PHYLOGENY AND CLASSIFICATION OF THE FAMILY LYCIDAE (INSECTA: COLEOPTERA)

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Abstract.— Lycidae, net winged beetles, have proved difficult to classify using morphological characters. Here, using a previously published molecular phylogeny, comparing the results with morphological data and re-analyzing previously published morphological data set, we propose a revised classification of Lycidae. All analyses support the monophyly of Lycidae, but phylogeny inferred from molecular data is in conflict with the current classification. The adult larviform females evolved in several lineages and never switched back to a winged form. Therefore, neotenic development of females is not a synapomorphy of Lycidae and the neotenic lineages do not form a basal paraphylum with respect to remaining Lycidae as previously proposed. As a consequence morphological similarities resulting from neoteny are homoplasies and cannot be used for definition of monophyletic lineages. The major result of this study is delineation of five basal clades, which are given subfamily rank: Libnetinae Bocak et Bocakova, 1990, **stat. nov.**, Dictyopterinae Kleine, 1928, **stat. nov.**, Lyropaeinae Bocak et Bocakova, 1989, Ateliinae Kleine, 1928 and Lycinae Laporte, 1836, **sensu nov.** Dexorinae Bocak et Bocakova, 1989, **stat. nov.** were not available for molecular analyses and their position is inferred from morphology alone. Further, Lycinae are redefined. Leptolycini are nested among Neotropical Lycini and render them paraphyletic. Slipinskiini are shown to group with Erotini. The distant position of Macrolycini and Dilophotini is demonstrated and Dilophotini are transferred from Calochrominae to Ateliinae. Four new tribes are proposed: Lycoprogenthini **trib. nov.** in Dictyopterinae, Alyculini **trib. nov.** and Antennolycini **trib. nov.** in Lyropaeinae, Dihammatini **trib. nov.** in Lycinae. Calochromini Lacordaire, 1857, **stat. nov.** and Leptolycini Leng et Mutchler, 1922, **stat. nov.** are lowered to the tribal status in Lycinae. The validity of Thonalmini Kleine, 1933 stat. rev. is re-established.

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Key words.— Elateroidea, taxonomy, new tribes, subfamilies, mtDNA, rDNA, morphology.

INTRODUCTION

With more than 4 000 described species, Lycidae, net winged beetles, are one of major elateroid lineages. The family occurs throughout the World (Kleine 1933, Bocak and Bocakova 1990), but they are most diverse and abundant in humid tropics. We know only a fragment of their diversity in tropical regions as exemplified by several recently published alpha taxonomic studies (e.g., Bocakova 1997a, 1999a, Dvorak and Bocak 2007, Tvardik and Bocak 2001). The poor condition of higher-level classification is reflected by conflicting opinions published by various authors (Bocak and Bocakova 1990, Miller 2002, Kazantsev 2005).

The present study is based on previously reported phylogenetic analyses of an extensive molecular data set (Levkanicova and Bocak, in press) and reanalysis of the morphological data published by Kazantsev (2005). We did not expand available morphological data herein for several reasons. First of all, there are no homologues when we compare larviform and fully metamorphosed females; secondly, females of most supposedly neotenous lineages are unknown as these animals have cryptic life habits. The present knowledge of immature stages is also far from complete (Bocak and Matsuda 2003) and therefore, any attempt to compile a matrix of morphological data results in a high number of unknown or inapplicable character states and consequently low resolution and weak support of most clades (e.g., Kazantsev's matrix of larval characters includes question marks for 69% of parsimony informative ingroup character states and female morphology is not used at all [Kazantsev 2005]). Additionally, Miller (1991) discussed the potential influence of neoteny not only on female morphology where neotenous traits are very prominent, but also in a smaller degree on males of these taxa. Considering the hypothesized multiple origins of neoteny (Levkanicova and Bocak in press) these neoteny affected characters can increase the proportion of homoplasies in data sets. In an attempt to avoid such impact on the phylogenetic hypothesis we propose the classification on the basis of phylogeny inferred from six molecular markers.

Levkanicova and Bocak (in press) discussed the origin and macroevolutionary consequences of neoteny in Lycidae, but did not discuss the relationships of nonneotenic lineages and impact of new findings on the formal classification of Lycidae. The aims of this study are to discuss the monophyly of various previously hypothesized lycid lineages, to investigate their mutual relationships and to evaluate the congruence between phylogenetic hypotheses based on morphology and molecular markers. Additionally, we re-analyze the morphological data set published by Kazantsev (2005). The inferred phylogenetic hypothesis (Levkanicova and Bocak, in press) is used as a basis for the here proposed classification of Lycidae.

Biology. Lycidae are terrestrial beetles with strong association with forest habitats. Lycid larvae usually occur in dead wood in various stages of decomposition, in forest litter, and soil with high content of organic material. Moist shaded decaying microhabitats that promote microbial growth are typical for Lycidae (Bocak and Matsuda 2003). The food of lycid larvae was a subject of long lasting controversy (Shelford 1916, Miller 1988). Many authors reported feeding on fermenting juices and this is considered now the principal way of feeding (for a review see Bocak and Matsuda 2003). Adults of most species avoid sunny places and remain under canopy, where they sit or sluggishly move on leaves or decaying wood. It seems that most adult lycids are short living and do not take any food in adult stage; only flower frequenting species consume nectar. Adults are capable of spontaneous bleeding. The drops of hemolymph appear on margins of elytra, antennae, and on femur – tibial joints when the individual is strongly disturbed. The hemolymph is malodorous and protects lycids from predators. There are observations available that both vertebrate and invertebrate predators avoid lycids as a prey (Linsley *et al*. 1961). The chemical composition of bitter and foulsmelling substances in lycid body was studied by Moore and Brown (1981) and Eisner *et al*. (2008). Similarly to other chemically protected organisms, lycids are very often aposematically colored and have a tendency to aggregate. Various insects resemble sympatrically occurring lycids and the most common mimics belong to Coleoptera. E.g., Buprestidae, Meloidae, Oedemeridae, Cerambycidae, and Belidae mimic lycids in the Australian region (Lawrence and Britton 1991) and Cantharidae, Eucnemidae, Chrysomelidae in the Oriental region. Some other insect orders, mostly Lepidoptera and Heteroptera are often represented by a few species in mimicry assemblages. The Müllerian type of mimicry is assumed to operate in interactions among unpalatable Lycidae and the Batesian type in interactions between lycids and non-protected insects from other beetle families and insect orders. Most taxa are winged in both sexes, but a limited number of genera have neotenous larviform females (Bocak and Bocakova 1990, Bocakova *et al*. 2007, Levkanicova and Bocak, in press). Female neoteny was observed in *Duliticola* Mjöberg (Mjöberg 1925, Wong 1996) and further cases in *Platerodrilus* Pic and *Macrolibnetis* Pic were identified by molecular markers (Levkanicova and Bocak in press). Gravely (1915) described the female of *Lyropaeus* Waterhouse, and Miller (1991) described the larviform female of *Leptolycus heterocornis* Leng et Mutchler from West Indies.

Systematic history. The phylogenetic relationships among tribes and subfamilies have remained contentious. The classification is not based on the thorough analysis of a large data set and recent contributions by various authors are not generally accepted (Bocak and Bocakova 1990, Miller 1997, 2002, Kazantsev 2005, Beutel *et al*. 2007).

The monophyly of Lycidae is supported by several synapomorphies in both larval and adult stages (Bocak and Bocakova 1990, Miller 2002, Bocak and Matsuda 2003, Kazantsev 2005) and no author has seriously questioned their monophyly. On the other hand, their relationships to other elateroid families remain controversial. Crowson (1972) considered Lycidae to be the sister group to Omalisidae. Beutel (1995) analyzed the head musculature of Elateriformia and suggested monophyly of Cantharoidea except Cantharidae and the

close position of Lycidae to Omalisidae, Lampyridae, and Phengodidae. Branham and Wenzel (2001) placed Lycidae in the clade with Cantharidae, Omethidae, Telegeusidae, and Phengodidae. Kazantsev's (2006) hypothesis on the sister group relationships of the lycid genus *Platerodrilus* to Neoptera was rejected by Beutel *et al.* (2007). The molecular phylogeny of Elateriformia was studied by Bocakova *et al.* (2007) and their results showed close relationships of Lycidae to Elateridae + Cantharidae + Lampyridae and a distant position of Telegeusidae and Omethidae.

The chaotic tribal classification of Lycidae (Kleine 1933) was modified by Bocak and Bocakova (1990) who defined 6 subfamilies, brought a detailed history of lycid supergeneric classification, and described thoroughly adult morphology. The classification was not based on a phylogenetic analysis, but merely critically considered taxa described by previous authors. A few modifications were introduced later: Medvedev and Kazantsev (1992) described one species from the large and frequently collected genus *Lyropaeus* as the monotypic genus *Paralycus* Medvedev and Kazantsev and established the subfamily Paralycinae Medvedev et

