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Phylogenomic analysis of the family Lycidae (Coleoptera: Elateroidea)

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Declaration

I declare that I worked on this master thesis entitled „Phylogenomic analysis of the family Lycidae (Coleoptera: Elateroidea)" on my own under supervision of Prof. Ing. Ladislav Bocák, Ph.D. and that I used only sources mentioned in the Bibliography section.

Olomouc, 24. 4. 2019 …….

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ABSTRACT

Net-winged beetles (Coleoptera: Lycidae) are a diverse group of elateroids known for the aposematism and neoteny. Phylogenetic analyses of morphological and molecular data have revealed different topologies with respect to within-group relationships. In this study, a highly supported phylogenomic phylogeny is recovered and seven subfamilies are identified: Dexorinae **stat. nov.**, Calochrominae **stat. nov.**, Erotinae, Ateliinae, Lycinae, Lyropaeinae **stat. nov.**, and Metriorrhynchinae **stat. nov.** The results suggest that female neoteny evolved multiple times. Therefore, the evolution of similar morphological modifications in neotenics may be linked and may have produced characteristics such as male body miniaturization, structural simplification, *i.e*., reduction of mouthparts, fewer antennomeres and palpomeres, uniquely shaped terminal palpomeres, shortened elytra, the loss of coadaptation between the elytra and pronotum, and others. Additional traits evolved in parallel due to similarities in biology, function, and sexual selection. These characteristics include mimetic similarities, the presence of the rostrum, pronotal carinae, and elytral costae, and the structure of male genitalia. By comparing the phylogenomic topology with the evolution of morphological characters, it was possible to identify evolutionary trends in lycids and compare them with similar traits in other neotenic elateroids. These traits have not been accepted as homoplasies due to the ambiguous phylogenetic signal from Sanger markers.

Key words: Coleoptera, Lycidae, phylogeny, transcriptome, genome, orthology, neoteny

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ABSTRAKT

Čeled Lycidae (Coleoptera: Lycidae) je diverzifikovanou skupinou elateroidních brouků známých především pro jejich aposematické zbarvení a neotenii. Fylogenetické analýzy morfologických znaků a molekulárních dat odhalily různé topologie uvnitř skupiny. V této práci byla vyprodukována vysoce podpořená fylogenomická hypotéza a je popsáno sedm podčeledí: Dexorinae **stat. nov.**, Calochrominae **stat. nov.**, Erotinae, Ateliinae, Lycinae, Lyropaeinae **stat. nov.**, and Metriorrhynchinae **stat. nov.** Výsledky potvrzují mnohonásobný vznik samičí neotenie. Výsledky ukazují, že vývoj podobných morfologických struktur neoteních linií je konvergentní a může mít za následek miniaturizaci samčího těla, zjednodušení tělní stavby, redukci čelistí, snižování počtu antennomer a palpomer, jedinečně tvarované terminální palpomery, zkrácené krovky, ztrátu koadaptace mezi krovkou a štítem atp. Další znaky se vyvíjely souběžně kvůli podobnostem v biologii, funkci a působením sexuálního výběru. Tyto znaky zahrnují mimetické podobnosti, výskyt rostra, areoly na štítu, žebra krovky a struktury samičích genitálií. Porovnáním fylogenomické topologie s evolucí morfologických znaků bylo možné identifikovat evoluční trendy v čeledi Lycidae a srovnat je s podobnými znaky v jiných liniích neotenických brouků. Tyto znaky nebyly klasifikovány jako homoplasie kvůli nejednoznačnému fylogenetickému signálu ze sekvencí vyprodukovaných Sangerovým sekvenováním.

Klíčová slova: Coleoptera, Lycidae, fylogeneze, genom, transkriptom, orthology, neotenie

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1. Introduction

1.1 Sequencing Strategies and Techniques

New possibilities come with new technologies. Recent progress in the development of next-generation sequencing technologies and its huge cost reduction create the possibility to produce a huge amount of genome-scale data even for non-model organisms (Bleidorn, 2015; Da Fonseca *et al., 2016*; Mardis, 2011). For example, the latest Illumina short read sequencer NovaSeq 6000 is capable to produce 2400–3000 Gb using 2x150 base pairs paired end approach just in 44 hours, with cost $0.05 to $0.15 per one million bases (1Mb) (www.illumina.com, April 2019). So, theoretically, it is possible in one run to sequence ~48 human genomes with 30x genome coverage in less than two days. Hand to hand with cheaper and more powerful computers this opportunity to produce huge amount of data in a short period of time with acceptable price and the possibility to analyze them brings many new possibilities to all fields of the biology (Garner *et al.,* 2016; Schuster, 2007; Valentini *et al.*, 2016). New fields of science rapidly develop i.e., metagenomics, functional genomics etc. (Seppey *et* al., 2018; Waldor *et al.,* 2015). These results for the first time provide information on the genetics basis of life diversity (Hug *et al*., 2016). New methods greatly facilitate the production of genome-scale data in systematics biology and enable generating of hundreds to thousands of loci suitable for phylogenetic analyses (Misof *et al*., 2014). Therefore, new big genomic data give us an insight into relationships of many groups of organisms and in many cases strongly reject earlier hypotheses (Crawford *et al*., 2015; Misof *et al.*, 2014; Niehuis *et al*., 2012; Prum *et al.,* 2015).

1.2 Homology, orthology, paralogy

The major crucial step before the analysis of phylogenetic interference is definition which pair of structures or genes have shared ancestry among different taxa, *i.e.*, if they are homologous (Owen, 1843). In case of phylogenomics, the organisms with precisely sequenced genomes and well predicted genes sets are needed (Gabaldón, 2008). In most cases, these organisms are models for molecular biology or important crop pests. The Coleoptera model species *Tribolium castaneum* (Shelton *et al*., 2015; Richards *et al*., 2008), *Agrilus planipennis* (Poelchau *et al*., 2014) invasive member of Buprestidae and dangerous pests of *Fraxinus* in America, *Leptinotarsa decemlineata* (Poelchau *et al*., 2014) important pests on *Solanum tuberosum* were studied in detail and their well sequenced genomes are now available in public databases. The number of well sequenced genomes is getting

bigger every year and they now represent distant families of Coleoptera. Currently, ~11 well sequenced coleopteran genomes are available (McKenna, 2018).

Two genes can be similar in their sequence by percentage identity, but that does not necessary imply their homology which is important. We need to identify homologs because the gene homology implies a genealogical relationship. The similarity between sequences can be achieved not only by the common origin but also by other evolutionary processes such as convergence, which result in analogy among unrelated organism. Together with parallelisms we group these processes under the term homoplasy (Jensen, 2001; Koonin, 2005). Homologous genes in a group of species which resulted from speciation event are orthologs (Fitch, 1970). Conversely, paralogs are also homologous genes, but they result from a duplication event within an organism (Ohno, 1970). Other terms to describe relationships between paralog genes are outparalogs, inparalogs and co-orthologs (Remm *et al.*, 2001).

The precise graph-based algorithms with reciprocal best hits (RBH) improvement are used to identify orthology in genome scale data (Altenhoff *et al*., 2012). These methods have been recently implemented in many public databases: COG (clusters of ortholog groups) (Tatusov *et al.,* 2003), InParanoid (Sonnhammer & Östlund, 2014), OrthoMCL (Li *et* al., 2003) and, for example, OrthoDB, which provides orthology relationships at many levels of the taxonomic tree (Zdobnov *et al.,* 2016). Information about which genes are orthologous among defined set of organisms are then used in Orthograph pipeline (Petersen *et al*., 2017) to search for those genes in non-model organism.

1.3 Transcriptome and other genomic partitioning strategies

The usage of transcriptome sequencing for phylogenetic interference have became a popular option recently (Pauli *et* al., 2018; Peters *et al.,* 2017; Vasilikopoulos *et al.*, 2019). This technique enables to sequence RNA which contains various parts of the genome transcribed from DNA to mRNA during transcription in whole organism or a tissue at the time it is fixed in the RNA later. The RNAlater fixation stabilizes and protects cellular RNA intact. The limitation of this method is a requirement of large quantity of high-quality RNA so samples must be fixed in RNAlater solution alive, at best in the field and then kept gently stored (Cronn *et al*., 2012; Gayral *et al*. 2011). Another problem is unpredictable availability of the samples in non-model lineages. Because this method is destructive, we must be sure what we sample already in the field. Such requirement call for the participation of an expert in the studied group already at the beginning of the project, especially in diversified groups as insects. The best possible way is to get as many information for future identification as possible. For example, the mitochondrial DNA from the sample can be sequenced for the cytochrome oxidase amplicon. Such

information can help to identify organism to the group using huge databases of sequences from the same group. Further, a part of the body can be retained, and male genitalia can be dissected. We prefer also to take a detailed photograph of a specimen before fixation in RNAlater. If possible, specimens collected in copula provide material for both molecular and morphological investigation, if one of them is kept as a voucher in 96% alcohol.

Hybrid enrichment such as Anchored hybrid enrichment (Lemmon *et al.,* 2012) and ultra-conserved elements (Faircloth *et al.,* 2012) are another recently developed technique. These technologies have fewer limitations for the DNA quality and quantity but for each taxonomic group of interest are required specific hybridization baits and genomic resources are needed in advance for designation of these probe sets (Faircloth 2017; Faircloth *et al.,* 2012; Lemmon *et al.,* 2012).

Despite some limitations, new techniques have been successfully used in recent years to address many systematics and evolutionary questions (Pauli *et* al., 2018; Peters *et al.,* 2017; Vasilikopoulos *et al.*, 2019). The part-genome strategies pose less computational requirements and a lower cost over whole genome sequencing. Their biggest limitations and shortcoming are the narrow utility of the generated data which are rarely used outside phylogenetics (Allen *et al.*, 2017). This can be a problem in small rare organism with limited availability if we are interested in another genes and questions beside phylogeny (Zhang *et al.*, 2019).

1.4 Whole genome sequencing for phylogenomics

Use of the whole genome sequences for phylogenetics is the most recent technique (Zhang *et al.*, 2019). In this case, all genomic components, introns, exons, repetitive elements etc., are sequenced. Advantages over genome partitioning techniques are mainly in the diversity of targeted markers and the future availability of produced data for other studies. Additionally, the laboratory DNA extraction is easier than in case of RNA-based methods. The capacity of produced data to answer unrelated questions is essential in the case of rare specimens or dry unique museum specimens. One of major limitations of whole genome sequencing in phylogenetics was its high cost and computational challenges. Another problem is the genome size of the targeted organism which is unknown for most groups because alive specimen is needed for measurements of genome size. The genome size can vary by many orders of magnitude even in closely related organism (Lower *et al.,* 2017). Although the genome sequencing is readily available concerning laboratory techniques the further steps following assembly, gene annotation and classification of suitable genes for phylogenetic interreferences are more difficult (Jarvis *et al*., 2014). To overcome these limitations, methods for automated target

restricted assembly were developed: aTRAM (Allen *et al*., 2015; Allen *et al*., 2017), HybPiper (Johnson *et al*., 2016), Kollector (Kucuk *et al.,* 2017)). These approaches assemble only genes of interest rather than whole genome from all reads. This method can be used if target sequences from closely related organism are available, but most of the pipelines mentioned contain BLAST (Cock *et al*., 2015) and are computationally extensive. With the development of fast and memory efficient de Bruijn graph algorithms we have tools suitable for whole genome assembly of low coverage genome data (Bankevich *et* al., 2012; Chikhi *et al.*, 2016; Chikhi & Rizk, 2013). This approach enables to use another promising method for mining suitable loci for phylogenetic interferences directly from genome assemblies, i.e., BUSCO: benchmarking universal single copy orthologs (Waterhouse *et al*., 2017). BUSCO pipeline is based on OrthoDB database (Zdobnov *et al*., 2016) which contains the list of near-universal single copy orthologs across diverse taxa. BUSCO was applied to address phylogenetic relationships in many groups of organisms: insects (Ioannidis *et al*., 2017), yeasts (Shen *et al*., 2016) and spiders (Fernández *et al*., 2018).

1.5 Advantage of phylogenomics

Until recently, the phylogenetic studies have been based on a limited amount of information. The history of phylogenetics start with early Henning's studies using manual consideration of morphological characters. Later, the computers opened the era of large morphology-based dataset, but 'large' meant that time up to a hundred of taxa and a hundred of characters. Seldom larges datasets were analyzed and the difficult homologation of trait lead to disputable results (Lawrence et al. 2011). The morphology-based studies are affected by a subjective decision of an examiner which morphological structures are homologous and suitable for phylogenetic interference.

In most cases, the growing amount of information can provide better resolution and improve its statistical significance. The first studies based on molecular characters, provided a lot of new information and shred a new light on many parts of the Tree of Life (Regier *et al.*, 2005). The early works were based as a rule on single or few genes and often lead to apparently conflicting results. To overcome limitations of few-genes data, a genome-scale approaches were applied. These combine a hundred to thousands of genes. Although not always decisive results may be attained, they mean very often a decisive progress and they end many disputes in phylogenetics. Ongoing genome sequencing projects have led to phylogenetics approaches based on genome-scale data, which shed light on longstanding unresolved phylogenetic issues such as the monophyly of large insect orders (Inward *et* al., 2007; Misof *et al.*, 2014; Wang *et al*., 2017).

Why robust phylogenetic hypothesis is needed? Famous Theodosius Dobzhansky once said, "nothing in biology makes sense except in the light of evolution" (Dobzhansky, 1964). Simply said, without robustly supported phylogenetic hypothesis, the evolution of any trait cannot be discussed. For example, Niehuis *et al*. 2012 sequenced and assembled the first Strepsiptera genome and the first partial genome of a beetle *Priacma serrata* from the suborder Archostemata. They also used the sequences from other 13 insect genomes and were able to robustly recover the phylogenetic placement of such long enigmatic insect order as Strepsiptera (Niehuis *et al*. 2012), historically considered as beetle ingroup (McKenna & Farrell, 2010). Other recent studies have used data from genome and/or transcriptome sequences to reconstruct difficult phylogenies that include beetles (Vasilikopoulos *et al.*, 2019), wasps (Peters *et al.*, 2018), basal relationships among holometabolous groups of insects (Peters *et* al., 2014) or they develop target enrichment-based approaches, such as anchored hybrid enrichment (Lemmon *et al.,* 2012), for reconstructing phylogenetic relationships in cerambycid (Haddad *et* al., 2018) and curculionids (Shin *et al.*, 2017).

1.6 Pitfalls of phylogenomics

Despite the obvious benefits of the genome-scale data new set of challenges appears (Yeates *et al.*, 2016). The main sources of error and incongruence in phylogenomic analyses can be: (1) violations of the orthology assumption generated by mechanisms such as gene duplication, horizontal gene transfer or an incomplete lineage sorting (citation), (2) the stochastic error related to the shortness of the genes, and (3) the systematic error leading to tree reconstruction artifacts generated by the presence of a non-phylogenetic signal in the data (Jeffroy *et al*., 2006). The first two problems can be theoretically solved just by the usage of genome-scale data. In the case of the systematic error which results from non-phylogenetic signals in the data, such as compositional heterogeneity of nucleotides among species (Jermiin *et al*., 2004), rate variation across lineages, and within-site rate variation (Rosenberg & Kumar, 2003) the solution is more difficult. We can encounter the bias causing systematic error as a signal because, contrary to stochastic noise, it does not average out over many sites. With a strong bias, the noise can dominate over the true phylogenetic signal. Then, the tree reconstruction method is inconsistent and recovers an incorrect, but highly supported tree (Felsenstein, 1978; Phillips *et al*., 2004).

Therefore, the usage of genome-scale data will not end the presence of incongruent hypotheses. As these can be caused by the use of different methods, taxon samplings, different data types or different character partitions of the same dataset (Jeffroy *et al*., 2006). Unlike previous methods, we are now able to statistically evaluate the inconsistencies and much better support our

best hypothesis (Dell'Ampio *et al*., 2013). The experience from last decade history of large dataset highlights the benefits of integration of and congruence among multiple sources of phylogenetic evidence. This integrative approach includes rich new evidence from paleontological, molecular and morphological data (Niehuis *et al*. 2012). All of this will dramatically improve our ability to assess the accuracy of our hypotheses of the evolutionary relationships among organisms.

1.7 Group of study: Lycidae

Despite repeated attempts over the last three decades, the evolutionary history of net-winged beetles (Elateroidea: Lycidae) remains unresolved. This includes both the position of Lycidae within Elateroidea and the relationships among subfamilies and tribes. Previous phylogenetic studies based on morphological data produced large datasets supposedly rich in phylogenetic information, but these phylogenies were largely incompatible with those produced from molecular analyses (Bocak & Bocakova, 1990, 2008; Branham & Wenzel, 2003; Kazantsev, 2005, 2013; Bocakova *et al.*, 2007; Lawrence *et al.*, 2011; Bocak *et al.*, 2016; Kundrata *et al.*, 2014; McKenna *et al.*, 2015; Masek *et al.*, 2018; Zhang *et al.*, 2018).

Based on morphology, net-winged beetles are hypothesized to be a deep branch of the "cantharoid" clade (Lawrence *et al.*, 2011) or sister to Cantharidae, Omethidae, Telegeusidae, and Phengodidae (Branham & Wenzel, 2003). Likewise, the use of Sanger markers has led to contradictory outcomes regarding deep-level relationships in the Elateroidea. Nevertheless, results from molecular analyses have revealed that the cantharoid clade may not be monophyletic after all (Bocakova *et al.*, 2007; Hunt *et al.*, 2007; Kundrata *et al.*, 2014; Bocak *et al.*, 2016; McKenna *et al.*, 2015; Zhang *et al.*, 2018). Molecular analyses were only moderately supported and seemingly counterintuitive, and

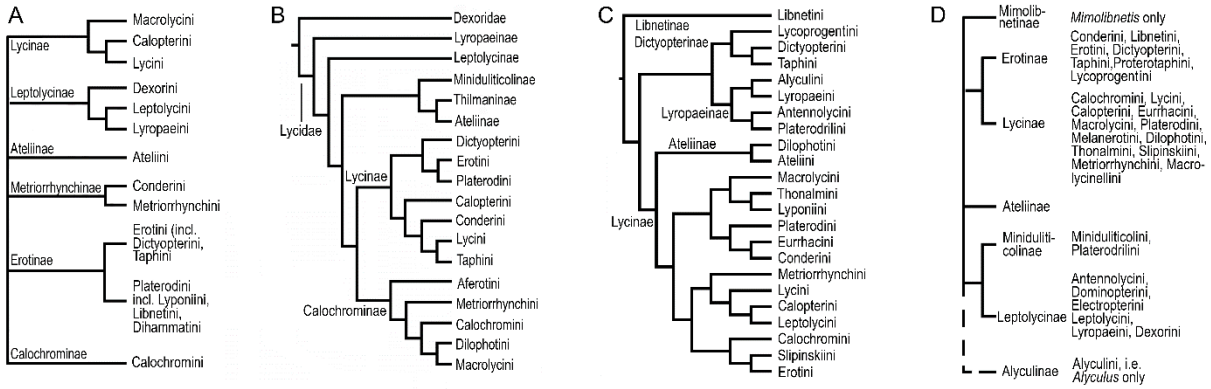

Figure 1. Overview of earlier net-winged beetle classifications. (A) Bocak & Bocakova 1990; (B) Kazantsev (2005), compare with Figs. S1, S2; (C) Bocak *et al.*, (2008); (D) Kazantsev (2013), compare with Fig. S3.

therefore some researchers have rejected these findings and continued to use the traditional classification of cantharoid families (Lawrence *et al.*, 2011; Beutel & Leschen, 2016). Recently, net-winged beetles and soldier beetles have been recovered as successive sister groups to luminescent elateroids (Lampyridae, Phengodidae, and Rhagophthalmidae) and click beetles (Elateridae; Kusy *et al.*, 2018b). Iberobaeniidae was identified as sister to Lycidae (Bocak *et al.*, 2016), but no material from this family is available for genomic analyses.

The phylogenetic relationships among net-winged beetles are also unresolved. The lycid phylogenies based on morphological traits are unstable and poorly supported, with ambiguous phylogenetic signals and unstable inferred trees. Results from morphological analyses suggested that neotenic lineages from different biogeographic regions are closely related (Fig. 1; Bocak & Bocakova 1990; Miller, 1991; Kazantsev, 2005, 2013). In contrast, molecular phylogenies suggest that neoteny has multiple origins and neotenics occur in limited ranges (Bocak *et al.*, 2008; Masek *et al.*, 2018). Therefore, we aimed to test whether neotenic taxa evolved repeatedly in Lycidae, in congruence with evolutionary trends for soft-bodiedness and neoteny in Elateroidea (Kundrata & Bocak, 2011; Kundrata *et al.*, 2014; Bocak *et al.*, 2018; Kusy *et al.*, 2018a, b). We used genomic data, as these can provide independent and decisive phylogenetic information to analyze the distribution of homoplasy in the morphological phylogeny (Misof *et al.*, 2014; Peters *et al.*, 2017).

Figure 2. Net-winged beetles in nature. (A) *Platerodrilus* sp., the female larva; (B) *Cautires* sp.; (C) *Diatrichalus aeneus* Bocak (D) *Metriorrhynchus* sp.; (E) *Platerodrilus* sp., the female larva; (F) *Scarelus anthracinus* Bocakova & Bocak, 1999; (G) *Porrostoma* sp. (H) head and antennae of *Cladophorus* sp. All photographs © authors of Kusy *et al., 2019*.

Previous studies have reported on the evolution of neoteny (Crowson, 1972; Bocak et al., 2008; Masek et al., 2015; Kazantsev, 2013; McMahon & Hayward, 2016), speciation of neotenic

lineages (Malohlava & Bocak 2010; Bray & Bocak, 2016), chemical protection and mimicry (Linsley et al., 1961; Moore & Brown, 1980, 1989; Eisner et al., 1962, 2008; Bocak & Yagi 2010; Motyka et al., 2018), dispersal history (Sklenarova et al., 2013; Li et al., 2015; Motyka et al., 2017; Bocek & Bocak, 2019), and morphological evolution (e.g., Bocak & Bocakova, 1990; Miller, 1991; Bocakova 2001, 2003, 2005; Kazantsev, 2005, 2006, 2013) in net-winged beetles. Additionally, detailed phylogenetic and taxonomic studies have focused on specific groups within Lycidae (e.g., Kazantsev, 2002, 2004, 2012; Bocakova, 2003, 2004; Sklenarova et al., 2014; Bocek & Bocak, 2016; Masek et al., 2014; Li et al., 2016, 2017, 2018; Ferreira et al., 2018). Although net-winged beetles have potential as models for macroevolutionary studies, indecisive phylogenetic data and weakly-supported phylogenies complicate further research of this group (Fig. 1; Bocak & Bocakova 2008; Kazantsev, 2005, 2013).

The assessment of levels of morphological homoplasy in a system is feasible with independent robust phylogenies (Koehler & Criscione, 2015; Sansom *et al.*, 2017). In this study, we considered some inherent properties of net-winged beetles to investigate the links between the development and function of morphological characters. There are more than 100 neotenic species of Lycidae, *i.e*., approximately 3% of 4,300 formally described species (Table S1; Kazantsev, 2013; Masek *et al.*, 2018). A morphological homoplasy could have evolved along similar lines, as a result of modified metamorphosis (Bocak *et al.*, 2018; Kusy *et al.*, 2018b; Motyka *et al.*, 2018). Additionally, the appearance of miniaturization could obscure trait homology in large- and small-bodied net-winged beetles (Kazantsev, 2002, 2005, 2013; Polilov, 2015). The beetles' external morphology might also be affected by adaptations compensating for weak sclerotization, such as the development of pronotal carinae and elytral costae (Fig. 2). The pronotal carinae generally exhibit simple patterns, therefore the similarity in patterns across species may have resulted from multiple cases of evolution due to similar functions, or from parallel reduction (Sklenarova *et al.*, 2014). The number of longitudinal elytral costae is also a plastic trait; some costae can be short or absent. Further, some species only have irregularly punctured interstices, whereas others have numerous clearly defined cells with varying shapes (Fig. 2; Bocak & Bocakova, 1990, 2008; Kazantsev, 2005; Bocakova, 2006). All net-winged beetles are members of mimicry complexes, which contain similar-looking but unrelated taxa and their mimics from other beetle families and insect orders (Linsley *et al.*, 1961, 1962). Therefore, the external morphology of aposematically colored and unpalatable lycids can be strongly affected by natural selection for similar body sizes and forms (Motyka *et al.*, 2018). As a result, these similar but convergently evolved traits could have been coded with the same character state in morphological phylogenies, which would have masked their homoplasy (Kazantsev, 2005, 2013). Hence, morphological datasets containing neotenics could produce inaccurate trees as has been

demonstrated for click beetles (Lawrence *et al*. 2011; Kundrata & Bocak, 2011; Kundrata *et al.*, 2014; McKenna *et al.*, 2015; Zhang *et al.*, 2018; Kusy *et al.*, 2018b). Due to these inconsistencies, several incompatible classifications at the subfamily level have been proposed to date for net-winged beetles (Fig. 1; Tables S1–S3; Bocak & Bocakova, 1990, 2008; Kazantsev, 2005, 2013; Masek *et al.*, 2018).

In this study, we used new data that can provide insight into the evolution of net-winged beetles, *i.e*., by using transcriptomic and genomic data to form a new phylogenomic phylogeny. These data were used to confirm the position of net-winged beetles in the Elateroidea, and to resolve relationships at the subfamily and tribal level. Molecular relationships are compared with a previously published morphological phylogeny (Kazantsev, 2013) to identify traits with high levels of homoplasy, and to construct hypotheses for the factors causing these morphological similarities. We recommend that highly homoplastic characters should be identified, and the general morphological trends in the evolution of neoteny considered, when studying insect groups with modified metamorphosis. Finally, we propose a new phylogeny for Lycidae, which can provide a framework for further comparative research on the macroevolutionary origins of female neoteny, lycid phylogeography, and the evolution of aposematism across biogeographic ranges and net-winged beetle lineages (Felsenstein, 1985; Wiley & Liebermann, 2011).

2. Aims of the work

- Reconstruct the robust phylogeny of Lycidae using genome-scale data.
- Investigate if the neoteny evolved multiple times and if it affected morphological traits.
- Recover of the convergent evolution of morphological characters was affected by biology and function.

3. Methods and material

3.1 Material collection

Our sample comprised 9 outgroups and 22 lycid species, including 6 neotenic taxa (Tables 1, S4–S5). All zoogeographical regions and almost all major extant lineages were represented (Table S1). Each tribe was represented by one species, as tribal monophyly was well-supported by previous molecular and most morphological analyses (Bocak *et al.*, 2008; Masek *et al.*, 2014, 2018; Motyka *et al.*, 2017, 2018). The eight tribes missing from the analysis represented approximately 4% of net-winged beetle

diversity (Masek *et al.*, 2018) and we were able to obtain Sanger data for most of them. Molecular data were unavailable for six species in five tribes (Melanerotini, Miniduliticolini, Mimolibnetini, Lampyrolycini, and Vikhrevini). The subfamily classification used throughout this study was based on our phylogenetic results, and thus did not match previous taxonomic classifications (Supplementary Text). GenBank accession numbers are provided in Table 1. RNA samples were fixed in the field in RNAlater (Ambion, Inc., Austin, TX, USA). DNA samples were preserved in 96% ethyl alcohol and stored at -80ºC.

Subfamily	**Tribe**	**Species**
Dexorinae	Dexorini	*Dexoris ruzzieri*
Calochrominae	Calochromini	*Lygistopterus sanguineus*
Erotinae	Erotini	*Konoplatycis otome*
	Dictyopterini	*Dictyoptera* sp.
	Taphini	*Taphes brevicollis*
Ateliinae	Ateliini	*Scarelus anthracinus*
	Lyponiini	*Ponyalis quadricollis*
	Macrolycini	*Macrolycus* sp.
Lycinae	Conderini	*Conderis signicollis*
	Leptolycini	*Leptolycus* sp.
	Platerodini	*Plateros* sp.
	Calopterini	*Calopteron* sp.
	Lycini	*Lycostomus kraatzi*
Lyropaeinae	Antennolycini	*Antennolycus constrictus*
	Lyropaeini	*Lyropaeus optabilis*
	Platerodrilini	*Platerodrilus* sp.
Metriorrhynchinae	Libnetini	*Libnetis* sp.
	Dilophotini	*Dilophotes* sp.
	Metriorrhynchini	*Cautires* sp.
		Sulabanus sp.
	Dihammatini	*Dihammatus* sp.
	Lycoprogentini	*Lycoprogentes* sp.

Table 1. The list of newly produced samples for the transcriptomic and genomic analysis. All samples are included in the BioProject no. PRJNA507451. Additional information on taxa is provided in Tables S4, S5.

3.2 Transcriptomes sequencing, assembly and quality control

Fourteen transcriptomes were prepared and sequenced, and the raw reads were filtered at the Beijing Genomics Institute (Guangzhou, China). All sample libraries were constructed using RNA TruSeq (Illumina, San Diego, CA, USA) and pair-end sequencing of 150 bp was conducted using HiSeq X-ten (Illumina). Filtration was carried out as follows: [1] adapter-contaminated read pairs were removed; adapter alignment length ≥15 bp with no more than three mismatches; [2] the last 60 bp of all reads were trimmed, as they may contain adaptor sequences when the PE150 sequencing strategy is used. The remaining PE90 sequence was used for transcriptome assembly, with a TruSeq library insert size of approximately 160 bp. [3] Read pairs were removed if one read had ≥10 undefined bases (Ns) and [4] if one read had ≥50% of base pairs with quality scores ≤Q35. The transcriptomes of *Sulabanus* sp., *Conderis signicollis*, *Dictyoptera* sp*. Dihammatus* sp., and *Konoplatycis otome* were prepared and sequenced by Novogene Co., Ltd. (Beijing, China) on the same platform. The removal of low-quality reads and TruSeq adaptor sequences were performed with Trimmomatic-0.36 (Bolger *et al.*, 2014) using command ILLUMINACLIP:TruSeq3-PE-2.fa:2:30:10 LEADING:28 TRAILING:28 SLIDINGWINDOW:4:15 MINLEN:50. All paired-end transcriptomic reads were assembled using SOAPdenovo-Trans-31mer (Xie *et al.*, 2014).

3.3 Genomes sequencing, assembly, quality control and genes prediction

Additionally, the total DNA (~30 Gbp each) of *Dexoris ruzzieri* Bocak, 2018, *Leptolycus* sp., and *Cautires* sp. was shotgun-sequenced on the same platform by Novogene Co., Ltd. (Beijing, China) used for 150 bp paired-end reads. Raw paired-end reads were filtered using fastp v. 0.13.2 (Chen *et al.*, 2018) with the following parameters: -q 5 -u 50 -l 50 -n 15. Default values were used for the other settings. Read pairs were removed if at least one read was contaminated by adapters, if more than 50% of the bases were of low quality, or if at least one read contained more than 15 Ns. Read quality was visualized with FastQC (http://www.bioinformatics. babraham.ac.uk/projects/fastqc). The draft genomes of were assembled using MEGAHIT v. 1.1.3 (Li *et al.*, 2015, 2016), with all parameters set to default values and k-mer sizes of 31, 59, 87, 115 and 143. Contig sequences were used to train the AUGUSTUS software (Stanke & Waack, 2003) for species-specific gene models with BUSCO 3 (Waterhouse *et al.*, 2017). Settings were: -long option, the conserved genes in the Endopterygota set (n = 2,442), and -sp tribolium2012 as the closest relative. The predicted species-specific gene models were then used for *ab initio* gene predictions in AUGUSTUS, and predicted protein coding sequences were used in Orthograph v. 0.6.1 (Petersen *et al.*, 2017). Outgroup data were assembled as described in previous studies (Kusy *et al.*, 2018a, b).

3.4 Assembly completeness and Orthology prediction

The completeness of transcriptomes, genomes and predicted protein-coding gene sets were evaluated with BUSCO using Endopterygota single-copy orthologs as targets. BUSCO quantitatively assesses completeness using evolutionarily conserved expectations of the gene content.

The ortholog set was collated by searching the OrthoDB 9.1 database (Zdobnov *et al.*, 2016) for single copy orthologs in six beetle genomes (Table S4; Richards *et al.*; 2008, Keeling *et al.*, 2013; Shelton *et al.*, 2015; Poelchau *et al.*, 2015; McKenna *et al.*, 2017). OrthoDB 9.1 predicted 4,225 single copy orthologs for beetle species and Coleoptera reference node. We used Orthograph with default settings to search in our assemblies for presence of specified single copy orthologs. From the recovered 4,214 orthologs, terminal stop codons were removed, and internal stop codons at the translational and nucleotide levels were masked using the Perl script summarize_orthograph_results.pl (Petersen *et al.*, 2017).

3.5 Multiple sequences alignment and masking

The amino acid sequences were aligned using MAFFT v. 7.394 with the L-INS-i algorithm (Katoh & Standley, 2013). The alignments from each ortholog group were then checked for the presence of outliers using the script from https://github.com/mptrsen/scripts/blob/master/ outlier_check.pl, according to previously published methods (Misof *et al.*, 2014; Peters *et al.*, 2017). The corresponding multiple sequence alignments of nucleotides were generated using Pal2Nal (Suyama *et al.*, 2006). We removed sequences of non-elateriform taxa leaving *Agrilus planipennis* only. Then, all gap-only sites were removed from alignment. To identify random or ambiguous similarities within alignments, we used Aliscore v. 2.076 with the maximum number of pairwise comparisons, option -e, and other parameters set to default values. Any random or ambiguous similarities were masked using Alicut 2.3 (Kück *et al.*, 2010). Alinuc.pl was then used to apply the Aliscore results to match amino acids to the nucleotide data (Peters *et al.*, 2017). MARE v. 0.1.2-rc was used to calculate the information content of each gene partition in terms of amino acid coding (Misof *et al.*, 2013). Partitions with zero information content (IC0) were removed from the datasets. We present summary statistics of alignments using AMAS (Borowiec, 2016) and pairwise coverage of the datasets using AliStat 1.7 (https://github.com/thomaskf/ AliStat).

