolonizovali Nearktickou oblast v malém počtu druhů. Na základě fylogeneze, tektoniky a paleoklimatických údajů byly definovány základní dispersní bariéry pro čeleď Lycidae. Ty se přitom částečně liší od podobných bariér definovaných na základě obratlovců a sloužících k delimitaci základních zoogeografických oblastí. V celé čeledi bylo identifikováno pouze několik případů disperse přes úzké mořské úžiny a nebyl zjištěn žádný případ délkové kolonizace přes otevřený oceán. Lycidae a zvláště jejich neotenní linie jsou velmi vhodnou modelovou skupinou pro studium konektivity suchozemských oblastí za dlouhá geologická období. Byl potvrzen starý vznik neotenních linií a poprvé přinesen důkaz na základě molekulární fylogeneze, že neotenní linie z Orientální, Afrotropické a Panamské oblasti mají monofyletický původ. Tato příbuznost poukazuje na jejich vznik v době, kdy tyto oblasti byly propojené souší.

Výsledky dalších studií tvořících tuto disertaci jsou uvedeny v abstraktech, v následující části tohoto autoreferátu.

Abstrakty prací

Bocak L, Grebennikov VV, Masek M (2013) A new species of Dexoris (Coleoptera: Lycidae) and parallel evolution of brachyptery in the soft-bodied elateroid beetles. Zootaxa, 3721 (5): 495–500.

Dexoris chome sp. nov. is described from South Pare mountains, Tanzania, based on a male specimen. This is the only Dexoris with shortened elytra, rudimentary hind wings and large, larviform abdomen. Unlike males of other species in the genus, D. chome sp. nov. has a modified number of palpomeres and remarkably short, robust legs and antennae. Such modifications are similar to those in the neotenic female of Omalisus fontisbellaquei Fourcroy, 1785 (Omalisidae), sug-gesting analogous morphological changes in unrelated lineages supposedly caused by similar modifications of their meta-morphosis. The distribution of all 11 known species of African Dexoris closely overlap with the location of the hypothesized centres for evolution of new species in the Afrotropical region.

Masek M, Ivie MA, Palata V, Bocak L (2014) Molecular phylogeny and classification of Lyropaeini (Coleoptera: Lycidae) with description of larvae and new species of *Lyropaeus*), Raffles Bulletin Of Zoology, 62: 136–145.

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).

Masek M, Bocak L (2014) The taxonomy and diversity of *Platerodrilus*. ZooKeys, 426: 29–63.

The Oriental neotenic net-winged beetles attracted attention of biologists due to conspicuous large-bodied females; nevertheless phylogenetic relationships remain contentious and only a few species are known in both the fully metamorphosed males and neotenic females. The phylogenetic analyses and morphology of larvae and adults provide data for investigation of relationships and species delineation. Platrilus Kazantsev, 2009, Platerodriloplesius Wittmer, 1944, and Falsocalochromus Pic, 1942 are synonymized to Platerodrilus Pic, 1921. Platrilus hirtus (Wittmer, 1938) and Pl. crassicornis (Pic, 1923) are transferred to Platerodrilus Pic, 1921. Platerodrilus hoiseni Wong, 1996 is proposed as a junior subjective synonym of Falsocalochromus ruficollis Pic, 1942. Platerodrilus is divided in three species-groups: P. paradoxus, P. major, and P. sinuatus groups defined based on the shape of genitalia and molecular phylogeny. The following species are described: Platerodrilus foliaceus sp. n., P. wongi sp. n. (P. paradoxus group); P. ngi sp. n., P. wittmeri (P. major group), P. ijenensis sp. n., P. luteus sp. n., P. maninjauensis sp. n., P. montanus sp. n., P. palawanensis sp. n., P. ranauensis sp. n., P. sibayakensis sp. n., P. sinabungensis sp. n., P. talamauensis sp. n., and P. tujuhensis sp. n. (P. sinuatus group). P. korinchiana robinsoni Blair, 1928 is elevated to the species rank as P. robinsoni Blair, 1928, stat. n. The conspecific semaphoronts are identified using molecular phylogeny for P. foliaceus sp. n., P. tujuhensis sp. n., P. montanus sp. n., P. maninjauensis sp. n.; additional female larvae are assigned to the species-groups. Diagnostic characters are illustrated and keys are provided for P. paradoxus and P. major groups.

Masek M, Palata V, Bray TC, Bocak L (2015) Molecular Phylogeny Reveals High Diversity, Geographic Structure and Limited Ranges in Neotenic Net-Winged Beetles *Platerodrilus* (Coleoptera: Lycidae). PLoS One, 10(4): DOI:10.1371/journal.pone.0123855