Kazantsev, 1992 (a junior synonym of Lyropaeinae Bocak et Bocakova, 1989). The rest of Lycidae was considered to be a subfamily Lycinae and authors did not discuss the status of previously described family-level taxa within Lycidae. Miller (1997) described immature stages of *Plateros floralis* (Melsheimer) and elevated Platerodini to the subfamily level. Kazantsev (2002) formally described Duliticolinae in the sense proposed by Mjöberg (1925). Bocak and Matsuda (2003) reviewed the literature on lycid immature stages, described further immature stages, and discussed incongruence of some larval characters with the actual classification based on adult morphology. Recently, Kazantsev (2005) proposed a new classification of Lycidae (Fig. 1): Dexorini were removed from Lycidae and given family status; 7 subfamilies were defined: Lyropaeinae, Leptolycinae, Ateliinae, Thilmaninae, Miniduliticolinae (= Duliticolinae, invalid name), Lycinae and Calochrominae. Thilmaninae were later returned to Omalisidae by Bocak and Brlik (2008). Kazantsev's conclusions on the phylogeny of Lycidae are unconvincing for several reasons: e.g., only 22 ingroup taxa were included in the data set; several lineages were
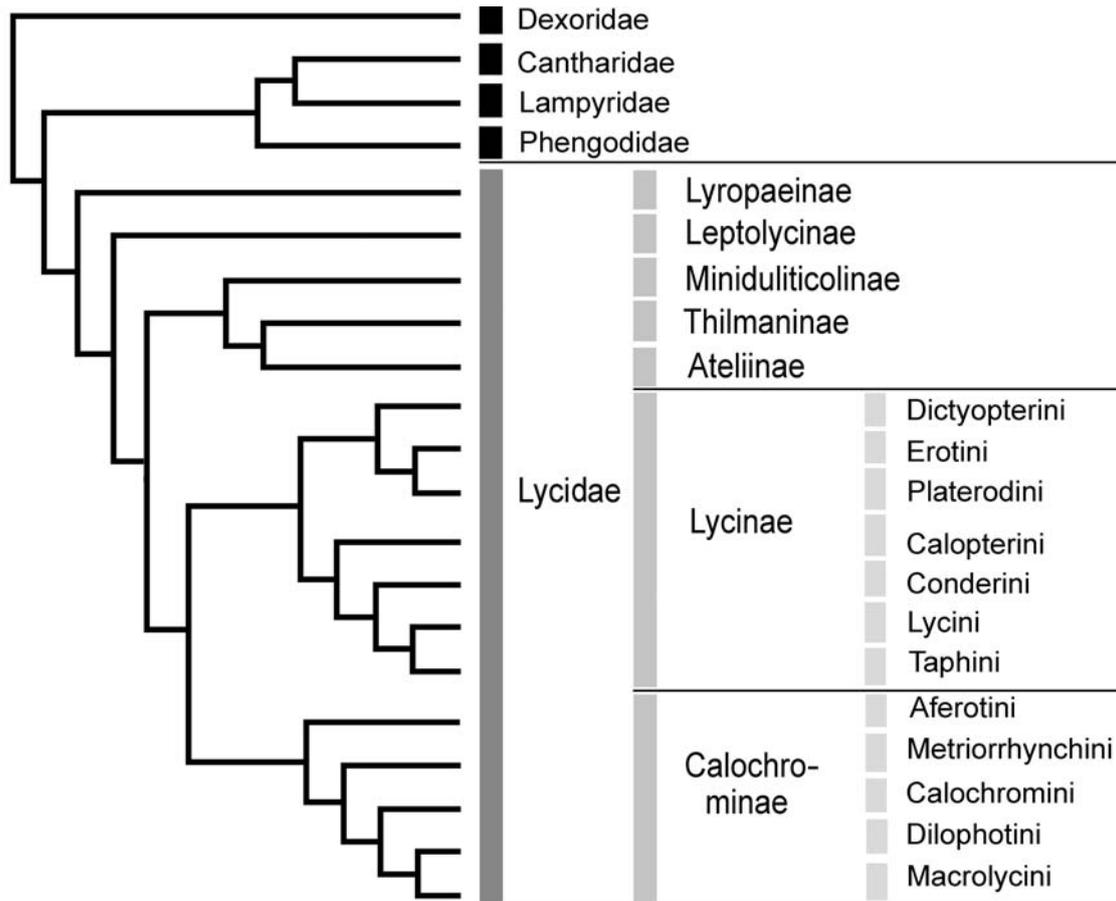

Figure 1. The presumed phylogeny of Lycidae used as a basis for previous classification (redrawn from Kazantsev 2005, Figs 599 and 600).

omitted although specimens are widely available, the monophyly of most taxa was either not tested as only one representative was included in the data set or their polyphyly in majority of his analyses was simply ignored. Additionally, the classification was not based on the results of the presented phylogenetic analyses, but on a different phylogenetic tree which was figured without any explanation (Kazantsev 2005, compare Figs 595–600).

MATERIAL AND METHODS

The laboratory procedures and methods of phylogenetic analyses were described by Levkanicova and Bocak (in press). Here, only facts specifically related to the re-analysis of the morphological dataset and sampling of important non-neotenic lineages are pointed out.

Sampling. A representative sampling of previously described subfamilies and tribes of Lycidae was available for molecular study. With an exception of Dexorinae and Miniduliticolini we sampled all taxa which were given subfamily or tribe rank and are classified in Lycidae at present (Kleine 1933, Bocak and Bocakova 1990, Miller 2002, Kazantsev 2005). The position of *Thilmanus* Gemminger as the single genus classified in Thilmaninae (Kazantsev 2005) was extensively discussed by Bocak and Brlik (2008). Outgroups are restricted here to only 6 taxa, for which sequences of all six genes were available. The complete list of sequenced taxa was given by Levkanicova and Bocak (in press) and their identification is shown in Fig. 2.

Phylogenetic analyses. Six molecular markers were used for analyses. These included both highly conservative genes as 18S rRNA and 28S rRNA and fast evolving genes as *rrnL*, *cox1*, *nad5*, and *cob* mtDNA. The two-step phylogenetic analyses of each alignment and analyses under direct optimization (Wheeler 1996) were carried out under parsimony criterion (MP) using PAUP* v.4.0b10 and POY 3.0.11 (Swofford 2002, Wheeler *et al.* 2002). Gaps were considered as missing or 5th character in the analyses. The procedures were reported by Levkanicova and Bocak (in press). The settings of parameters are listed in Table 3.

Re-analysis of morphological data set published by Kazantsev (2005). The matrix of morphological characters as published by Kazantsev (2005) was re-analyzed under parsimony criterion by PAUP* v.4.0b10. All data were included in the analysis and equal weights were assigned to all characters. Heuristic searches used 1000 random-addition-sequence starting trees for tree-bisection-reconnection (TBR) swapping on best trees. All trees were counted as unrooted, all branches were collapsed if maximum

branch length was zero and no topological constrains were used. The roots of trees were designated subsequently. The support for individual clades was estimated by bootstrap analysis (1000 pseudoreplicates with 100 random taxon additions and 100 starting trees for TBR swapping). We did not repeat Kazantsev's analyses using *a priori* weights, because we consider *a priori* weighting of selected character five times or nine times as unjustified.

RESULTS

The basic information on results of analyses was reported by Levkanicova and Bocak (in press). Levkanicova and Bocak (in press) discussed only the origin and position of neotenic lineages. Therefore, we describe here the relationships of all lycid lineages and their classification.

The matrices of 73 ingroup and 6 outgroup taxa and three ribosomal (18S rRNA, 28S rRNA, and *rrnL*) and three mitochondrial protein coding (*cox1*, *cob*, and *nad5* mtDNA) genes contained 5742–5975 characters after various alignment parameters we used in the prior alignment procedures (Table 3). The total number of characters and number of constant, variable and parsimony informative characters for selected settings are given in Table 3. We found usual difference in base composition between nuclear ribosomal and mitochondrial genes (Table 2). The genes 18S rRNA and 28S rRNA were considerably more conservative than all mitochondrial genes. The maximum genetic distances within ingroup taxa in 18S and 28S rRNA genes were 5.60 and 7.68%, respectively. The variability in the mtDNA genes was highest in the protein coding fragments (Table 2). The *rrnL* fragment had slightly lower variability than protein coding genes and with higher content of indels in the alignment it was more similar to nuclear rRNAs. No variability was found in closely related species (*Thonalmus* spp.) in nuclear genes. The mitochondrial genes showed 0.68 per cent or more of variable sites in such taxa. The numbers of variable sites were counted for pairs of species of *Dictyoptera*, *Benibotarus*, *Lopheros*, and *Eropterus* to document variability within genera. We found 0.16–0.43% of variable sites in 18S rRNA, 0.48–0.97% in 28S rRNA, 4.2–10.6% in *rrnL*, 11.5–19.6% in *cox1*, 14.9–19.1% in *cob*, 13.4–19.1% in *nad5*.

Two-step analyses under maximum parsimony criterion. Each analysis produced 1-9 most parsimonious trees with lengths 27911–31051 steps depending on alignment settings and gap handling (Table 4). Fig. 2 shows one of three trees recovered under default settings for alignment (gap: extension penalty 15: 6.66) and handling gaps as 5th character. This tree was chosen as the preferred phylogenetic hypothesis on the

Phengodidae
Rhagophthalmidae
Lampyridae
Omalisidae
Cantharidae

Outgroups

Phengodes sp.
Ochotyra sp.
Bicladodrilus sp.
Luciolinae gen., sp.
Omalisus fontisbellaquei
Cantharis decipiens
Libnetis sp.B
Libnetis granicollis
Libnetis sp.A
Libnetis sp.C
Lycoprogenthes sp.A
Lycoprogenthes sp.B
Lycoprogenthes sp.C
Lycoprogenthes sp.D
Taphes brevicollis
Dictyoptera elegans
Dictyoptera speciosa
Pyropterus nigroruber
Beniboratus nigripennis
Beniboratus spinicoxis
Alyculus kurbatovi
Lyropaeus sp.B
Lyropaeus sp.A
Lyropaeus sp.C
Antennolycus constrictus
Microlyropaeus dembickyi
Macrolibnetis sp.
Pendola sp.
Horakiella emasensis
Platerodrilus sp.A
Platerodrilus sp.B
Platerodrilus sp.C
Platerodrilus sp.D
Dilphotes sp.
Scarelus sp.B
Scarelus sp.A
Scarelus sp.C
Dihammatus sp.A
Dihammatus sp.B
Dihammatus sp.C
Dihammatus sp.D
Eurrhacus sp.
Conderis signicollis
Conderis rufohumeralis
Plateros sp.A
Plateros sp.C
Plateros sp.E
Plateros sp.B
Plateros sp.D
Macrolycus sp.A
Macrolycus sp.B
Thonalmus sinuaticostis
Thonalmus hubbardi
Lyponia delicatula
Lyponia sp.
Lyponia nigrohumeralis
Lyponia quadricollis
Lycus sp.
Lycostomus sp.
Idiopteron biplagiatum
Calopteron sp.
Pseudoceratoprion sp.
Cautires sp.B
Cautires sp.A
Leptotrichalus sp.
Metriorrhynchus lineatus
Microtrichalus sp.
Calochromus sp.A
Calochromus sp.D
Calochromus sp.B
Calochromus sp.C
Flagrax sp.
Konoplatycis otome
Lopheros sp.A
Lopheros sp.B
Platycis minutus
Platycis nasutus
Eropterus nothus
Eropterus sp.