Figure 3. Simplyfied methodological workflow.

3.6 Concatenation and Phylogenetic analysis

Finally, matrices with multiple partitions were assembled using FASconCAT-G to elucidate the robustness of the analyses (Table 2; Kück & Longo, 2014; Reddy *et al.*, 2017). All homologous fragments (Datasets A, C) or only fragments with complete data in all taxa were included to calculate the impact of missing data (Dataset B). The raw nucleotide and amino acid datasets were not filtered before analysis to calculate the impact of applied analytical procedures (Datasets D). Alternatively, six non-elateriform Polyphaga and *Agrilus planipennis* (datasets C, D) or only *Agrilus* (datasets A, B) were

left as non-Elateroidea outgroups. The four datasets were analyzed three ways: [1] nucleotides at all positions, [2] nucleotides without the third codon, and [3] amino acids sequences (Table 2).

IQ-TREE v. 1.6.8 (Nguyen *et al.*, 2015) was used to construct maximum likelihood (ML) trees, partitions and models were identified using Model Finder (Kalyaanamoorthy *et al.*, 2017, Chernomor *et al.*, 2016). The ultrafast bootstrap option with 5,000 bootstrap iterations was selected (Hoang *et al.*, 2018). The IQ-TREE analyses were run with the -spp parameter to allow each partition to have its own evolutionary rate. Four cluster Likelihood Mapping (FcLM) analysis was used to investigate alternative topologies (Strimmer & von Haeseler, 1997; Misof *et al.*, 2014). This analysis also determines if incongruent or confounding signals, which may be obscured in a multi-species phylogenetic tree, are present in the amino acid datasets. The tree-likeness graph for the three possible quartet topologies shows the support for each topology based on terminal quartets randomly drawn from the tree that represent one terminal from each focal taxon. Seven areas that record topology distribution are represented in the graph. We tested the hypotheses described in Fig. 3D–E in this analysis. Further, ASTRAL v. 5.6.1 (Sayyari & Mirarab, 2016) was used to construct coalescent species trees from individual ML topologies based on nucleotides and amino acids (Dataset A).

Dataset	**Level characters (10^6)**	
A (4165 orthologues); all data,	NT (1,2,3)	5.755
aliscore, outliers out, IC0 out,	NT (1 + 2)	3.837
outgroup Buprestoidea	AA	1.918
B (1713 orthologues) as dataset A,	NT (1,2,3)	2.251
only partitions with complete	NT (1 + 2)	1.501
information included	AA	0.750
C (4165 orthologues) as dataset A,	NT (1,2,3)	6.041
but six Polyphaga as outgroups	NT (1 + 2)	4.027
	AA	2.014
D (4214 orthologues) no *fi*ltering, six	NT (1,2,3)	9.576
Polyphaga as outgroups	NT (1 + 2)	6.384
	AA	3.192

Table 2. The list of analyzed dataset.

3.7 Morphological analysis

For inferring the evolution of morphological traits, we used the morphological dataset published by Kazantsev (2013) that included 65 characters, 43 net-winged beetle taxa, and 1 outgroup. We removed 13 uninformative characters from the dataset for our study (52 characters left; Table S9). The modified dataset was analyzed using TNT v. 4.0a (http://www.lillo.org.ar/phylogeny/tnt) with the parsimony optimality criterion, and with application of the 'New Technology Search', ratchet, drift, and tree fusion. All characters were considered to be unordered and of equal weight. The majority consensus tree was produced from all TNT-trees using IQ-TREE with options -t and -minsup 0.5. The length, consistency index (CI), and retention index (RI) of the characters in the recovered topology were evaluated (Fig. S11). We also analyzed the dataset with a fixed topology that was congruent with the result of the transcriptomic analysis (Fig. S12) and reevaluated the tree and character scores. The taxa absent from the phylogenomic analysis were positioned to match the relationships inferred from the morphological analysis. For example, a taxon recovered outside the tribe was set as sister to the tribe. The resulting tree length, CU, and RI were then compared with values from the other analyses. Phylogenetic trees were visualized in FigTree 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/).

4. Results

4.1 Phylogenomics

A total of 19 transcriptomes were produced for the phylogenomic analysis of 4,165 orthologs (Fig. S1); the additional homologous fragments were obtained from three assembled genomes. The list of datasets analyzed and the lengths of individual alignments are displayed in Table 2. Datasets A and B were 63.4% and 81.8% complete, respectively (Fig. S2).

All phylogenetic analyses produced fully resolved trees with robust support at almost all nodes. Tree topologies were similar across datasets and analytical settings (Table 2). The first split separated Dexorinae from other net-winged beetles. Then, successive split separated Calochrominae + Erotinae, which were sisters to the rest of the clade. The position of Calochrominae was affected by the exclusion of non-elateriform outgroups and fragments with incomplete information (Figs. 3A, B). Ateliinae was regularly recovered as the next branch. The terminal clade in all trees consisted of three monophyletic groups: Lycinae, Lyropaeinae, and Metriorrhynchinae. However, short internal branches in these three subfamilies indicated that diversification was rapid in these groups. Ateliinae was positioned in the terminal clade only in the coalescent tree based on nucleotide analysis (Fig. S6).

Therefore, this phylogenetic signal was further tested using the FcLM method (Fig. 3D, E). Lycinae consists of Conderini and four Gondwanan tribes: Leptolycini, Platerodini, Lycini, and Calopterini. In our analysis, Lycinae was sister to Lyropaeinae, which contains all Asian neotenic beetles except Ateliini, and to Metriorrhynchinae, which contains Lycoprogenthini, Dihammatini, Dilophotini, Libnetini, and Metriorrhynchini. We observed one ambiguity in the internal topology of these terminal clades. Platerodini and Leptolycini were either successive branches basal to Calopterini and Lycini, or a clade that is sister to Calopterini and Lycini (Fig. 3A, C).

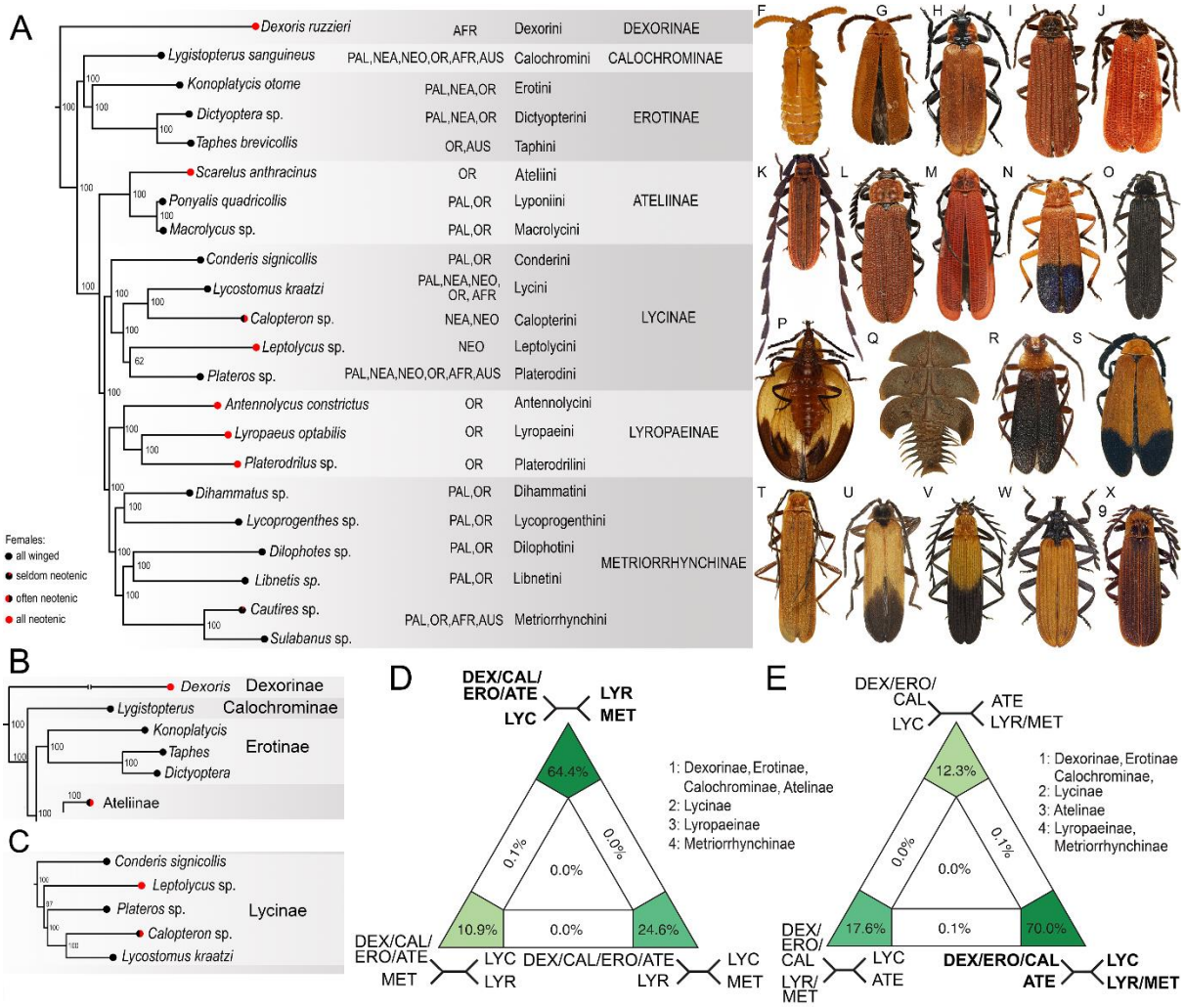

Figure 3. (A) Maximum likelihood (ML) tree obtained from the analysis of the 4165 ortholog dataset at amino acid level with *Agrilus* outgroup; (B) The alternative ML topology of Calochrominae and Erotinae obtained from the analysis of the 1713 ortholog dataset at the nucleotide level with *Agrilus* outgroup. (C) The alternative ML topology of Lycinae obtained from the analysis of the 4165 ortholog dataset at the nucleotide level with *Agrilus* outgroup; numbers at branches designate bi(D–E) 2D simplex graphs obtained from the four cluster likelihood mapping analysis; the support values in cells show support for each of the three topologies illustrated. General appearance, dorsal view: (F) *Dexoris*

chome Bocak *et al.*, 2013; (G) *D. ruzzieri* Bocak, 2018; (H) *Lygistopterus sanguineus* L., 1758; (I) *Dictyoptera aurora* Herbst, 1784; (J) *Taphes brevicollis* Waterhouse, 1878; (K) *Atelius kadoorieorum* Li *et al.*, 2018; (L) *Ponyalis* sp.; (M) *Conderis signicollis* (Kirsch, 1879); (N) *Thonalmus* sp.; (O) *Plateros* sp.; (P) *Lycus* sp., ventral view; (Q) *Platerodrilus foliaceus* Masek & Bocak, 2014, female larva; (R) *Platerodrilus* sp., male; (S) *Lyropaeus* sp.; (T) *Dilophotes* sp. (U) *Libnetis* sp.; (V) *Metriorrhynchus doleschali* Redtenbacher, 1868; (W) *Porrostoma* sp.; (X) *Cautires* sp. Abbreviations: PAL – Palearctic; OR – Oriental; NEA – Nearctic; NEO – Neotropical; AFR – Afrotropical; AUS – Australian. All photographs © authors of Kusy *et al., 2019.*

4.2 Morphology

We used 52 of 65 morphological traits defined by Kazantsev (2013) in our analysis of Lycidae. Characters are described in Table S8 and coded according to Kazantsev (2013). The tree recovered from the modified matrix had a length of 294 steps, suggesting that the clade of neotenic beetles is extensive (Fig. S8–S11). Detailed analysis of individual traits indicated that most traits only provide ambiguous support for the recovered topology (Table S10). The morphological characters require additional evolutionary steps when mapped onto the transcriptomic tree, which had a length of 384 steps. As with neoteny, the rostrate cranium could have at least four origins (Fig. S9). Multiple origins are also likely for the short third antennomere (Fig. 4), the similar patterns of the pronotal carinae (Fig. 5), and the transverse elytral costae (Fig. 6). Further, the short and lost parameres were likely to have origins with 16 and 19 steps, respectively. Detailed information on individual characters is listed in Tables S8–S10.

5. Discussion

In this study, we used a large phylogenomic dataset to recover Lycidae as sister to luminescent elateroids and Elateridae in general (Figs. 3A, S1–7; Kusy *et al.*, 2018). As the sister clade contains both soft-bodied and sclerotized beetles, the morphological diversity may have contributed to the failure of earlier morphological analyses to identify the sister clade to net-winged beetles and properly root the Lycidae tree (Branham & Wenzel, 2003; Lawrence *et al.*, 2011; Kazantsev 2005, 2013). Likewise, the trees recovered by Sanger analyses have been variably rooted with poor support for early divergence. These trees could not be used in robust classification even if datasets were more complete or densely sampled (Townsend & Lopez-Giraldez, 2010; Bocak & Bocakova, 2008; Masek *et al.*, 2018; Fig. 1).

Here, we present our phylogenomic analysis, which is appropriate for the investigation of deep-level relationships (Misof *et al.*, 2014; Peters *et al.*, 2018) and the identification of homoplasy in morphological datasets. We were able to resolve three previously contentious issues: [1] the tribe- and subfamily-level classification; [2] the number of origins of female neoteny and shared morphological traits in males having neotenic females; and [3] the evolution of morphological traits, especially those with an adaptive function, associated with mimicry, or affected by sexual selection.

5.1 Classification of net-winged beetles

The phylogenomic analyses confirmed the monophyly of Lycidae with a high amount of nucleotide or amino acid synapomorphies, as indicated by root length (Figs. 3A–C and S3–S6; Bocak *et al.*, 2008, 2016; Kundrata *et al.*, 2014; Masek *et al.*, 2018). In terms of morphological characters, the lycid clade was robustly supported by unique larval mandibles adapted for sucking (Cicero, 1988, 1994; Bocak & Matsuda, 2003; Kazantsev, 2005; Lawrence *et al.*, 2011). The additional morphological characters shared by all or most lycids were long trochanters, the presence of pronotal carinae and elytral costae, and a weakly sclerotized body. In previous studies, lycid taxa have rarely been classified outside the family (only *Aporrhipis* Pascoe, 1887 and *Platerodrilus* Pic, 1921) and a few non-lycid taxa have been erroneously included (*e.g.*, the firefly *Pristolycus* Gorham, 1883 and the neotenic click-beetle *Thilmanus* Gemminger, 1869; Winkler, 1952; Kazantsev, 2005; Ferreira *et al.*, 2018).

Recovered relationships had high bootstrap values and were supported by FcLM analyses (Figs. 3D, E, S7). We did not have many species samples per tribe, but tribal classification was robustly inferred using a densely sampled molecular dataset (Masek *et al.*, 2018). The molecular tribal classification is generally consistent with classification based on morphology (Bocak & Bocakova, 1990, 2008; Kazantsev, 2005).

Our recovered topologies suggest that the present classification of Lycidae should be revised. We propose that the seven major clades within Lycidae – Dexorinae **stat. nov.**, Calochrominae **stat. rev.**, Erotinae, Ateliinae, Lycinae, Lyropaeinae **stat. nov.**, and Metriorrhynchinae **stat. nov.** should be given the subfamily rank. The classification is supported by all phylogenomic trees (Figs. 3A–B, S3–S7). Dexorinae should be sister to the rest of Lycidae (Fig. 3A). Then, Calochrominae + Erotinae and Ateliinae are the successive sister groups to the remaining clades. Alternatively, Calochrominae and Erotinae could be serial branches (Fig. 3A, B, S3–7). In terms of radiation, the terminal subfamilies and some of their constituent tribes were characterized by very short internal branches, which might represent ancient and rapid diversification events. Additionally, the position of Ateliinae in the coalescent tree based on the nucleotide dataset had ambiguous support (Fig. S6A). Thus, we tested

whether Metriorrhynchinae is sister to neotenic Lyropaeinae (Fig. 3A) and whether Ateliinae is sister to the three terminal subfamilies. Based on the FcLM analysis (Figs 3C, D, S7), the topology displayed in Fig. 3A was preferred.

Alyculini was placed within the monophyletic Lyropaeinae based on Sanger data, but no information was available for transcriptomic analysis (Bocak *et al.*, 2008; Masek *et al.*, 2018). The relationship between Slipinskiini and Erotini was also supported by Sanger markers, and now unavailable Slipinskiini was placed within the newly defined Erotinae (Table S1, S2). The other monophyletic clades proposed here each consisted of several tribes and the justification for the classification proposed in this study can be found in the Supplementary Text.

The morphological phylogeny was based on a modified morphological dataset and constructed using algorithms that were different from those used in a previous study. Thus, our tree topology differed slightly from the previously published results (Kazantsev, 2013; Figs. 1, S9–S11, Table S1). Morphological analyses consistently proposed that taxa with neotenic and putatively neotenic females were closely related, in contrast to results from molecular analyses (Bocak *et al.*, 2008; Masek *et al.*, 2018; Figs. 3A, S3–6). Given the amount of data used and the level of support, we consider the transcriptomic phylogeny to be more robust. Below, we discuss how character development and ecological and functional constraints could affect individual characters and generate a false phylogenetic signal.

5.2 Morphological characters affected by neoteny

Neoteny in net-winged beetles was first identified in female individuals of *Lyropaeus* and *Duliticola* (Gravely, 1915; Mjöberg, 1925). Since then, larviform females have been identified in other lycid taxa. Additional presumed neotenics are currently known in a high number of males and their relationships, morphology, and distribution indicate a possibility that conspecific females are larviform, although this hypothesis has not been verified (Crowson, 1972; Cicero, 1988; Bocak & Bocakova, 1990; Miller, 1991; Bocak *et al.*, 2008; Masek *et al.*, 2015, 2018; McMahon & Hayward, 2016; Kazantsev, 2005, 2013). We considered these taxa to be neotenic in our analysis in agreement with the opinion of above listed authors. Details of the neotenic taxa are described in Table S1 (the list of neotenic taxa) and in Tables S8 and S9 (character 52).

Initially, neotenic net-winged beetles were thought to be 'primitive' (Crowson 1972), and they were consistently positioned at the earliest divergences in morphological analyses (Kazantsev, 2005, 2013; Figs. 6, S9–S11). In contrast, all of the molecular analyses conducted to date proposed that

neoteny has multiple origins and is present in unrelated lineages (Bocak *et al.*, 2008; Kundrata *et al.*, 2014; Masek *et al.*, 2018). Our phylogenomic analysis confirms the multiple origins of neoteny in deep and terminal lineages (Figs. 3A, 6, S3–7). Therefore, we hypothesize that the similar morphological traits in neotenic taxa are homoplasies.

Unlike lycid species in which both sexes undergo full metamorphosis, the males of species with neotenic females are commonly characterized by miniaturized bodies (known in most neotenics, but also in a low proportion of taxa with fully-metamorphosed females, *e.g.*, some Libnetini and Dihammatini), fewer antennomeres (six neotenic genera, but not present in other Lycidae), miniaturized or reduced mouthparts, *i.e.*, rudimentary mandibles, distally pointed maxillary and labial palpi, simplified labium, the reduced number of labial palpomeres, no mesoscutellum posterior processes (the character state present mostly in neotenics, but also in a few other lycids), shortened male elytra (only neotenics, e.g., *Mimolibnetis apicalis* Kazantsev, 2018, *Alyculus* spp.), loss or severe reduction of wings (*Dexoris chome* Bocak *et al.*, 2013, *Cautires apterus* Bocak *et al.*, 2014; Fig. 3F), structural simplifications such as the loss of strengthening costae and carinae (common in neotenics), elytra that are not co-adapted with the pronotum (the neotenic lycids apart from *Nanolycus* Kazantsev, 2013), shortened discrimen, no metendosternite transverse sutures, no tibial spurs (found also in some non-neotenic taxa, but more common in neotenics), and slender tarsomeres with reduced tarsal pads (Fig. 4U; Bocak & Bocakova, 1998, 1990, 2008; Kazantsev, 2005, 2013). The miniature adult males may have evolved as a mating adaptation to the low dispersal capacity of larviform and highly immobile females (Bocak *et al.*, 2008). Almost all males with putatively neotenic females have been collected only in the lowest stratum of tropical forests, either from the herbaceous vegetation or from sifted soil which supports the link between limited mobility and miniaturization. (Bocak *et al*., 2013, 2014), The miniaturized body evolved independently in some Lyropaeinae (Alyculini, Antennolycini, some Platerodrilini), all Leptolycini, and most neotenic Calopterini (Bocakova, 2003, 2005; Bocak & Bocakova, 2008; Kazantsev 2013). Given that neotenic females are developmentally truncated, male morphological traits may be affected by incomplete structural differentiation of the appendages, especially the legs and their derived structures (Bocak & Bocakova, 1990, 2008; Kazantsev, 2005, 2013). In general, ontogenetic reprogramming may affect both sexes, but males are modified less markedly.

Without understanding the molecular mechanisms, we cannot differentiate between morphological traits modified due to adaptive evolution or premature arrest, such as incomplete metamorphosis. For example, reduced mouthparts could have evolved from a short lifespan and the absence of feeding in the adult stage, or from the limited differentiation of several body parts during

metamorphosis. In contrast with mouthparts, the short lifespan hypothesis cannot be applied to modifications of the tarsomeres. It is likely that traits were modified in tandem as described for other neotenic elateroids (Telegeusidae, Lampyridae, Rhagophthalmidae, Phengodidae, and Elateridae: Agrypninae: Drilini, Omalisinae and Plastocerinae; Bocakova *et al.*, 2007; Kundrata & Bocak, 2011; Bocak *et al.*, 2018; Kusy *et al.*, 2018), but the mechanism producing the modifications remains unknown.

Several closely related neotenic taxa, such as the lyropaeine and dexorine tribes, were very diverse morphologically (Kazantsev, 2002, 2013; Bocakova, 2006, 2014; Masek *et al.*, 2013, 2015). For example, *Platerodrilus* spp. do not have neither small body nor reduced mouthparts, *Alyculus* spp. have miniaturized bodies, and *Lyropaeus* spp. have large body and reduced and simplified mouthparts (Bocakova, 2006; Masek *et al.*, 2014, 2015). Conversely, morphologically similar taxa can be unrelated according to molecular phylogenies. For example, neotenic Calopterini were placed to Leptolycini (Miller, 1991; Kazantsev, 2013), but the molecular analyses rejected such placement (Masek *et al.*, 2018; Kalousova, 2019). Based on results from previous studies and our transcriptomic phylogeny (Figs. 3A–C, S1–S6; Bocak *et al.*, 2008; Masek *et al.*, 2015, 2018), we propose that the adult male morphology is considerably affected by the ontogenetic reprogramming that produces larviform females, and that common occurrences of parallel evolution could obscure morphological analyses.

5.3 Morphological characters affected by biology and function

The first non-topological analysis of Lycidae classified tribal and sub familial taxa based on putative morphological synapomorphies (Bocak & Bocakova, 1990). Two topologies based on morphological phylogenetic analysis were subsequently published (Kazantsev, 2005, 2013). Although these topologies were based on a high number of characters and involved detailed study, they were unstable (Fig. 1, S9–S11). With our robust topology based on >4,000 orthologs, we were able to analyse the evolution of additional morphological characters (Table S8).

In addition to the wide and short cranium typical of lycids (Figs. 3, 4), two other cranial types have been observed: [1] the rostrate crania of flower-visiting species (Fig. 4A), and [2] the prolonged crania of some neotenic taxa that are associated with miniaturized mouthparts (Fig. 4B, C). The angle between the vertex and frons defines these types of cranium (Kazantsev, 2013). A sharp angle codes for neotenic taxa, and a blunt angle codes for taxa with rostrate heads. Unrelated neotenic taxa, such as *Leptolycus* spp. (Lycinae; Fig. 4B, 5R), *Dexoris* spp. (Dexorinae; Fig. 4C, 5A, B), and *Lyropaeus* spp. (Lyropaeinae, Fig. 5K) can share a prolonged cranium with tiny mouthparts. Unrelated *Lygistopterus*

spp. (Calochrominae, Fig. 3H), *Lycostomus* spp. (Lycinae; Fig. 3P), and *Metriorrhynchus* spp. (Metriorrhynchinae; Fig. 3W) have rostrate crania (Fig. 4A). Our phylogeny indicates that the absence or presence of prolonged hypognathous head and the rostrate head have multiple antecedents (length=13 steps, CI=0.154, Table S10). Rostrum presence is associated with taxa inhabiting semiarid regions where net-winged beetles visit flowers (all except *Aferos* spp.). In these areas, it is advantageous to have a prolonged rostrum. The taxa with rostrate crania also have exposed labrum (Table S8, character 7), long setose mala, and short mandibles. Therefore, these traits are linked and coding for these traits increases the weight of the rostrate cranium as a character in a morphological analysis, thus incorrectly placing all genera with a rostrate cranium in a single terminal clade in morphology-based trees (Figs. S10, S11).

Antennae are also unstable morphological characters (length=3–17 steps, CI=0.13–0.67). Neotenic taxa such as *Lyropaeus* spp. (Lyropaeinae), *Mimolibnetis* sp. (Dexorinae), *Neolyrium* spp., *Tishechkinia* sp. (Lycinae) have only 10 antennomeres, but these subfamilies were unrelated in our phylogenomic phylogeny (Figs. 3A, 4D–S). A large antennal surface improves pheromone communication, and lamellae have been shown to have evolved multiple times in several taxa (length=17 steps, CI=0.176, RI=0.333, Fig. 4R). Further, the lengths of the second and third antennomere and the relative length of the fourth antennomere are variable and do not distinguish any tribes or subfamilies (Fig. 4; Table S10, characters 5 and 6; length 3 and 15 steps, CI=0.667 and 0.133, RI=0.00 and 0.350; Kazantsev, 2013). Certain shapes of the basal antennomeres and the presence of lamellae are only found in some genera or species groups, but deep-level phylogenetic relationships were not corroborated by these traits.

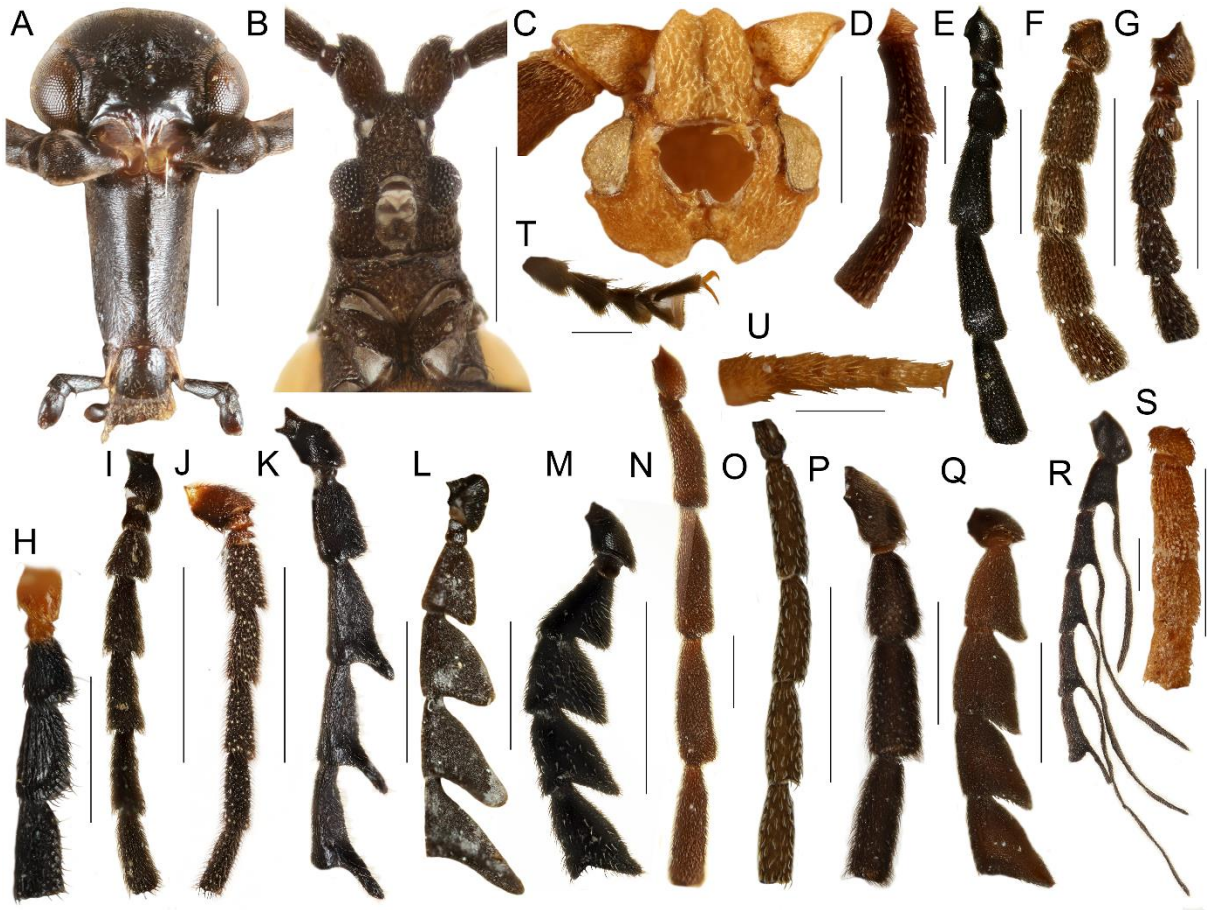

Figure 4. Head. (A) *Lycostomus flavotestaceus* Kleine, 1926, dorsal view; (B) *Leptolycus* sp., ventral view; (C) *Dexoris grandis* Bocak et Bocakova, 1988, ventral view; Basal part of antenna. (D) *D. ruzzieri* Bocak, 2018; (E) *Micronychus* sp.; (F) *Dictyoptera aurora* Herbst, 1784; (G) *Pyropterus nigroruber* De Geer, 1774; (H) *Staepteron cyanoxanthum* (Bourgeois, 1884); (I) *Erotides nasutus* (Kiesenwetter, 1874); (J) *Platerodrilus* sp.; (K) *Thonalmus* sp.; (L) *Ponyalis limbaticollis* (Pic, 1926); (M) *Plateros* sp.; (N) *Scarelus anthracinus* Bocak & Bocakova, 1999; (O) *Leptolycus* sp.; (P) *Lycoprogenthes* sp.; (Q) *Diatrichalus ruficollis* Bocak, 2000; (R) *Cladophorus* sp.; (S) *Lyropaeus* sp.; Tarsus. (T) *Lycoprogenthes* sp.; (U) *Lyropaeus* sp. Scales 0.5 mm. All photographs © authors of Kusy *et al., 2019*.

The short, y-shaped prosternum is characteristic of net-winged beetles and other soft-bodied elateroids (Fig. 5X; Bocak *et al.*, 2018; Kusy *et al.*, 2018), whereas the outgroup *Thilmanus* has a long prosternum. *Leptolycus* Leng et Mutchler, 1922 also has a long prosternum, but is a derived lycid (Figs. 3; 4B). The characters 17–26 code mesothoracic morphology and their fit with DNA and morphology-based phylogenies is low and these characters did not provide any clear synapomorphy (Tables S8–S10, Supplementary Text).

Figure 5. Head and pronotum, dorsal view: (A) *Dexoris chome* Bocak *et al.*, 2014; (B) *D. ruzzieri* Bocak, 2018; (C) *Micronychus* sp.; (D) *Staepteron cyanoxanthum* (Bourgeois, 1884); (E) *Taphes brevicollis* Waterhouse, 1878; (F) *Dictyoptera aurora* Herbst, 1784; (G) *Erotides nasutus* (Kiesenwetter, 1874); (H) *Scarelus* sp.; (J) *Ponyalis* sp.; (K) *Lyropaeus aurantiacus* Bourgeois, 1908; (L) *Pendola* sp.; (M) *Conderis signicollis* (Kirsch, 1879); (N) *Thonalmus* sp.; (O) *Plateros* sp.; (P) *Calopteron* sp.; (Q) *Lycostomus flavotestaceus* Kleine, 1926 (R) *Leptolycus* sp.; (S) *Lycus trabeatus* Guérin-Méneville, 1835; (T) *Lycoprogenthes* sp.; (U) *Dihammatus* sp.; (V) *Dilophotes* sp.; (W) *Libnetis* sp.; (X) *Cautires* sp., ventral view; (Y) *Metanoeus dispar* Waterhouse, 1879; (Z) *Diatrichalus ruficollis* Bocak, 2000; (AA) *Leptotrichalus* sp.; (AB, AC) *Cautires* spp. Scales 0.5 mm. All photographs © authors of Kusy *et al., 2019*.

Additionally, pronotal keels have been used as a character in previous morphological analyses (Figs. 2, 5), but their evolution is likely affected by their strengthening function. They can also be lost during miniaturization in both neotenic and fully metamorphosed forms (Fig. 5; Bocakova, 2004; Bocak *et al.*, 2016). The pronotal carinae were evolved and lost multiple times (length=12 steps, CI=0.167; Table S10). Lycids with a median rhomboidal areola also do not form a clade; Dictyopterini (Fig. 5E), Slipinskiini (Fig. 5C), Conderini (Fig. 5L), Lycoprogenthini (Fig. 5S), and some Metriorrhynchini (Figs. 5Z–AB) have similar areolae. Several lineages, including Macrolycini and Libnetini (Figs. 5G, H), and almost all members of the west Gondwanan clade of Lycinae, have longitudinal keels and no lateral carinae. The presence or absence of these structures may represent phylogenetic relationships in some cases, but could also be misleading (Figs. 5A–AC; Sklenarova *et al.*, 2014).