The neotenic Platerodrilus net-winged beetles have strongly modified development where females do not pupate and retain larval morphology when sexually mature. As a result, dispersal propensity of females is extremely low and the lineage can be used for reconstruction of ancient dispersal and vicariance patterns and identification of centres of diversity. We identified three deep lineages in Platerodrilus occurring predominantly in (1) Borneo and the Philippines, (2) continental Asia, and (3) Sumatra, the Malay Peninsula and Java. We document limited ranges of all species of Platerodrilus and complete species level turnover between the Sunda Islands and even between individual mountain regions in Sumatra. Few dispersal events were recovered among the major geographical regions despite long evolutionary history of occurrence; all of them were dated at the early phase of Platerodrilus diversification up to the end of Miocene and no exchange of island faunas was identified during the Pliocene and Pleistocene despite the frequently exposed Sunda Shelf as sea levels fluctuated with each glacial cycle. We observed high diversity in the regions with persisting humid tropical forests during cool periods. The origins of multiple species were inferred in Sumatra soon after the island emerged and the mountain range uplifted 15 million years ago with the speciation rate lower since then. We suppose that the extremely low dispersal propensity makes Platerodrilus a valuable indicator of uninterrupted persistence of rainforests over a long time span. Additionally, if the diversity of these neotenic lineages is to be protected, a high dense system of protected areas would be necessary.

Motyka M, Masek M, Bocak L (in press) Congruence between morphology and molecular phylogeny: the reclassification of Calochromini (Coleoptera: Lycidae) and their dispersal history. Zoological Journal of the Linnean Society.

Calochromini is a tribe of net-winged beetles (Elateroidea: Lycidae) with 284 described species, which have a global distribution. Historically, the species have been placed in eight genera, however the morphological boundaries between genera have been poorly defined. We assembled a five-marker DNA dataset (18S, 28S rRNA and rrnL, nad5, cox1 mtDNA) with 89 terminals, representing 61 calochromine species from eight genera and from all geographic regions. The analyses recovered a well-resolved phylogeny of Calochromini and identified major lineages, which were tested by the detailed evaluation of the adult morphology. The inferred topology is in conflict with the traditional morphology-based concepts of genera and highlighted that historically used diagnostic characters such as the prolonged rostrum are homoplastic. New morphological diagnostic characters are defined here, mainly in male genitalia, that are congruent with the DNA-based topology. We delimit the genera Calochromus Guérin-Méneville, 1833 (incl. the subgenera Flabellochromus Pic, 1925 and Paracalochromus subgen. nov.), Micronychus Motschoulsky, 1861, Macrolygistopterus Pic, 1929, Lucaina Dugčs, 1879, Lygistopterus Mulsant, 1838, Parantis gen. nov., and Caloptognatha Green, 1954. Micronychus Motschoulsky, 1861 is removed from synonymy with Calochromus Guérin-Méneville, 1833 and Adoceta Bourgeois, 1882 syn. nov. is proposed as a junior synonym of Lygistopterus Mulsant, 1838. These changes in the generic classification resulted in 145 new combinations. Additionally, we estimated divergence dates and dispersal history of the tribe. Calochromini originated in continental Southeast Asia in the Paleocene (56 mya), dispersed two times to the New World, in Lower Eocene (51 mya, Lucaina and Macrolygistopterus) and in Upper Oligocene (28 mya, Lygistopterus). Our results indicate that the Western Palearctic region was colonized by extant Lygistopterus (28 mya), and the Afrotropical region by Micronychus (29 mya). Dispersal routes are discussed in the context of the tectonic and paleoclimatic history. The highest phylogenetic diversity was identified in Southern China and Indo-Burma where most principal lineages occur. Conversely, the highest alpha diversity was identified in the semiarid areas of Southern India.

Literatura

Ahearn GA (1970) The control of water loss in desert tenebrionid beetles. Journal of Experimental Biology, 53: 573–595.

Belshaw R & Katzourakis A (2005) BlastAlign: a program that uses blast to align problematic nucleotide sequences. Bioinformatics, 21: 122–123.

Bielejec F, Rambaut A, Suchard MA, Lemey P (2011) SPREAD: spatial phylogenetic reconstruction of evolutionary dynamics. Bioinformatics, 27(20): 2910–2912.

Bocak L & Bocakova M (2008) Phylogeny and classification of the family Lycidae (Insecta: Coleoptera). Annales Zoologici, 58: 695–720.

Bocak L & Matsuda K (2003) Review of the immature stages of the family Lycidae (Insecta: Coleoptera). Journal of Natural History 37: 1463–1507.

Bocak L, Bocakova M, Hunt T and Vogler AP (2008) Multiple ancient origins of neoteny in Lycidae (Coleoptera): consequences for ecology and macroevolution. Proceedings of the Royal Society B, 275: 2015–2023.

Bocakova M, Bocak L, Hunt T, Teravainen M, Vogler AP (2007) Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminiscence and neoteny. Cladistics, 23: 477–496.

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu C-H, Xie D, Suchard MA, Rambaut A Drummond AJ (2014) BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. PLoS Computational Biology, 10(4): e1003537.

Cicero JM (1994) Composite, haustellate mouthparts in netwinged beetle and firefly larvae (Coleoptera, Cantharoidea: Lycidae, Lampyridae). Journal of Morphology, 219(2): 183–192.

Crowson RA (1960) The phylogeny of Coleoptera. Annual Review of Entomology, 5: 111–134.

Crowson RA (1972) A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families: Cneoglossidae and Omethidae. Revista de la Universidad de Madrid, 21: 35–71.