LIBNETINAE
DICTYOPTERINAE
LYROPAEINAE
ATELIINAE
LYCINAE

Lycoprogenthini
Taphini
Dictyopterini
Lyropaeini
Antennolycini
Platerodrilini
Dilophotini
Ateliini
Dihammatini
Eurrhacini
Conderini
Platerodini
Macrolycini
Thonalmini
Lyponiini
Lycini
Leptolycini
Metriorrhynchini
Calochromini
Slipinskiini
Erotini

Branch support values:
100/100
54/66
96/100
100/100
61/69
-/53
100/100
60/59
100/100
89/105
100/100
-/61
4/5
87/95
10/14
100/100
-/58
4/5
75/86
95/92
100/100
53/64
4/3
85/98
12/25
100/100
89/97
60/56
56/95
7/14
100/100
-/84
1/9
100/100
45/53
54/55
1/3
100/100
98/98
100/100
-/58
4/5
-/93
4/25
96/97
9/23
96/100
98/99
17/23
100/100
100/100
-/95
2/17
95/98
14/15
50/58
97/100
20/19
100/100
100/100
64/58
100/100
195/199
-/51
100/100
48/53
100/100
-/78
3/14
100/100
90/92
12/17
100/100
37/37
100/100
97/95
50/-
100/100
100/100
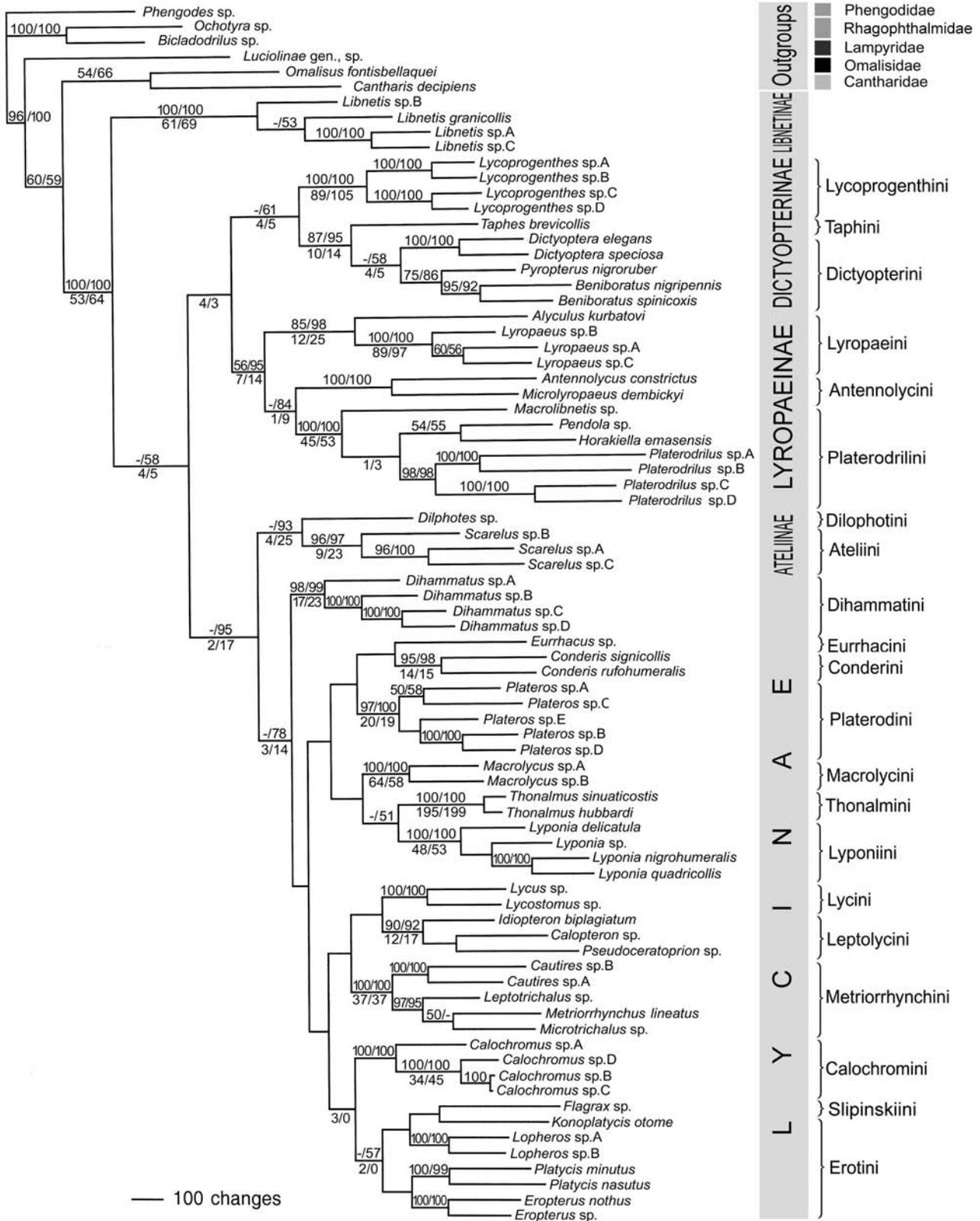34/45
100
3/0
-/57
2/0
100/99
100/100

— 100 changes

Figure 2. Phylogenetic hypothesis of 73 lycid taxa and 6 outgroups. One of five most parsimonious tree produced under default settings for ClustalX alignment, analyzed under maximum parsimony criterion by Paup*, when indels were handled as missing characters. The topology is similar with the one of most parsimonious trees produced by the same data set when indels were handled as 5th character. Numbers over branches refer to bootstrap proportions (if above 50%) for missing and 5th character gap handling, respectively; numbers under selected branches give Bremer support values.

Table 1. Base composition and uncorrected genetic distances within Lycidae.

	A	C	G	T	No. sites	Distance min.	max.
18S rDNA	0.24082	0.24271	0.27841	0.23896	1855	0.00	5.60
28S rDNA	0.25470	0.23555	0.30996	0.19978	627	0.00	7.68
rrnL	0.34031	0.08603	0.15567	0.41799	499	1.00	25.56
cox1 mtDNA	0.35312	0.18391	0.13270	0.33027	790	0.76	30.51
cob mtDNA	0.32389	0.20329	0.10808	0.36474	403	0.74	37.01
nad5 mtDNA	0.30768	0.07759	0.14600	0.46873	1198	0.68	38.01

basis of the lowest ILD values (Levkanicova and Bocak, in press). Additionally, this tree represents most frequently encountered topology of main basal branches of Lycidae and it produces the lowest conflict with morphologically defined lineages. The analyses of alignments produced by extreme gap : extension penalty values did not support monophyly of genera or tribes which were regularly encountered in most analyses and are well supported by morphological characters.

The analyses of the complete data set always returned Lycidae as a monophyletic group. The clade was regularly supported by 100% bootstrap values. The major lineages defined on the basis of adult and larval morphology were recovered under almost all settings. On the other hand, the relationships between subfamilies and internal clades of Lycinae often received weak support. The bootstrap values were low for relationships among Libnetinae, Dictyopterinae and Lyropaeinae and for most clades grouping tribes within Lycinae (Fig. 2).

Several analyses produced an alternative topology. Libnetines were under some settings nested inside Dictyopterinae clade and the clade was in the sister group position to Lyropaeinae. Eventually, Lycoprogenthini were in the most basal position and *Taphes* (*Dictyoptera* (*Pyropterus* + *Benibotarus*) formed a clade with Libnetinae (Figs 4A, B). Two settings of direct optimization procedure proposed the relationships of *Libnetis* spp. and *Lycoprogenthes* spp. placed outside Dictyopterinae. The recovery of selected clades under various settings is depicted in Fig 3.

We tested some previously proposed morphology-based phylogenetic hypotheses by constraining of hypothesized nodes and rerunning a parsimony analysis. Constraining Erotini + Dictyopterini (Kleine 1933, Bocak and Bocakova 1990, Kazantsev 2003) resulted in additional 27 and 62 steps, when matrices produced by default ClustalX parameters were analyzed with indels treated as missing or 5th character state; Libnetini + Platerodini (Bocak and Bocakova 1990) in additional 41 and 75 steps; basal position of neotenics and

reversal of "higher lycids" to winged forms (Crowson 1972, Kazantsev 2005) in 53 and 94 steps.

Analyses under direct optimization. The six settings of POY analyses yielded the similar topology (Figs 3, 5A–C). The setting of gap: transversion: transition 4:1:1 produced the tree representing the most frequently encountered topology and it was similar to the preferred trees inferred by the two-step parsimony analysis. Lycidae were found to be monophyletic in all analyses and the main clades based on morphology were regularly recovered. The conflicting topology was found in the Lycinae clade in the two-step analyses. The clade Leptolycini gen., spec. (= the taxon Pseudoceratoprion *in litt.* as designated by Miller, 1991 in the manuscript) + *Idiopteron* + *Calopteron* was not recovered under four settings, when the taxon Pseudoceratoprion (*in litt.*) was found in the sister group position to *Eurrhacus* Waterhouse. The frequency, in which individual clades were returned under various settings, is depicted in Figs 3, 5A–C.

Re-analysis of Kazantsev's data set. The analysis of the whole data set with equal weights assigned to all characters resulted in four trees of 217 steps, $ci = 0.409$, $ri = 0.527$ when uninformative characters were excluded; the bootstrap analysis with 1000 pseudoreplicates and 100 searches for each replicate showed very low support for most branches when only three nodes got support over 50 percent. Most branches of Lycinae collapsed in the strict consensus tree (Fig. 6).

DISCUSSION

The monophyly of Lycidae

All analyses provide strong molecular evidence with high bootstrap proportions for the monophyly of Lycidae as concluded by recent authors (e.g., Crowson 1972, Bocak and Bocakova 1990, Miller 2002). Due to the unavailability of material for DNA study, the position of dexorines (previously elevated to the family level [Kazantsev 2005]) could not be tested by molecular

Table 2. Number of constant, uninformative and parsimony informative characters across studied genes and selected gap cost settings. * The protein coding mtDNA genes were aligned by eye and the short tRNAs by default settings and they were attached to matrices of rDNA genes.

Gap costs	5:1				10:6.66				15:6.66				20:6.66			
Characters	all	const.	uninf.	inf.	all	const.	uninf.	inf.	all	const.	uninf.	inf.	all	const.	uninf.	inf.
18SrDNA	1882	1488	161	233	1876	1477	159	242	1875	1464	169	242	1871	1455	171	245
28SrDNA	656	482	71	103	656	475	72	109	647	472	68	107	647	470	70	107
rrnL	560	202	55	303	529	189	46	285	516	186	46	284	514	183	45	286
cdsmtDNA*	2495	615	201	1643	2459	615	201	1643	2495	615	201	1643	2495	615	201	1643
all genes	5557	2787	488	2282	5510	2756	476	2278	5497	2737	484	2276	5491	2723	487	2281

data. Dexorines are considered herein to be a lineage of Lycidae on the basis of previous opinions (Bocak and Bocakova 1988, 1989, 1990) and results of re-analysis of Kazantsev's data set (Fig. 6).