Elytral costae are another plastic trait (Fig. 6). Closely related groups, such as the dictyopterine genera *Pyropterus* spp. and *Dictyoptera* spp. (Figs. 6C, D), have either four or nine costae. Fewer primary costae are usually associated with slender-bodied taxa, such as e.g., *Scarelus* spp. (Ateliinae; Fig. 6H), *Leptolycus* spp. (Lycinae; Fig. 6M; *Dilophotes* spp. (Metriorrhynchinae; Fig. 6R). The Libnetini and Dilophotini tribes have similar simple longitudinal costae with no reticulation, but they are a crown lineage within an extensive tribal clade associated with up to nine reticulated costae (Figs. 3A, 6). Additionally, the transverse elytral costae are often variable in closely related taxa (*e.g.*, *Lycus* sp. and *Lycostomus* sp.; Figs. 6N, O). While these external structures can support some lycid relationships proposed by the phylogenomic analysis, their evolution has to be explained using a robust molecular phylogeny. The presence or absence of the transverse costae was only costal character used in the morphological analysis (character 28, length=3, CI=0.667, RI=0.000; Table S10).

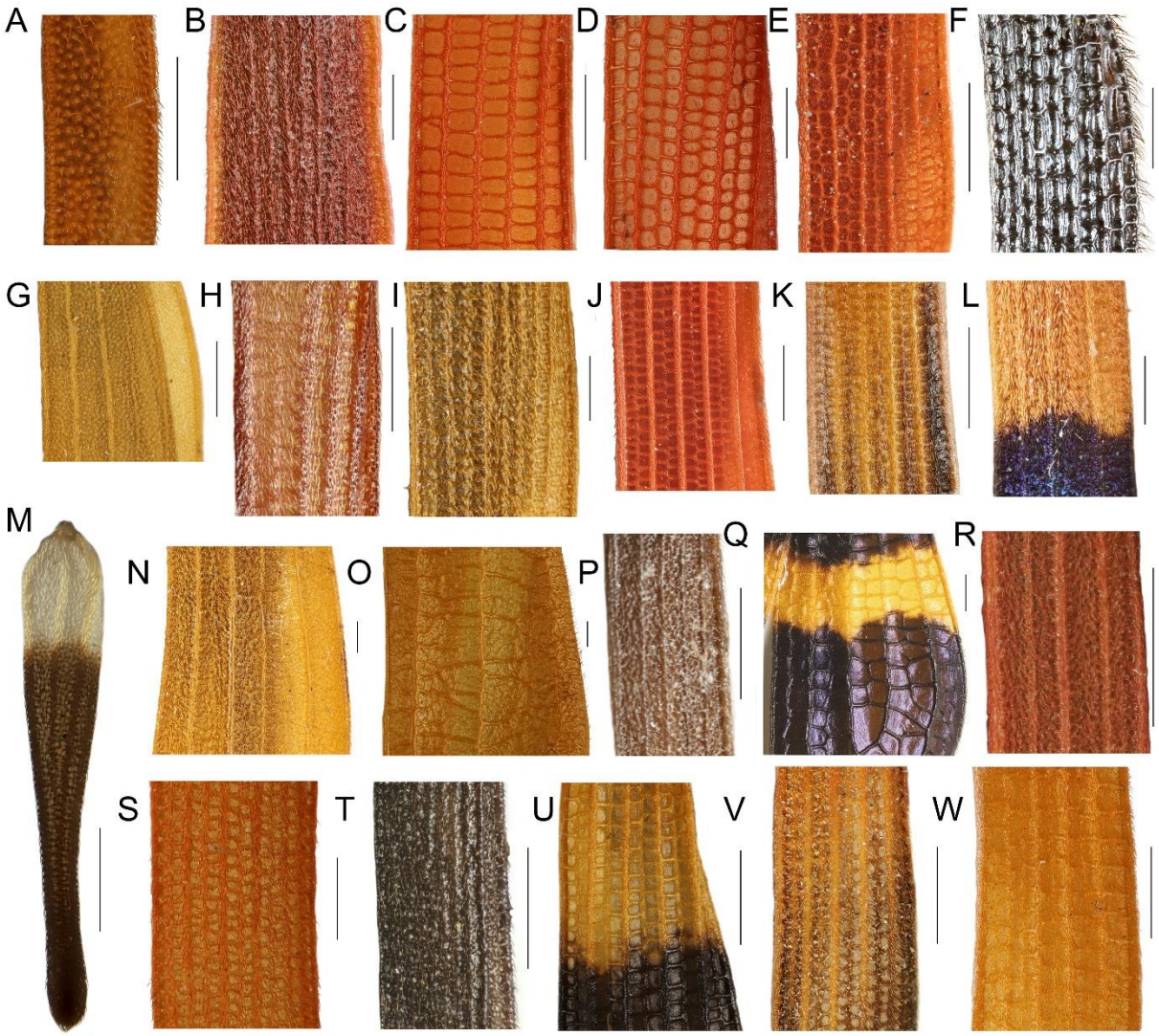

Figure 6. Elytron, right, middle part: (A) *D. ruzzieri* Bocak, 2018; (B) *Micronychus* sp.; (C) *Pyropterus* sp.; (D) *Dictyoptera aurora* Herbst, 1784; (E) *Taphes brevicollis* Waterhouse, 1878; (F) *Staepteron cyanoxanthum* (Bourgeois, 1884); (G) *Lyropaeus aurantiacus* Bourgeois, 1908; (H) *Scarelus* sp.; (I) *Ponyalis* sp.; (J) *Conderis signicollis* (Kirsch, 1879); (K) *Plateros* sp.; (L) *Thonalmus* sp.; (M) *Leptolycus* sp.; (N) *Lycostomus flavotestaceus* Kleine, 1926; (O) *Lycus trabeatus* Guérin-Méneville, 1835; (P) *Libnetis* sp.; (Q) *Calopteron* sp.; (R) *Dilophotes* sp.; (S) *Lycoprogenthes* sp.; (T) *Dihammatus* sp.; (U) *Cautires* sp.; (V) *Metanoeus dispar* Waterhouse, 1879; (W) *Xylobanus* sp. Scales 0.5 mm. All photographs © authors of Kusy *et al., 2019*.

The level of coadaptation between the elytra and abdomen was used as a morphological character (Table S8, character 27). We assume that the dilated elytra and slender, short abdomen (Fig. 3P) evolved independently due to the expansion of the elytra for aposematic signalling. Similarly, modified elytra are found in the unrelated *Calopteron* spp., *Lycus* spp. and *Lycostomus* spp. (Figs. 3P,

6N, O, Q). Unpalatable species of net-winged beetles have largely evolved to have similar phenotypes, which led to the constrained evolution of body size and shape (Motyka *et al.*, 2018). The characters that coevolved with aposematic traits could be a source of homoplasy in morphological analyses.

Six characters related to male genitalia were examined in this study (Table S10). However, they were only able to classify some tribes but not subfamilies. Genitalia are highly variable in net-winged beetles. Genitalia diversity in groups such as Platerodini and Ateliini can be used to identify speciation events (Eberhard, 1985; Malohlava & Bocak, 2010; Bray & Bocak 2016), but their plasticity makes genital characters inappropriate for deep-level phylogenetic inference (CI=0.08–0.33, see Tables S8–10). For example, paramere shape requires 16 steps to be mapped onto the morphological topology and 19 steps for the transcriptomic topology (character 51, ci=0.188 and 0.158, ri=0.500 and 0.385). The morphological characters and their states are discussed in the Supplementary Text.

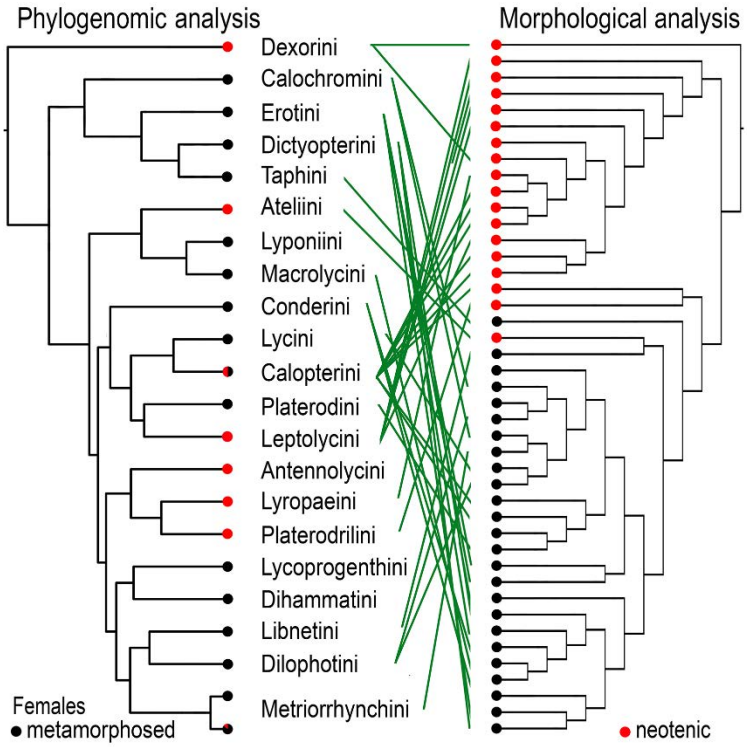

Figure 7. Comparison of inferred phylogenomic relationships compared with previous morphology-based phylogeny.

Overall, our results revealed high levels of homoplasy in the lycid morphological phylogeny. When morphological characters were mapped onto the phylogenomic topology, the multiple origins of homoplastic traits contributed to the increased length of the tree (384 vs. 294 steps). Because the phylogenomic analysis was information-rich (>4,000 orthologs) and produced stable topologies (Figs. 3, 7, S3–12), it was considered more robust than the morphological analysis.

6. Conclusions

Our phylogenomic phylogeny indicates that several morphological characters of net-winged beetles have a higher level of homoplasy and a more complicated evolutionary history than previously assumed. First, we confirmed that clades with larviform adult females were dispersed throughout the tree, *i.e*., female neoteny evolved independently on many occasions. Neotenic taxa with absent or modified phenotypic characters were initially considered 'primitive' (Crowson, 1972; Kazantsev, 2005, 2013, 2018), but these characters resulted from truncated metamorphosis and are actually derived. Ontogenetic modifications affected both male and female semaphoronts, though at different intensities. These modifications resulted in great morphological diversity in related taxa, which led to the description of several ambiguously supported family groups within Lycidae (Kazantsev, 2002, 2005, 2013, 2018). The homology of morphological traits in lineages with truncated metamorphosis also causes taxonomic confusion in other insect taxa. Analog taxonomic classifications for neotenic Elateridae based on morphological characters were recently deemed as incorrect (Crowson, 1972; Lawrence & Newton, 1995; Bocakova *et al.*, 2007; Lawrence *et al.*, 2011; Kundrata *et al.*, 2014; McKenna *et al.*, 2015; Beutel & Leschen, 2016; Kundrata & Bocak 2011, 2017; Bocak *et al.*, 2018; Kusy *et al.*, 2018b). Other morphological characters may be affected by their strengthening function in soft-bodied beetles, the parallel evolution of aposematic signals, modifications of mouthparts and crania in taxa that visit flowers, and the high plasticity of genital characters due to sexual selection. For closely related groups with potentially non-homologous morphological traits, phylogenomic data are useful for the construction of robust trees and can validate the homology of morphological characters.

6.1 Highlights:

- This study presents the first densely sampled phylogenomic analysis of net-winged beetles (Coleoptera: Lycidae) and compares results with morphology-based hypotheses.
- Multiple origins of female neoteny were recovered and the parallel morphological evolution in males is discussed in detail.
- Seven major clades – Dexorinae, Erotinae, Calochrominae, Ateliinae, Lyropaeinae, Lycinae and Metriorrhynchinae – are given subfamily rank in the new classification based on the genomic analysis.

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Supplements

Supplementary Text

1. Classification of Lycidae subfamilies.
2. Overview of subfamily and tribe taxa with diagnoses and justification of their limits.

Supplementary Tables

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Supplementary Text

1. Classification of Lycidae subfamilies

The classification of Lycidae have been based on morphological (Leconte 1881, Leng & Mutchler 1921, Kleine, 1926, 1928, 1933, Crowson 1972, Bocak & Bocakova 1990, Kazantsev 2005, 2013) and Sanger molecular analyses (Bocak & Bocakova 2008, Masek et al. 2018). Present results use genomic data and resolve long-standing debates on the net-winged beetle classification (Figs 1, 3, S3–S7). Using transcriptomic analyses, we propose the new delimitation of subfamilies (Tabs S1, S2). The recovered topology was robust regardless used dataset, levels of analyses and settings apart from a few alternative relationships which are not in conflict with the here proposed classification (see the main text for details).

a/ Dexorinae

Unlike previous analyses, the present results recovered *Dexoris* as the sister to the rest of net-winged beetles and the Dexorini needs to be excluded from the subfamily Leptolycinae *sensu* Kazantsev (2013) and elevated to the subfamily rank Dexorinae **stat. nov.** The Dexorini were given family rank when the earlier morphology-based tree was incorrectly interpreted (Fig. S8; Kazantsev 2005) and were kept as a subfamily in the classification proposed by Bocak & Bocakova (2008). Later, they were placed in the Leptolycinae as a tribe (Tab. S1, Fig. 1, Kazantsev 2013). The external morphology of Dexorinae differs from other net-winged beetles in the attachment of femora to trochanters (Tab. 9; character 36, an oblique attachment); further the Dexorini have an unique arrangement of pronotal carinae and papillae on elytra (in *Dexoris*, but other tribes of Dexorinae; Bocak & Bocakova 1988, 1989, Kazantsev 2013, Bocakova 2014, Masek *et al*. 2018). The putatively neotenic tribe Mimolibnetini which is currently unavailable for the genomic analysis should be placed here if it is not synonymized with Dexorinae as proposed by Bocakova (2014) and as indicated by the shape of trochanters. The Mimolibnetini have the similar shape of basal antennomeres, cranium, and similarly modified mouthparts as Dexorini and differ in the structure and the shape of the pronotum and the presence of elytral costae (Kazantsev 2013, 2015, Bocakova 2014). Recently, Lampyrolycini Kazantsev, 2018 were erected and three of five genera of Dexorinae have a separate tribe. Analogically to the morphological differences between Mimolibnetini and Dexorini, we identified morphologically distant but phylogenetically close forms in Lyropaeinae (*e.g*. *Lyropaeus* Waterhouse, 1878 and *Microlyropaeus* Pic, 1929, Masek et al. 2015, 2018).

b/ Calochrominae

Based on the present analysis, the Calochrominae **stat. nov.** must be given subfamily rank (Kleine 1928, Bocak & Bocakova 1990, Kazantsev 2005) and, in contrast with previous concept presented by Kazantsev (2005), the Calochrominae now contain only the nominotypical tribe. The latest classification placed Calochromini in Lycinae (Kazantsev 2013). Motyka *et al*. (2017) revised the

generic classification of Calochromini and based its monophyly on the absence of transverse pronotal costae, asymmetrical phallobase, wide parameres, and long baculi of female genitalia. The Calochrominae is for the first time recovered in a molecular analysis as one of the early branches of Lycidae. Their relationships to Erotinae (without Dictyopterini) was inferred in previous molecular analyses, but due to different rooting of recovered trees, these tribes had a terminal position and were included in the widely defined Lycinae (Bocak *et al*. 2008, Bocak & Bocakova 2008).

c/ Erotinae

The Erotinae **stat. rev.** consists of three lineages in the currently recovered topology: Erotini, Dictyopterini, and Taphini (Fig. 3A). Until now, the molecular analyses have not suggested relationships of Dictyopterini + Taphini to Erotini and their relationships has been inferred only from morphological analyses (Bocak & Bocakova 1990), but often in the clade which included additional tribes (Kazantsev 2005, 2013). The Slipinskiini retain tribal rank and are transferred to Erotinae from Lycinae *sensu* Kazantsev (2013). The tribe was unavailable for the current analysis and belongs here based on the morphology and earlier molecular analyses of rRNA and mtDNA markers which indicated the close relationships to the Erotini (Bocak & Bocakova 2008, Masek et al. 2018). Proterotaphini are kept as an separate tribe, till more data are available (Kazantsev 2012, 2013). Unlike earlier molecular analyses (Bocak et al. 2008, Masek et al. 2018), Lycoprogenthini are unrelated to Erotinae, despite their general similarity (Fig. 3A, 4–6, S3–S6). The relationships of the tribes currently included in Erotinae is supported by a few shared external morphological traits (Bocak & Bocakova 1990, Kazantsev 2013) and they are difficult to identify with clear synapomorphies present in all taxa: most Erotini have multiple pronotal carinae which may form a median areola with widely open frontal carinae (Fig. 5G, *Erotides*, *Platycis*) or their pattern is simple and their form a median carina and incomplete lateral carinae (*Lopheros*, *Eros*, *Eropterus*), male genitalia are trilobed, phallus usually laterally compressed, long to short parameres in some taxa, elytra with four or nine longitudinal costae and transverse cells. Dictyopterini are similar in general appearance, they have regularly median areola in the pronotum and unlike other tribes of Erotinae their ovipositors have long baculi.

d/ Ateliinae

The Ateliinae **stat. rev.** is another deeply rooted lineage that keeps the subfamily rank (Bocak & Bocakova 1990, 2008, Kazantsev, 2013). The subfamily contains supposedly neotenic Ateliini (*Atelius* and *Scarelus*) and the closely related, but morphologically very disparate Lyponiini and Macrolycini. The Ateliini were sister to Dilophotini in earlier molecular analyses (Bocak et al. 2008) or alternatively to Lyponiini (Masek et al. 2018). The maximum likelihood analysis of the mtDNA and rRNA dataset published by Bocak et al. (2008) suggested relationships Macrolycini + Lyponiini. Due to the absent support from morphology and low bootstrap values, these relationships have not been seriously considered. Now, the relationships of Ateliini to Lyponiini is confirmed and the Macrolycini is added (Fig. 3A). All Ateliinae share the pronotum without transverse carinae. Ateliini and

Macrolycini have a sharp longitudinal median carina which is absent in Lyponiini. At least some genera and species in each tribe have extensive triangular antennomeres 3–5 (Li *et al*. 2013, 2015a, b, Fig. 4).

e/ Lycinae

Furthermore, we newly delimit the subfamily Lycinae **stat. rev.** containing Conderini as sister to the rest of this subfamily which is represented by Lycini, Calopterini, Platerodini, Eurrhacini, and Thonalmini. Although ambiguously indicated also by some previous molecular analyses (Bocak et al. 2008, Masek et al. 2018), the position of Conderini in this clade is difficult to support by morphological characters. This tribe resembles Dictyopterini in general appearance, but differs in the shape of the median areola and male and female genitalia. Their earlier putative, already rejected, relationships to Metriorrhynchini was defined based on the circular phallobase (Bocak & Bocakova 1990, Bocak 2002, Bocak et al. 2008). Due to morphological similarity, the Conderini were placed in Erotinae by Kazantsev (2013). Further, the clade of Lycini, Calopterini, Platerodini, and Leptolycini was recovered in the present analyses (designated as the West Gondwanan clade). The relationships among Platerodini + Calopterini + Lycini was weakly supported already in the analyses of the Sanger dataset (Bocak et al. 2008, Masek et al. 2018). The Eurrhacini and Thonalmini should be placed here based on morphology and in case of Eurrhacini also on previous molecular analyses (Bocakova 2001, Bocak et al. 2008 Masek et al. 2018, Kalousova 2019). Leptolycini have been given repeatedly the subfamily rank and were merged in morphology-based studies with neotenic groups from the Afrotropical and Oriental regions (i.e., Dexorinae and Lyropaeinae; Bocak & Bocakova 1990, Kazantsev 2005, 2013) and this wide concept is refused based on the present phylogenomic analysis. The taxa of the West Gondwanan tribes never have transverse pronotal carinae, the parameres, if present, are short, and most taxa do not have dense regular transverse costae (clear transverse costae are present only in some *Plateros*). The constituting tribes are well-defined by unique synapomorphies, but their morphology provides only a very limited phylogenetic signal for their inter-relationships, apart from a few exceptions.

f/ Lyropaeinae

The further large clade is the Lyropaeinae **stat. nov.** and consists of three lineages with neotenic larviform females in the present topology: Antennolycini, Lyropaeini and Platerodrilini. Additional two tribes of Asian neotenics should be placed here: Miniduliticolini Kazantsev, 2003 and Alyculini Bocak & Bocakova 2008 (Kazantsev 2003, Bocak et al. 2008, Bocak & Bocakova 2008). These tribes were unavailable for genomic analysis and the memberships of Alyculini in this clade is based on rRNA and mitochondrial DNA topologies (Bocak et al. 2008, Masek et al. 2018). Miniduliticolini are more difficult to be placed in the phylogenetic system. *Miniduliticola* Kazantsev, 2002, the nominotypical genus of this tribe, is known in a single species and a single heavily damaged male specimen (Kazantsev 2002). Kazantsev (2013) merged Miniduliticolini and Platerodrilini in Miniduliticolinae, but *Platerodrilus* Pic, 1921 is a terminal branch in sister clade to Lyropaeinae which includes several successively split lineages of

small-bodied Lyropaeinae (Masek et al. 2015). Further data are needed to solve the relationships among numerous morphologically modified and miniaturized neotenics in this subfamily. If *Miniduliticola* is not the sister to all Platerodrilini in the analysis by Masek et al. (2015), Platerodrilini would have to be synonymized with Miniduliticolini or all successive lineages between Miniduliticolini and Platerodrilini would have to get tribal rank. Alternatively, *Miniduliticola* can be a sister to *Alyculus*, *Antennolycus* or an independent deeply rooted branch in the sister position to Lyropaeini + Platerodrilini. Under any considered topology, Miniduliticolinae do not deserve the subfamily rank recently proposed by Kazantsev (2013).

g/ Metriorrhynchinae

The last subfamily is Metriorrhynchinae **stat. nov.** and consists of the Dihammatini + Lycoprogenthini, Metriorrhynchini, and Dilophotini + Libnetini (Fig. 3A). Their relationships have never been inferred from morphological analyses (Bocak & Bocakova 1990, Kazantsev 2005, 2013). Some poorly supported clades consisting of two or three tribes, now placed in Metriorrhynchini, were identified by Bocak et al. (2008) and in the latest molecular study by Masek et al. (2018), but due to low support values and a conflict with morphological delimitation, they have not been seriously considered. The Libnetini and Dilophotini share the pronotum with a longitudinal keel and elytra without transverse costae, but they differ substantially in the structure of male genitalia. Some Metriorrhynchini are characterized by a circular phallobase (e.g. *Cautires*), resembling those of distantly related Conderini. Most Metriorrhynchini can be characterized by the presence of seven pronotal areolae, but they can be substantially reduced and as a result, the arrangement of carinae may be similar to those in Conderini and some Dictyopterinae as in *Stadenus*, *Falsoenylus* and *Wakarumbia* (Bocak 2002, Sklenarova et al. 2014, Bocek & Bocak 2017, Fig. 5). The phallobase has different forms in various lineages (Bocak 2002, Sklenarova et al. 2014, Kubecek et al. 2011).

2. The overview of subfamilies and tribes with diagnoses, descriptions and justification of their placement.

Dexorinae Bocak & Bocakova, 1989, **stat. nov.**

Type genus. Dexoris Waterhouse, 1878.

Diagnosis. Adult. Body small to medium sized, head small, hypognathous, mouthparts reduced, maxillary palpi 4-segmented, labial palpi 3- or 1-segmented, antennae 10 or 11-segmented. Pronotum prolonged to transverse, with two longitudinal carinae or without carinae. Elytra without costae (*Dexoris*) or longitudinal costae and vestiges of transverse costae present (*Lolodorphus*), femora obliquely attached to trochanters. Male genitalia simple, parameres and phallobase absent in some taxa Females and larvae unknown.

Remarks. The Dexorinae is the sister to other Lycidae and the current relationships was robustly inferred from the phylogenomic dataset. Kazantsev's elevation of Dexorini (represented by *Dexoris* only in the analysis) to the family level was unsupported by his analyses (see Fig. S8, Kazantsev 2005, Bocak & Bocakova 2008) and even if they are now found as the sister to other net-winged beetles we do not consider their morphological disparity sufficient for family rank. The earlier morphology-based analyses suggested the relationships with Lyropaeini and Leptolycini (Bocak & Bocakova 1989, Kazantsev 2005, Masek et al. 2018), primarily based on the similar modification of the cranium and reduction of mouth parts (Fig. 4).

Dexorini Bocak & Bocakova, 1989
Type genus. Dexoris Waterhouse, 1878

Diagnosis. Adult. Body smaller to medium sized, head small, hypognathous, mouthparts reduced maxillary palpi 4-segmented, labial palpi 3- or 1-segmented, antennae 10 or 11-segmented. Pronotum transverse, with two longitudinal carinae or without carinae. Elytra without costae (*Dexoris*). Male genitalia simple, parameres and phallobase absent. Females and larvae unknown.

Remarks.
The nominotypical tribe is characteristic in divergent v-shaped carinae in the pronotum (Bocak & Bocakova 1988). The tribe contains a species with brachelytrous male (Bocak et al. 2013).

Mimolibnetini Kazantsev, 2013
Type genus. Mimolibnetis Pic, 1936.

Diagnosis. Adult. Body smaller to medium sized, head small, hypognathous, mouthparts reduced maxillary palpi 4-segmented, labial palpi 3- or 1-segmented, antennae 10 or 11-segmented. Pronotum transverse, with two longitudinal carinae or without carinae. Elytra without costae (*Dexoris*) or longitudinal costae and vestiges of transverse costae present (*Lolodorphus*). Male genitalia simple, parameres and phallobase absent. Females and larvae unknown.

Remarks.
Mimolibnetini are closely related to Dexorini and placed in Dexorinae. Their relationships is supported also by Kazantsev's studies which alternatively placed *Lampyrolycus* Burgeon, 1937 either in Dexorini or Mimolibnetini (Kazantsev 1999, 2018) before he erected a separate tribe for the genus (Kazantsev, 2018). Bocakova (2014) synonymized Mimolibnetinae to Dexorinae (Bocakova 2014), but Kazantsev (2015) refused the synonymization and recently proposed the additional tribe Lampyrolycini Kazantsev, 2018 in Mimolibnetinae (Kazantsev 2018). The lower number of antennomeres is common in neotenics and this trait was used to delimit Miniduliticolini (Kazantsev 2006). The morphological diversity of neotenics is a possible reason for the ongoing inflation of family-group taxa defined within lineages with larviform females. Analogically to the earlier studies of neotenics, *e.g*., Elateridae: Omalisinae (see Bocek et al. 2018, Kusy et al. 2018), inappropriately high rank was given to incompletely metamorphosed taxa. The classification of Dexorinae which contains only neotenic genera is complex and regularly the genera are placed in their own family (e.g., Dexoridae), subfamily (e.g. Miniduliticolinae) or tribe (Lampyrolycini) in various studies by Kazantsev (2005, 2013, 2015, 2018). We propose to include Lampyrolycini in Mimolibnetini as a subtribe.

Calochrominae Lacordaire, **stat. nov.**

Calochromines Lacordaire, 1857: 301.
Type genus. Calochromus Guérin-Méneville, 1833.

Diagnosis. Adult. Body medium to large-sized. Head prolonged in rostrum (*Lygistopterus* Mulsant, 1838, *Macrolygistopterus* Pic, 1929, *Lucaina* Dugès) or rostrum absent (other genera). Antennae 11-segmented, filiform to serrate, seldom flabellate (*Flabellochromus*). Mouthparts, especially mandibles, miniaturized when rostrum developed, mala long, densely setose in rostrate forms. Pronotum without sharp carinae, only with bulges at lateral margins. Elytra parallel-sided, seldom considerably widened posteriorly, four indistinct costae in each elytron, transverse costae absent or irregular and rudimentary. Male genitalia with asymmetrical phallobase, parameres robust, approximately as long as phallus. Female genitalia slender, long, with paraproctal baculi multiple times longer than coxites. Larva (*Lygistopterus*, *Calochromus*). Body cylindrical. Antennal peg small, slender, mala sclerotized, dorsally attached to palpifer, thoracic terga incompletely divided in two parts by very narrow median longitudinal suture, terminal abdominal segment with long, fixed urogomphi.

Remarks. Calochrominae were treated as an independent subfamily and/or tribe since proposed by Lacordaire (1857) (Kleine 1933, Bocak & Bocakova 1990) and Kazantsev (2005) combined them with Metriorrhynchini, Dilophotini, Macrolycini, and Slipinskiini solely on the basis of an asymmetrical phallobase and in conflict with the results of the majority of his analyses. The coding of an asymmetrical phallobase is affected by incomplete sampling in Kazantsev's analyses. The symmetrical phallobase is found in many Metriorrhynchini (Bocak 2002) and asymmetrical one in many Platerodini and Lycini (Bocak & Bocakova 1990, Bocakova 2001). Our analyses of molecular data do not support close relationships of any of these taxa and Calochromini and we classify the Calochromini as an independent subfamily based on the present phylogenomic topology. Already Bocak & Bocakova (1990)

suggested relationships between Erotini and Calochromini and it was weakly supported by the analysis of the Sanger dataset (Bocak et al. 2008, Masek et al. 2018). The results of the present molecular analyses reopen such a possibility. Considering alternative relationships (Figs 3A, B, S3–S6), morphological divergence and the diversity of both lineages, we assign subfamily rank to both of them.

Erotinae Leconte, 1881, **stat. rev.**

Type genus. *Eros* Newman, 1838.

Diagnosis. Adult. Head with antennal tubercles, antennae 11-segment, filiform in both sexes. Pronotum with closed median areola, with simple cross-like structure of carinae or with obtuse highly reduced carinae. Elytra with four primary costae (*Pyropterus*) and sometimes also with five secondary costae (*Dictyoptera*, *Platycis*, *Lopheros*), reticulate cells in intercostal intervals sometimes reduced and irregular (*Erotides*). Male genitalia with long parameres, sometimes shortened, as long as half of phallic length. Female genitalia slender, with long to medium sized paraproctal baculi, spiculum ventrale shortened or long with processes at base. Larva (*Pyropterus*, *Eros*, *Lopheros*, and *Platycis*). Body sub-parallel; lateral part of epicranium well sclerotized and pigmented; terga transverse, pleurites indistinct, tergum A9 simply rounded, urogomphi absent (Bocak & Matsuda 2003).

Remark. The current analyses indicate that Erotini, Dictyopterini, and Taphini are close relatives as earlier suggested by Bocak & Bocakova (1990). The previous molecular analyses supported the close relationships of Dictyopterini and Taphini, but not Erotini as a sister to them (Bocak et al. 2008, Masek et al. 2018). Kazantsev (2005) supposed their paraphyly with respect to Platerodini. The Erotinae as one of major lineages of Lycidae keeps the subfamily status as proposed by Bocak & Bocakova (1990) and Kazantsev (2013), but unlike the latter classification three tribes, the Conderini, Lycoprogentini, and Libnetini have to be excluded (Fig. 1, Tab. S2). Erotinae is a species poor lineage occurring mostly in the Palearctic and Nearctic regions, a few species are known from the Oriental region and only one of constituent tribes, Slipinskiini, occurs in the Afrotropical region (Masek et al. 2018). A few species of Taphini reach to Australia.

Erotini Leconte, 1881.

Type genus. *Eros* Newman, 1838.

Diagnosis. Adult. Body medium sized, parallel-sided. Head with antennal tubercles, antennae 11-segment, filiform in both sexes. Pronotum with median areola or with simple cross-like structure. Elytra with four primary and five secondary costae, reticulate cells in intercostal intervals sometimes reduced (*Erotides*). Male genitalia with long parameres, sometimes shortened, as long as half of phallic length. Female genitalia slender, with spiculum ventrale short with processes at base or shortened. Larva (*Eros, Lopheros, and Platycis*).

Remark. The Erotini were recently redefined based on the analysis of a Sanger dataset and it includes also the tribe Lopherotini Kazantsev, 2012 and subtribe Pseudaplatopterina Kazantsev, 2012 which represent terminal branches or a paraphylum within Erotini, respectively. Therefore, they were synonymized to Erotini (Li et al. 2017). Kazantsev (2005) supposed the paraphyly of Erotini with respect to Platerodini and similarly, the current re-analysis of the morphological dataset does not support their monophyly.

Slipinskiini Bocak & Bocakova, 1992, **stat. rev.**
Type genus. *Slipinskia* Bocak & Bocakova, 1992.

Diagnosis. Adult. Body small to medium-sized, antennal tubercles weakly prominent, eyes small in both sexes. Antennae filiform, antennomeres circular in cross section. Maxillary palpi slender, terminal palpomere weakly widened distally, securiform. Labial palpi 3-segmented, terminal palpomeres strongly widened distally. Pronotum with sharp lanceolate median longitudinal areola, and lateral oblique fold in most species. Each elytron with nine costae, four primary costae conspicuously stronger, secondary costae often interrupted, sometimes with large elytral cells. Female terminal abdominal segment with short spiculum ventrale. Male genitalia usually with parameres, sometimes parameres reduced or fused. Phallus 2–3 times longer than phallobase. Female genitalia with long rod-like paraproctal baculi, 1.5 times as long as coxites. Larva unknown.

Remark. Slipinskiini were repeatedly inferred in relationships to Erotini (Bocak & Bocakova 2008, Masek et al. 2018) and they are placed here even if phylogenomic data remain unavailable. Afrotropical Flagraxini Kazantsev, 2002 and Aferotini Kazantsev, 2004 are placed here. *Flagrax* Kazantsev, 1992 is a senior synonym of *Slipinskia* Bocak & Bocakova 1992, *Aferos* Kazantsev, 1992 is morphologically close to Slipinskiini.