Cruaud A, Jabbour-Zahab R, Genson G, Couloux A, Yan-Qiong P, Rong YD, Ubaidillah R, Pereira RAS, Kjellberg F, Noort S, Kerdelhue C, Rasplus JY (2011) Out of Australia and back again: the world-wide historical biogeography of non-pollinating fig wasps (Hymenoptera: Sycophaginae). Journal of Biogeography, 38: 209–225.

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research, 32: 1792–1797.

Fabre PH, Moltensen M, Fjeldsa J, Irestedt M, Lessard JP, Jonsson KA (2014) Multiple waves of colonization by monarch flycatchers (Myiagra, Monarchidae) across the Indo-Pacific and their implications for coexistence and speciation. Journal of Biogeography, 41: 274–286.

Gomez-Rodriguez C, Freijeiro A, Baselga A (2015) Dispersal and ecological traits explain differences in beta diversity patterns of European beetles. Journal of Biogeography, 42: 1526–1537.

Holt B, Lessard JP, Borregaard MK, Fritz SA, Araujo MB, Dimitrov D, Fabre PH, Graham CH, Graves GR, Jonsson KA, Nogues-Bravo D, Wang ZH, Whittaker RJ, Fjeldsa J, Rahbek C (2013) An update of Wallace's zoogeographic regions of the world. Science, 339: 74–78.

Katoh K & Standley DM (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. Molecular Biology and Evolution, 30: 772–780.

Kleine R (1933) *Coleopterorum Catalogus auspiciis et auxilio W. Junk editus S. Schenkling*. Pars 128: Lycidae. W. Junk, Berlin.

Masek M, Palata V, Bray TC, Bocak L (2015) Molecular phylogeny reveals high diversity and geographic structure in Asian neotenic net-winged beetles *Platerodrilus* (Coleoptera: Lycidae). PLoS One, 10(4): e0123855.

Sklenarova K, Kubecek V, Bocak L (2014) Subtribal classification of Metriorrhynchini (Insecta: Coleoptera: Lycidae): an integrative approach using molecular phylogeny and morphology of adults and larvae. Arthropod Systematics & Phylogeny, 72(1): 37–54.

Stamatakis A, Ludwig T, Meier H (2005) RAxML-III: a fast program for maximum likelihood-based inference of large phylogenetic trees. Bioinformatics, 21: 456–463.

Thompson J, Higgins D, Gibson T (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignments through sequence weighting, position specific gap penalties and weight matrix choice. Nucleic Acids Research, 22: 4673–4680.

Seznam publikovaných prací
(s uvedením impakt faktoru)

Bocak L, Grebenikov VV, Masek M (2013) A new species of *Dexoris* (Coleoptera: Lycidae) and parallel evolution of brachyptery in the soft-bodied elateroid beetles. Zootaxa, 3721 (5): 495–500. (IF = 1.06; 73/153).

Masek M, Ivie M, Palata V, Bocak L (2014) Molecular phylogeny and classification of *Lyropaeini* (Coleoptera: Lycidae) with description of larvae and new species of *Lyropaeus*). Raffles Bulletin Of Zoology, 62: 136–145. (IF = 1.047; 77/154).

Masek M, Bocak L (2014) The taxonomy and diversity of *Platerodrilus*. ZooKeys, 426: 29–63. (IF = 0.933; 86/154).

Masek M, Palata V, Bray TC, Bocak L (2015) Molecular Phylogeny Reveals High Diversity, Geographic Structure and Limited Ranges in Neotenic Net-Winged Beetles *Platerodrilus* (Coleoptera: Lycidae). PLoS One, 10(4): DOI:10.1371/journal.pone.0123855 (IF = 3.057; 11/63).

Motyka M, Masek M, Bocak L (in press) Congruence between morphology and molecular phylogeny: the reclassification of *Calochromini* (Coleoptera: Lycidae) and their dispersal history. Zoological Journal of the Linnean Society. (IF = 2.316; 16/161).

Curriculum vitae

Jméno: Michal Mášek

Datum a místo narození: 1.8.1985, Hlinsko

E-mail: michal.masek@seznam.cz

Vzdělání:

2011 - dosud: doktorské studium (Zoologie, PřF UP, Olomouc)

2009 - 2011: Učitelství biologie a geografie v ochraně životního prostředí, PřF UP, Olomouc (Mgr.)

2006 - 2009: Učitelství biologie a geografie, PřF UP, Olomouc (Bc.)

Zahraniční stáže a pobyty:

2012 - Ege University, Izmir-Bornova, Turecko

2014 - Queensland University of Technology, Brisbane, Austrálie

Ocenění:

2012 - Cena rektora UP za nejlepší vědeckou práci studentů magisterských studijních programů v oboru Biologie

Magisterská práce na téma Klasifikace druhové skupiny *Cautires Pauper* (Coleoptera: Lycidae)

Pedagogická činnost:

Podíl na výuce:	ZOO/SBP Fylogeneze a systém bezobratlých
	ZOO/CTP Zoologická cvičení v terénu
	ZOO/BIKZ Biologická klasifikace živočichů

Oponentské posudky bakalářských prací (2x)