Phylogeny of Lycidae and comparison with the existing classification

Basal lineages of Lycidae. The only phylogenetic analysis has been published by Kazantsev (2005). Lyropaeinae, Leptolycinae, Ateliinae, and Miniduliticolinae were a paraphylum with respect to other lycids. Assuming basal position of neotenic lineages, Kazantsev predicted violation of Dollo's law by re-evolution of wings in Lycinae and Calochrominae. Additionally, Kazantsev (2005, 2006) hypothesized that *Platerodrilus* is the sister group to whole Neoptera and that several lycid lineages may deserve being separated at the suborder level in Coleoptera (Kazantsev 2005, 2006). Only three branches obtained some support from the bootstrap analysis of Kazantsev's dataset (Fig. 6), but these lineages were not used for classification (Kazantsev 2005). Further shortcomings of Kazantsev's studies were evaluated by Beutel *et al*. (2007). The relationships proposed by Kazantsev (2005) were never found in our analyses and are strongly rejected by considerable increase of the tree length when such topology was forced on our data. Our data set suggested independent origins of neotenic lineages. Similarly with our findings, Bocakova *et al*. (2007) favored multiple origins of neoteny and absence of reversals to fully metamorphosed forms in several families of Elateroidea. The position of *Platerodrilus* as a member of Lycidae within Elateroidea was supported also by comprehensive phylogeny of Coleoptera (Hunt *et al*. 2007).

The analyses of all available molecular data regularly returned fully resolved dichotomies for basal lineages in strict consensus trees, but the earliest divergence was unstable across analysis parameters and we found three competing topologies. The best supported hypothesis suggested the basal position of Libnetinae, the monophyly of Dictyopterinae, Lyropaeinae and the sister group position of Ateliinae and Lycinae (Fig. 3). This topology was indicated in majority of cases, had the lowest ILD values and limits of all these basal lineages were well supported by morphology in previous studies (Bocak and Bocakova 1990). The basal position of Libnetinae, although surprising, was found frequently also in partitioned analyses of both ribosomal and protein coding genes.

Dictyopterinae is an extensive group, which branched off consistently early in lycid evolution. Dictyopterines formed either a clade with Lyropaeinae (Figs 2, 3) or these lineages were in the paraphyletic position with respect to Ateliinae and Lycinae (Figs 4A, B). Neither

Table 3. Number of trees, consistency and retency indexes and ILD values under various alignment procedures and parameter settings as analyzed by Bocak *et al.* (2008).

Setting	Trees	Length	ci/ri	ILD
2:1 miss.	2	28124	0.191/0.356	0.00441
5th	3	30435	0.213/0.379	0.00624
2:0.1 miss.	1	27911	0.193/0.357	0.00448
5th	2	30538	0.217/0.381	0.00671
3:1 miss.	1	28210	0.190/0.358	0.00421
5th	2	30460	0.211/0.380	0.00630
3:0.1 miss.	1	28129	0.190/0.357	0.00388
5th	2	30488	0.212/0.380	0.00653
5:1 miss.	1	28513	0.187/0.359	0.00383
5th	2	30471	0.200/0.379	0.00704
5:0.1 miss.	2	28460	0.188/0.358	0.00397
5th	1	30444	0.208/0.380	0.00568
10:6.66 m.	2	28818	0.184/0.361	0.00385
5th	2	30182	0.196/0.377	0.00918
10:0.1 m.	1	28765	0.184/0.360	0.00379
5th	1	30372	0.195/0.376	0.00380
15:6.66 m.	5	28904	0.185/0.361	0.00374
5th	3	30039	0.194/0.378	0.00336
20:6.66 m.	1	28953	0.185/0.363	0.00356
5th	1	30167	0.195/0.379	0.00348
25:6.66 m.	1	29016	0.186/0.363	0.00406
5th	1	30507	0.203/0.382	0.00439
30:6.66 m.	6	29609	0.186/0.363	0.02276
5th	1	30597	0.203/0.381	0.00536
35:6.66 m.	3	29084	0.186/0.364	0.00461
5th	4	30598	0.203/0.381	0.00592
45:6.66 m.	2	29148	0.186/0.365	0.00446
5th	1	30624	0.204/0.381	0.00519
55:6.66 m.	3	29223	0.187/0.366	0.00486
5th	3	30719	0.204/0.386	0.00531
75:6.66 m.	1	29344	0.187/0.371	0.00460
5th	1	30850	0.205/0.389	0.00570
100:6.6 m.	9	29560	0.189/0.367	0.00626
5th	4	31051	0.206/0.386	0.00734
1:1:1 5th	2	29683	0.218/0.382	0.00286
2:1:1 5th	1	29689	0.206/0.372	0.00310
2:2:1 5th	1	29801	0.208/0.370	0.00386
3:1:1 5th	1	29787	0.205/0.368	0.00356
3:2:1 5th	1	29776	0.204/0.369	0.00319
3:3:1 5th	1	29912	0.208/0.372	0.00314
4:1:1 5th	1	29848	0.205/0.371	0.00285
4:2:1 5th	1	29886	0.205/0.370	0.00977
4:4:1 5th	1	29996	0.207/0.370	0.00423
8:1:1 5th	1	30251	0.204/0.367	0.00569
8:4:1 5th	1	30446	0.202/0.368	0.00670
8:8:1 5th	1	30679	0.202/0.363	0.00958

of these topologies showed bootstrap proportions over 50%. The basal position of these lineages was recovered also under most direct optimization analyses. We have not found any morphological character clearly supporting the relationships of these two lineages, although *Taphes* Waterhouse, (Dictyopterinae) was found in the sister position to *Lyroneces* (Lyropaeinae) in the tree inferred from the morphological data set (Fig. 6). Additionally, the metathoracic spiracles are known in larvae of *Lycoprogenthes* Pic and *Duliticola* and the cup shaped pedicels are known in *Taphes* and some Lyropaeines and nowhere else. The rejection of close relationships of Erotini and Dictyopterini (Bocak and Bocakova 1990, Kazantsev 2005) is rather surprising concerning adult morphology, but already Bocak and Matsuda (2003) reported similarity of *Pyropterus* Mulsant and *Lycoprogenthes* (= *Pseudosynchonnus* Pic) larvae and the lack of any larval character supporting the traditional perception of Erotini + Dictyopterini as closely related lineages.

Unlike all other basal lineages, Dictyopterinae in the sense proposed here, were not found monophyletic in all analyses and obtained low bootstrap support (Fig. 2). The alternative topologies suggest the clade lycoprogenthines (libnetines + dictyopterines) (Fig. 4A) or polyphyly of dictyopterines (Fig. 4B). Concerning morphology, *Lycoprogenthes* is very close to *Taphes* and dictyopterines and the position of *Lycoprogenthes* outside Dictyopterinae is highly improbable. *Taphes* and *Lycoprogenthes* share similarly shaped pronotum, similar structure of elytral costae, male and female genitalia and larval morphology (Bocak and Matsuda 2003). Libnetines differ morphologically from dictyopterines in male and female genitalia, absence of pronotal and elytral costae, and shape of cranium (Bocakova 2004) and therefore we accept their deeply rooted position within Lycidae. Their relationships with Platerodini as previously suggested (Bocak and Bocakova 1990, Bocakova 2001a) or placement of dictyopterines in Lycinae (Kazantsev 2005) are strongly rejected by molecular data. On the basis of both larval and adult morphological characters and the prevailing position in the molecular analyses, we propose the broad definition of Dictyopterinae as depicted in Fig. 2.

Lyropaeinae is a well supported clade comprising most Southeast Asian lycids with larviform females. We found this clade in all analyses among basal lineages and well supported with bootstrap proportions between 56 and 95 percent. The clade contains not only *Lyropaeus* and closely related genera (Bocakova 2006) but also Miniduliticolinae as understood by Kazantsev (2005). Kazantsev (2005) proposed distant position of Lyropaeinae and Miniduliticolinae regardless high similarity of larvae of *Lyropaeus* and *Duliticola* (Gravely 1915, Wong 1996). Clades representing

Table 4. Previous and current higher classifications of Lycidae.

Bocak and Bocakova 1990		Kazantsev, 2005	Present study
Leptolycinae	Dexorini	Dexoridae	Dexorinae
	Leptolycini		Libnetinae
	Lyropaeini	Lycidae	Lyropaeinae
Ateliinae	Ateliini	Leptolycinae	Dictyopterinae
			Lycoprogenthini
		Lyropaeinae	Dictyopterini
Lycinae	Lycini	Ateliinae	Taphini
	Calopterini	Thilmaninae	Ateliinae Ateliini
	Macrolycini	Miniduliticolinae	Dilophotini
	(incl. *Dilophotes*)	(=Lyropaeinae pars)	
		Lycinae	Lycinae Dihammatini
		Platerodini	Eurrhacini
Erotinae	Erotini (incl. Dictyopterini,	Erotini	Conderini
	Taphini)	Dictyopterini (incl. *Flagrax*)	Platerodini
	Platerodini (incl. Libnetina,	Taphini	Macrolycini
	Dihammatus)	Lycini	Thonalmini
	Lyponiini	Conderini	Lyponiini
		Calopterini	Lycini
Calochrominae	Calochromini	Libnetini	Metriorrhynchini
		Calochrominae	Calopterini
Metriorrhynchinae		Macrolycini	Leptolycini
	Conderini	Dilophotini	Metriorrhynchini
	Metriorrhynchini	Calochromin i	Erotini
	Trichalini	Aferotini	Slipinskiini

lyropaeine tribes were found in all analyses and with high Bremer and bootstrap values, but their mutual relationships remain ambiguous and further data should be included in the analyses to obtain more robust support. The *Antennolycus + Microlyropaeus* clade was found in the sister group position to Miniduliticolini or *Lyropaeus + Alyculus* or they formed a clade with *Alyculus* (Figs 2–4). Both, *Antennolycus* and *Microlyropaeus* had long branches, but they share several morphological characters, which support their close position.

Dexorines were included only in the re-analysis of the morphological data set and they were found to be an internal branch within Lycidae in the sister group position to *Lyropaeus s. l.* as was previously proposed by Bocak and Bocakova (1989, 1990). Therefore, Dexoridae cannot be accepted as an independent family under principles of phylogenetic systematics (Fig. 6). Kazantsev (2005) presented four phylogenies based on partial data sets and different weighting schemes and a hand drawn tree, which should depict the presumed phylogeny of Lycidae. The hand drawn tree presents some topologies, which were not found in any of his

analyses (Fig. 1). For example Dexoridae are depicted as the sister group to all Lycidae, although they were in internal positions under all Kazantsev's settings (Kazantsev 2005, Figs 595–598). Our bootstrap analysis of the morphological data set suggested high support for the *Lyropaeus s. l. + Dexoris* clade, but considering the possible morphological convergence due to the neoteny in both groups the rigorous testing of this relationships should be based on independent source of data or at least on known morphology of females and larvae of both groups.