Dictyopterini Kleine Houlbert, 1922.
Type genus. *Dictyoptera* Latreille, 1829.

Diagnosis. Adult. Head with conspicuous antennal tubercles divided by deep groove, antennae filiform in both sexes, pronotum always with median areola. Elytra with nine costae (*Dictyoptera*), only primary costae in some genera (*e.g.*, *Pyropterus* Mulsant, 1838), or elytral costa 3 shortened (*Benibotarus* Kōno, 1932). Male genitalia with long parameres, paraproctal baculi in female genitalia long, very slender. Larva (*Pyropterus* Mulsant, 1838, *Dictyoptera* sp.). Body cylindrical; head transverse, pleural part of head membranous; thoracic and abdominal terga divided by longitudinal median line in two parts, thoracic pleurites small; tergum A9 emarginate at apex, urogomphi absent (Bocak & Matsuda 2003, Levkanicova & Bocak 2009).

Remark. The Dictyopterini is a species poor lineage, which occurs mainly in the Palearctic and Nearctic regions (Kleine 1933). Previous molecular analyses of Sanger datasets and morphological analyses always robustly supported their monophyly (Bocak &

Bocakova 1990, Bocak et al. 2008, Masek et al. 2018). They were classified for a long time with Erotini (Kleine 1933, Nakane 1969, Bocak & Bocakova 1990), but this position has not been supported by Sanger data. Only phylogenomic analysis confirmed such relationships.

Taphini Bocak & Bocakova, 1990.
Type genus. *Taphes* Waterhouse, 1878.

Diagnosis. Adult. Antennal tubercles inconspicuous, shallow depression only behind tubercles, antennae filiform to slightly serrate, pronotum always with median areola of very specific shape. Male genitalia with parameres shorter than phallus, lateral margins concave. Female genitalia with well developed proctiger, paraproctal baculi about 1.5 length of coxites. Larva unknown.

Remark. The subtribe Taphina was proposed for genera *Taphes* Waterhouse, 1878 and *Coloberos* Bourgeois, 1905 in Dictyopterini and they were placed in Lycinae in sister position to Lycini by Kazantsev (2005). Here, they are classified as the tribe in Erotinae and their placement in this subfamily is well supported by both molecular and morphological data (Fig. 3, Bocak & Bocakova 1990, Bocak et al. 2008, Masek et al. 2018). The monophyly of Taphini was not recovered in the latest analysis based on Sanger dataset (Masek et al. 2018) and further investigation is needed to clarify their status.

Proterotaphini Kazantsev, 2012.
Type genus: *Proterotaphes* Kazantsev, 2006 (=*Proteros* Kazantsev, 2004, a homonym)

Diagnosis. Adult. Body medium-sized, externally similar to other Dictyopterinae, maxillary palpi four-segmented, labial palpi three segmented, apical palpomeres pointed, labrum divided, eyes small, antennae reaching middle of elytra, pronotum with median areola, elytra with four primary costae and secondary costae present only in basal and apical part of elytra, trochanters short, male genitalia trilobate, phallus with dentate lateral edges. Female and larva unknown.

Remark. Proterotaphini were proposed for a single species of *Proterotaphes* Kazantsev, 2006 known in a single male specimen which was placed in Taphini (Kazantsev 2004) and later designated as the type-genus of Proterotaphini (Kazantsev 2012). Here, the tribe is placed in Erotinae as proposed by the author, but the taxon needs further investigation (Kazantsev 2004, 2013). Its dubious relationships was already expressed by the naming of the taxon originally as a primitive Eros ("pro" and Eros) or later using the stepm 'Taphes'. The tribe is kept in Erotinae close to Erotini, Taphini and Dictyopterini as was proposed in earlier publications by Kazantsev (2002, 2004, 2006, 2013). The male mouthparts are similarly reduced as in *Taphes* and neotenic net-winged beetles with pointed apical palpomeres. Similarly to earlier studies (Kazantsev 2004, 2005, 2006, 2013) it has been suggested in the description that a taxon with incompletely differentiated mouthparts must be the most archaic member of the subfamily (Kazantsev 2004). The consideration of morphological traits lead earlier to the proposal that net-winged beetles represent the deepest lineages of Neoptera and that net-

winged beetle subfamilies should obtain order rank (Kazantsev, 2006, see Beutel et al. 2007 for the rebuttal). The possibility that incompletely metamorphosed taxa are considered primitive was discussed by Crowson (1972).

Ateliinae Kleine, 1928, **stat. rev.**

Type genus. *Atelius* Waterhouse, 1878.

Diagnosis. Adult. Head small, with long slender or deeply serrate antennae, commonly longer than body (only Ateliini, Figs 3–4), at least some taxa in all tribes with flat, triangular male antennomeres 3–6 (Fig. 4; *Macrolycus*, *Ponyalis*, *Atelius*). Pronotum with median longitudinal keel at least in anterior part of pronotum (Fig. 5N). Elytra parallel-sided, with four longitudinal costae, which may be reduced in various degree and absent secondary costae (Fig. 6H) and reticulation (Macrolycini) or with reticulate cells (Fig. 6H; Ateliini) and sometimes with secondary costae (Fig. 6I; Lyponiini). Phallus usually long and slender, and short parameres in Ateliini and some Macrolycini, long phallobase present in most taxa. Females larviform (Ateliini) or fully metamorphosed (Lyponiini, Macrolycini).

Remark. The redefined Ateliinae merge three tribes and their only putative synapomorphy are flat, triangular male antennomeres 3–6(10). Although the shape of antennae, *e.g*., the presence of lamellae and compression of antennomeres are generally very variable characters, we found in this case that triangular antennomeres supports the relationships inferred from the phylogenomic analysis. The lamellae are present only in Macrolycini and most Lyponiini, but not in the neotenic Ateliini. Acute triangular antennomeres are well-developed in *Atelius* Waterhouse, 1878 (Fig. 3K; Ateliini), *Ponyalis* Fairmaire, 1899 (Fig. 3L; Lyponiini) and almost all *Macrolycus* Waterhouse, 1878 (Macrolycini), We suppose that it was secondarily lost in *Scarelus* Waterhouse, 1878 (Fig. 4N; and *Lyponia* s. str. The current analysis suggests the very close relationships of Macrolycini and Lyponiini (Fig. 3) and we keep the tribal status of these two lineages due to their morphological differences. Their relationships has been only ambiguously proposed based in some earlier analyses of Sanger data (Bocak et al. 2008, Masek et al. 2018).

Ateliini Kleine, 1928.
Type genus. Atelius Waterhouse, 1878.

Diagnosis. Adult. Head small, sometimes long, bearing long slender antennae, antennae always longer than body, with triangular antennomeres (Fig. 3K; most *Atelius*) or with parallel sided antennomeres (Fig. 4N; *Scarelus*, some *Atelius*). Pronotum with median longitudinal keel (Fig. 5H). Elytra parallel-sided, with four longitudinal costae, which may be reduced in various degree, especially in small-bodied species (Fig. 6H). Phallus long, slender, parameres short. Females and larvae unknown.

Remark. All species are known only in males and neotenic females are supposed in all Ateliini, when hundreds of specimens were collected (Malohlava & Bocak 2010, 2011, Bray & Bocak 2016).

Lyponiini Bocak & Bocakova, 1990, **stat. rev.**
Type genus. *Lyponia* Waterhouse, 1878.

Diagnosis. Adult. Body small to medium sized. Head prognathous, antennae filiform to flabellate in males, filiform to serrate in females, antennomeres 3–6 triangular in *Ponyalis* (Fig. 4L). Pronotum subquadrate, with median line (Fig. 5J). Elytra with nine costae and well developed reticulate cells (Fig. 6I). Male genitalia without parameres, apical part of phallus often with pair of lateral spines, phallobase annuliform. Female genitalia elongate, paraproctal baculi fused with coxites, terminal abdominal sternum with short spiculum ventrale. Larva (*Ponyalis*). Body subparallel-sided, flat, head with two membranes in lateral part of cranium, antennal peg pointed, mandibles very long, slender, terga undivided, with four processes at posterior margins, metathoracic spiracles well developed, terminal abdominal segment with slender, fixed urogomphi (Bocak & Matsuda 2003).

Remark. Lyponiini were originally delimited in Platerodinae as a subtribe (Bocak & Bocakova 1990). Kazantsev (2005) transferred Lyponiini to Calochrominae *incertae sedis* and recently, he omitted Lyponiini from his classification (Kazantsev 2013). The current analysis indicates close relationships to Macrolycini and Ateliini and the tribe is transferred to Ateliinae (Fig. 3A).

Macrolycini Kleine, 1928, **stat. rev.**
Type genus. Macrolycus Waterhouse, 1878.

Diagnosis. Adult. Body medium sized to large. Head without rostrum, antennae flabellate in males, serrate in females, always strongly compressed, with triangular basal antennomeres in almost all species. Pronotum with sharp median carina frontally (Fig. 5I). Elytra with four longitudinal costae, intercostal intervals irregularly punctured, without reticulate cells. Claws bifid at apex. Phallus long, slender, often with processes at apex, parameres mostly absent. Female genitalia wide, with short styli, coxites short, paraproctal baculi widened at base. Spiculum ventrale short. Larva (*Macrolycus*). Similar to Calochromini in shape and longitudinal division or terga T2–T3 and transverse head capsule, abdominal terga of *Macrolycus* only partly divided, sterna T2 and T3 considerably reduced, sickle-like (Bocak & Matsuda 2003).

Remark. Macrolycini were classified in Lycinae by Bocak & Bocakova (1990, 2008) and Kazantsev (2013) and as a sister group of Dilophotini in Calochrominae (Kazantsev 2005). They were recovered as a sister to Lyponiini and are transferred to Ateliinae in this study.

Lycinae Laporte, 1836.

Type genus. *Lycus* Fabricius, 1787.

Diagnosis. There is no clear morphological synapomorphy supporting this clade. It consists of the morphologically distant Conderini characterized by a small median pronotal areola, circular phallobase, characteristic long parameres and arcuate phallus (Bocak & Bocakova 1990, Bocak 2002) and from the West Gondwanan clade (Thonalmini, Leptolycini, Platerodini, Eurrhacini, Calopterini, and Lycini). These tribes share shortened parameres, absent reticulate cells in elytra (except some *Plateros* Bourgeois, 1879), and short paraproctal baculi.

Remark. Most lycid lineages were included in Lycinae by Bocak & Bocakova (2008). The relationships between tribes and groups of tribes were weakly supported and only current analyses provided sufficient support for relationships among the tribes now included in Lycinae (see Bocak & Bocakova 1990, 2008, Kazantsev 2005, 2013, Masek et al. 2018). We propose to abandon the wide definition of Lycinae and to define separate subfamilies Lyropaeinae (neotenics from the Oriental region), Lycinae (Conderini and the clade of mostly West Gondwanan lineages) and Metriorrhynchinae (the clade of mostly East Asian lineages; all except a part of Metriorrhynchini). Although the morphology-based definition of these subfamilies is poorly supported, their classification as subfamilies is robustly supported phylogenomic relationships, some subclades were earlier supported by Sanger data analyses, their relationships is additionally supported geographical distribution. Ontogenetic modifications define Lyropaeinae and Lycinae: Leptolycini. The largest part of net-winged beetles diversity is concentrated in Lycinae (1812 spp.) and Metriorrhynchinae (1647 spp.; Masek et al. 2018).

The tribes Conderini, Thonalmini, Leptolycini, Platerodini, Eurrhacini, Calopterini, and Lycini are classified in Lycinae. Except Conderini, these tribes are represented by at least some genera and species in the Neotropical region. Conderini are morphologically and zoogeographically distant lineage which we prefer to include in Lycinae based on the present phylogenomic analysis. Although their subfamily status could be justified by morphological disparity, we prefer not to inflate the number of subfamilies, especially when a limited number of Conderini is known (42 spp.; Masek *et al*. 2018).

Conderini Bocak & Bocakova, 1990
Type genus. *Conderis* Waterhouse, 1879.

Diagnosis. Adult. Body medium sized, parallel-sided. Head without rostrum, antennae serrate in both sexes. Pronotum with five areolae. Elytra always with four primary longitudinal costae, secondary costae well developed or absent. Male genitalia with circular phallobase, slender strongly arcuate phallus, parameres slender, divergent. Ovipositor with wide, plate-like coxites, slender, curved paraproctal baculi. Larva (*Xylobanellus* Kleine, 1930). Body parallel-sided; lateral part of epicranium deeply and widely emarginate in posterior half; mala slender, long, membranous; terga T1–T3 and A1–A8 large, divided by longitudinal membranous area in two tergites; urogomphi finger-like, fixed (Burakowski 1989).

Remark. The analyses support independent position of Conderini in Lycinae. They are very characteristic and unlike other Lucinae tribes have long parameres, circular phallobase, sharp pronotal carinae forming a central areola (Fig. 5M) and vll developed elytral costae (Fig. 6J). Conderini was previously classified with Metriorrhynchinae on the basis of the circular phallobase and the presence of the median areola (Bocak 2002). Conderini differ from Metriorrhynchini in the structure of genitalia (the presence/absence of parameres and unpaired vaginal gland) and larval mouth parts (presence/ absence of mala; Bocak 2002, Bocak & Matsuda 2003).

Thonalmini Kleine, 1933
Type genus. *Thonalmus* Bourgeois, 1882.

Diagnosis. Adult. Body small to medium sized, all species with orange pronotum and basal part of elytra and metallic blue apical part of elytra. Head without rostrum and prominent antennal tubercles, apical palpomeres securiform; antennae 11-segmented, antennomere 2 very short, antennomeres 3–11 parallel-sided, strongly compressed. Pronotum with elevated lateral margins and median longitudinal carina with inconspicuous areola basally (Fig. 5N). Elytra with three longitudinal costae, costa 3 usually much stronger; reticulate cells irregular, weak, sometimes apparent only in apical part of elytra, inconspicuous and covered by dense pubescence basally (Fig. 6L) . Male genitalia without parameres, phallus slender, tubular, terminal orifice situated dorsally, phallobase small, rather hemispherical, as long as 1/6 of phallus. Female genitalia with plate-like coxites, paraproctal baculi widened basally, spiculum ventrale absent. Larva unknown.

Remarks. Bocak & Bocakova (1990) classified the genus in Lycini on the basis of the structure of elytral and pronotal costae. The recent molecular analysis indicated the close relationships of *Thonalmus* and Eurrhacini or Eurrhacini and Platerodini (Masek et al. 2018) and the current phylogenomic analysis confirmed the relationships of Platerodini within west Gondwanan lineages (Fig. 3). The Thonalmini were not included in the dataset. We justify their position using the results of previous analyses by Masek et al. (2018) and place Thonalmini as a tribe in Lycinae.

Lycini Laporte, 1836.
Type genus. *Lycus* Fabricius, 1787.

Diagnosis. Adult. Body medium to large sized. Head small, with rostrum. Antennae 11-segmented, strongly compressed, pedicel short, antennae often serrate from antennomere 3. Pronotum with median longitudinal carina in anterior part of pronotum, changing in depression posteriorly (Figs 5Q-S). Elytra slightly widened posteriorly to hemispherically expanded, each elytron with four longitudinal costae, reticulate costae reduced, irregular (Fig. 6N, O). Male genitalia with long slender aedeagus, parameres short, rarely reaching half ofphallic length. Female genitalia with extensive plate- like coxites, paraproctal baculi separate, slender, slightly longer than coxites. Larva (*Lycus* and *Lycostomus*). Body flat, widest at basal abdominal segments, often brightly coloured. Epicranium more or less prolonged, praementum divided in two segment-like parts. Pronotum elongated. Tergum T1 undivided or

only partly divided, divided terga T2–T3 and A1–A8, considerably reduced sterna T2 and T3.

Remark. Lycini show close affinities to Calopterini in both morphological and genetic resemblance. Their relationships is well supported also by the current phylogenomic analysis.

Calopterini Green, 1949
Type genus. *Calopteron* Castelnau, 1838.

Diagnosis. Adult. Medium-sized to large lycid beetles. Head without rostrum, usually with conspicuous antennal tubercles. Antennae strongly compressed, 11-segmented, serrate to flabellate in males and serrate in females, antennomere 2 very short (Fig. 5P). Maxillary palpi four-segmented, labial palpi three-segmented. Pronotum with median longitudinal carina sometimes forming longitudinal areola posteriorly; transverse pronotal carinae absent (Fig. 5P). Anterior thoracic spiracles mostly tubular. Elytra with 3–4 primary costae, secondary costae sometimes absent, reticulate cells mostly distinct, sometimes irregular (Fig. 6Q). Female terminal sternum with short spiculum ventrale. Male genitalia with phallus ventro-basally emarginate, parameres short, at most 3/4 as long as phallus. Female genitalia short to elongate, paraproctal baculi fused basally forming median bridge. Larva (*Calopteron*, *Caenia* Fabricius, 1801). Larva of Calopteron is very similar to *Lycostomus*. *Calopteron* differs in entire spiracular plates A1–A8. *Caenia* differs substantially from both *Calopteron* and *Lycostomus*, but only exuviae were available for the study (Bocak and Matsuda 2003).

Remarks. Calopterini were morphologically defined by Bocakova (2003, 2005) who revised their classification. The recent studies by Masek et al. (2018) and Kalousova (2019) confirmed relationships among Neotropical neotenic lineages and the fully-metamorphosed Calopterini. Calopterini formed a paraphylum with respect to the taxon Pseudoceratoprion (*in litt.*) which represented the neotenic calopterine genera in the analysis by Bocak & Bocakova (2005) and Masek et al. (2018). Numerous neotenics earlier placed by Kazantsev (2013) the subfamily Leptolycinae were included in the analysis of Calopterini and Eurrhacini by Kalousova (2019) and they were recovered in relationships to fully metamorphosed genera. They are placed in the lineages close to the concept of the subtribe Acroleptina erected in Calochromini by Bocakova (2003). Miller (1991) discussed the possibility of multiple origins of neoteny in the terminal clades of Lycidae and our analyses and classification reflects his view. The reanalysis of the morphological dataset did not recover the monophyly of Calopterini, but various genera were found in distant positions in relationships Platerodini (*Calopteron*), and Erotini (*Caenia*) and the neotenic calopterine genera were recovered in close relationships to Leptolycini (Fig. S10).

Leptolycini Leng & Mutchler, 1922, **stat. nov.**
Type genus. *Leptolycus* Leng & Mutchler, 1922.

Diagnosis. Adult. Body often very slender, small to medium sized. Head protruded anteriorly (Fig. 5R), mouthparts vertical, mandibles strongly reduced, labium with weakly sclerotized mentum (Fig. 4B). Antennae 10- or 11-segmented, with very short

antennomere 2 (Fig. 4O). Pronotum without carinae or with short median carina (Fig. 5R). Each elytron with two or three longitudinal costae, inter-costal intervals irregularly punctured or with irregular reticulate cells (Fig. 6M). Male genitalia often reduced, heterogeneous in shape. Females neotenic (Miler 1991). Larva. Numerous larvae were collected by M. Ivie (personal communication), but have not yet been described.

Remarks. Leptolycini had been considered as an independent clade in Lycidae (Leng & Mutchler 1922, Kleine 1933) until Bocak & Bocakova (1990) combined them with Oriental and Afrotropical neotenic lineages in Leptolycinae. Similarly, Kazantsev (2013) merged them with Dexorini and a part of Lyropaeinae. The Leptolycini from Caribbean islands were represented in the present analysis by *Leptolycus* sp. and found as a terminal lineage in Lycinae, either as the successive serial branch with Conderini and Platerodini or as the sister to Platerodini (Figs. 3A, C, S3–S6). Both topologies justify the tribal rank for Leptolycini in Lycinae and reject an independent position among the deepest splits (Kazantsev 2005, 2013). Similarly, their relationships to Lyropaeinae and Dexorinae is robustly falsified (Bocak & Bocakova 1989, Kazantsev 2013, Masek et al. 2018). The putatively neotenic taxa from the continental part of the Neotropical region were regularly recovered in Calopterini (Bocak et al. 2008, Masek et al. 2018, Kalousova 2019). We propose that all continental South American neotenics do not belong to Leptolycini and form a terminal clade within Calopterini, *i.e*., Acroleptina Bocakova, 2005 (Kalousova 2019).

The latest classification of Leptolycinae by Kazantsev (2013, 2018) was very wide and the subfamily consisted of unrelated taxa. Apart from tribes representing some Oriental and Afrotropical neotenic, Kazantsev (2013) proposed the tribes Electropterini Kazantsev, 2013 and Dominopterini Kazantsev, 2013. These tribes contain further Caribbean Leptolycinae *sensu* Kazantsev, 2013. These taxa supposedly have larviform females. We propose that these lineages do not merit the tribe rank, but they should be at most subtribes within Leptolycinae if all lineages are mutually monophyletic. Only if they do not form a monophylum within Lycinae and represent a series of successive branches, they would have to be recognized as separate tribes having the same rank as Leptolycini. Then, we would have to propose multiple origins of neotenic development in three lineages of Caribbean Lycinae or a unique not yet robustly documented reversal back to fully metamorphosed females in Platerodini or Platerodini, Lycini and Calopterini (Figs 3A,B, S3–S6). The reversal would falsify the Dollo's law (Dollo 1893, Whiting et al. 2003). Although, these taxa were unavailable for molecular analyses, based on the morphology and available information on relationships, we lower them to subtribe rank in Leptolycini, *i.e*., Dominopterina new stat. and Electropterina new stat.

Eurrhacini Bocakova, 2005
Type genus. *Eurrhacus* Waterhouse, 1878.

Diagnosis. Adult. Head with small eyes, antennae flabellate, very long, terminal palpomeres of both palpi elongate, securiform. Pronotal median longitudinal carina double in median portion forming longitudinal areola, terminal palpomeres of maxillary and labial palpi large, elongate, elytra with nine longitudinal costae, hind trochanters with spine. Male genitalia slender, tubular parameres fused

to phallus, phallus slightly laterally distorted. Female genitalia elongate, paraproctal baculi twice longer than coxites, convergent basally and forming long, thin ventral bridge. Spiculum ventrale absent. Larva unknown.

Remarks. Eurrhacini were described as a subtribe in Calopterini and are well morphologically defined based (Bocakova 2003, 2005). The tribe was not available for the phylogenomic analysis and its position is based on the previous molecular analysis by Masek et al. (2018) and morphological analysis by Bocakova (2005). The tribal rank is kept as earlier proposed (Bocak & Bocakova 2008). Their internal relationships has been inferred by Kalousova (2019).

Platerodini Kleine,1928
Type genus. *Plateros* Bourgeois, 1879.

Diagnosis. Adult. Body small to medium sized (Fig. 3O). Head without rostrum, antennal tubercles inconspicuous, antennae slightly serrate to flabellate in males, serrate in females (Fig. 4M). Pronotal carinae absent, at most vestiges present at margins (Fig. 5O); elytra with nine longitudinal costae, usually similar in strength, reticulate cells often reduced, irregular (Fig. 6K). Male genitalia with long (*Teroplas* Gorham, 1884) to absent parameres (*Plateros*); female genitalia, with basally widened paraproctal baculi, spiculum ventrale absent. Larva (*Plateros* spp.). Body parallel-sided, all terga except last one tripartite, formed by small, strongly prolonged, oblong or quadrate mediotergite and two laterotergites, precoxale fused to prosternum, abdominal segments A1–A8 with only one lateral pleurite, terminal abdominal tergite undivided, mostly simply rounded.

Remarks. Platerodini is classified in Lycinae as a tribe. The generic revision of the tribe was presented by Bocakova (2001). Their relationships with Calopterini and Lycini was supported only ambiguously by Sanger data analyses (Bocak & Bocakova 2008, Masek et al. 2018). The present topology recovered this tribe robustly in Lycinae, but alternative relationships were recovered: Platerodini were found either in a single clade with Leptolycini or as an independent successive lineage in Lycinae (Figs. 3A, S3–S6).

Lyropaeinae Bocak & Bocakova, 1989

Type genus. *Lyropaeus* Waterhouse, 1878.

Diagnosis. Adult. Males very small (1–5 mm, *Alyculus* Kazantsev, 2002 and others) to medium sized (8–12 mm, *Lyropaeus*, *Platerodrilus* Pic, 1921). Head small, hypognathous, often with reduced mouth parts (Fig. 5K); alternatively head prognathous with long mandibles (*Platerodrilus*). Maxillary palpi with terminal palpomere apically pointed, labium reduced. Antennae 10–11 segmented. Pronotum usually trapezoidal, without carinae (Fig. 5L), sometimes with median longitudinal groove posteriorly, posterior angles of pronotum projected obliquely backwards (Fig. 5K), alternatively flat laterally dilated pronotum known in *Platerodrilus* (Fig. 3R). Each elytron with 4–9 weak longitudinal costae, costae sometimes indistinct. Intercostal intervals with irregular reticulate cells or punctures, sometimes elytra almost glabrous (Fig. 6G). Male genitalia trilobate, phallobase always present, sometimes fused with

parameres. Parameres apically pointed, with sharp ventro-basal projection, sometimes very short with long filament (Platerodrilus). Females larviform as proved for *Lyropaeus*, *Macrolibnetis*, and *Platerodrilus* (Wong 1996, 1998, Levkanicova & Bocak 2009, Masek & Bocak 2013, Masek et al. 2014, 2015) or unknown. Larva. Only large-bodied female larvae are known, most females have not been discovered (Wong 1996, Bocak & Matsuda 2003).

Remarks. The Lyropaeinae is a morphologically diverse group of Oriental lycids with proved or presumed neotenic females and consists of the following tribes: Lyropaeini, Alyculini, Antennolycini, Miniduliticolini, and Platerodrilini (Bocak & Bocakova 1989, 2008, Kazantsev 2002, Kazantsev 2005, Bocak et al. 2008, Masek et al. 2018). The relationships of Lyropaeini, Alyculini, Antennolycini and Platerodrilini was repeatedly recovered in Sanger-are analyses of Lycidae using rRNA and mtDNA markers as well as in the current analysis (Fig. 3; Bocak & Bocakova 2008, Masek & Bocak 2013, Masek et al. 2014, 2015, 2018).

Kazantsev (2005) separated Oriental lyropaeine neotenic net-winged beetles in two subfamilies: the Lyropaeinae and Miniduliticolinae (incl. Platerodrilini). Later, he placed the Lyropaeini genera in three subfamilies: Miniduliticolinae (incl. Platerodrilini), Alyculinae and Leptolycinae. The latter contained not only lyropaeine taxa but also Afrotropical Dexorinae and Lycinae: Leptolycini and Lycinae: Calopterini, part. (Kazantsev 2013). The morphological disparity caused such high level of phylogenetic uncertainty and high inflation of family-group taxa. Considering the robustness of morphological analyses, we propose that disparate adult male morphology is produced as a result of ontogenetic reprogramming in females and similar morphology evolved repeatedly due to the similar developmental path.

Neotenic females have been confirmed for some species when they were collected in copula (Gravely 1915, Mjöberg 1925, Wong 1996, 1998) Further large-bodied larvae were identified to species-level using DNA markers and supposedly remain larviform when sexually mature (Bocak & Matsuda 2003, Levkanicova & Bocak 2009, Masek & Bocak 2014, Bocak et al. 2014). Other genera are known only in males. High numbers of males have been collected, so we suggest the similar modification of ontogeny in these closely related taxa.

Despite the fact that all lyropaeine females are larviform and we could expect the similar morphology of males, no synapomorphy is available for the definition of this subfamily and the Lyropaeinae consists of morphologically very disparate taxa. The subfamily includes small-bodied, brachelytrous forms (Alyculini), small-bodied forms with fully developed elytra (Antennolycini Miniduliticolini, numerous Platerodrilini), large-bodied forms with reduced mouthparts and characteristically modified cranium (Lyropaeini) and large-bodied forms with fully-developed mouthparts and long mandibles (Platerodini: *Platerodrilus*). Similar variability is seen in the morphology of male genitalia. All non-ateliine neotenics known from the Oriental region are placed here.

Alyculini Bocak & Bocakova, 2008
Type genus. *Alyculus* Kazantsev, 1999: 252.

Description. Adult. Body very small, subtle, 1.3–2.5 mm long. Head small, with large, hemispherically prominent eyes, Antennae filiform, slender, antennomere 1 long, 2 small, 3 slightly longer than 1. Mouthparts tiny, with reduced mandibles. Maxillary palpi 4-segmented, apical palpomere conspicuously pointed. Pronotum transverse, widest at basal margin, anterior margin straight, lateral

margins strongly concave, posterior margin bisinuate. Scutellum apically deeply emarginate, distal tips projected obliquely backwards. Elytra shortened, tapering to apex, distal portion rounded, densely punctured, with- out any traces of costae or reticular cells. Wings fully developed. Abdominal sternum 8 simple, 9 elongate. Legs slender, tarsomere 4 lobed. Male genitalia with slender phallus widened basally. Females and larva unknown.

Remarks. Alyculini is the monotypic tribe. *Alyculus* is the only brachelytrous genus in Lyropaeinae. All known species have very small body (<2.5 mm) and strongly transverse pronotum. They differ in 11-segmented antennae from Lyropaeini.
Alyculini was unavailable for genomic study and it is classified as the tribe and placed here on the basis of earlier molecular analyses of the Sanger dataset by Bocak & Bocakova (2008) and Masek et al. (2015, 2018).

Antennolycini Bocak & Bocakova, 2008
Type genus. *Antennolycus* Bocakova & Bocak, 1999.

Diagnosis. The tribe is characterized by the unique shape of male genitalia within the subfamily Lyropaeinae (Bocakova and Bocak 1999, Bocakova 2006).

Description. Adult. Body small, weakly sclerotized, dorso-ventrally flattened, subparallel-sided. Head small, shallowly retracted in pronotum. Eyes small, antennae 11-segmented, filiform in *Microlyropaeus* Pic, 1929, strongly modified in *Antennolycus*, antennomeres 2 and 3 very small, subequal, mouthparts hypognathous, labium and maxillae tiny, palpi with pointed terminal palpomere. Pronotum transverse, without carinae, sometimes with basal longitudinal groove. Scutellum emarginate apically. Elytra with four or nine costae, sometimes partly shortened. Legs slender, trochanters long, tibial spurs tiny. Male genitalia with stout phallus and very short parameres, each paramere with setose process apically. Females unknown. Larva unknown.

Remarks. Antennolycus was recovered in the phylogenomic analysis as the sister group to Lyropaeini and Platerodrilini (Fig. 3). Their independent position was recovered also in earlier analyses (Bocak et al. 2008, Bocak & Bocakova 2018, Masek et al. 2015, 2018).

Lyropaeini Bocak & Bocakova, 1989
Type genus. *Lyropaeus* Waterhouse, 1878.

Diagnosis. Adult. Head small, mouthparts vertical, mandibles small, reduced, curved apically. Antennae 10- segmented, laterally compressed (Fig. 4S). Maxillary palpi with terminal palpomere small, apically pointed. Labium reduced, labial palpi 1-segmented, apically pointed. Pronotum trapezoidal, without carinae, scutellum considerably emarginate apically (Fig. 5K). Elytra flat, each elytron with four weak longitudinal costae, costa 3 vestigial, intercostal intervals finely punctured, without reticulate cells (Fig. 6G). Male genitalia trilobate, phallobase long, as long as aedeagus. Parameres robust, with ventro-basal process. Larva. Larva was

described by Gravely (1915), but no specimen was found in collections. It reminds larva of *Platerodrilus* and *Duliticola* by large body size and unique structure of terminal antennomere and was recently identified using molecular markers by Masek et al. 2014. It resembles *Platerodrilus* larva in general appearance, but parallel evolution of large bodied Lyropaeinae larvae must be hypothesized based on the earlier published molecular phylogenies (Bocak et al. 2008, Masek et al. 2018).

Remark. Lyropaeini were revised by Bocakova (2006) in a wider sense including Alyculini and Antennolycini as proposed here. High morphological disparity was identified also in this tribe (Bocakova 2006).

Platerodrilini Kazantsev, 2005.
Type genus. *Platerodrilus* Pic, 1921.

Diagnosis. Adult. Body small to medium sized. Head without rostrum, transverse, with conspicuous antennal tubercles, mouthparts vertical, mandibles very long, slender, curved. Antennae 11-segmented, antennomeres 2 and 3 very short, subequal in length, antennomeres 3–11 parallel-sided, compressed, seldom flabellate in males (Fig. 4J); apical palpomeres pointed. Pronotum without any carinae (Fig. 5L), with longitudinal depression at lateral margins. Elytra with inconspicuous vestiges of longitudinal costae at humeri, usually densely pubescent. Male genitalia trilobate, with fused bases of phallus and parameres, phallus slender, usually curved, parameres robust basally, very slender apically, shorter than phallus. Females larviform. Larva (*Platerodrilus*). Body shape trilobite-like. Apical antennomere with several peg-like processes. Spiracles situated at margin of deep, large cavities surrounding spiracular scar in mature larvae, additional spiracles in bottom of cavity. Meso- and metasternum with paired tubercles. Sclerites of A1–A8 with at least one process at posterior margin.

Remarks. Masek et al. (2015) showed that Platerodrilini as defined by Kazantsev (2005) form only a terminal branch within Lyropaeinae with several close relatives in the lyropaeine clade (e.g., *Pendola* Bocak 2002). The phylogeny of this clade was studied by Masek et al. (2015). Kazantsev (2013) placed Platerodrilini in relationships to the Miniduliticolini.

Miniduliticolini Kazantsev, 2005.
Type species. Miniduliticola Kazantsev, 2002.