Ateliinae is another Oriental clade branching off early in the evolution of Lycidae. Ateliinae were considered to be an independent lineage by Bocak and Bocakova (1990) and Kazantsev (2005). Herein, they were found regularly as a sister group of Lycinae. Unlike all previous studies, molecular data show very close relationships between Dilophotini and Ateliini (Figs 2 and 3). The name Dilophotini was erected for *Dilophotes* Waterhouse by Kleine (1928) and later synonymized to Macrolycini (Bocak and Bocakova 1990). They were resurrected by Kazantsev (2005), but they were still considered to be the sister-group of
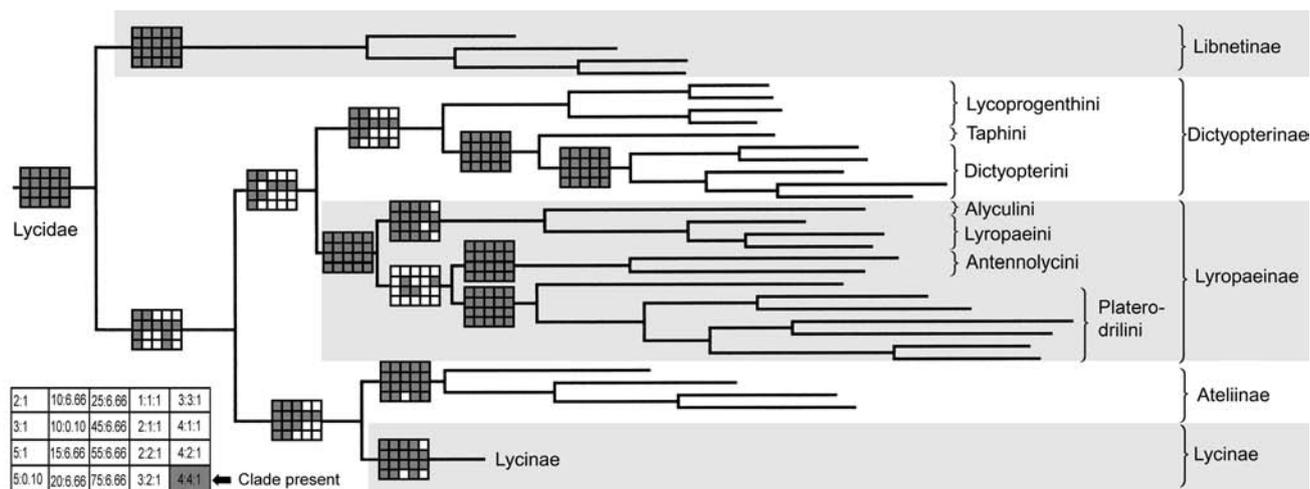
Figure 3. The topology of the basal part of Lycidae tree obtained under various settings. The sensitivity landscapes show the presence/absence of the given clade under specific parameters.

Macrolycini in Calochrominae. The clade Dilophotini + Ateliini was obtained in all two-step analyses, but it got very high bootstrap support only in analyses considering gaps to be the 5th character state. When we handled indels as the missing character the maximum bootstrap support values reached 60%. Under direct optimization two settings produced alternative topologies. Either *Dilophotes* was found in Lycinae as the sister group to Metriorrhynchini or Antennolycini were a part of the *Dilophotes + Scarelus* clade. Both topologies did not get any support from other analyses or morphological data. We do not know immature stages of either tribe and additionally, females of Ateliini are also unknown.

Monophyly and composition of Lycinae. Lycinae is by far the largest subfamily representing 93% of described species. There are several large genera in Lycinae with hundreds of species (e.g., *Plateros* Bourgeois, 1879 in Platerodini, *Lycus* Fabricius, *Lycostomus* Motschoulsky and *Calopteron* Castelnau in Lycini, *Metriorrhynchus* Gemminger and Harold, *Cautires* Waterhouse, *Xylobanus* Waterhouse, and *Cladophorus* Guérin Méneville in Metriorrhynchini, and *Calochromus* Lacordaire in Calochromini). These groups represent four most species rich tribes in the whole family. Our data favored the broad definition of Lycinae (Fig. 2, 5), although the evidence was far from definitive for relationships among included lineages. Lycinae were recovered in all two-step analyses except two. Neither molecular data nor Kazantsev's morphological data set did not lend any support for separation of subfamilies Lycinae and Calochrominae as proposed by Kazantsev (2005). Kazantsev's proposal was based on a single analysis using unjustified weighting scheme. Additionally, these groupings were not supported by our re-analysis of morphological data (Fig. 6). Therefore, we propose the new broad delineation of Lycinae.

The relationships among tribes of Lycinae remain weakly supported. We have not found any stable arrangement, which would be consistently present in all analyses and get reasonably high bootstrap values. A few groupings of tribes appeared regularly under various settings of analysis parameters, but their robustness was generally low. There is also a high uncertainty about the most basal clade of Lycinae, Metriorrhynchini and Dihammatini being in such position in most analyses (Figs 2, 5A–B). On the other hand, our data lent good support for the monophyly of most tribes as defined by morphology-based studies. The clades Metriorrhynchini (bootstrap proportions 99–100%), Dihammatini (94–100%), Platerodini (93–100%), Lyponiini (100% in all analyses), Calochromini (100% in all analyses), and Erotini (up to 91%, but see discussion further) were present in all analyses. These clades were represented either by several genera or at least a higher number of distant species. Further lineages were represented by two species from the same genus, so their high support values were expected from the beginning.

Dihammatini is a small Southeast Asian group, which was previously included in Platerodini (Bocak and Bocakova 1990). Based on morphology of the internal female genitalia Bocakova (2001a, 2004) classified *Dihammatus* Waterhouse within libnetines. The hypothesized homologies were rejected by molecular analyses as the position of Dihammatini was distant from libnetines in all analyses. We do not know immature stages of these groups and neither of these lineages was included in the Kazantsev's study (Kazantsev 2005).
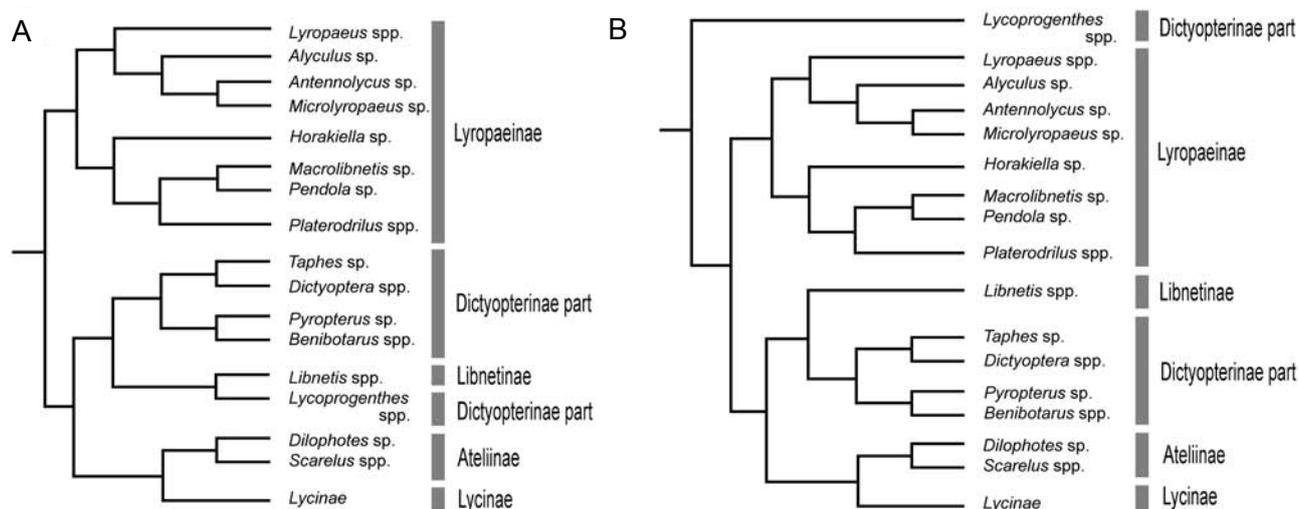
Figure 4. (A) Tree topology of the basal part of Lycidae based on the combined analysis of all genes aligned with gap opening / extension penalties 2:1 and analyzed under MP criterion by Paup*, when indels were considered missing character. (B) The same under alignment parameters 10:6.66.

Metriorrhynchini are one of the largest groups of Lycidae (Bocak 2002b). Metriorrhynchine clade was recovered in all analyses and got strong support. The lineage is well characterized by adult and larval morphology (Bocak 2002b, Bocak and Matsuda 2003).

Platerodini is the second largest group of Lycinae. Platerodine clade is clearly defined by larval morphology (Miller 1997) and was consistently present in our analyses. Although their exact position was variable, some arrangements were prevailing. Most frequently they are found in the sister-group position to the clade *Eurrhacus + Conderis* with Lycini basally to them or Lycini are the sister group of Platerodini with Metriorrhynchini basally to them. These topologies are not sufficiently corroborated by the adult or larval morphology and need further investigation.

The clade *Eurrhacus + Conderis* was found in most two-step analyses (Fig. 5A), but it did not get bootstrap support proportions over 50% in any case. Both these groups are small in number of species. Eurrhacini is a tribe with six genera and altogether 90 species (Bocakova 2005). Conderini include only *Conderis* Waterhouse and *Xylobanellus* Kleine with less than 30 species (Kleine 1933). These groups are endemics to the Neotropical Region and Oriental and Palaearctic Regions, respectively. As few taxa were sequenced for these groups, we should postpone further considerations until more data are obtained. Under direct optimization we found the conflicting *Eurrhacus* + the taxon Pseudoceratoprion (*in litt*.) clade several times.

The clade Macrolycini + Thonalmini + Lyponiini is another frequently encountered lineage (Figs 2, 5A). Thonalmini is a small group of very distinctive lycids from West Indies, the other two tribes are known from the Eastern part of the Palaearctic Region and the northernmost areas of the Oriental Region. Macrolycini were originally classified in Lycinae in restricted sense (Bocak and Bocakova 1990) and their position was doubted on the basis of larval morphology (Bocak and Matsuda 2003). The adults of both sexes and larvae are known for *Macrolycus* Waterhouse and *Lyponia* Waterhouse, but no evident synapomorphy indicates their relationships.

The clade (Lycini (Calopterini (Leptolycini)) was found with high frequency in our two-step analyses, but without sufficient bootstrap support. Larvae of *Lycus* and *Calopteron* show the close relationships of these two groups (Bocak and Matsuda 2003). Based on adult morphology, these two tribes were both classified in the subfamily Lycinae in the restricted sense (Bocak and Bocakova 1990) and molecular data support this view. Most analyses showed the taxon Pseudoceratoprion (*in litt*.) as a member of the calopterini clade (Fig. 5A). We got this taxon from the collection of Richard Miller (Bozeman) and based on extensive knowledge of the morphology he classified it as a leptolycine. The present analysis included it in Calopterini as understood until now and it is in agreement with the possibility discussed by Miller (1991) and findings of Bocakova (2003, 2005) who considered several similar taxa to be related to *Idiopteron* Bourgeois. Unfortunately, *Leptolycus* Leng et Mutchler, the type species of the group, was not available for the study and should be studied to confirm the present hypothesis.

Calochromini were classified as a subfamily for long time and this subfamily was redefined by Kazantsev (2005) who added Metriorrhynchini, Dilophotini, Macrolycini, and Slipinskiini. Most Kazantsev's (2005) analyses proposed different topologies and he found this clade under single setting with selected characters
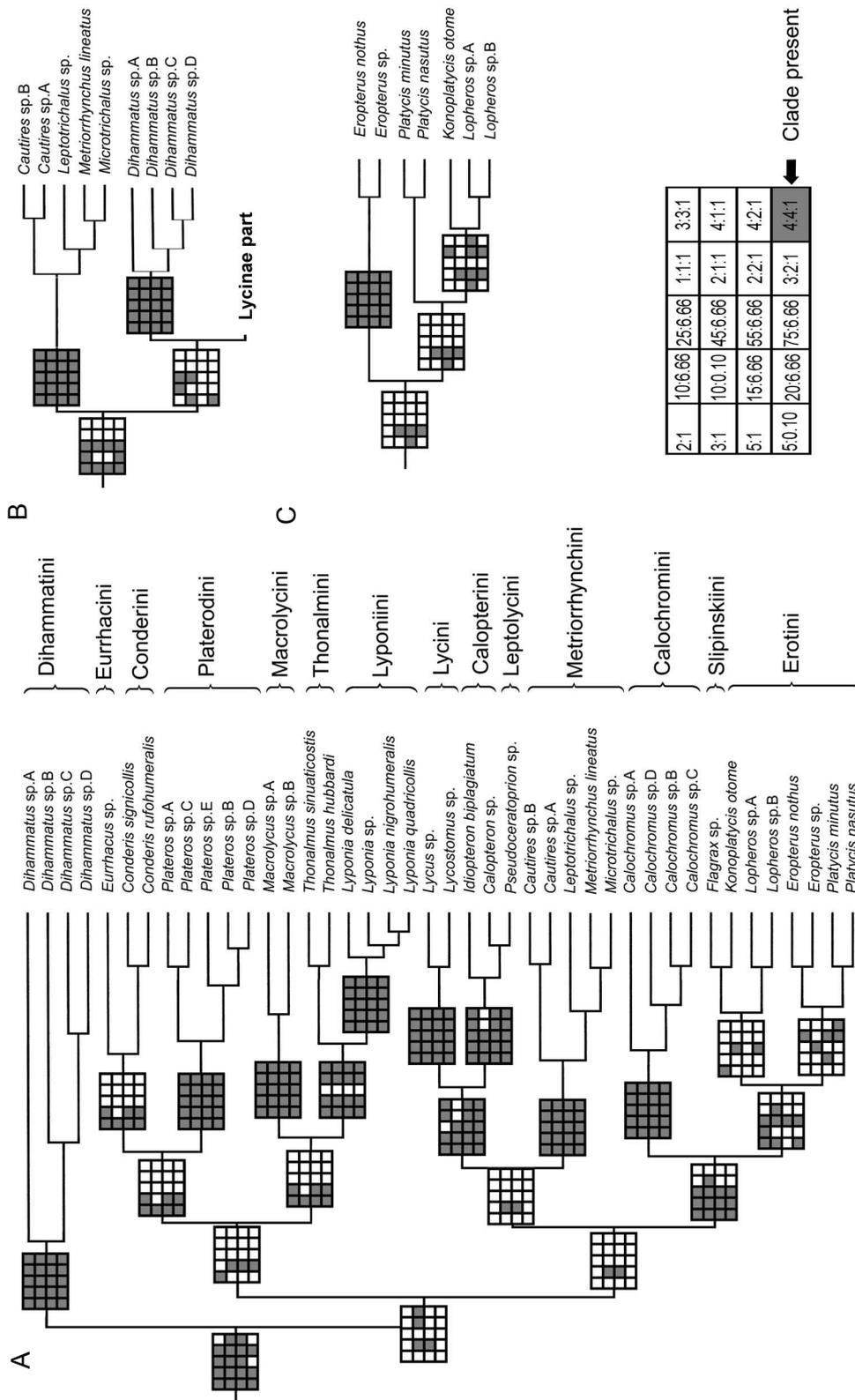
Figure 5. (A) Phylogenetic hypothesis of Lycinae taxa. One of the most parsimonious trees produced under default settings for ClustalX alignment, analyzed under parsimony criterion by Paup*, when indels were considered 5th character. The sensitivity landscape is depicted on basal nodes with boxes representing presence/absence under specific parameters. (B) Alternative topology for basal lineages of Lycinae. (C) Alternative topology for the Erotini clade.

a priori reweighted five times. Our re-analysis of Kazantsev's data did not reveal the proposed relationships (Fig. 6). His view is strongly contradicted by molecular data as analyses revealed no topology reminding his concept. Calochromini were frequently found closely related to Erotini in our two-step analyses and other groups were regularly in a distant position. Larvae are known for erotine genera *Lopheros* Leconte and *Platycis* Thomson and they resemble *Calochromus* in some aspects (Bocak and Matsuda 2003). The direct optimization analyses supported the relationships of Calochromini + Erotini only under one setting and most analyses suggested relationships of *Calochromus* to *Lyponia*. Kazantsev (2005) classified Lyponiini in Calochrominae, although *Lyponia* was omitted from his morphological data set for some reason.

Erotini were hypothesized to be related to some Dictyopterini and *Flagrax* Kazantsev was classified with Dictyopterini by Kazantsev (2005). Molecular data do not provide any support for these relationships under any setting. Erotini were consistently found to be a member of Lycinae in all two-step analyses either with *Flagrax* included in Erotini or in various positions outside *Calochromus* + Erotini clade. The clade obtained low bootstrap proportions when *Flagrax* was included, but the clade (*Eropterus* (*Platycis* (*Konoplatycis, Lopheros*)) got high support under some settings and relationships among genera was stable (Fig.
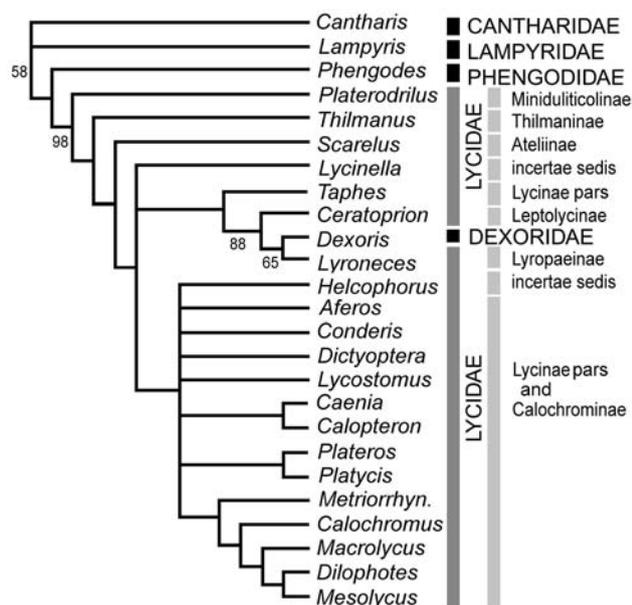
5C). Direct optimization provided lower support for Erotini, but similar topologies were found in majority of direct optimization analyses. The unstable position of *Flagrax* (Slipinskiini) can be a reason for lower bootstrap support values for Erotini. As the presence and/ or absence of *Flagrax* in the clade affected the internal topology of Erotini we cannot suggest any hypothesis about the internal relationships among erotine genera until the position of *Flagrax* is solved. Unfortunately, *Flagrax* is the only representative of the Afrotropical tribe Slipinskiini in the analysis and only more taxa in the analysis can clarify its position.

Congruence with morphology-based phylogeny.
Kazantsev (2005) has been the only author who presented a formal analysis of the morphological data set for Lycidae. He reported four analyses: unweighted and *a priori* weighted adult characters and both adult and larval characters combined and again unweighted and *a priori* weighted. Kazantsev (2005) figured one arbitrarily selected tree for each analysis. The trees were rooted by *Dexoris* which is considered to be lycid (Bocak and Bocakova 1988, 1990) and no information about tree lengths, indexes and branch support was reported. We re-analyzed his data set and we found the very low branch support for all branches except three (Fig. 6). Additionally, most taxa, even those proposed by Kazantsev in his formal classification, were not found to be monophyletic in the majority of his analyses. Kazantsev's results are in a deep conflict with previous morphological studies (Bocak and Bocakova 1990, Bocak and Matsuda 2003) and topologies produced by the analyses of the molecular dataset, therefore we refuse his hypothesis on lycid phylogeny (Fig. 1) as weakly supported and unsuitable as a basis for classification.

The lycid classification was traditionally based on morphology of pronotal carinae and elytral costae, which are characteristic for most lycid lineages and can be easily used as diagnostic characters. We suppose that these costae and ridges have an important adaptive function in the soft-bodied lycids as strengthening structures and molecular phylogeny suggests their multiple origins in independent lineages. As an example we can consider the presence of the lanceolate median areola in the middle of the pronotal disc. The molecular analyses showed multiple origins of this structure as it is present in all Dictyopterinae, in some tribes of Lycinae (Conderini, Slipinskiini and in *Achras* Waterhouse, *Wakarumbia* Bocak, and *Hemiconderis* Kleine in Metriorrhynchini). None of our analyses united at least two of these lineages and therefore the multiple origins of median areola are strongly indicated. Similarly, the number of longitudinal elytral costae is a very unstable character and most lineages comprise genera with secondary costae present or absent. Additionally, these structures have a tendency

Figure 6. The strict consensus tree obtained by the nonadditive parsimony re-analysis of the morphological data set published by Kazantsev (2005). The numbers below branches indicate bootstrap proportions if above 50%. Classification of the family level taxa follows Kazantsev (2005).

to be simplified in small or slender bodied taxa (e.g., Leptolycini, Dilophotini).