Diagnosis. Adult. Body small. Head elongate, not narrowed behind eyes, labrum indistinguishable. Mandibles long and slender, projected forwards. Maxillary palpi 4-segmented, slender, palpomere 4 elongate, pointed distally. Labial palpi 3-segmented, slender and short, with pointed apex. Antennae 11-segmented, antennomere 2 small, filiform. Pronotum transverse, trapezoidal, posterior angles prominent laterally. Anterior thoracic spiracles small. Scutellum subquadrate, parallel-sided, weakly emarginate apically. Elytra long, shining, finely punctured with no trace of costae, broad basally and slightly narrowing distally. Legs with femora relatively robust, conspicuously less flattened than tibiae, trochanters long, attached to femora obliquely in middle. Tarsomeres narrow without

apical plantar pads, claws simple. Female unknown, probably larviform. Larva unknown.

Remarks. Kazantsev (2005) had to replace Duliticolinae by Miniduliticolinae Kazantsev 2002 because the name Duliticolinae was invalid in the sense of the article 13.2 (ICZN 1999). Considering morphological differences we keep the position of Miniduliticolini close to Platerodrilini as proposed by Kazantsev (2002), but their relationships to the small-bodied Platerodrilini remain obscure. The Miniduliticolini is known in a single damaged male specimen. Kazantsev (2013) merged Platerodrilini and Miniduliticolini in Miniduliticolinae in an apparent conflict with the previously published molecular phylogenies (Bocak & Bocakova 2008, Masek & Bocak 2013, Masek et al. 2015, 2018).

Metriorrhynchinae Kleine, 1926, stat. nov.
Type genus. *Metriorrhynchus* Gemminger & Harold, 1869.

Diagnosis. Body small to large, with a reduced keel in frontal part of pronotum (Figs. 5V, W; Dilophotini and Libnetini), vestigial carinae at pronotal margins (Fig. 5U; Dihammatini), with median areola (Fig. 5T; Lycoprogenthini) or with seven areolae (Fig. 5 AC; Metriorrhynchini), reduced patterns of areolae are known in some Metriorrhynchini (Figs 5Y–AB; *Trichalus*, *Leptolycus*, *Wakarumbia* etc.). Antennae with antennomere 2 much shorter than antennomere 3, except *Libnetisia* and *Dihammatus*, filiform, serrate or flabellate (Figs. 4P–R). Male genitalia with parameres (Dihammatini, Libnetini, Lycoprogenthini) or only phallus and phallobase present (Metriorrhynchini, Dilophotini). Female genitalia similarly variable. Larva (*Cautires*, *Metriorrhynchus*, *Leptotrichalus*, *Lycoprogenthes*). Variable in shape and modification of terga even within some tribes (Bocak & Matsuda 2003).

Remark. The subfamily contains morphologically diverse lineages which cannot be identified by any morphological synapomorphy, but the monophyly of the clade which contains Dihammatini, Lycoprogenthini, Dilophotini, Libnetini and Metriorrhynchini was robustly recovered by the current phylogenomic analysis and some relationships obtained a weak support already in the analyses of Sanger datasets (Bocak & Bocakova 2008, Masek et al. 2018). *E.g.*, Dilophotini + Libnetini were recovered as a monophylum or paraphylum by Masek et al. (2018) and the possible relationships between Dihammatini + Metriorrhynchini was discussed by Bocak & Bocakova (2008). Morphological traits define very well the tribes, but do not indicate relationships among them within the subfamily as a whole.

Dihammatini Bocak & Bocakova, 2008
Type genus. *Dihammatus* Waterhouse, 1879.

Diagnosis. Dihammatini externally resemble *Plateros*, but differ in the short 3rd antennomere (Fig. 5U) and the structure of both male and female genitalia (Bocakova 2001a). Male genitalia with dorsally and sometimes also ventro-proximally fused parameres,

phallobase elongate. Female genitalia with stick-like paraproctal baculi, coxites and paraproctal baculi separate, paraprocts present, but reduced. Besides proximal vaginal glands, additional pair of tubular glands attached to vagina near vulva (collateral glands *sensu* Bocakova 2001), female terminal sternum with spiculum ventrale as long as segment. Larva unknown.

Remarks. *Dihammatus* was classified in Platerodini for a long time and only Bocakova (2001a) transferred the genus to Libnetini on the basis of similar four accessory glands in female genitalia. Molecular data do not support close relationships of *Dihammatus* and *Libnetis* and we found *Dihammatus* as a basal clade in Metriorrhynchinae with Lycoprogenthini as their sister-tribe and the Libnetini as a subclade in relationships with Dilophotini and Metriorrhynchini (Fig. 3; all Metriorrhynchinae). The morphology of Dihammatini and Lycoprogenthini does not provide a morphological evidence for neither their sister-relationships nor their relationships to other Metriorrhynchinae. Conversely, current phylogenomic data provide strong support for the recovered topology. We prefer to include Dihammatini and Lycoprogenthini in the widely defined Metriorrhynchinae which contain predominantly East and Southeast Asian lycid lineages in contrast with the predominantly Neotropical Lycinae (Fig. 3). The erection of a separate taxon for these two tribes is useless.

Lycoprogenthini Bocak & Bocakova, 2008
Type genus. *Lycoprogentes* Pic, 1915: 6.

Diagnosis. Adult. Body small to medium sized, slender. Pronotum with median areola broadly attached to basal margin of pronotum, areola widest at the frontal third, and lateral pronotal costae straight and conspicuous; male genitalia characteristic, with long phallobase and robust rounded parameres; ovipositor wide, with complex paraprocts and short, free valvifers. Larva (*Lycoprogenthes*). *Lycoprogenthes* is characterized by the sclerotized pleural part of cranium, well developed metathoracic spiracles, undivided thoracic and abdominal tergites, and long, fixed urogomphi (Bocak & Matsuda 2003).

Remarks. The listed characters, along with the structure of pronotal carinae, distinguish Lycoprogenthini from other tribes of Metriorrhynchini and from Dictyopterini which are similar in general appearance. *Lycoprogenthes* was originally classified in Calochromini (Pic, 1915, Kleine 1933) and transferred to Erotinae by Bocak (2002b). Such classification was accepted by Kazantsev (2013). Their relationships with Dihammatini and Metriorrhynchini is unexpected and morphologically unsupported. The presence of median rhomboidal areola, nine elytral costae in most species and filiform antennae are shared with Dictyopterini. Conversely, these species differ in the structure of male and female genitalia. Ambiguous morphological signal caused their inconsistent placement by various authors.

Dilophotini Kleine, 1928.
Type genus. *Dilophotes* Waterhouse, 1879: 72.

Diagnosis. Adult. Body small to medium sized, slender. Head small, sometimes shortly rostrate, most species without rostrum, mouthparts well-developed, antennae filiform to flabellate. Pronotum with longitudinal keel in anterior part. Elytra with three longitudinal costae, intercostal intervals without reticulate cells, densely punctured. Male genitalia with long phallobase, slender to robust phallus, parameres absent. Female genitalia with long styli, short coxites and basally fused paraproctal baculi. Larva unknown.

Remark. Dilophotini is sister to Libnetini and their current position in the phylogenomic tree places it in the relationships with Metriorrhynchini and justifies their transfer to Metriorrhynchinae. The Dilophotini was studied by Motyka et al. (2018).

Libnetini Bocak & Bocakova, 1990, **stat. nov.**
Type genus. *Libnetis* Waterhouse, 1878.

Diagnosis. Adult. Body small, antennae filiform, rarely weekly serrate, pronotal areolae absent (Fig. 5W), median longitudinal keel present in anterior part of pronotum, each elytron with four primary costae, secondary costae and reticulate cells absent, interspace irregularly punctured (Fig. 6P). Male genitalia with short basally fused parameres. Larva unknown.

Remark. The Libnetini was recovered as the sister to Dilophotini, unlike some earlier studies when the tribe marked the most basal split in Lycidae and was gibed subfamily rank (Bocak et al. 2008, Bocak & Bocakova 2008). Their relationships to Dilophotini was suggested by some analyses of rRNA and mtDNA, but without acceptable statistical support (Masek et al. 2018). The Dilophotini and Libnetini share the pronotum with incomplete longitudinal keel and only longitudinal costae in their elytra (Fig. 6P, R). These tribes differ in the shape of male genitalia. Due to their terminal position close to Metriorrhynchini, Libnetini must be given tribal rank and transferred from Erotinae (*sensu* Kazantsev, 2013) to Metriorrhynchinae.

Metriorrhynchini Kleine, 1926.
Type genus. *Metriorrhynchus* Gemminger & Harold, 1869.

Diagnosis. Adult. Body small to large, head small, sometimes with rostrum (Figs. 3V–X) Antennae serrate to flabellate in males, serrate in females (Figs 4Q, R). Pronotum always with slender median areola and lateral carinae which form up to seven pronotal areolae (Figs 5Y–AC). Elytra with four primary longitudinal costae and five secondary costae which may be absent in some genera (Figs 6U–W). Male genitalia mostly with slender phallus, internal sac often with sclerites of various shape, parameres absent, phallobase circular. Ovipositor with plate-like simple coxites and rod-like paraproctal baculi. Vagina with unpaired median gland. Larva (*Cautires* Waterhouse, 1879, *Xylobanus* Waterhouse, 1879, *Metriorrhynchus* Gemminger & Harold, 1969, *Porrostoma*

Castelnau, 1838, *etc*.). Body parallel-sided to slightly widened at base of abdomen, mala considerably reduced, sclerites with tergal and pleural processes of variable length; sclerotization of the lateral part of epicranium, arrangement of tergites, and shape and presence of urogomphi variable (Bocak & Matsuda 2003, Levkanicova & Bocak 2009).

Remark. Metriorrhynchini were redefined by Bocak & Bocakova (1990) when Cladophorini and Dilolycini were synonymized with the tribe and the Trichalini placed in it. The generic classification was revised by Bocak (2002). Metriorrhynchini are the most species rich lineage in Lycidae with about 1400 described species (Masek et al. 2018). Their phylogeography was studied by Sklenarova et al. (2013).

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Supplementary Table S1. The overview of Lycidae classifications. Red dots designate taxa with proved of hypothesized female neoteny.

Kleine, 1933

Homalisinae Geoffroy, 1762
(now Elateridae: Omalisinae)
Lycinae Laporte, 1836
Macrolycini Kleine, 1928
Lycini Laporte, 1836
•Leptolycini Leng & Mutchler, 1922
Thonalmini Kleine, 1933
Calopterini Kleine, 1933
Dictyopterini Houlbert, 1922
incl. Erotini Leconte, 1881
Ateliini Kleine, 1928
Metriorrhynchini Kleine, 1926
Cladophorini Kleine, 1926
(now Metriorrhynchini)
incl. *Taphes*, *Conderis*, etc.
Trichalini Kleine, 1926 (now
Metriorrhynchini)
Dilolycini Kleine, 1926 (now
Metriorrhynchini)
Platerodini incl. *Libnetis*, *Lyponia*
Lygistopterini Kleine, 1933
(=Calochromini)
Dilophotini incl. •*Lyropaeus*
•Dexorini Kleine, 1933

Bocak & Bocakova, 1990

•Leptolycinae Leng & Mutchler, 1922
•Dexorini Bocak & Bocakova, 1989
•Leptolycini Leng & Mutchler, 1922
•Lyropaeini Bocak & Bocakova, 1989
•Ateliinae Kleine, 1928
•Ateliini Kleine, 1928
Lycinae Laporte, 1836
Lycini Laporte, 1836
Calopterini Green, 1949
Macrolycini Kleine, 1928, incl.
Dilophotini
Erotinae Leconte, 1881
Erotini Leconte, 1881
Dictyopterini Houlbert, 1922
Taphini Bocak & Bocaková, 1990
Platerodini Kleine, 1929, incl.
Libnetis, *Dihammatus*
Lyponiini Bocak & Bocakova, 1990
Calochrominae Lacordaire, 1857
Calochromini Lacordaire, 1857
Metriorrhynchinae Kleine, 1926
Conderini Bocak & Bocakova, 1990
Metriorrhynchini Kleine, 1926
Trichalini Kleine, 1926

Kazantsev, 2005

Lycidae Laporte, 1836
•Leptolycinae Leng & Mutchler, 1922
•Lyropaeinae Bocak & Bocakova, 1989
•Ateliinae Kleine, 1928
•Thilmaninae Kazantsev, 2005 (now
Elateridae)
•Miniduliticolinae Kazantsev, 2003
(=Lyropaeinae pars)
Lycinae Laporte, 1836
Platerodini Kleine, 1929
Erotini Leconte, 1881
Dictyopterini Houlbert, 1922 (incl.
Slipinskiini Bocak & Bocakova, 1992)
Taphini Bocak & Bocaková, 1990
Lycini Laporte, 1836
Conderini Bocak & Bocakova, 1990
Calopterini Green, 1949 (except
neotenics)
Calochrominae Lacordaire, 1857
Macrolycini Kleine, 1928
Dilophotini Kleine, 1929
Calochromini Lacordaire, 1857
Aferotini Kazantsev, 2002
(=Slipinskiini part)

Excluded from Lycidae:
•Dexoridae Bocak & Bocakova, 1989

Supplementary Table S1. Continued.

Bocak & Bocakova, 2008

•Dexorinae Bocak & Bocakova, 1989
Libnetinae Bocak &Bocakova, 1990
•Lyropaeinae Bocak & Bocakova, 1989
    •Lyropaeini Bocak & Bocakova, 1989
    •Antennolycini Bocak & Bocakova, 2008
    •Lyropaeini Bocak & Bocakova, 1989.
    •Miniduliticolini Kazantsev, 2003
    •Platerodrilini Kazantsev, 2004
Dictyopterinae
    Lycoprogenthini Bocak & Bocakova, 2008
    Dictyopterini Houlbert, 1922
    Taphini Bocak & Bocaková, 1990
Ateliinae Kleine, 1928
    •Ateliini Kleine, 1928
    Dilophotini Kleine, 1928
Lycinae Laporte, 1836
    Conderini Bocak & Bocakova, 1990
    Calopterini Green, 1949 (• a part)
    •Leptolycini Leng & Mutchler, 1922
    Lycini Laporte, 1836,
    Thonalmini Kleine, 1933
    Eurrhacini Bocakova, 2005
    Platerodini Kleine, 1929
    Metriorrhynchini Kleine, 1926
    Dihammatini Bocak & Bocakova, 2008
    Erotini Leconte, 1881
    Slipinskiini Bocak & Bocaková, 1992
    Lyponiini Bocak & Bocakova, 1990
    Macrolycini Kleine, 1928

Kazantsev, 2013

•Mimolibnetinae Kazantsev, 2013
•Ateliinae Kleine, 1928
    •Ateliini Kleine, 1928
•Alyculinae Bocak & Bocakova, 2008
•Miniduliticolinae Kazantsev, 2003
    Miniduliticolini Kazantsev, 2003
    Platerodrilini Kazantsev, 2004
•Leptolycinae Leng & Mutchler, 1922
    •Antennolycini Bocak & Bocakova, 2008
    •Dexorini Bocak & Bocakova, 1989
    •Dominopterini Kazantsev 2013
    •Electropterini Kazantsev 2013
    •Leptolycini Leng & Mutchler, 1922
    •Lyropaeini Bocak & Bocakova, 1989
Erotinae Leconte, 1881
    Conderini Bocak & Bocakova, 1990
    Dictyopterini Houlbert, 1922
    Erotini Leconte, 1881
    Lopherotini Kazantsev, 2012
    Libnetini Bocak & Bocakova, 1990
    Taphini Bocak & Bocaková, 1990
    Proterotaphini Kazantsev, 2012.
    Lycoprogenthini Bocak & Bocakova, 2008
Lycinae Laporte, 1836
    Calochromini Lacordaire, 1857
    Calopterini Green, 1949
    Lycini Laporte, 1836,
    Macrolycini Kleine, 1929
    Macrolycinellini Kazantsev, 2012
    Melanerotini Kazantsev, 2010
    Metriorrhynchini Kleine, 1926
    Platerodini Kleine, 1929
    Slipinskiini Bocak & Bocaková, 1992
    Thonalmini Kleine, 1933
    Dilophotini Kleine, 1929
    Eurrhacini Bocakova, 2005

Current study

•Dexorinae Bocak & Bocakova, 1989
    •Dexorini Bocak & Bocakova, 1989
    •Mimolibnetini Kazantsev, 2013
Calochrominae Lacordaire, 1857
    Calochromini Lacordaire, 1857
Erotinae Leconte, 1881
    Erotini Leconte, 1881
    Slipinskiini Bocak & Bocaková, 1992
    Dictyopterini Houlbert, 1922
    Taphini Bocak & Bocaková, 1990
    Proterotaphini Kazantsev, 2012
Ateliinae Kleine, 1928
    •Ateliini Kleine, 1928
    Macrolycini Kleine, 1928
    Lyponiini Bocak & Bocakova, 1990
Lycinae Laporte, 1836
    Conderini Bocak & Bocakova, 1990
    Thonalmini Kleine, 1933
    Eurrhacini Bocakova, 2005
    •Leptolycini Leng & Mutchler, 1922
    Platerodini Kleine, 1929
    Calopterini Green, 1949 (• a part)
    Lycini Laporte, 1836
•Lyropaeinae Bocak & Bocakova, 1989
    •Antennolycini Bocak & Bocakova, 2008
    •Lyropaeini Bocak & Bocakova, 1989.
    •Miniduliticolini Kazantsev, 2003
    •Platerodrilini Kazantsev, 2004
Metriorrhynchinae Kleine, 1926
    Dihammatini Bocak & Bocakova, 2008
    Lycoprogenthini Bocakova & Bocak, 2008
    Dilophotini Kleine, 1929
    Libnetini Bocak & Bocakova, 1990
    Metriorrhynchini Kleine, 1926
        (• *C. apterus* only)
incertae sedis
    Melanerotini Kazantsev, 2010
    Vikhrevini Kazantsev, 2013
    Macrolycinellini Kazantsev, 2012

Supplementary Table S2. The list of currently accepted subfamily and tribe taxa with their revised placement.

SUBFAMILY	TRIBE	REMARK
Dexorinae **stat. nov.**	✓Dexorini	raised to subfamily rank, redefined limits
	×Mimolibnetini **stat. nov.**	down-ranked to tribe, transferred to Dexorinae
Calochrominae **stat. nov.**	✓Calochromini	raised to subfamily rank, redefined limits
Erotinae **stat. rev.**		redefined limits
	✓Erotini	
	×Slipinskiini **stat. rev.**	transferred from Lycinae
	✓Dictyopterini	
	✓Taphini	
	×Proterotaphini	
Ateliinae **stat. rev.**		redefined limits
	✓Ateliini	
	✓Macrolycini **stat. rev.**	transferred from Lycinae
	✓Lyponiini **stat. rev.**	transferred from Lycinae
Lycinae **stat. rev.**		redefined limits
	✓Conderini **stat. rev.**	transferred from Erotinae
	×Eurrhacini	
	×Thonalmini	
	✓Leptolycini **stat. nov.**	down-ranked to tribe, transferred to Lycinae
	✓Platerodini	
	✓Lycini	
	✓Calopterini	
Lyropaeinae **stat. nov.**		raised to subfamily rank, redefined limits
	×Alyculini	transferred from Leptolycinae
	✓Antennolycini **stat. rev.**	transferred from Leptolycinae
	✓Lyropaeini	
	×Miniduliticolini **stat. nov.**	down-ranked to tribe, transferred to Lyropaeinae
	✓Platerodrilini **stat. rev.**	transferred from Miniduliticolinae
Metriorrhynchinae **stat. nov.**		raised to subfamily rank, redefined limits
	✓Dihammatini **stat. rev.**	transferred from Lycinae
	✓Lycoprogenthini **stat. rev.**	transferred from Erotinae
	✓Dilophotini **stat. rev.**	transferred from Lycinae
	✓Libnetini **stat. rev.**	transferred from Erotinae
	✓Metriorrhynchini	transferred from Lycinae
incertae sedis	×Vikhrevini	Placed in Lycinae by Kazantsev (2013)
	×Macrolycinellini	Placed in Calopterini by Kleine (1933) and Dictyopterinae by Kazantsev (2012) and Lycinae by Kazantsev (2013)
	×Melanerotini	Never placed in a subfamily, relationships to Ateliinae: Ateliini, Macrolycini and Metriorrhynchinae: Dilophotini discussed in the original description.

Legend: ✓included and/or ×absent in the current study

Supplementary Table S3. The overview all family-group taxa described or temporarily placed in Lycidae

Original rank	Author	Orig. placement	Other ranks/placements	Author	Current rank (this study)
Lycidae (as Lycusites)	Castelnau, 1840	Malacodermes	Lycidae: Lycinae	Kleine (1933)	Lycidae/Lycinae/Lycini
Acroleptina	Bocakova, 2005	Calopterini			Calopterini: Acroleptina
Aferotini	Kazantsev, 2004	Dictyopterini	Calochrominae: Aferotini	Kazantsev (2005)	
			syn. of Slipinskiini	Bocak et al. (2008)	
Alyculini	Bocak & Bocakova, 2008	Lyropaeinae	Lycidae: Alyculinae	Kazantsev (2013)	Lyropaeinae: Alyculini
Antennolycini	Bocak & Bocakova, 2008	Lyropaeinae	Leptolycinae: Antennolycini	Kazantsev (2013)	Lyropaeinae: Antennolycini
Ateliinae	Kleine, 1928	Lycidae	Ateliinae: Ateliini	Kleine (1933)	Ateliinae/Ateliini
Calochromini (as Calochromides)	Lacordaire, 1857	Malacodermes	Calochrominae	Kleine (1926)	Calochrominae
			Lycidae: Calochromini	Kleine, 1933	
			Calochrominae: Calochromini		
			Lycinae: Calochromini	Bocak et al. (2008)	
Calopterini	Green, 1949	Lycinae			Lycinae: Calopterini
Cautirina	Sklenarova et al. 2014	Metriorrhynchini			Metriorrhynchini: Cautirina
Cladophorinae	Kleine, 1928	Lycidae	Lycinae: Cladophorini	Kleine (1933)	
			syn. of Metriorrhynchini	Bocak & Bocakova (1990)	
Conderini	Bocak & Bocakova, 1990	Metriorrhynchinae	Lycinae: Conderini	Bocak & Bocakova (2008)	Lycinae: Conderini
			Lycinae: Conderini	Kazantsev (2005)	
			Erotinae: Conderini	Kazantsev (2013)	
Dexorinae	Bocak & Bocakova, 1989	Lycidae: Dexorini	Lyropaeinae: Dexorini	Bocak & Bocakova (1990)	Dexorinae: Dexorini
			Elateroidea: Dexoridae	Kazantsev (2005)	
			Leptolycinae: Dexorini	Kazantsev (2013)	
Dictyopterini	Houlbert, 1922	Lycidae	Dictyopterinae	Kleine, 1928	Erotinae: Dictyopterini
			syn. of Erotinae	Bocak & Bocakova (1990)	
			Dictyopterinae: Dictyopterini	Bocak et al. (2008)	
			Lycinae: Dictyopterini	Kazantsev (2005)	
			Dictyopterinae	Kazantsev (2012)	
			Erotinae: Dictyopterini	Kazantsev (2013)	
Dihammatini	Bocak & Bocakova, 2008	Lycinae			Metriorrhynchinae: Dihammatini
Dilolycinae	Kleine, 1926	Lycidae	syn. of Metriorrhynchini	Bocak & Bocakova (1990)	
Dilophotinae	Kleine, 1928		Lycidae: Dilophotini	Kleine (1933)	Metriorrhynchinae: Dilophotini
			synonym of Macrolycini	Bocak & Bocakova (1990)	
			Calochrominae: Dilophotini	Kazantsev (2005)	
			Ateliinae: Dilophotini	Bocak & Bocakova (1990)	
			Lycinae: Dilophotini	Kazantsev (2013)	
Dominopterini	Kazantsev, 2013	Leptolycinae	Dominopterina	stat. nov.	Lycinae: Leptolycini (1)
Duliticolinae	Kazantsev, 2002	invalid name			
Electropterini	Kazantsev, 2013	Leptolycinae	Electropterina	stat. nov.	Lycinae: Leptolycini (1)
Erotini (as Erotes)	Leconte, 1881		Erotinae	Bocak & Bocakova (1990)	Erotinae:/Erotini
			Lycinae: Erotini	Kazantsev (2005)	

Eurrhacina	Bocakova, 2005	Calopterini
Flagraxini	Kazantsev, 2002	Dictyopterinae
Hemiconderina	Bocak & Bocakova, 1990	Metriorrhynchini
Lampyrolycini	Kazantsev, 2018	Mimolibnetinae
Leptolycini	Leng & Mutchler	Lycidae
Libnetina	Bocak & Bocakova, 1990	Platerodini
Lopherotini	Kazantsev, 2012	Erotinae
Lycoprogenthini	Bocak et al. 2008	Dictyopterinae
Lygistopterini (as Lygistopteri)	Leconte, 1881	Lycidae
Lyponiina	Bocak& Bocakova, 1990	Platerodini
Lyropaeini	Bocak & Bocakova, 1989	
Macrolycinellini	Kazantsev, 2012	Lycinae
Macrolycinae	Kleine, 1928	Lycidae
Melanerotini	Kazantsev, 2010	*incertae sedis* (4)
Metanoeina	Sklenarova et al. 2014	Metriorrhynchini
Metriorrhynchinae	Kleine, 1928	Lycidae
Mimolibnetinae	Kazantsev, 2013	
Miniduliticolini	Kazantsev, 2002	
Platerodinae	Kleine, 1928	Lycidae
Paralycinae	Medvedev & Kazantsev, 1992	Lycidae
Platerodrilini	Kazantsev, 2005	Duliticolinae
Pristolycini	Winkler, 1952	
Proterotaphini	Kazantsev, 2012	Erotinae (1)
Pseudaplatopterina	Kazantsev, 2012	Lopherotini
Slipinskiini	Bocak & Bocakova 1992	Erotinae
Taphina	Bocak & Bocakova, 1990	Dictyopterini
Thilmaninae	Kazantsev, 2005	Lycidae
Thonalmini	Kleine, 1933	Lycinae
Trichalinae	Kleine, 1928	Lycidae
Vikhrevini	Kazantsev, 2013	*incertae sedis*

Erotinae: Erotini	Kazantsev (2013)	
Lycinae: Eurrhacini	Bocak et al. (2008)	Lycinae: Eurrhacini
syn. of Slipinskiini	Bocak & Bocakova (2008)	
syn. of Metriorrhynchini	Bocak et al. (2008)	
Lampyrolycina	new stat.	
Leptolycinae	Bocak & Bocakova (1990)	Lycinae: Leptolycini
Libnetinae	Bocak et al. (2008)	Metriorrhynchinae: Libnetini
Erotinae: Libnetini	Kazantsev (2013)	
syn. of Erotini	Li et al. 2017	
Erotinae: Lycoprogenthini	Kazantsev (2013)	Metriorrhynchinae: Lycoprogenthini
Lygistopterini	Kleine (1933)	
syn. of Calochrominae	Bocak & Bocakova (1990)	
Lycinae: Lyponiini	Bocak et al. (2008)	Ateliinae: Lyponiini
		Lyropaeinae/Lyropaeini
incertae sedis (6)		
Macrolycini	Kleine (1933)	Ateliinae: Macrolycini
		Metriorrhynchini: Metanoeina
Metriorrhynchini	Kleine (1933)	Metriorrhynchinae
Calochrominae: Metriorrhynchini	Kazantsev (2005)	
Lycinae: Metriorrhynchini	Kazantsev (2013)	
syn. of Dexorinae	Bocakova (2014)	Dexorinae: Mimolibnetini
		Lyropaeinae: Miniduliticolini
Platerodini	Kleine (1933)	Lycinae: Platerodini
Erotinae: Platerodini	Bocak & Bocakova (1990)	
Lycinae: Platerodini	Kazantsev (2013)	
syn. of Lyropaeini	Kazantsev (2002)	
Miniduliticolinae: Platerodrilini	Kazantsev (2005)	Lyropaeinae: Platerodrilini (3)
Lyropaeinae: Platerodrilini	Bocak et al. (2008)	
transferred to Lampyridae	Bocak & Bocakova (1990)	
		Erotinae: Proterotaphini
syn. of Erotini	Li et al. 2017	
Lycinae: Slipinskiini	Bocak et al. (2008)	Erotinae: Slipinskiini
Lycinae: Taphini	Kazantsev (2005)	Erotinae: Taphini
Dictyopterinae: Taphini	Bocak et al. (2008)	
Erotinae: Taphini	Kazantsev (2013)	
transferred to Omalisidae	Bocak & Brlik (2008)	Elateridae: Omalisinae (2)
syn. of Lycini	Bocak & Bocakova (1990)	Lycinae: Thonalmini
Trichalini	Bocak & Bocakova (1990)	
Trichalina	Bocak, 2002	
syn. of Metriorrhynchina	Sklenarova et al. (2014)	
		incertae sedis (5)

(1) The monotypic tribe with unclear affinities to Erotini and Taphini.
(2) Kusy et al. (2018).
(3) Platerodrilini limits remain unclear and previous studies recovered *Platerodrilus* as a terminal lineage in the widely defined Lyropaeinae (Masek et al. 2014).
(4) *Melaneros* is similarly to *Dilolycus* a highly modified Melanesian genus. It is unavailable for a molecular study.
(5) *Vikhrevia* Kazantsev is a highly modified monotypic genus, currently unavailable for a molecular study.
(6) Macrolycinellini are left in Lycidae as a tribe *incertae sedis* due to ambiguous information on their relationships (Kazantsev 2010, 2012, 2013, Figs S10–S12). *Macrolycinella* was earlier placed in Calopterini (Kleine 1933, Bocakova 2003) or Dictyopterinae (Kazantsev 2010) and inferred within a paraphylum containing Caenia and Calopteron (both Calopterini) and Lycostomus (Lycini) by Kazantsev (20130). The characters shown by Kazantsev (2010, 2012) do not robustly support the relationships with Dictyopterini. If the proposed relationships in Dictyopterini holds, the Macrolycinellini must be down-ranked to the subtribe Macrolycinellina in Dictyopterini in the current classification. Alternatively, they can return to Calopterini as earlier suggested.

Supplementary Table S4. The list of outgroup taxa included in the phylogenomic dataset.

Species	Accession	# of contigs	Source	Download Date	Reference
Outgroups:					
Onthophagus taurus (ref)	PRJNA167478	17483	i5K	5.3.2017	1
Tribolium castaneum (ref)	PRJNA12540	16631	iBeetle	5.3.2017	2,3
Dendroct. ponderosae (ref)	PRJNA360270	13088	ENS Metazoa	5.3.2017	4
Anoploph. glabripennis (ref)	PRJNA167479	22035	i5K	5.3.2017	5
Leptinotarsa decemlin. (ref)	PRJNA171749	24671	i5K	5.3.2017	1
Buprestoidea					
Agrilus planipennis (ref)	PRJNA230921	15497	i5K	5.3.2017	1
Elateroidea					
Chauliognathus flavipes	PRJNA347807	92143	NCBI,SRA	5.3.2017	6
Rhagophthalmus sp.	PRJNA339505	38989	NCBI,SRA	5.3.2017	7
Phrixothrix hirtus	RJNA347807	31428	NCBI,SRA	5.3.2017	6
Photinus pyralis	PRJNA321737	174087	NCBI,SRA	5.3.2017	8
Asymmetricata circumdata	PRJNA339505	55590	NCBI,SRA	10.1.2017	7
Aquatica ficta	PRJNA339505	70558	NCBI,SRA	10.1.2017	7
Pyrocoelia pectoralis	PRJNA339505	76908	NCBI,SRA	10.1.2017	7
Melanotus cribricollis	PRJNA417752	38705	NCBI,SRA	15.4.2017	9
Ignelater luminosus	PRJNA418169	27553	fireflybase.org	15.4.2017	10

(ref) - reference taxon

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Supplementary Table S5. The list of ingroup taxa included in the analysis. All samples are included in the BioProject No. PRJNA123456.

Subfamily Tribe	Species	Geographic origin	GenBank SRA Acc. No.
Dexorinae			
Dexorini	*Dexoris ruzzieri* Bocak, 2018	Sierra Leone	ABC123456
Calochrominae			
Calochromini	*Lygistopterus sanguineus* L., 1758	Turkey	ABC123456
Erotinae			
Erotini	*Konoplatycis otome* Kōno, 1932	Japan	ABC123456
Dictyopterini	*Dictyoptera* sp.	Japan	ABC123456
Taphini	*Taphes brevicollis* Waterh., 1879	Malaysia	ABC123456
Ateliinae			
Ateliini	*Scarelus anthracinus* Bocakova & Bocak, 1999	Malaysia	ABC123456
Lyponiini	*Ponyalis quadricollis* Kiesw., 1874	Japan	ABC123456
Macrolycini	*Macrolycus* sp.	Japan	ABC123456
Lycinae			
Conderini	*Conderis signicollis* Kirsch, 1875	Malaysia	ABC123456
Leptolycini	*Leptolycus* sp.	Cuba	ABC123456
Platerodini	*Plateros* sp.	Malaysia	ABC123456
Calopterini	*Calopteron* sp.	USA: Illinois	ABC123456
Lycini	*Lycostomus kraatzi* Bourgeois, 1882	Turkey	ABC123456
Lyropaeinae			
Antennolycini	*Antennolycus constrictus* Bocakova & Bocak, 1999	Malaysia	ABC123456
Lyropaeini	*Lyropaeus optabilis* Kleine, 1926	Malaysia	ABC123456
Platerodrilini	*Platerodrilus* sp.	Malaysia	ABC123456
Metriorrhynchinae			
Dihammatini	*Dihammatus* sp.	Malaysia	ABC123456
Lycoprogentini	*Lycoprogentes* sp.	Malaysia	ABC123456
Dilophotini	*Dilophotes* sp.	Malaysia	ABC123456
Libnetini	*Libnetis* sp.	Malaysia	ABC123456
Metriorrhynchini	*Cautires* sp.	Malaysia	ABC123456
	Sulabanus sp.	Indonesia	ABC123456

Supplementary Table S6. Number of identified target genes in the analyzed transcriptomes and draft genomes.