Another source of homologies lies in supposed multiple origins of neoteny in Lycidae (Levkanicova and Bocak, in press) and resulting parallel modifications of morphology. The characters used for definition of Leptolycinae in the sense of Bocak and Bocakova (1990), e.g., shape of cranium in males and reduction of mouth parts, are supposed to be homoplastic characters as many males are tiny, short living and very probably they do not take any food as adults. As neotenic females remain larviform when sexually mature, the analyses suffer from the high portion of the inapplicable character states for females. The molecular markers should not be biased by life histories and modification of ontogeny and therefore we expect them to provide an independent insight into lycid phylogeny.

TAXONOMY

The phylogenetic hypothesis presented by Levkanicova and Bocak (in press) and briefly described above can serve as a basis for modified higher classification of Lycidae. We compare the results with morphological data and we propose a new classification as given in Tab. 4. This section includes formal descriptions of new tribes, proposals of new status of some taxa and brief information on all tribes and subfamilies in Lycidae. The classification of genera is based mostly on previously published revisions (Bocak 1998a, 2002a, b, Bocak and Bocakova 1990, Bocakova 2001a, 2003, 2004, 2005, 2006, Bocakova and Bocak 1999, Kazantsev 2002, 2005). Larval morphology of Lycidae was recently reviewed by Bocak and Masuda (2003) and it is only briefly mentioned further.

Libnetinae Bocak et Bocakova, stat. nov.

Libnetina Bocak et Bocakova, 1990: 652 (in Erotinae: Platerodini).
Libnetini: Bocakova 2001a: 65 (in Platerodinae), Kazantsev 2005: 217 (in Lycinae).

Type genus. Libnetis Waterhouse, 1878.
Diagnosis. Adult. Body small, antennae filiform, rarely weekly serrate, pronotal areolae absent, median longitudinal keel present in anterior part of pronotum, each elytron with four primary costae, reticulate cells absent. Male genitalia with short basally fused paramerae. Larva unknown.
Genera. Libnetis Waterhouse, 1878, *Libnetisia* Pic, 1921, *Prolibnetis* Bocakova, 2004.
Remark. Libnetini were described as a subtribe in Platerodini and when Platerodini obtained subfamiliar status (Miller, 1997), they were treated as a tribe (Bocakova 2001a, 2004). The present analyses support their

basal position within Lycidae and they are given a subfamily status for that reason. We propose their independent position from Dictyopterinae on the basis adult morphology (Bocak and Bocakova 1990). These groups differ in the shape of genitalia in both sexes, presence and/or absence of pronotal cells and transverse elytral costae, shape of pronotum, and in the general appearance. The diversity of Oriental and East Palaearctic Libnetini was studied by Bocakova (2000, 2001a).

Dictyopterinae Kleine, stat. nov.

Dictyopterinae Kleine, 1928: 222.
Dictyopterini: Kazantsev 2005: 217 (in Lycinae).

Type genus. Dictyoptera Latreille, 1829.
Diagnosis. Adult. Head with antennal tubercles divided by groove, antennae filiform to slightly serrate in both sexes, pronotum always with median areola. Elytra with nine costae, four of them stronger (primary costae), five weaker (secondary costae) or only with primary costae, always with well developed reticulate cells in intervals between costae. Male genitalia with long paramerae; ovipositor with paraproctal baculi very slender (Dictyopterini) or shortened (Taphini, Lycoprogenthini), ultimate female sternite with long spiculum ventrale.
Remark. The genera classified in Dictyopterinae were considered a part of Erotinae until Kazantsev (2005) supposed paraphyly of Dictyopterini and Erotini with respect to Platerodini and separated Taphini as an independent lineage. None of our analyses indicated that Erotini and Dictyopterini are close lineages and all analyses supported close relationships of Dictyopterini and Taphini. Dictyopterinae as one of basal lineages of Lycidae are given the subfamily status. Dictyopterinae consist of three tribes: Dictyopterini, Taphini and Lycoprogenthini trib. nov.

Dictyopterini Kleine

Dictyopterinae Kleine, 1928: 222.
Dictyopterini: Kazantsev 2005: 217 (in Lycinae).

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 whole length (*Pyropterus* Mulsant, 1838), or elytral costa 3 shortened (*Benibotarus* Kono, 1932). Male genitalia with long paramerae, paraproctal baculi in female genitalia long, very slender. Larva (*Pyropterus*). 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.

Genera and distribution. E.g., *Benibotarus* Kono, 1932, *Chinotaphes* Bocak et Bocakova, 1999, *Dictyoptera* Latreille, 1829, *Greenarus* Kazantsev, 1995, *Laterialis* Kazantsev, 1990, *Punicealis* Kazantsev, 1990, *Pyropterus* Mulsant, 1838. Nearctic, Palaearctic, and Oriental regions.

Remark. Dictyopterinae are a species poor lineage, which occurs mainly in the Palaearctic and Nearctic regions (Kleine 1933). They were classified long time with Erotini (Kleine 1933, Nakane 1969, Bocak and Bocakova 1990).

Lycoprogenthini trib. nov.

Type genus. Lycoprogenthes Pic, 1915: 6.

Differential diagnosis. Lycoprogenthini have very characteristic male genitalia with long phallobase and short rounded paramerae. The ovipositor is wide, with the complex paraprocts and short, free valvifers. These characters together with the structure of pronotal carinae distinguish them from both Dictyopterini and Taphini.

Description. Adult. Body small to medium sized, dorsoventrally flattened, subparallel-sided. Head small, prognathous, without rostrum. Eyes large, hemispherically prominent. Frontal margin of clypeus straight or projected in middle. Maxillary palpi 4-segmented, labial palpi 3-segmented, apical palpomere similar in shape, parallel-sided, obliquely cut at apex. Mandibles long, slender, falciform. Antennae filiform, antennomere 2 very short, 3 long, similar to antennomere 4. Pronotum with median areola broadly attached to basal margin of pronotum, widest at frontal third, lateral pronotal costae straight, conspicuous. Scutellum bilobe at apex. Elytra subparallel-sided, usually with nine longitudinal costae; only four costae often conspicuous in apical half of elytra when body small. Legs slender, compressed; trochanters slender, long, tarsomeres 1-2 laterally compressed, with sharp keel dorsally, tarsomeres 3 and 4 deeply bilobe. Male genitalia with long phallobase and robust rounded paramerae. Female genitalia with complex paraprocts and free paraproctal baculi. Larva (*Lycoprogenthes*). Body shape, limited sclerotization, and pigmentation of tergites and pleurites remind *Pyropterus nigroruber. Lycoprogenthes* is characterized by sclerotized pleural part of cranium, well developed metathoracic spiracles, undivided thoracic and abdominal tergites, and long, fixed urogomphi.

Genus and distribution. Lycoprogenthes Pic, 1915. Oriental region.

Remarks. Lycoprogenthes was originally classified in Calochromini (Kleine 1933) and transferred to Erotinae by Bocak (2002b). *Lycoprogenthes, Coloberos* Bourgeois, 1885 and *Taphes* Waterhouse, 1878 formed the tribe Taphini in Erotinae, but the analyses shoved the close relationships of *Taphes* with the clade of (*Dictyoptera* (*Pyropterus* (*Benibotarus*)). The tribal status must be given to *Lycoprogenthes*, which is in the basal position to the (*Taphes* (Dictyopterini)) clade.

Taphini Bocak et Bocakova

Taphina Bocak et Bocakova, 1990: 650.
Taphini: Kazantsev; 2005: 217.

Type genus. Taphes Waterhouse, 1878 (in Lycinae).

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 paramerae shorter than phallus, lateral margins concave. Female genitalia with well developed proctiger, paraproctal baculi about 1.5 length of coxites. Larva unknown.

Genera and distribution. Coloberos Bourgeois, 1905, *Taphes* Waterhouse, 1878. Oriental and Australian regions.

Remark. Taphina were proposed for genera *Taphes* and *Coloberos* Bourgeois, 1885 in Dictyopterini and they were placed in Lycinae in the sister-group position with Lycini by Kazantsev (2005). Here, they are classified as the tribe in Dictyopterinae and their placement is well supported by both molecular and morphological data.

Lyropaeinae Bocak et Bocakova

Lyropaeini Bocak et Bocakova, 1989: 718.
Lyropaeinae: Kazantsev, 2005: 216.
= Paralycinae Medvedev et Kazantsev, 1992: 55; Kazantsev 2002: 18 (Type genus: *Paralycus* Medvedev et Kazantsev, 1992, a junior synonym of *Lyropaeus* Waterhouse, 1878).

Type genus. Lyropaeus Waterhouse, 1878.

Diagnosis. Adult. Morphologically diverse group of Oriental lycids with neotenous females. Males very small (*Alyculus* Kazantsev, 2002) to medium sized. Head small, mouth vertical, often reduced. Maxillary palpi with terminal palpomere apically pointed, labium reduced. Antennae 10–11 segmented. Pronotum usually trapezoidal, without carinae, sometimes with median longitudinal groove posteriorly, posterior angles of pronotum projected obliquely backwards. Each elytron

with 4–9 weak longitudinal costae, costae some-times indistinct. Intercostal intervals with irregular reticulate cells or punctures, sometimes elytra almost glabrous. Male genitalia trilobate, phallobase always present, sometimes fused with paramerae. Paramerae apically pointed, with sharp ventrobasal projection. Females unknown except *Lyropaeus*, *Duliticola* Mjöberg, 1925, *Macrolibnetis* Pic, 1939, and *Platero-drilus* (Wong 1996, 1998, Bocak and Matsuda 2003). Larva. Only large bodied female larvae are known; many of them are characteristic in wide expanded thoracic terga (Gravely 1915, Bocak and Matsuda 2003).

Remark. Lyropaeinae are redefined and consist of the following tribes: Lyropaeini Bocak and Bocakova, 1989, Alyculini trib. nov., Antennolycini trib. nov., Miniduliticolini Kazantsev, 2002, and Platerodrilini Kazantsev, 2005. Females of *Lyropaeus*, *Duliticola*, *Macrolibnetis*, and *Platerodrilus* are exceptionally large and remain larviform when sexually mature. The remaining genera of the subfamily are known only in males.

Lyropaeini Bocak et Bocakova

Lyropaeini Bocak et Bocakova, 1989: 718.

Type genus. *Lyropaeus* Waterhouse, 1878.
Diagnosis. Adult. Head small, mouthparts vertical, mandibles small, reduced, curved apically. Antennae 10-segmented, laterally compressed. Maxillary palpi with terminal palpomere small, apically pointed. Labium reduced, labial palpi 1-segmented, apically pointed. Pronotum trapezoidal, without carinae, scutellum considerably emarginate apically. Elytra flat, each elytron with four weak longitudinal costae, costa 3 vestigial, intercostal intervals finely punctured, without reticulate cells. Male genitalia trilobate, phallobase long, as long as aedeagus. Paramerae robust, with ventrobasal projection. 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.