Species name	Data type	Orthologs found	Orthologs after outliers and IC0 removal
Ingroups			
Antennolycus constrictus	RNA-Seq	3739	3655
Calopteron sp.	RNA-Seq	3668	3645
Conderis signicollis	RNA-Seq	3678	3659
Dexoris ruzzieri	shotgun genome	3897	3794
Dictyoptera aurora	RNA-Seq	3401	3344
Konoplatycis otome	RNA-Seq	3516	3480
Leptolycus sp.	shotgun genome	3797	3714
Lycostomus kraatzi	RNA-Seq	3501	3472
Lygistopterus sanguineus	RNA-Seq	3694	3675
Lyropaeus optabilis	RNA-Seq	3529	3507
Macrolycus sp.	RNA-Seq	3656	3638
Platerodrilus sp.	RNA-Seq	3283	3258
Plateros sp.	RNA-Seq	3661	3640
Ponyalis quadricollis	RNA-Seq	3563	3543
Sulabanus sp.	RNA-Seq	3775	3749
Scarelus anthracinus	RNA-Seq	3744	3724
Taphes brevicollis	RNA-Seq	3710	3697
Cautires sp.	shotgun genome	3780	3705
Dihammatus sp.	RNA-Seq	3731	3708
Dilophotes sp.	RNA-Seq	3715	3699
Libnetis sp.	RNA-Seq	3732	3710
Lycoprogenthes sp.	RNA-Seq	3686	3667
Outgroups			
Buprestoidea			
Agrilus planipennis (ref)	proteome	4214	4165
Elateroidea			
Chauliognathus flavipes	RNA-Seq	3669	3611
Rhagophthalmus sp.	RNA-Seq	3769	3750
Phrixothrix hirtus	RNA-Seq	2878	2846
Photinus pyralis	RNA-Seq	3403	3376

Asymmetricata circumdata	RNA-Seq	3603	3580
Aquatica ficta	RNA-Seq	3703	3684
Pyrocoelia pectoralis	RNA-Seq	3767	3750
Melanotus cribricollis	RNA-Seq	3683	3665
Ignelater luminosus	proteome	3869	3840

Supplementary Table S7. The list of taxa included in the morphological analysis (modified from Kazantsev 2013); their original and revised placements are given.

A. Lycid taxa with proved or presumed larviform adult females as designated by Kazantsev (2013):

	Placement *sens*u Kazantsev (2013)	Revised placement (this study)
Dexoris tessmani Bocak & Bocakova, 1988	Leptolycinae: Dexorini	Dexorinae: Dexorini
Mimolibnetis patruelis Kazantsev, 2013	Mimolibnetinae	Dexorinae: Mimolibnetini
Lyropaeus optabilis (Kleine, 1926) (as *Lyroneces*)	Leptolycinae: Lyropaeini	Lyropaeinae: Lyropaeini
Platerodrilus svetae Kazantsev, 2009	Miniduliticolinae: Platerodrilini	Lyropaeinae: Platerodrilini
Cessator luquillonis Kazantsev, 2009	Leptolycinae: Electropterini	Lycinae: Leptolycini
Dominopteron hispaniolum Kazantsev, 2013	Leptolycinae: Dominopterini	Lycinae: Leptolycini
Electropteron nepos Kazantsev, 2013	Leptolycinae: Electropterini	Lycinae: Leptolycini
Leptolycus heterocornis Leng & Mutchler, 1922	Leptolycinae: Leptolycini	Lycinae: Leptolycini
Nanolycus gnomus Kazantsev, 2013	Leptolycinae: Electropterini	Lycinae: Leptolycini
Tainopteron milleri Kazantsev, 2009	?Leptolycinae: Leptolycini	Lycinae: Leptolycini
Ceratoprion sobrinus Kazantsev, 2013	Leptolycinae: Leptolycini	Lycinae: Calopterini
Prioceraton ignavum Kazantsev, 2008	Leptolycinae: Leptolycini	Lycinae: Calopterini
Pseudacroleptus gorgonus Kazantsev, 2013	Leptolycinae: Leptolycini	Lycinae: Calopterini
Pseudacroleptus lamellifer Kazantsev, 2008	Leptolycinae: Leptolycini	Lycinae: Calopterini
Neolyrium duidaense Kazantsev, 2005	Leptolycinae: Leptolycini	Lycinae: Calopterini
Lycinella parvula Gorham, 1884	Ateliinae (?)	Lycinae: Calopterini
Tishechkinia carltoni (Kazantsev, 2007)	Leptolycinae: Leptolycini	Lycinae: Calopterini
Scarelus umbrosus Kleine, 1932	Ateliinae	Ateliinae: Ateliini

B. Lycid taxa with fully metamorphosed adult females:

	Placement *sensu* Kazantsev (2013)	Revised placement (this study)
Calochromus glaucopterus (Guerin-Men., 1833)	Lycinae: Calochromini	Calochrominae: Calochromini
Lygistopterus sanguineus (Linnaeus, 1758)	Lycinae: Calochromini	Calochrominae: Calochromini
Aferos dewittei Kazantsev, 2000	Lycinae: Slipinskiini	Erotinae: Slipinskiini
Aplatopterus rubens (Gyllenhal, 1817)	Lycinae: Lopherotini	Erotinae: Erotini
Pseudaplatopterus trilineatus (Melsheimer, 1846)	Lycinae: Lopherotini	Erotinae: Erotini
Eros humeralis (Fabricius, 1801)	Lycinae: Erotini	Erotinae: Erotini
Eulopheros harmandi (Bourgeois, 1902)	Lycinae: Lopherotini	Erotinae: Erotini
Platycis minuta (Fabricius, 1787)	Lycinae: Erotini	Erotinae: Erotini
Lopheros fraternus (Randall, 1838)	Lycinae: Lopherotini	Erotinae: Erotini
Helcophorus miniatus Fairmaire, 1891	Erotinae: Dictyopterini	Erotinae: Dictyopterini
Dictyoptera aurora (Herbst, 1784)	Erotinae: Dictyopterini	Erotinae: Dictyopterini

Taphes brevicollis Waterhouse, 1878	Erotinae: Taphini	Erotinae: Taphini
Cerceros flabellatus (Motschulsky, 1860)	Lycinae: Macrolycini	Ateliinae: Macrolycini
Mesolycus shelfordi (Bourgeois, 1906)	Lycinae: Dilophotini	Ateliinae: Dilophotini
Conderis signicollis (Kirsch, 1875)	Erotinae: Conderini	Lycinae: Conderini
Xylobanellus erythropterus (Baudi, 1871)	Erotinae: Conderini	Lycinae: Conderini
Caenia kirschi Bourgeois, 1880	Lycinae: Calopterini	Lycinae: Calopterini
Calopteron reticulatum (F., 1775)	Lycinae: Calopterini	Lycinae: Calopterini
Lycostomus praeustus (Fabricius, 1792)	Lycinae: Lycini	Lycinae: Lycini
Plateros flavoscutellatus Blatchley, 1914	Lycinae: Platerodini	Lycinae: Platerodini
Macrolycinella dichroma Kazantsev, 2010	Lycinae: Macrolycinellini	Macrolycinellini, *incertae sedis*
Melaneros acuticollis Fairmaire, 1879	Lycinae: Melanerotini	Melanerotini, *incertae sedis*
Metriorrhynchus thoracicus (Fabricius, 1801)	Lycinae: Metriorrhynchini	Metriorrhynchinae: Metriorrhynchini
Libnetus corporaali Pic, 1921, Libnetini	Erotinae: Conderini	Metriorrhynchinae: Libnetini
Dilophotes depressicornis Pic, 1921	Lycinae: Dilophotini	Metriorrhynchinae: Dilophotini
Outgroup		
Thilmanus obscurus (Baudi, 1871)	Drilidae: Thilmaninae	Elateridae: Omalisinae

Supplementary Table S8. The list of characters coded in the morphological dataset.

The set of morphological characters defined by Kazantsev (2013) and here, it is used for the morphological analysis (Tab. S9). The original dataset contained 65 characters and only male characters were coded. Some important character systems including female and larval morphology could not be considered due to the high proportion of missing data owing to unknown females of presumably neotenic lineages and a poor knowledge on net-winged beetle larvae.

The uninformative characters (uniform for all taxa, characters containing only a single state and several unknown character states or autapomorphies were excluded from the original dataset (all remaining characters are related to males, except the character 52 which designates proved or hypothesized larviform females). Kazantsev (2013) defined characters 62–65 only with character states either "0" or "?". As these character states are uninformative, they were also erased from the dataset for the purpose of the present analysis. The characters excluded from the original dataset: 9, 11, 19, 33, 38, 47, 50, 55, 56, 62, 63, 64, 65. The modified dataset is presented in Tab. S9. The illustrations of characters and their detailed descriptions were given by Kazantsev (2005, 2013), further structures have been displayed in dozens of morphological studies dealing with various tribes and genera (see References). Some potential miscoding were identified, but, as we do not have the same species at our disposal, we are not able to reliably recode the character states and we keep characters states as originally published. The descriptions of morphological traits was slightly modified from Kazantsev (2013) and all comments on used characters are clearly separated and provided by the authors of this study.

The evolution of characters was investigated on the topology inferred from the morphological dataset (Tab. S9) and on the topology with basal relationships forced to the relationships inferred from the genomic analysis and the terminal branches unavailable in the phylogenomic analysis forced to relationships as much as possible following the topology recovered from the morphological analysis (i.e., the members of tribes if they were recovered in a distant position were considered as a sister to the remaining taxa from the same tribe and if a taxon was incorrectly inferred as a member of distant tribe, the relationships of the given tribe follows the topology after an alien taxon was pruned out. The tree used for the inference of character statistics is shown in Fig. S10.

1. Gula: 0, absent (ventral closure represented by an occipital sulcus); 1, short, located anteriad of posterior tentorial pits; 2, short, transverse, located posteriad of posterior tentorial pits; 3, elongate, located posteriad of posterior tentorial pits.

Comment. The shape of gula is highly variable in net-winged beetles, but the distribution of character states does not support neither relationships proposed by the morphological nor phylogenomic analysis and its length is very high on both topologies (Tab. S10).

2. Fastigium (the angle between the vertex and the frons): 0, acute; 1, more or less right-angled; 2, blunt.

Comment: The shape of the head is variable in net-winged beetles and the taxa with apparently reduced mouthparts have small, mouth opening and hypognathous head. As a result, multiple taxa with presumed neoteny, share the acute angle between vertex and frons. *Platycis* is coded with these taxa due to the presence of prolonged cranium, unlike its close relatives (*Pseudaplatopterus*, *Eros*, *Lopheros*, *etc*.). The taxa with more or less prominent rostrum share obtuse, to straight angle between vertex and thorax. The presence of the rostrum is known in taxa which visit flowers and take nectar (*Lycostomus*, *Lygistopterus*, *Macrolygistopterus*, *Lucaina*, *Mesolycus*, some *Metriorrhynchus, Porrostoma, Leptotrichalus, etc*.). Multiple origins of rostrum has been documented in flower visiting Metriorrhynchini (*Leptotrichalus*, *Porrostoma*, some *Metriorrhynchus*; Sklenarova et al. 2014). As a result, the character has much lower fit with the genomic topology than with the topology inferred exclusively from morphological data which suggest relationships of rostrate taxa. We recovered following characteristics for this trait: length (L) 6 and 13 steps, ci=0.333 and 0.154 on the morphological and genomic topology.

3. Antenna, the number of antennomeres: 0, 11; 1, 10.

Comment. The number of antennomeres is reduced in some taxa with presumed larviform females (*Lyropaeus*, *Mimolibnetis*, *Neolyrium*, *Tishechkinia*). The shorted antennae, sometimes with randomly fused antennomeres are known in the neotenic lineages of click-beetles (Omalisinae, Agrypninae: Drilini). The differentiation of antennomeres is connected with metamorphosis and a modified or weakly sclerotized apical antennomere is encountered in some incompletely sclerotized elateroid beetles. The character fits poorly with both topologies (Tab. S10).

4. Antennomeres: 0, filiform; 1, flattened, but more or less parallel-sided; 2, flattened and dentate; 3, flabellate.

Comment: The shape of antennae is variable and sometimes internal clades or closely related species can have distinct modifications of antennae. The common multiple origins of the similar antennal morphology was demonstrated by several molecular analyses (Sklenarova et al. 2014, Bocek & Bocak 2017). The character is coded in the original dataset for a single species which represent a genus or a tribe and dataset does not reflect potential ambiguity of the coding when different types of antennae are encountered within studied genera or tribes.

5. Pedicel (antennomere 2): 0, elongate, subequal in length to antennomere 3; 1, elongate, but conspicuously shorter than antennomere 3; 2, transverse.

Comment. The length of the pedicel seems incorrectly coded for some taxa in the original dataset. E.g., *Lyropaeus* (=*Lyroneces*) and *Scarelus* have antennomere 2 transverse, although shorter than antennomere 3 (Kazantsev 2003, Fig. 173, 174); *Ceratoprion* has the antennomere 2 slightly longer than antennomere 3 (Kazantsev 2003; Fig. 172). When the shape of antennomere 2 is re-investigated, a higher variability than suggested by Kazantsev (2013) is encountered. Nevertheless, the shared shape and length merely defines tribes or clades of closely related genera, but it does not support deeper relationships. See Fig. 4.

6. Antennomere 3: 0, elongate, subequal in length to antennomere 4; 1, elongate, but conspicuously shorter than antennomere 4; 2, transverse or subquadrate.

Comment. The relative length of antennomere 3 is similarly variable and the closely related taxa can have very different shape of antennomere 3. For example, *Lyropaeus* and *Platerodrilus*, despite being placed in the same subfamily by previous and current analyses, have very different antennae (Fig. 4; Bocak & Bocakova 2008, Masek et al. 2014), similarly *Libnetis* and *Libnetisia* or *Pyropterus* and *Dictyoptera* differ in the shape of antennae (Kleine, 1942, Bocak & Bocakova 1987, Bocakova 2001). The shape of basal antennomeres should not be so affected by the olfactory function of antennae as terminal segments, but a high level of variability has nevertheless been identified. This character does not fit well neither with morphological or genomic topology (L=11 and 15, respectively; Tab. S10).

7. Labrum: 0, free, at least proximally located inside oral cavity, 1, free, but entirely located anteriad of epistoma.

Comment. Four apparently unrelated taxa have fully exposed labrum: *Lycostomus*, *Lygistopterus* and *Metriorrhynchus* which have long slender rostrum and their labrum cannot be retracted to the rostrum and *Libnetis*. These taxa are unrelated and all origins must be considered independent and the distribution of this character state does not contribute to any recovered topology (L=5 in both cases, Tab. S10).

8. Mandibles: 0, developed; 1, rudimentary.

Comment. The rudimentary mandibles are characteristic for most males of neotenic taxa (except *Lycinella* and *Platerodrilus*) and we hypothesize that either miniaturization or the modification of ontogeny resulting in female neoteny commonly causes incomplete differentiation of mouthparts in conspecific males (see further characters describing the mouthparts and the main text). These modifications in neotenic taxa affect antennae (lower number of antennomeres, incomplete sclerotization of apical antennomeres, much more common irregular fusion of some antennomeres than in the non-neotenic lineages), mouthparts (general miniaturization of mandibles, palpomeres, labium and the loss of some structures, *e.g.*, a lower number of labial palpomeres, a slender and pointed apex of the terminal palpomeres). The separate coding of all these structures in the morphological analysis causes a relative over-representation of linked traits. We suggest that all these traits are affected by a single evolutionary modification and the trait are also exposed to the similar selection (short life span, no feeding in the adult stage, miniaturization). The character needs a higher number of steps on the genomic topology due to inferred multiple origins of neotenic lineages (L=3 and 5, Tab. S10).

9. Maxillae, ultimate palpomere: 0, distally pointed, 1, distally flattened and more or less dilated; 2, palpi absent.

Comment. Similarly to antennae, the males of the taxa with proved or presumed larviform females have commonly modified apical palpomeres. Seldom the number of palpomeres is lowered, but the apical palpomere is commonly slender, pointed in contrast with flat, widened palpomeres in other taxa. The similar shape of pointed terminal palpi is known in two taxa with winged females: *Libnetis* and *Taphes*. The character fits well with the morphology based topology (L=1) in contrast with the genomic topology (L=8; Tab. S10).

10. Labium, praementum: 0, free; 1, rigidly connected to (mentum and) gula.

Comment. The fused praementum and gula in known in two distantly related taxa: *Helcophorus* (Erotinae: Dictyopterini) and *Mimolibnetis* (Dexorinae: Mimolibnetini). The character does not contribute to the topology and two independent origins have to be hypothesized (Tab. S10).

11. Labium, praementum: 0, divided into a pair of sclerites; 1, divided by median suture; 2, undivided.

Comment. Most net-winged beetles have compact praementum and the praementum is modified only in a few taxa. The fragmented praementum is encounter only in *Calopteron* (autapomorphy) and the longitudinal suture is present in *Cerceros* (Ateliinae: Macrolycini) and *Caenia* (Lycinae: Calopterini). The character does not contribute to the topology (Tab. S10).

12. Labium, number of palpomeres: 0, 3 palpomeres; 1, one palpomere or palpi reduced to sensillae.

Comment. The similar modifications of labial and maxillary palpomeres palpomere are observed in most neotenic taxa. See above the discussion of the modification of mouthparts in general. Some neotenic taxa have unmodified labial palpi, i.e., *Dominopteron* (Lycinae: Leptolycini) and *Scarelus* (Ateliinae: Ateliini).

13. Labium, ultimate palpomere: 0, distally pointed; 1, distally flattened and more or less dilated; 2, palpi absent.

Comment. See above the discussion of the modification of the maxillary palpomeres. The shape of labial palpi mostly resembles those of maxillary palpi. Some non-neotenic taxa can have also a modified apical palpomere (*Taphes*, *Libnetis*, *Mesolycus*). Contrary, some neotenic taxa have apical palpomere similar to the majority of net-winged beetles (*Dominopteron*, *Lycinella*, *Platerodrilus*, *Scarelus*). In

most cases, i.e. except *Dominopteron*, the parallel evolution of several characters defined on mouthparts is encountered. This characters needs 5 steps on the morphology-based topology, but 11 steps on the phylogenomic topology. The separate coding of labial and maxillary palpi gives an inappropriate weight to the traits which develop in tandem owing to the neotenic development of females.

14. Pronotum, median carina (sometimes bifurcate posteriorly or taking shape of a diamond): 0, complete; 1, incomplete, present only anteriorly or posteriorly; 2, absent.

Comment. The net-winged beetles have commonly variably arranged pronotal carinae which are in many cases used as a diagnostic character for the delimitation of genera and sometimes also higher taxa. Previous studies have shown, that a very similar pattern of carinae can evolve repeatedly in quite distant lineages (Sklenarova et al. 2014). When the character is mapped on the phylogenomic tree, we recovered the fit of this character with molecular relationships in some cases, such as the absence of lateral carinae in all Ateliinae and most Lycinae and distinct, although variably arranged carinae in all Erotinae. Conversely, Metriorrhynchini are the only lineage of Metriorrhynchinae with apparent fronto-lateral carinae and seven areolae arranged in a complex pattern (Fig. 5). The parallel evolution of the similar pattern was recovered in Conderini, a tribe in a sister position to other Lycinae. Their characteristic arrangement of pronotal carinae generally resemble some Erotinae, especially Dictyopterini, distantly related Lycoprogenthini (Metriorrhynchinae) and several Metriorrhynchini (*Hemiconderis*, *Wakarumbia*; Sklenarova et al. 2014). The coding of this trait as proposed by Kazantsev (2013) needs 9 steps on the morphology-based topology and even three more steps on the phylogenomic topology (Tab. S10).

15. Prosternum: 0, tripartite, divided into prosternum proper and a pair of sterno-pleural sclerites; 1, representing a single sclerite.

Comment. The defined character states evolved six times and very low ci was characteristic for this character. The topology recovered from transcriptomes suggests additional two steps.

16. Prosternum: 0, triangular or Y-shaped, narrow and medially concave; 1, sub-rectangular, relatively broad and anteriorly straight or convex.

Comment. The length of the prosternum is commonly correlated with soft-bodiedness in Elateroidea. All well-sclerotized elateroids have long prosternum with an apparent prosternal process and the soft-bodied forms show a strong trend for the shortened prosternum. Its evolution was discussed in detail for modified neotenic lineages of Elateridae (Bocak et al. 2018, Kusy et al. 2018). The prosternum is very short in most net-winged beetles (Fig. 5X), only *Leptolycus* has a longer prosternum (Fig. 4B). Intermediate forms are known in some other forms (Kazantsev 2013). Two steps are needed for evolution of this trait on both topologies.

17. Mesoscutum, scutellum: 0, small, with respect to scuta; 1, subequal in size to each of the scuta; 2, large, surpassing each of the scuta in size.

18. Mesoscutum, scutellum: 0, not reaching anterior margin; 1, touching anterior margin; 2, making conspicuous part of the anterior margin.

19. Mesoscutum, scutellum: 0, with median suture; 1, without median suture.

20. Mesoscutum, scuta: 0, both undivided; 1, each divided by a transverse or oblique suture.

21. Mesoscutum, posterior process of scutellum: 0, vestigial, with considerable elytro-scutellar dehiscence; 1, developed and functional, locking folded elytra.

Comment. The reduced posterior processes are recorded mostly in taxa with presumably larviform females. There is a possibility that premature arrest of metamorphosis results in incomplete development of these structures characteristic for taxa fully metamorhosed in both sexes.

22. Mesoventrite: 0, separated from mesepisternum (by suture or suture and additional sclerite); 1, semi-fused with mesepisternum; 2, fused with mesepisternum.

23. Mesoventrite, sterno-pleural sclerite: 0, present; 1, absent.

24. Mesoventrite: 0, divided by median suture; 1, without median suture.

25. Mesepimeron: 0, subequal in length to mesepisternum; 1, considerably shorter than mesepisternum.

26. Mesepimeron: 0, subequal in width to mesepisternum; 1, considerably narrower than mesepisternum.

Comment. The detailed study of the thoracic morphology was published by Kazantsev (2005) and the characters 17–26 describe various mesothoracic traits. These characters have generally a low fit with morphology-based topology and 3 to ten steps are needed to explain their evolution (Tab. S10). In most cases, the topology based on transcriptomic data suggest even more complicated evolution for all but three of these characters [characters 19 (4 steps), 22 and 24 (both 3 steps)]. As a possible explanation for such variability, we may consider the absence of evolutionary constraints in poorly flying and soft-bodied net-winged beetles. The loosely connected, weakly sclerotized sclerites might readily change their shape and position compared to their relatives with a compact and fully-sclerotized body.

27. Elytron: 0, not coadapted with thoracic and abdominal structures; 1, coadapted with thoracic, but not with abdominal structures; 2, coadapted with thoracic and abdominal structures.

Comment. The level of the coadaptation in Elateroidea is tightly connected with the level of sclerotization, *i.e*., with the completeness of final stages of the metamorphosis (Kundrata & Bocak 2011, Bocak et al. 2018, Bocek et al. 2018, Kusy et al. 2018) and we can expect a similar evolution of this trait in net-winged beetles. The males of some net-winged beetles have even shortened elytra (Alyculini, *Cautires apterus*) and resemble in some aspects the incompletely metamorphosed females of some click beetles (Elateridae: Omalisinae; Bocak et al. 2013, Palata & Bocak 2012, Bocek et al. 2018).

Further phenomenon affecting the modification of elytra is the evolution of aposematic signaling. The widened and in extreme cases globular elytra evolved in multiple net-winged beetles and their expansion automatically results in the loss of any coadaptation between the short and narrow abdomen and dilated elytra. As an example we can propose *Broxylus* Waterhouse, 1878 from Sulawesi which was incorrectly placed in Calopterini possibly owing to the similar structure of elytra (Bocakova 2003). Dilated elytra in various degrees are characteristic for Lycini and numerous Calopterini.

Kazantsev (2013) coded for most neotenic the loss of coadaptation and as the result this trait supported the rare origin of neoteny in his topology (2 steps). The character need 5 steps on the phylogenomic topology (Tab. S10).

28. Elytron: 0, with longitudinal costae and reticulation; 1, with longitudinal costae but without reticulation; 2, without longitudinal costae and reticulation.

Comment. The elytral costae have apparently the strengthening function in the soft-bodied net-winged beetles and their reduction is commonly connected with miniaturization (common in the males of taxa with larviform females). The coding might be problematic in some cases – we identified the presence and absence of transverse costae in closely related taxa (Figs 6N, O). Additionally, the costae are less apparent in taxa with a slender body(Fig. 6M). The character needs three steps in both topologies.

29. Elytron, epipleuron: 0, absent; 1, present at the base of elytron.

Comment. The absent epipleuron was coded for most taxa, only *Aferos* and *Thilmanus* were designated as taxa without epipleuron by Kazantsev (2013), but this character is variable and elytral epipleuron is developed in some degree also in other net-winged taxa which are absent from the analysis. For example, some *Lycus* have elevated costa 4 and apparent epipleuron in the basal part of elytra.

30. Metaventrite, discrimen (metasternal suture): 0, reaching anterior margin; 1, not reaching anterior margin.

Comment. The discrimen and metendosternite are structures on which the metathoracic muscles are attached. As a result their reductions can be affected by the flight activity and the general activity of adults. There are several hypothesized reasons for low activity of net-winged beetle adults. They are chemically protected and depend on aposematic signaling much more than on the rapid escape reaction characteristic for their unprotected relatives such as click-beetles. Further, they usually do not take food in an adult stage, which makes higher energetic investment in adult activity problematic. The net-winged beetles have a weakly sclerotized body which does not provide an adequate support for flight muscles. The reduction of the metasternal discrimen is more commonly encountered in multiple taxa with neotenic females, but also in some non-neotenic lineages: *Calopteron*, *Lycostomus* (both Lycinae), *Melaneros* (*incertae sedis*) and *Mesolycus* (Metriorrhynchinae: Dilophotini). The character needs 5 steps on the morphology-based topology, but 9 steps on the phylogenomic topology (Tab. S10).

31. Metendosternite, lateral arms: 0, absent; 1, present.

Comment. The lateral arms serve as an attachment point for thoracic muscles and their absence was recorded in several unrelated lineages. See discussion under the character 30. Multiple steps are need for this character on both topologies (8 and 5 steps, respectively; Tab. S10).

32. Metendosternite, transverse suture: 0, absent; 1, present.

Comment. The transverse suture strengthens the metendosternite which serves for the attachment of muscles and their absence was recorded in several unrelated lineages, with a more common absence in the lineages with neotenic females. See discussion under the character 31. The character needs 4 steps and 8 steps on morphological and phylogenomic topology, respectively.

33. Mesothoracic spiracles, orifice: 0, simple; 1, hooded dorsally.

Comment. Four taxa have hooded mesothoracic spiracles and they considered unrelated in both morphology and DNA-based classifications. Apart from genera included in the analysis (*i.e.*, Ateliinae: Macrolycini: *Cerceros* , Lycinae: Conderini: *Conderis*, Metriorrhynchinae: Dilophotini: *Mesolycus* and Metriorrhynchini: Metriorrhynchus), the hooded orifice is known also in some Lycini: *Lycus*.

34. Wing venation: wedge cell: 0, present; 1, absent.

35. Wing venation: cu-a brace: 0, absent; 1, located at or proximad of Cu fork; 2, located distad of Cu fork.
Comment. Wing venation does not contribute to the morphology-based topology and 7 steps are needed for character 34 and 12 steps for character 35 on morphology based topology. The phylogenomic topology needs slightly more steps for both characters (Tab. S10).

36. Trochanters; connection to femurs: 0, direct; 1, oblique (more than a half of their anterior surface incised).
Comment. The obliquely attached femora are known in Dexorinae, *i.e.* in *Dexoris* and *Mimolibnetis*. The characters needs 2 steps on morphology-based topology and only 1 step on the phylogenomic topology.

37. Femurs and tibiae: 0, both flattened; 1, femurs not or little flattened, tibiae flattened; 2, both not or little flattened.

38. Tibial spurs: 0, absent; 1, present.

39. Tarsomeres 3 and 4: 0, slender; 1, widened.
Comment. The slender tarsomeres are characteristic for small bodied males whose conspecific females are larviform. Due to the multiple origins of neoteny, this character state has a distribution highly inconsistent with phylogenomic topology. Highly similar distribution is observed in the presence of tarsal pulvilles (=tarsal pads). Besides the effect of miniaturization, the tendency to reduce differentiation of terminal body parts as in antennae and palpi can be hypothesized. Apart from neotenics, the slender tarsomeres were coded for *Taphes* (Dictyopterinae) who has additionally pointed palpomeres similarly to neotenics and for *Macrolycinella* (Calopterini) a member of the lineage with a high amount of presumably neotenic taxa. The same morphology was observed in Proterotaphes (type genus of Proterotaphini) which shows relationships to Taphini.

40. Tarsomere 1, plantar pad: 0, absent; 1, present.
Comment. See discussion under the character 39. The slender tarsomeres regularly do not have plantar pads. Apart from those with slender tarsomeres 3 and 4 (character 39), the absent tarsal pads were additionally coded for small-bodied *Mesolycus* and *Libnetis* (closely related tribes of Metriorrhynchinae; Dilophotini, Libnetini).

41. Tarsomere 3, plantar pad: 0, absent; 1, present.
Comment. See discussion under the character 39. Similarly to previous two characters, the absent pads in tarsomere 3 are known in neotenic forms including the outgroup (*Thilmanus*), but not in other net-winged beetles. Such character supports the deep position of neotenics which is in conflict with the phylotranscriptomic topology.

42. Abdomen, median suture on tergites: 0, present; 1, absent.
Comment. The median suture was coded for unrelated neotenics (Dexorinae: *Dexoris*, Lyropaeinae: *Lyropaeus*, Lycinae: Calopterini: *Ceratoprion*, *Prioceraton* and non-neotenic Ateliinae: *Dilophotes*. The character distribution is in conflict with the phylogenomic topology (6 steps) and it needs 2 steps on the morphology-based topology (Tab. S10).

43. Paraproct (male tergite 9): 0, divided by median suture; 1, not divided by median suture, but not fused with proctiger; 2, not divided and fused with proctiger.

Comment. This is one of ill-fitting character on both morphology- and DNA-based topology – 9 and 12 steps, ci=0.222 and 0.167, respectively; Tab. S10).

44. Male ultimate ventrite (sternite 9): 0, with short (not surpassing distal part of sternite in length) proximal process; 1, with long (surpassing distal part of sternite in length), but relatively broad proximal process; 2, with long and narrow proximal process (spiculum gastrale).
Comment. This is another ill-fitting character on both morphology- and DNA-based topology – 12 and 15 steps, ci=0.167 and 0.133, respectively; Tab. S10).

45. Abdominal spiracles, location: 0, on membrane between sternite and tergite; 1, at the edge of sternite; 2, on sternite, rather distant from the edge; 3, at the edge of tergite.

Comment. The location of spiracles is similarly variable also in net-winged beetles larvae (Bocak & Matsuda 2003). The character needs 14 steps on morphology-based topology and additional three steps on the phylogenomic topology (Tab. S10).

46. Male genitalia: phallobase: 0, noticeably composite; 1, uniform.

Comment. Three origins were inferred on both topologies. The composite phallobase was coded for *Dexoris*, *Leptolycus*, and *Platerodrilus* (Tab. S9). The character is variable within these taxa, some *Dexoris* does not have any sclerotized phallobase (Bocak & Bocakova 1988), some *Platerodrilus* have compact phallobase (Masek & Bocak 2014). All three taxa for which composite phallobase have proved (*Leptolycus* and *Platerodrilus*) or presumed (*Dexoris*) neotenic females. The fragmentation and substantial reduction of the phallobase may be connected to the neotenic development of females as female genitalia of these taxa are also similarly simplified (Wong 1996, Brlik & Bocak 2008).

47. Male genitalia: phallobase: 0, symmetric; 1, slightly asymmetric (in both halves same structures present); 2, strongly asymmetric.

Comment. The asymmetrical phallobase was earlier used to define Calochrominae sensu Kazantsev (2005). The character needs 6 steps in the current morphology-based topology and only slightly contributes to inferred relationships. The phylogenomic topology needs an additional step.

48. Male genitalia: phallobase, latero-proximal apodemes: 0, present; 1, absent.

49. Male genitalia: phallobase, median suture (or a pair of lateral sutures): 0, present or phallobase represented by a paired sclerite; 1, absent.

Comment. The distribution of character states needs multiple steps on both morphology- and DNA-based topology – 10 and 9 steps, ci=0.222 and 0.167, respectively; Tab. S10).

The character needs 10 steps on morphology-based topology and only a step less on the phylogenomic topology.

50. Male genitalia: phallus (=median lobe): 0, symmetrical; 1, asymmetrical.

Comment. The high variability of male genitalia is characteristic for insects with high numbers of sympatrically occurring species which use genital morphology as an isolating mechanism (Malohlava & Bocak 2010, Bocak& Yagi, 2010). Both character states are present in some lineages such as Metriorrhynchini, Lycini, and Platerodini. Conversely, some lineages have consistently a single type of the phallus

(see genus and tribe level revisions of net-winged beetles in References).

51. Male genitalia: parameres: 0, absent; 1, free, ca. half length of median lobe; 2, free, ca. as long as median lobe; 3, fused with median lobe.

Comment. The presence and modifications of parameres are traits with very low congruence with both topologies (16 and 19 steps, respectively). The morphology of male genitalia is very often species specific and the general of male genitalia is often stable within genera. This characters seems to be inappropriately variable for the inference of deep-level relationships.

52. Female: 0, winged, with complete metamorphosis; 1, larviform, without pupal stage, or unknown.

Comment. Kazantsev (2013) defined this trait and did not code any further female characters. The female characters are similarly variable as those defined in males and their inclusion in the analysis with a high number of only presumably neotenic, *i.e*., unknown, females, would result in a high proportion of missing data in the analysis. Additionally, the coding of larviform females in the molecular analysis becomes problematic due to the complicated homologation of states for larval and adults semaphoronts under a single defined character. Based on the molecular phylogenomic hypothesis, we strongly prefer multiple origins of larviform females in net-winged beetles, analogically to the evolution of various neotenic forms in other Elateroidea, including such morphologically conservative groups as click beetles (Bocakova et al. 2007, Bocak et al. 2008, 2018, Kusy et al. 2018). With the multiple-origin hypothesis based on an independent phylogenetic signal (Fig. 3), we propose that the female character states should be merely mapped on the tree inferred from molecular data than coded for the phylogenetic inference.

The assignment of some taxa as neotenics might be controversial, when females remain unknown, but there are reasons why we support Kazantsev's assignment which net-winged beetle lineages have larviform females (Bocak & Bocakova 1990, Bocak *et al*. 2008, Kazantsev 2005, 2013). The larviform adult females have been proved by the observed copulation only in the large-bodied taxa, i.e. in *Platerodrilus paradoxus* (Mjöberg, 1925 and *Platerodrilus ruficollis* Pic, 1921 (=*Duliticola hoiseni* Wong, 1996). The adult larviform female of *Leptolycus* was described by Miller (1991). Further conspecific large-bodied larvae and fully-metamorphosed males were identified using molecular data (*Macrolibnetis*, *Lyropaeus* and additional species of *Platerodrilus*; Levkanicova & Bocak 2009, Masek & Bocak 2014). In these cases, the larvae with the multiple times higher body mass than available conspecific males are expected to produce females of the same body mass and these cannot resemble an adult-like phenotype. We expect that other net-winged beetles have the females with the similar body mass as males even if they are larviform (*e.g*., similarly to the miniature female of *Thilmanus* in Elateridae: Omalisinae, Bocek *et al*. 2018). The small-bodied larviform females have not been collected and concerning the short and cryptic life of larviform females observed by Wong (1996), the chance to collect these small-bodied adult larviform females remains very low. For comparison, the mature females of *Platerodrilus* have been collected twice in the history despite the fact that the large-bodied larvae are aposematically coloured and so common that they are known to nature enthusiasts and figured on postcards issued by local tourist authorities (e.g., the well known females of *Platerodrilus* sp. in the Kinabalu and Crocker National Parks).

The evidence would be hardly obtainable for all supposedly neotenic taxa, because even if we collect larvae of presumably neotenic lineages, unlike large-bodied forms, the discovery of an immature larva does not necessarily mean that the adult female remains larviform when mature. Until now, our prediction of larviform females in numerous taxa holds when no adult-like female has been collected neither by soil sifting for any taxon with presumed larviform females or on vegetation together with adult males. Additionally, no collecting identified any incompletely metamorphosed female similar to those of incompletely metamorphosed *Omalisus*, *Thilmanus* or *Drilus*. As a supporting example, we can suggest Ateliini. Their neoteny was proposed quite recently by Bocak & Bocakova (1990) when a few dozens of specimens were available in World collections. Since that time, the number of known species is much higher and hundreds of males have been collected in many localities (Malohlava & Bocak 2011, Bray & Bocak 2016). Soil samples were taken in places where adults occur and no fully or

partly metamorphosed females were collected. Despite the unavailability of at least a single small-bodied sexually mature larviform female, all observation still support the hypothesized presence of larviform females in numerous net-winged beetle taxa.

Supplementary Table S9. The morphological dataset (modified from Kazantsev, 2013)

										1									2									3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Ceratoprion	0	0	0	2	2	2	0	1	0	0	2	2	2	1	1	0	0	0	1	0	0	0	1	1	0	1	0	0	0	0
Cessator	0	0	0	0	2	0	0	1	0	0	2	2	2	2	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1
Dexoris	1	0	0	1	2	0	0	1	0	0	2	2	2	1	1	0	0	1	1	0	0	0	1	1	0	0	0	2	0	0
Dominopteron	3	0	0	0	2	0	0	1	0	0	2	0	0	0	1	0	2	0	1	0	1	2	1	1	1	1	0	0	0	0
Electropteron	1	0	0	1	2	2	0	1	0	0	2	2	2	2	0	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0
Leptolycus	0	0	0	1	2	2	0	1	0	0	2	2	2	0	1	1	1	0	1	0	0	0	1	1	1	1	0	1	0	0
Lycinella	1	0	0	1	2	1	0	0	0	0	2	0	0	1	1	0	2	1	1	0	0	0	1	1	1	1	0	0	0	1
Lyroneces	0	0	1	1	2	0	0	1	0	0	2	2	0	0	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0
Mimolibnetis	3	0	1	0	2	0	0	1	0	1	2	2	2	0	1	0	1	0	1	0	1	1	1	1	0	0	1	0	0	1
Nanolycus	1	0	0	0	2	0	0	1	0	0	2	2	2	2	1	0	0	0	1	0	1	0	1	1	1	1	0	0	0	0
Neolyrium	0	0	1	1	2	0	0	1	0	0	2	2	2	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Platerodrilus	3	1	0	1	2	2	0	0	0	0	2	0	0	1	1	0	1	2	1	0	1	1	1	1	0	0	0	0	0	1
Prioceraton	0	0	0	1	2	2	0	1	0	0	2	2	2	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Pseudacroleptus A	1	0	0	3	2	2	0	1	0	0	2	2	2	1	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0
Pseudacroleptus B	1	0	0	3	2	2	0	1	0	0	2	2	2	1	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0
Scarelus	1	1	0	1	2	0	0	0	0	0	2	0	0	0	1	0	2	1	1	0	0	0	1	1	0	0	1	0	0	1
Tainopteron	0	0	0	0	2	2	0	1	0	0	2	2	2	1	1	0	1	0	1	0	0	0	?	1	?	?	0	0	0	0
Tishechkinia	0	0	1	1	2	0	0	1	0	0	2	2	2	0	1	0	1	0	1	1	0	0	0	1	1	1	0	0	0	0
Aferos	0	2	0	1	2	0	0	0	1	0	2	0	1	0	1	0	1	0	1	0	1	0	0	1	1	1	1	0	1	1
Aplatopterus	1	1	0	0	1	2	0	0	1	0	2	0	1	0	1	0	2	0	1	0	1	0	1	1	1	0	1	0	0	1
Caenia	1	1	0	3	2	2	0	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1
Calochromus	1	2	0	1	2	0	0	0	1	0	2	0	1	1	1	0	0	0	1	0	1	0	1	1	1	1	1	1	0	1
Calopteron	0	0	0	1	2	1	0	0	1	0	0	0	1	0	1	0	1	0	1	0	0	0	0	1	1	1	1	0	0	0
Cerceros	0	1	0	3	2	0	0	0	1	0	1	0	1	0	0	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Conderis	0	1	0	2	2	0	0	0	1	0	2	0	1	0	1	0	1	0	1	0	1	0	1	1	0	0	1	0	0	1
Dictyoptera	1	1	0	0	2	2	0	0	1	0	2	0	1	0	1	0	0	0	0	0	1	0	1	1	1	0	1	0	0	1
Dilophotes	0	1	0	2	2	0	0	0	1	0	2	0	1	0	1	0	1	1	0	0	1	0	0	1	1	1	1	0	0	1
Pseudaplatopterus	0	1	0	0	1	1	0	0	1	0	2	0	1	0	1	0	1	0	0	0	1	0	1	1	1	0	1	0	0	1
Eros	1	1	0	0	2	2	0	0	1	0	2	0	1	0	1	0	1	0	1	0	1	0	0	1	1	0	1	0	0	1
Eulopheros	1	1	0	0	2	2	0	0	1	0	2	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0	1	0	0	1
Helcophorus	1	1	0	0	2	1	0	0	1	1	2	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0	1	0	0	1
Libnetus	1	1	0	0	2	0	1	0	0	0	2	0	0	0	1	0	1	1	1	0	0	0	1	1	1	1	1	0	0	1
Lopheros	1	1	0	1	2	2	0	0	1	0	2	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0	1	0	0	1
Lycostomus	1	2	0	1	2	0	1	1	1	0	2	0	1	1	0	0	1	0	1	0	1	0	1	1	0	0	1	0	0	0
Lygistopterus	1	2	0	1	2	0	1	0	1	0	2	0	1	0	1	0	1	0	1	0	1	0	0	1	1	1	1	0	0	1

	1									2										3										
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Macrolycinella	1	1	0	0	2	0	0	0	1	0	2	0	1	0	1	0	1	0	1	0	1	0	0	1	1	1	1	0	0	1
Melaneros	0	1	0	0	2	1	0	0	1	0	2	0	1	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0
Mesolycus	1	2	0	1	2	0	0	0	1	0	2	0	0	1	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0
Metriorrhynchus	1	2	0	1	2	0	1	0	1	0	2	0	1	1	1	0	0	0	1	0	1	0	0	1	1	1	1	0	0	1
Plateros	0	1	0	1	2	1	0	0	1	0	2	0	1	1	1	0	1	0	1	0	1	0	0	1	0	1	1	0	0	1
Platycis	1	0	0	0	2	0	0	0	1	0	2	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0	1	0	0	1
Taphes	0	0	0	1	2	2	0	0	0	0	2	0	0	0	1	0	1	0	1	0	1	0	1	1	1	0	1	0	0	1
Xylobanellus	0	1	0	2	2	0	0	0	1	0	2	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0	1	0	0	1
Thilmanus	1	0	0	0	0	1	1	0	0	0	2	0	0	2	1	1	0	0	1	1	1	0	1	0	0	0	1	0	1	1

Supplementary Table S9. (continued)

	3									4										5		
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
Ceratoprion	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	2	0
Cessator	0	0	0	1	1	0	0	0	0	0	0	1	1	2	0	1	0	1	1	0	0	0
Dexoris	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0
Dominopteron	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	1	0	1	1	0	1	0
Electropteron	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0
Leptolycus	1	0	0	1	0	0	0	0	0	0	0	1	2	2	1	0	0	0	1	0	0	0
Lycinella	1	0	0	1	1	0	0	1	0	0	0	1	0	1	1	1	0	1	1	0	1	0
Lyroneces	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0
Mimolibnetis	0	0	0	0	1	1	0	1	0	0	0	1	1	0	3	1	0	0	1	0	1	0
Nanolycus	?	?	0	0	0	0	0	0	0	0	0	1	1	2	0	1	0	1	1	0	0	0
Neolyrium	1	0	0	1	0	0	0	0	0	0	0	?	0	1	3	1	0	1	1	0	1	0
Platerodrilus	1	1	0	1	0	0	0	1	0	0	0	1	1	1	0	0	0	1	1	0	2	0
Prioceraton	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	1	0
Pseudacroleptus A	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0
Pseudacroleptus B	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0
Scarelus	0	1	0	1	2	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	0
Tainopteron	?	?	0	1	0	0	0	0	0	0	0	1	1	0	?	1	0	1	1	0	1	0

Supplementary Table S9. (continued)

	3									4									5		
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
Tishechkinia	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	2	0
Aferos	1	1	0	0	2	0	0	1	1	1	1	1	1	2	2	1	2	1	1	0	1	1
Aplatopterus	1	1	0	1	1	0	0	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1
Caenia	1	1	0	1	2	0	0	1	1	1	1	1	1	0	0	1	0	1	0	0	1	1
Calochromus	1	1	0	1	2	0	1	1	1	1	1	1	0	1	1	1	2	1	1	1	2	1
Calopteron	1	1	0	1	1	0	0	1	1	1	1	1	1	0	0	1	0	1	0	0	1	1
Cerceros	0	1	1	1	0	0	0	1	1	1	1	1	0	1	2	1	2	1	0	1	3	1
Conderis	1	1	1	1	2	0	0	1	1	1	1	1	0	1	0	1	0	1	1	0	2	1
Dictyoptera	1	1	0	1	2	0	0	1	1	1	1	1	1	2	0	1	0	1	1	0	2	1
Dilophotes	0	1	0	0	1	0	0	0	0	0	1	0	1	2	1	1	2	1	0	1	0	1
Pseudaplatopterus	1	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	0	1	0	0	2	1
Eros	1	1	0	0	2	0	0	1	1	1	1	1	0	1	1	1	0	1	1	0	2	1
Eulopheros	1	1	0	0	1	0	0	1	1	1	1	1	0	0	1	1	0	1	0	0	3	1
Helcophorus	1	1	0	1	2	0	0	1	1	1	1	1	1	1	1	1	0	1	1	0	2	1
Libnetus	1	0	0	1	2	0	0	0	1	0	1	1	1	0	2	1	0	1	1	0	1	1
Lopheros	1	1	0	0	2	0	0	1	1	1	1	1	0	0	1	1	0	1	0	0	1	1
Lycostomus	1	1	0	1	2	0	0	1	1	1	1	1	1	0	1	1	1	1	0	0	3	1
Lygistopterus	1	1	0	0	2	0	1	1	1	1	1	1	1	2	1	1	2	1	0	0	2	1
Macrolycinella	1	1	0	1	2	0	0	1	0	0	1	1	1	0	1	1	0	1	0	0	1	1
Melaneros	1	1	0	1	2	0	0	1	1	1	1	1	1	2	2	1	1	1	1	1	3	1
Mesolycus	0	1	1	1	0	0	0	0	1	0	1	1	1	2	2	1	2	1	1	0	0	1
Metriorrhynchus	1	1	1	1	2	0	0	1	1	1	1	1	0	0	1	1	1	1	0	1	0	1
Plateros	1	1	0	1	2	0	0	1	1	1	1	1	1	0	2	1	0	1	1	1	3	1
Platycis	1	1	0	0	2	0	0	1	1	1	1	1	1	1	0	1	0	1	1	0	2	1
Taphes	1	0	0	1	1	0	0	1	0	0	1	1	1	2	0	1	0	1	1	0	1	1
Xylobanellus	1	1	0	0	2	0	0	1	1	1	1	1	0	2	0	1	0	1	1	0	2	1
Thilmanus	0	0	0	1	1	0	2	0	0	0	0	1	1	0	3	1	0	0	1	0	2	0

Supplementary Table S10. The tree and character statistics for trees based on the parsimony analysis of the morphological dataset . The length, consistency and retency indexes are recovered for morphological characters coded by Kazantsev (2013) (see Tab. S5 and S9) using the topologies inferred from morphological and phylogenomic analyses. The red-coloured values designate characters which have the considerably better fit with the morphology-based topology, blue-coloured values those with better fit with the phylogenomic topology. Character-status summary: Of 52 total characters all characters are all of the type unordered, equal weight, and parsimony-informative.

	Characters on the morphology based topology	Characters on genomic topology	Sum of min. possible lengths = 74 Sum of max. possible lengths = 656
Tree	#1	#1	
Length	294	384	
CI	0.252	0.193	
RI	0.622	0.467	

Version 4.0a (build 164) for 32-bit Microsoft Windows (built on Nov 1 2018 at 19:32:34)

Tree lengths (L), CI and RI for each character:

Character		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
morphology	L	11	6	3	14	3	11	5	3	1	2	3	2	5	9	6	2	10	6	4	3
based	CI	0.182	0.333	0.333	0.214	0.667	0.182	0.200	0.333	1.000	0.500	0.667	0.500	0.400	0.222	0.167	0.500	0.200	0.333	0.250	0.333
topology	RI	0.526	0.818	0.333	0.476	0.000	0.550	0.000	0.867	1.000	0.000	0.000	0.923	0.850	0.500	0.375	0.000	0.273	0.200	0.000	0.500
genomic	L	16	13	4	17	3	15	5	5	8	2	3	4	11	12	8	2	12	7	4	4
topology	CI	0.125	0.154	0.250	0.176	0.667	0.133	0.200	0.200	0.125	0.500	0.667	0.250	0.182	0.167	0.125	0.500	0.167	0.286	0.250	0.250
	RI	0.263	0.500	0.000	0.333	0.000	0.350	0.000	0.733	0.600	0.000	0.000	0.769	0.550	0.286	0.125	0.000	0.091	0.000	0.000	0.250

Character		21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
morphology	L	6	3	6	3	9	9	2	3	2	5	8	4	3	7	12	2	3	6	4	4
based	CI	0.167	0.667	0.167	0.333	0.111	0.111	0.500	0.667	0.500	0.200	0.125	0.250	0.333	0.143	0.167	0.500	0.667	0.167	0.250	0.250
topology	RI	0.688	0.000	0.688	0.000	0.500	0.600	0.933	0.000	0.000	0.750	0.222	0.800	0.333	0.333	0.583	0.000	0.000	0.688	0.857	0.842
genomic	L	7	3	10	3	8	7	5	3	2	9	5	8	4	8	14	1	2	6	8	8
topology	CI	0.143	0.667	0.100	0.333	0.125	0.143	0.200	0.667	0.500	0.111	0.200	0.125	0.250	0.125	0.133	1.000	1.000	0.167	0.111	0.125
	RI	0.625	0.000	0.438	0.000	0.563	0.700	0.733	0.000	0.000	0.500	0.556	0.533	0.000	0.222	0.500	1.000	1.000	0.688	0.667	0.632

Character		41	42	43	44	45	46	47	48	49	50	51	52
morphology	L	2	3	9	12	14	3	6	3	10	4	16	2
based	CI	0.500	0.333	0.222	0.167	0.214	0.333	0.333	0.333	0.100	0.250	0.188	0.500
topology	RI	0.944	0.500	0.500	0.500	0.500	0.000	0.500	0.333	0.357	0.400	0.500	0.944
genomic	L	6	5	12	15	17	3	7	4	9	5	19	6
based	CI	0.167	0.200	0.167	0.133	0.176	0.333	0.286	0.250	0.111	0.200	0.158	0.167
topology	RI	0.722	0.000	0.286	0.350	0.364	0.000	0.375	0.000	0.429	0.200	0.385	0.722

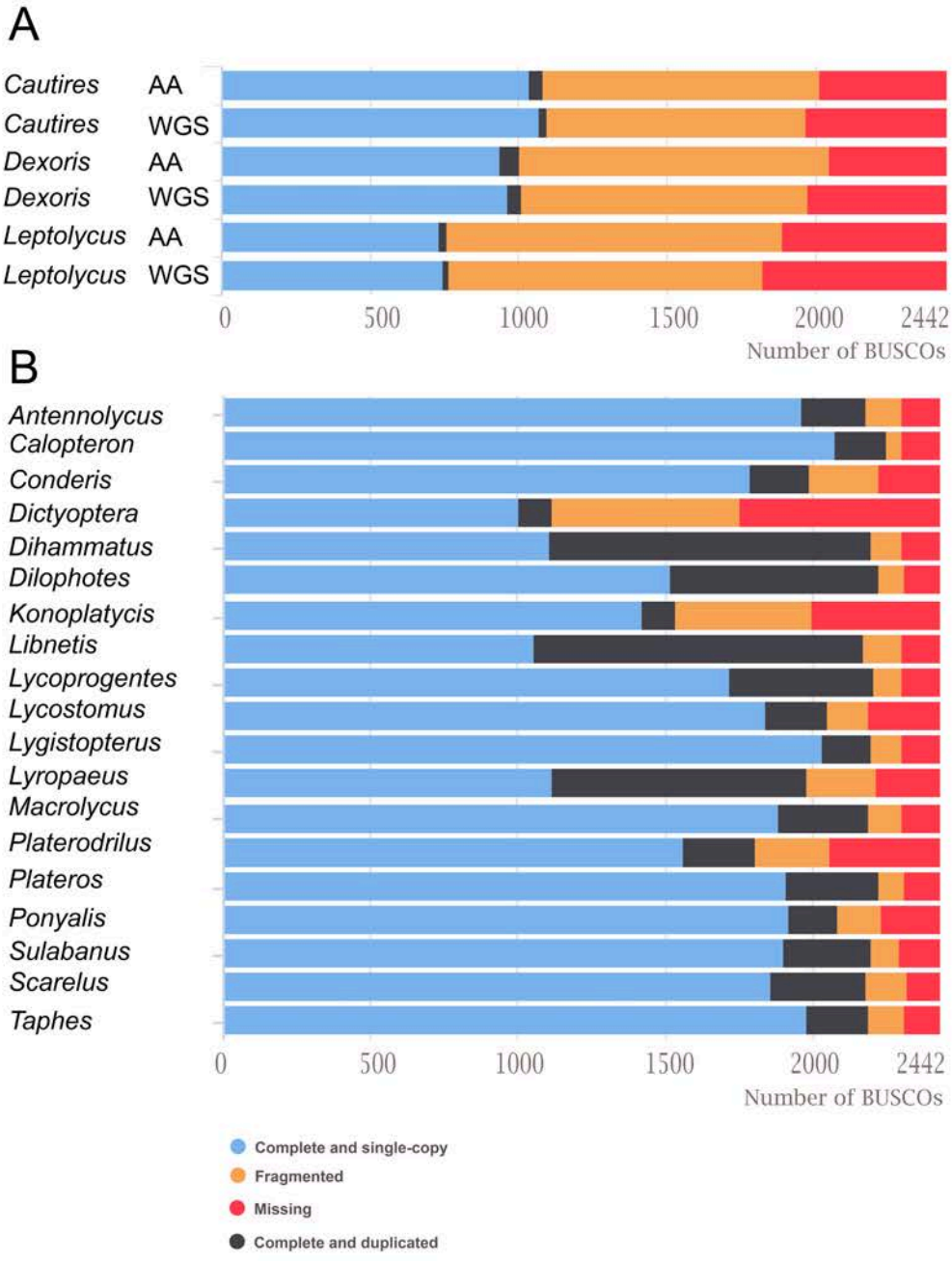

Figure S1. Summarized benchmarks in the BUSCO assessment. (A) assembled genomes and predicted gene sets. These estimations used 2442 expected Endopterygota genes as query; AA - predicted gene sets; WGS - whole assembled genomes.
(B) Summarized benchmarks in the BUSCO assessment - assembled transcriptomes.

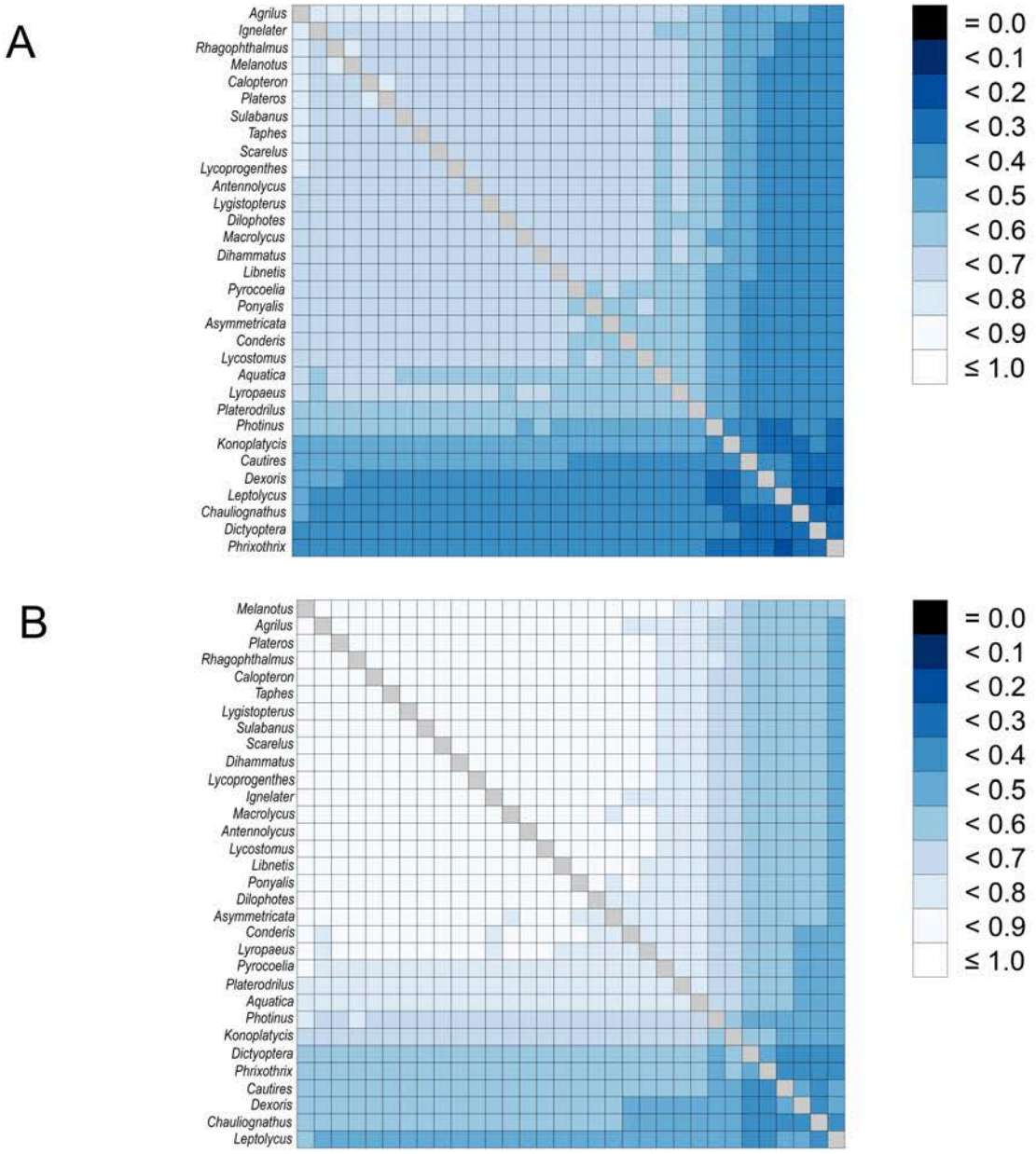

Figure S2. (A) AliStat rectangular heatmap for individual pairs of seqs (Cij) in phylogenomic Dataset A at nucleotide level with all codon positions kept; with Aliscore masking applied, partitions with incomplete information kept and outliers excluded.
(B) AliStat rectangular heatmap for individual pairs of seqs (Cij) in phylogenomic Dataset A at amino acid level; with Aliscore masking applied, partitions with incomplete information and outliers excluded.

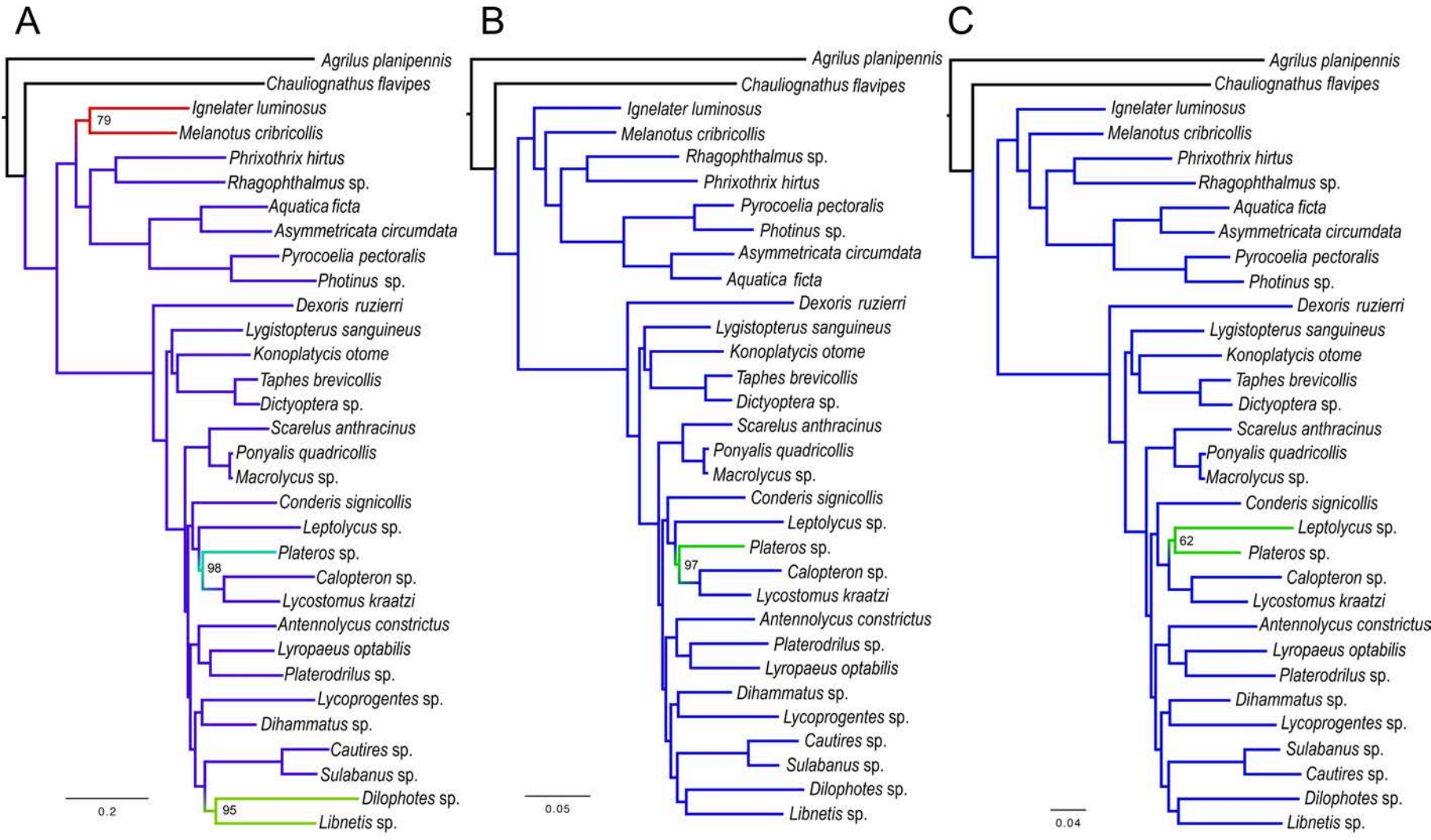

Figure S3. (A) Maximum likelihood tree obtained from the phylogenomics analysis of 31 Elateroidea and *Agrilus* outgroup dataset at nucleotide level with all codon positions kept, outliers removal, Aliscore masking, partitions with zero information content removed and full representation of fragments; (B) Maximum likelihood tree obtained from the phylogenomics analysis of 31 Elateroidea and *Agrilus* outgroup dataset at nucleotide level, with codon positions 1±2 kept, outliers removal, Aliscore masking, partitions with zero information content removed and full representation of fragments; (C) Maximum likelihood tree obtained from the phylogenomics analysis of 31 Elateroidea and *Agrilus* outgroup dataset at amino acid level, outliers removal, Aliscore masking, partitions with zero information content removed and full representation of fragments. Based on Dataset A. Only bootstrap support values lower than 100 are displayed.

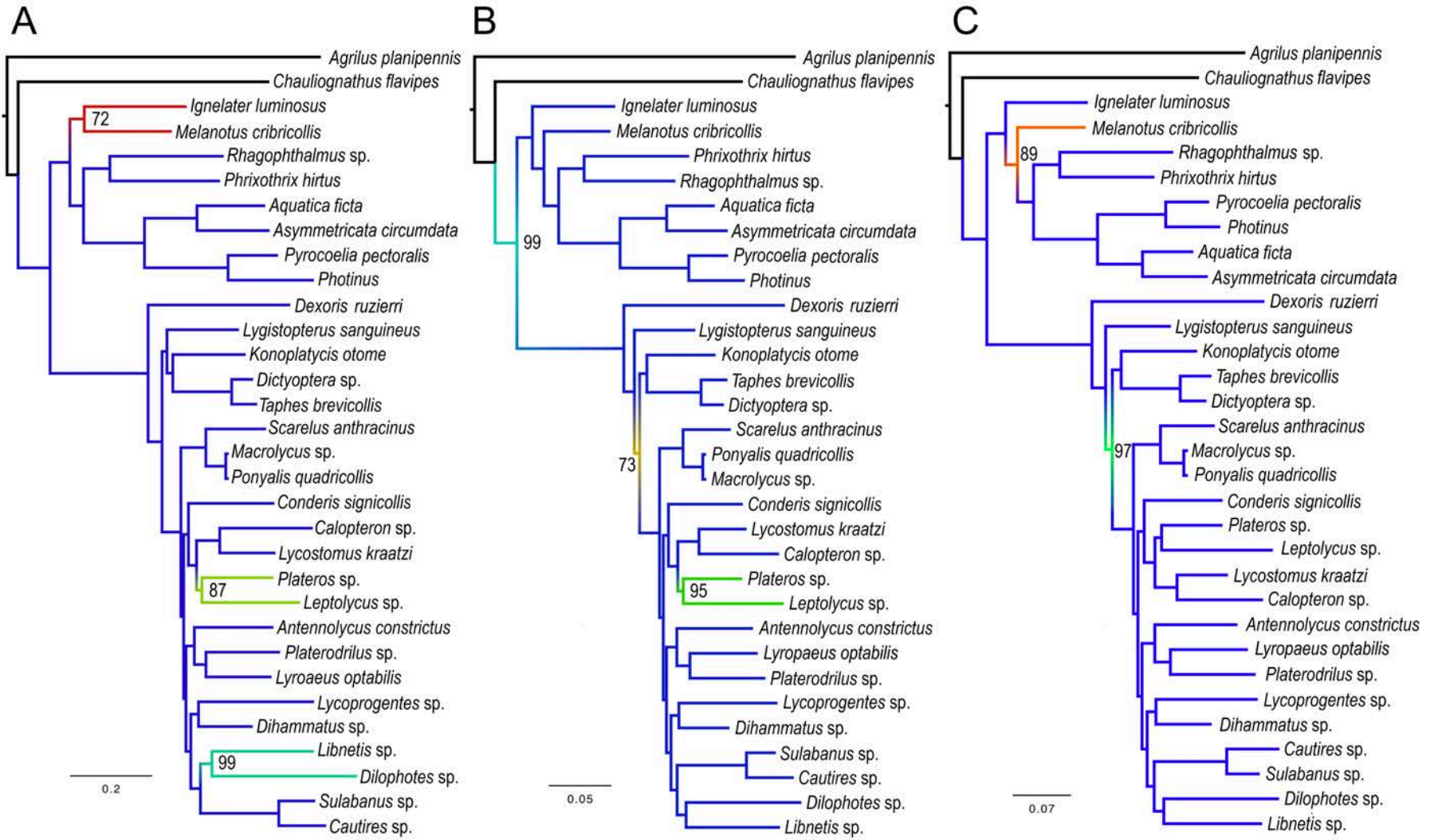

Figure S4 . (A) Maximum likelihood tree obtained from the phylogenomics analysis of 31 Elateroidea and *Agrilus* outgroup dataset at nucleotide level with all codon positions kept, outliers removal, Aliscore masking, partitions with zero information content and the fragments with incomplete data removed; (B) Maximum likelihood tree obtained from the phylogenomics analysis of 31 Elateroidea and *Agrilus* outgroup dataset at nucleotide level, with codon positions 1+2 kept, outliers removed, Aliscore masking, partitions with zero information content and the fragments with incomplete data removed; (C) Maximum likelihood tree obtained from the phylogenomics analysis of 31 Elateroidea and *Agrilus* outgroup dataset at amino acid level, outliers removal, Aliscore masking, partitions with zero information content and the fragments with incomplete data removed. Based on Dataset B. Only bootstrap support values lower than 100 are displayed.

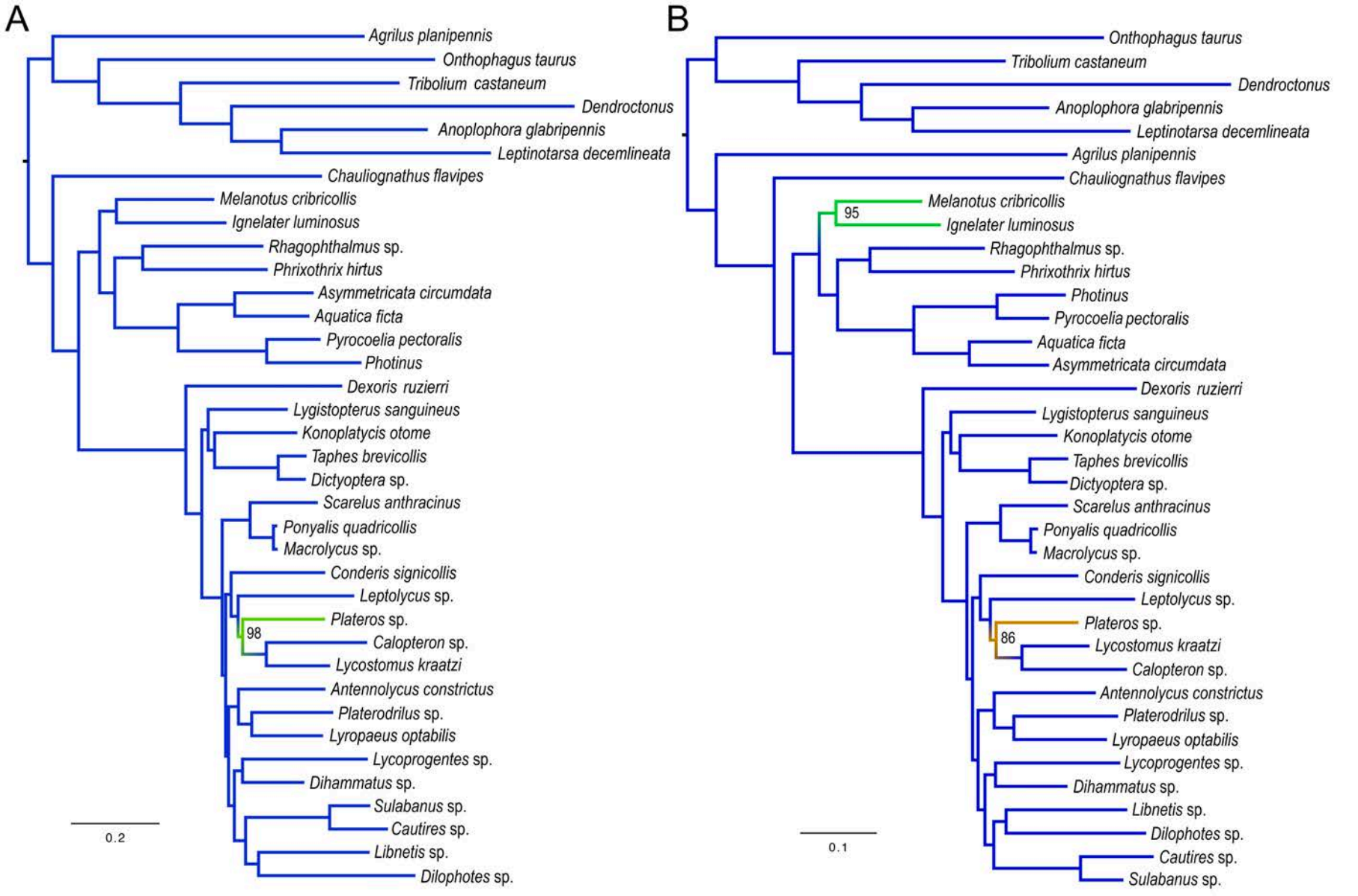

Figure S5. (A) Maximum likelihood tree obtained from the analysis of 32 Elateriformia and six Polyphaga outgroups dataset at nucleotide level, raw data without outliers removal and Aliscore masking; (B) Maximum likelihood tree obtained from the analysis of 32 Elateriformia and six Polyphaga outgroups at amino acid level, raw data without outliers removal and Aliscore masking. Based on Dataset D. Only bootstrap support values lower than 100 are displayed.

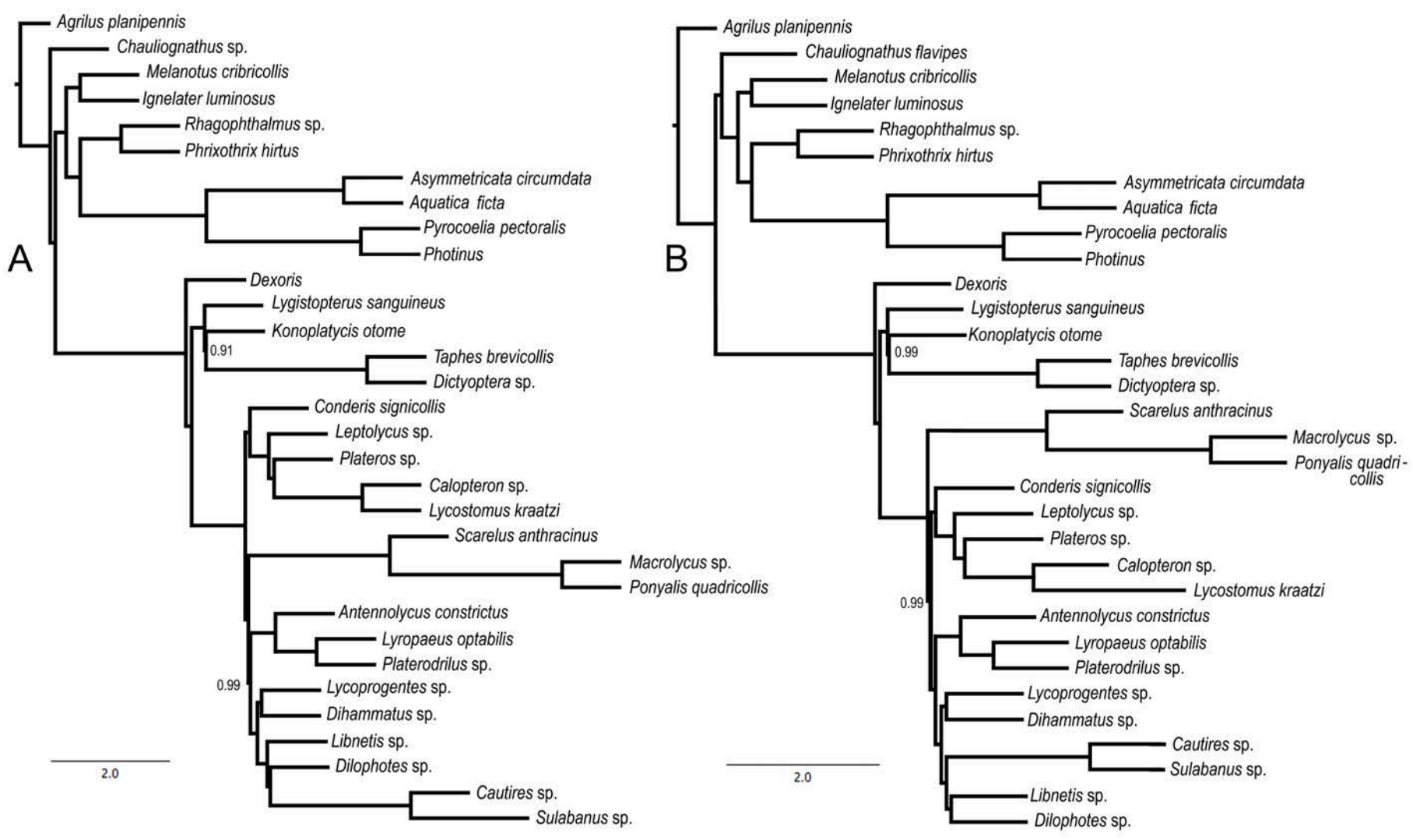

Figure S6 . (A) The coalescent ASTRAL tree constructed from individual maximum likelihood gene trees (n=3992) obtained from the phylotgenomics analysis of all orthologs, 31 Elateroidea ingroup and *Agrilus* outgroup dataset at nucleotide level with all codon positions kept, outliers removed, partitions with zero information content removal, and Aliscore masking; (B) The coalescent ASTRAL tree constructed from individual maximum likelihood trees (n=3992) obtained from the phylogenomics analysis of all orthologs, 31 Elateroidea and *Agrilus* outgroup dataset at amino acid level, partitions with zero information content removed, outliers removal and Aliscore masking. Based on Dataset A.

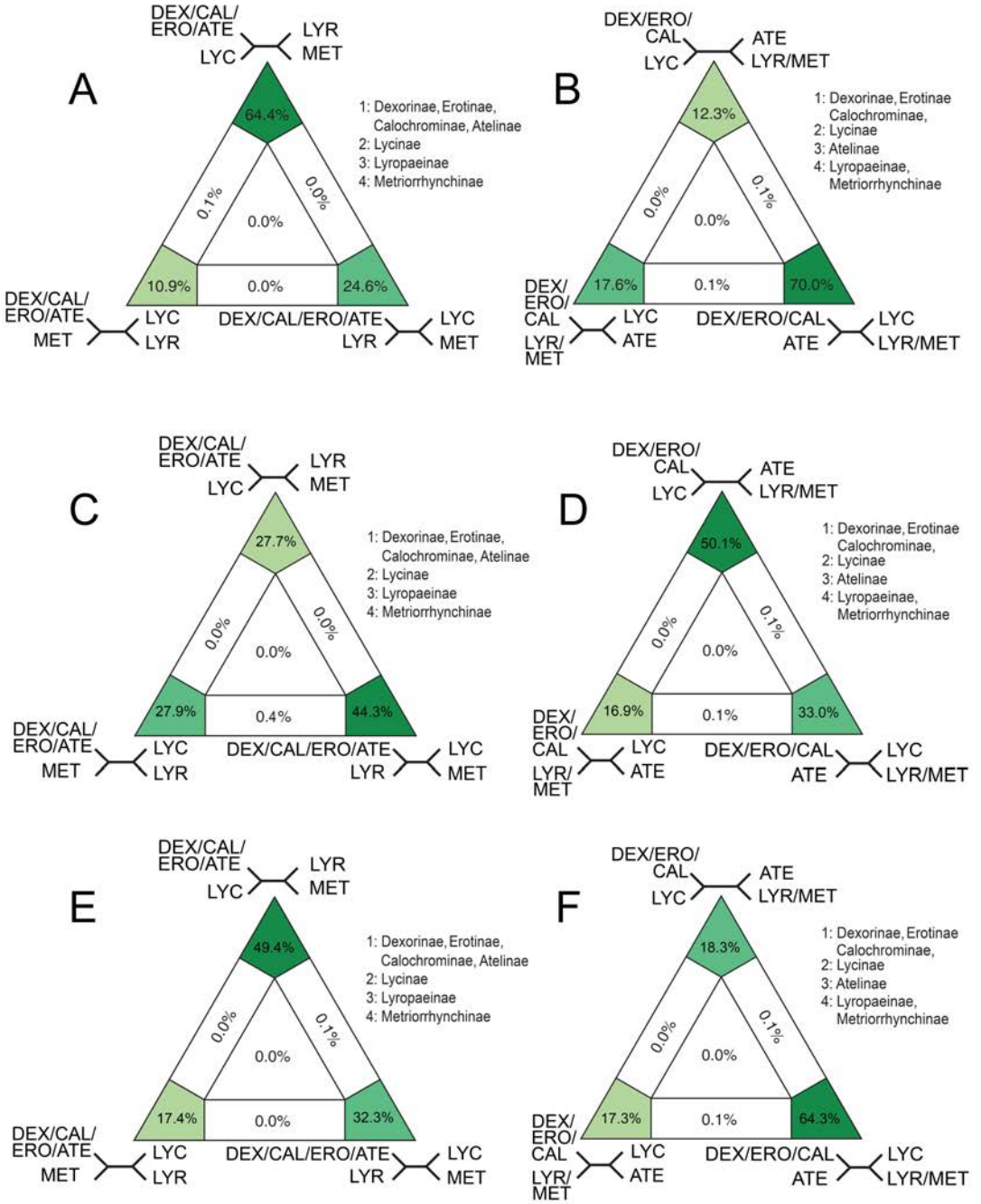

Figure S7. The Four cluster likelihood mapping analyses of alternative topology using phylogenomic Dataset B without outliers, Aliscore masking, partitions with zero information content excluded (A, B) at amino acid level; (C, D) at nucleotide level, with the 3rd codon position included; (E, F) at nucletide level with the 3rd nucletide codon position excluded.

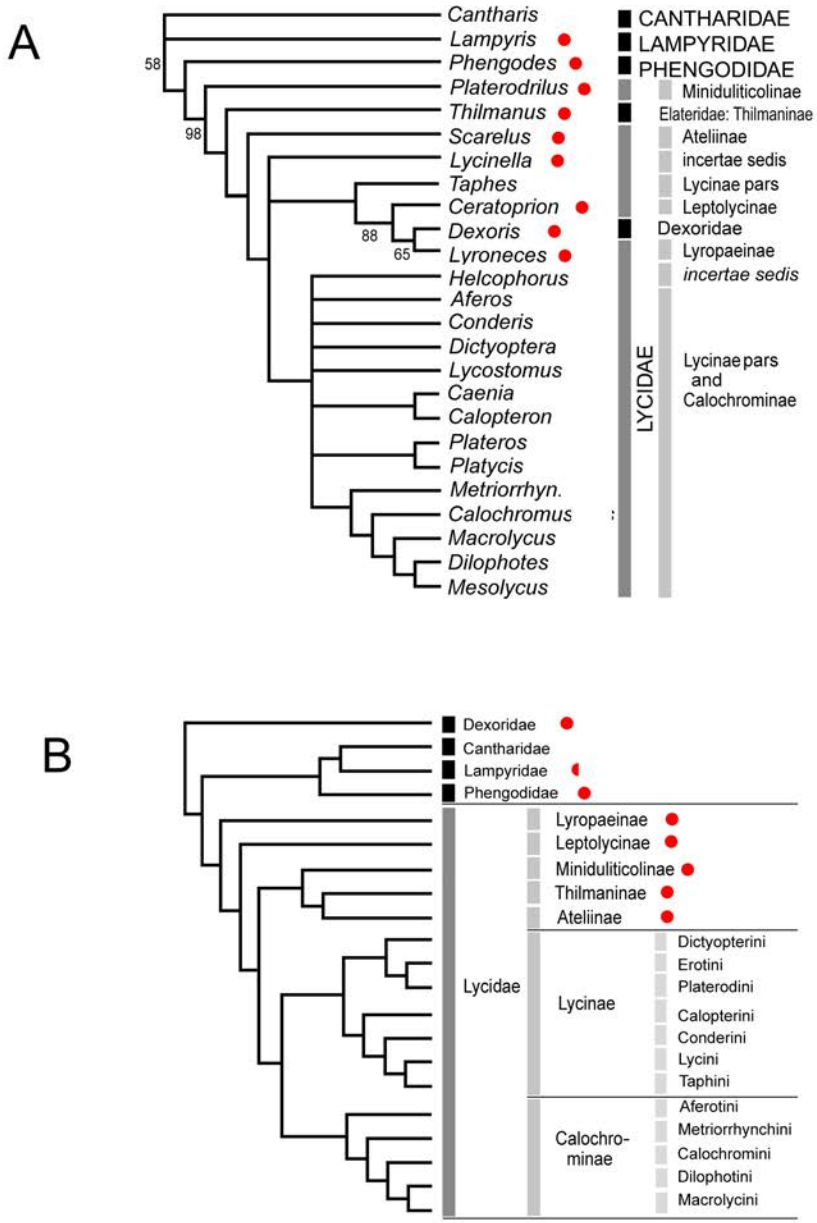

Figure S8. (A) The consensus of maximum parsimony trees recovered by the reanalysis of Kazantsev's (2005) morphological dataset;
(B) The classification of Lycidae proposed by Kazantsev (2005).

Both illustrations reprinted from Bocak & Bocakova (2008).

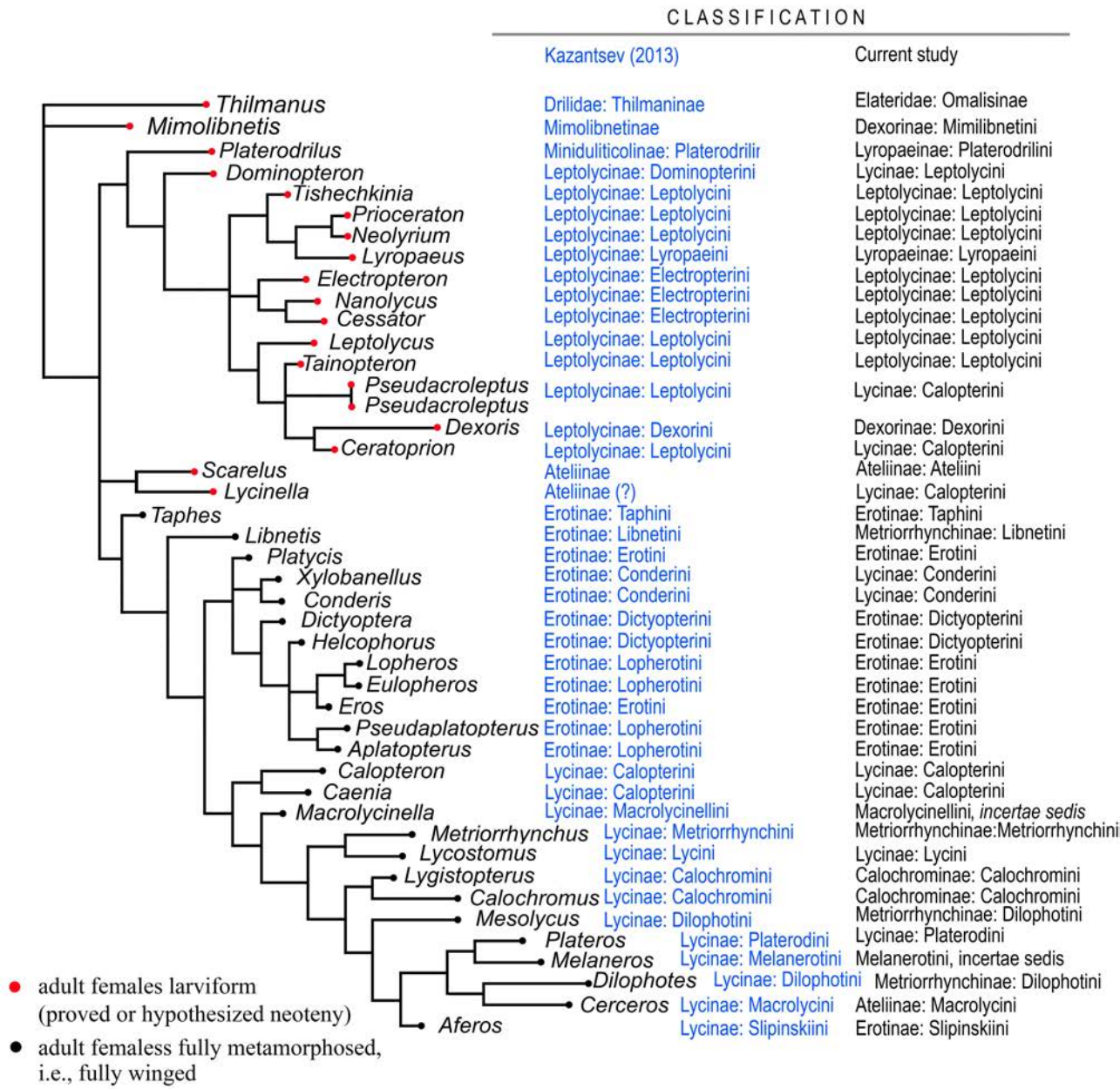

Figure S9. The tree produced by the analysis of the morphological dataset by Kazantsev (2013).

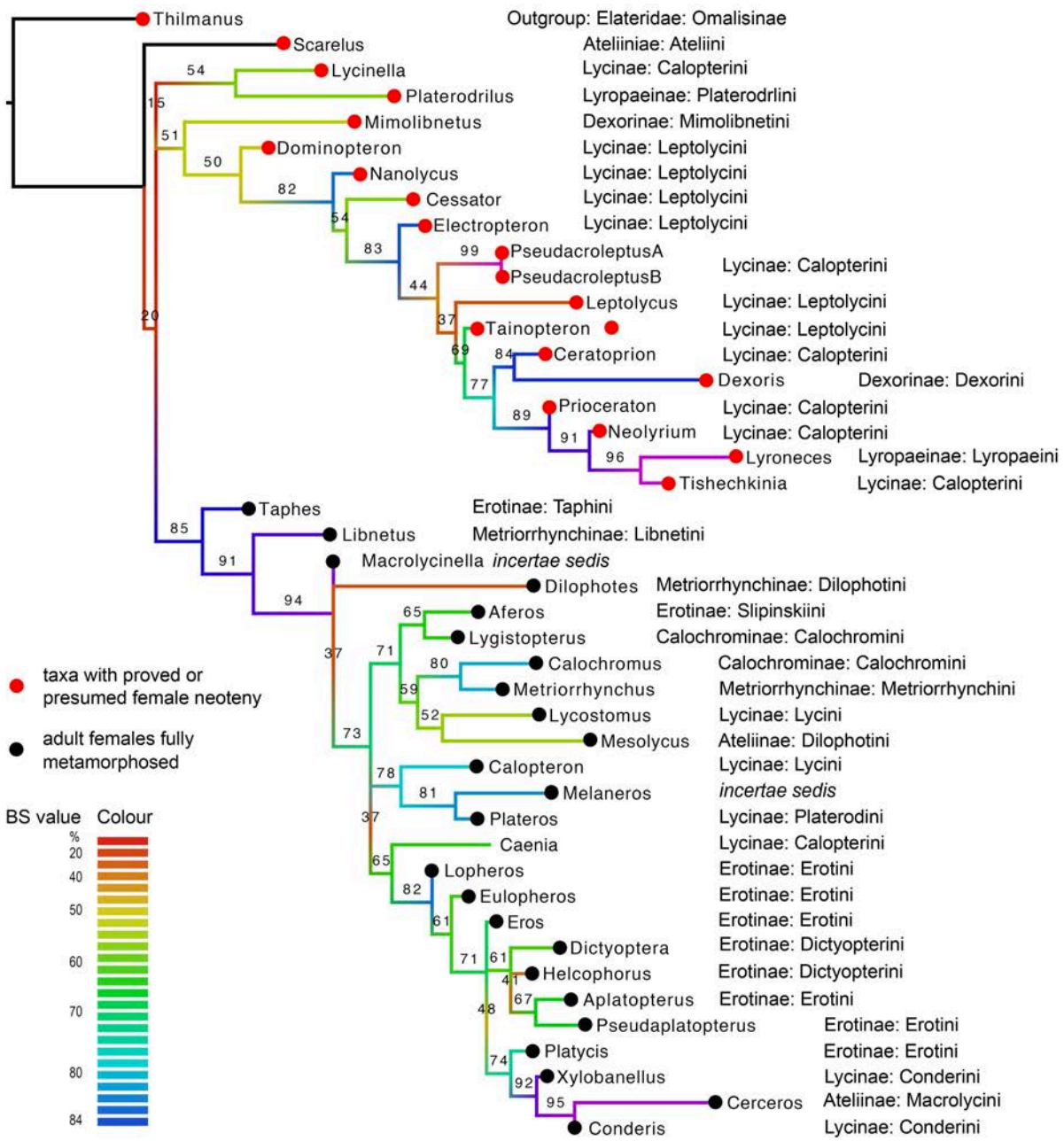

Figure S10. The majority consensus tree recovered from five most parsimonious trees produced by the analysis of the modified morphological dataset published by Kazantsev (2013). The values at branches designate bootstrap values.

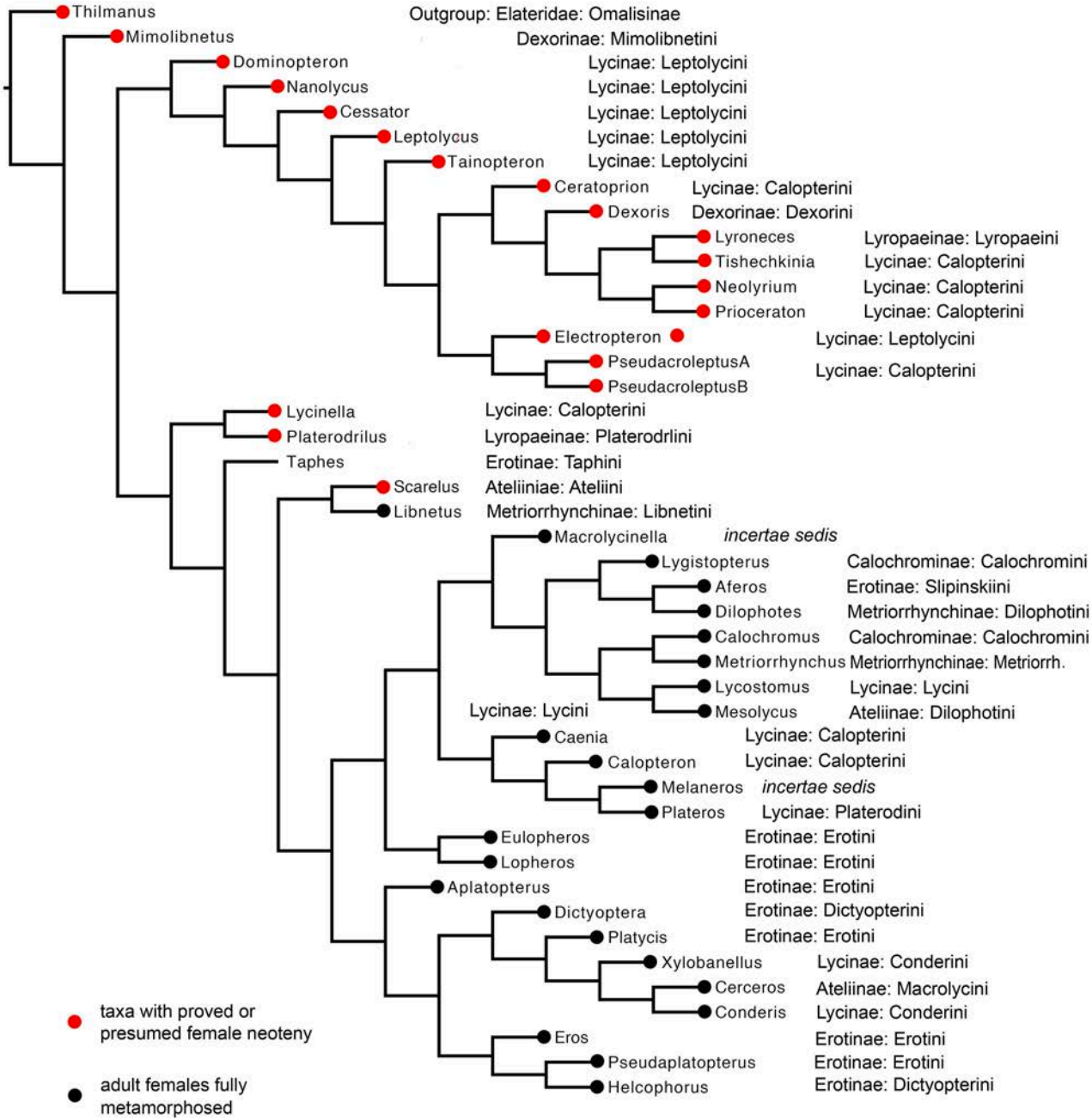

Figure S11. One of five most parsimonious trees recovered by the analysis of the modified morphological dataset published by Kazantsev (2013).

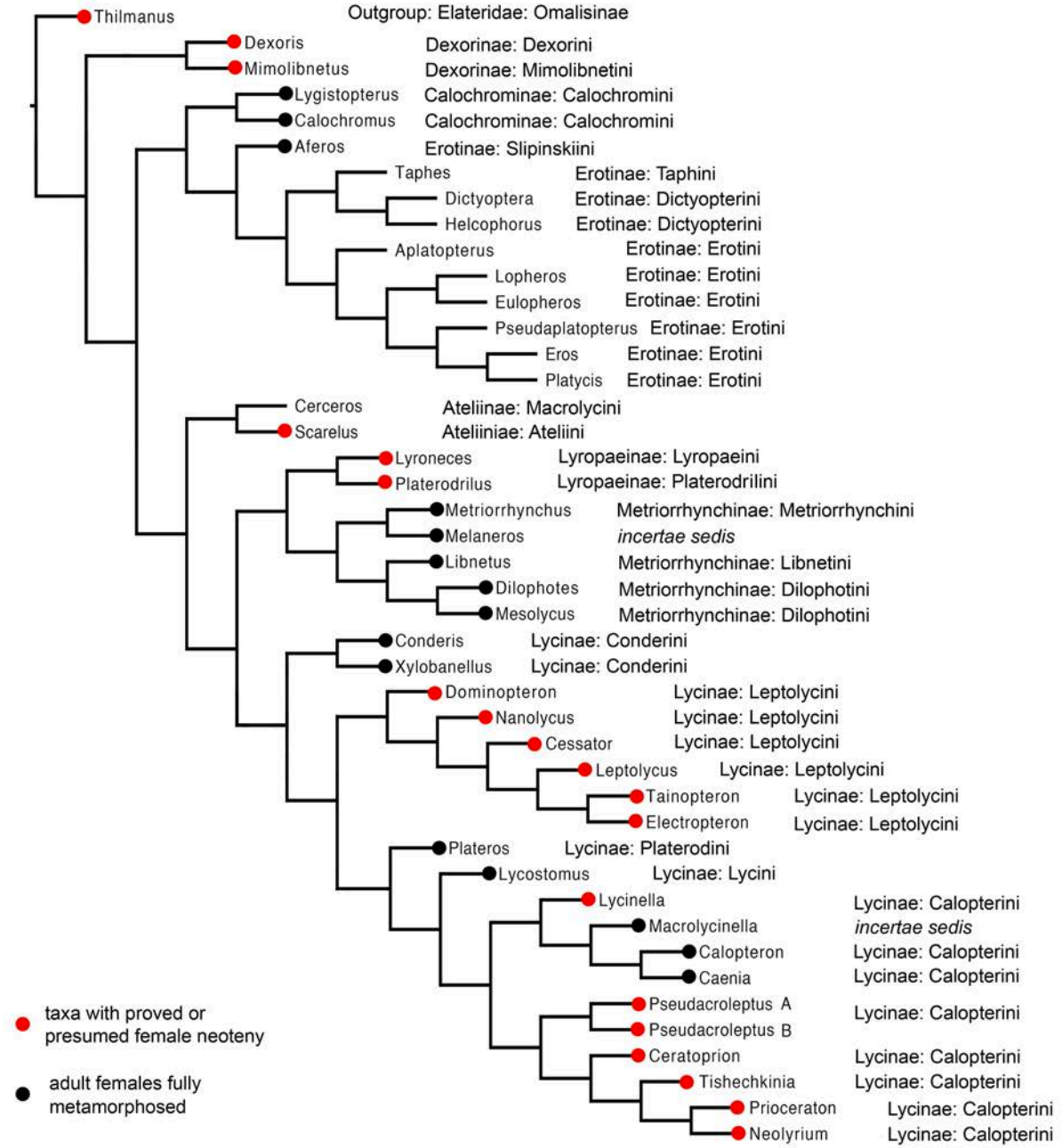

Figure S12. The constrained topology based on the phylogenomic analysis constructed for the comparison of the fit of morphological characters and the genomic topology. For the purpose of the present analysis, the taxa with controversal phylogenetic relationships are provisionally placed in the sister position to Metriorrhynchini (Melamerotini: *Melaneros* and Calopterini (*Macrolycinella*).