Genera and distribution. E.g., *Lybnopaeus* Kazantsev, 1998, *Lyroneces* Kazantsev, 1998, *Lyropaeus* Waterhouse, 1878. Oriental region.

Remark. Lyropaeini were recently revised by Bocakova (2006) in a wider sense including Alyculini and Antennolycini as proposed here.

Alyculini trib. nov.

Type genus. *Alyculus* Kazantsev, 1999: 252.
Differential diagnosis. Alyculini are the monotypic tribe. *Alyculus* is the only brachyelytrous genus in Lyropaeinae. All known species have very small body (slightly over 1 mm) and strongly transverse pronotum. They differ in 11-segmented antennae from Lyropaeini, which are supposed to be their sister group (Levkanicova and Bocak, in press).

Description. Adult. Body very small, subtle. 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 bilobed apically, distal tips projected obliquely backwards. Elytra shortened, tapering to apex, distal portion rounded, densely punctured, without any traces of costae or reticular cells. Abdominal sternum 8 simple, 9 elongate. Legs slender, tarsomere 4 lobed. Male genitalia with slender phallus widened basally. Females unknown. Larva unknown.

Genus and distribution. *Alyculus* Kazantsev, 1999. Oriental region.

Remarks. Kazantsev (1999) compared *Alyculus* with the Neotropical group Leptolycini and *Lyropaeus*. The analyses support relationships of *Alyculus* + *Lyropaeus* or *Alyculus* (*Antennolycus* + *Microlyropaeus*) as shown in Figs 2–4. These genera are morphologically very distant and we prefer to classify them in independent tribes.

Antennolycini trib. nov.

Type genus. *Antennolycus* Bocakova et Bocak, 1999: 105.
Differential 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, dorsoventrally 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 bilobed in distal half. Elytra with four or nine costae, sometimes partly shortened. Legs slender, trochanters long, tibial spurs tiny. Male genitalia with stout phallus and very short paramerae, each paramere with setose process apically. Females unknown. Larva unknown.

Genera and distribution. *Antennolycus* Bocakova et Bocak, 1999, *Microlyropaeus* Pic, 1929. Oriental region.

Remarks. The clade of *Antennolycus* + *Microlyropaeus* got a high support in our analyses and we found it in basal positions within Lyropaeinae. Additionally, these taxa show high morphological divergence from other lyropaeines. Therefore we propose a new tribe Antennolycini for these two genera.

Platerodrilini Kazantsev

Platerodrilini Kazantsev, 2005: 241.
= Duliticolinae Kazantsev, 2002: 20, invalid name.

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 3–11 parallel-sided, compressed, seldom flabellate in males; apical palpomere pointed. Pronotum without any carinae, 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 paramerae, phallus slender, usually curved, paramerae robust basally, very slender apically, shorter than phallus. Females larviform. Larva (*Duliticola* Mjöberg, 1925). Body shape characteristic, 'trilobite larva' of many authors. 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.

Genera and distribution. E.g., *Horakiella* Bocakova, 2006, *Macrolibnetis* Pic, 1938, *Pendola* Bocak, 2002, *Platerodriloplesius* Wittmer, 1941, *Platerodrilus* Pic, 1921, *Subdihammatus* Kleine, 1926. Oriental region and the northern part of the Australian region.

Remarks. We found that Platerodrilini as defined by Kazantsev (2005) form only one of terminal branches within Lyropaeinae with many common characters present in various representatives of the lyropaeine clade (e.g., *Lyropaeus* type of male genitalia in *Pendola*, which is close to *Macrolibnetis* and *Duliticola*; see Bocak 2002a). The taxa included in Lyropaeinae have neotenous females and the larvae of both *Lyropaeus* and *Duliticola* share unique modification of the terminal antennomere (Gravely 1915, Wong 1996, Bocak and Matsuda 2003). As we are not able to find any morphological character, which would enable clear separation of Lyropaeinae and Miniduliticolinae (Kazantsev 2002, 2005, Bocakova 2006), we combine them in one subfamily.

Kazantsev (2002) described Duliticolinae in the sense of Mjöberg (1925). As *Duliticola* and *Platerodrilus* were just studied by A. T. C. Wong (Singapore) and therefore all types were unavailable to Kazantsev, further chaos was introduced in the classification of the group. Both, *Platerodrilus* and *Duliticola* were considered valid by Wong (1998), but *Duliticola* was proposed to be a junior synonym of *Platerodrilus* by Kazantsev (2002) without study of types and simultaneously *Duliticola* was used as the type genus of Duliticolinae. Later, Kazantsev (2005) had to replace Duliticolinae by Miniduliticolinae Kazantsev 2002 and to describe Platerodrilini because the name Duliticolinae was invalid in the sense of the article 13.2 (ICZN 1999).

Miniduliticolini Kazantsev, stat. nov.

Miniduliticolini Kazantsev, 2002: 20.
Miniduliticolinae Kazantsev, 2005: 241.

Diagnosis. Adult. Body small. Head elongate, not narrowed behind eyes, Labrum indistinguishable, eyes prominent, small, eye diameter half as long as interocular distance. 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.

Genus and distribution. *Atamania* Kazantsev, 2004, *Autaphes* Kazantsev, 2004, *Microeron* Kazantsev, 2004, *Sinodulia* Kazantsev, 2002, *Miniduliticola* Kazantsev, 2002. Oriental region.

Remark. Considering morphological differences we keep the position of Miniduliticolini close to Platerodrilini as proposed by Kazantsev (2002).

Dexorinae Bocak et Bocakova, stat. nov.

Dexorinae Bocak et Bocakova, 1989: 718.
Dexoridae Kleine, 1933 [sic!]: Bocak and Bocakova 1990; Kazantsev 2005: 217.

Type genus. *Dexoris* Waterhouse, 1878.

Diagnosis. Adult. Body smaller to medium sized, head small, mouth part vertical, strongly reduced, labium with praementum divided in two sclerites, maxillary palpi 4-segmented, labial palpi 1-segmented. Antennae 11-segmented. Pronotum transverse, with two longitudinal carinae or with carinae vestigial. Elytra without costae (*Dexoris*) or longitudinal costae and vestiges of transverse costae present. Male genitalia simple, paramerae and phallobase absent. Females and larvae unknown.

Genera and distribution. Dexoris Waterhouse, 1878, *Elgodexoris* Bocak et Bocakova, 1988, *Lampyrolycus* Burgeon, 1937, *Mimolibnetis* Pic, 1936. Afrotropical region.

Remarks. The re-analysis of morphological data set as well as original Kazantsev's analyses (Kazantsev 2005) support the sister position of *Dexoris* Waterhouse, 1878 and the lyropaeine genus *Lyroneces* Kazantsev (=*Lyropaeus s. l.*). Kazantsev's elevation of dexorines to the family level is unjustified in terms of the contemporary phylogenetic systematics (Fig. 6) and we include dexorines in Lycidae on the basis of male adult morphology as demonstrated by Bocak and Bocakova (1989) and Kazantsev (2005, Fig. 595–598, but not Fig. 599). We can classify dexorines as a subfamily if we assume the close position of Dexorinae and any deeply rooted lineage of Lycidae or as a tribe in Lyropaeinae if Dexorini + Lyropaeini form a clade. The exact classification cannot be solved without further data from larval and female morphology or from DNA markers and we propose tentatively the subfamily status for dexorines.

Kazantsev (2005) did not respect the fact that Bocak (1998a) used the Art. 13 of the then valid Code (ICZN 1985) and refused Kleine's authorship of names Calopterini and Dexorini (Kleine 1933). Bocak (1998a) designated as the first author(s) who fulfilled the requirements of the Code Green (1949) in the case of Calopterini and Bocak and Bocakova (1989) in the case of Dexorini. Using the Art.13.2.1 of the Code (ICZN 1999) the act of Bocak (1998a) is valid.

Ateliinae Kleine

Ateliinae Kleine, 1928: 222; Bocak and Bocakova 1990: 640.
Ateliini: Kleine 1933: 68.

Type genus. Atelius Waterhouse, 1878.
Diagnosis. Adult. Head small, frons strongly arcuate. Mouth parts well developed, maxillary palpi 4-segmented, labial palpi 3-segmented or 2-segmented (*Scarelus* Waterhouse, 1878). Antennae 11-segmented, filiform to serrate, sometimes longer than body (Ateliini). Pronotum with median longitudinal keel in anterior part. Elytra with four primary costae, often reduced in various degree, intercostal intervals with transverse costae (Ateliini) or irregularly punctured (Dilophotini). Male genitalia with long phallus and long slender phallobase, paramerae short (Ateliini) or absent (Dilophotini). Female unknown in Ateliini. Larva unknown.

Remark. Ateliinae have been considered to be an independent lineage of Lycidae since proposed by Kleine (1928). Here, we combine for the first time dilophotines and ateliines in the single taxon on the basis of the present analysis. These taxa remind each other in the structure of pronotal carinae and male genitalia, but these morphological characters were not strong enough to recognize the relationships of these taxa.

Ateliini Kleine

Ateliinae Kleine, 1928: 222; Bocak and Bocakova, 1990: 640.
Ateliini: Kleine, 1933: 68.

Type genus. Atelius Waterhouse, 1878.
Diagnosis. Adult. Head small, bearing long slender antennae, antennae always longer than body. Pronotum with median longitudinal keel. Elytra parallel-sided, with four longitudinal costae, which may be reduced in various degree. Phallus long, slender, phallobase long. Females unknown. Larva unknown.

Genera and distribution. E.g., *Atelius* Waterhouse, 1878, *Scarelus* Waterhouse, 1878. Oriental region.

Remark. All species are known only in males and female neoteny is supposed in Ateliini (Levkanicova and Bocak, in press). Reviews of *Scarelus* were published by Bocak (1995, 1997).

Dilophotini Kleine

Dilophotinae Kleine 1928: 222.
Dilophotini: Kleine, 1933: 110; Kazantsev 2005: 217 (in Calochrominae).

Type genus. Dilophotes Waterhouse, 1879: 72
Diagnosis. Adult. Body small to medium sized, slender. Head small with well developed mouth parts, 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, paramerae absent. Female genitalia with long styli, short coxites and basally fused paraproctal baculi. Larva unknown.

Genera and distribution. Dilophotes Waterhouse, 1879. Oriental region and Eastern part of the Palaearctic region.

Remark. Dilophotini were listed as the tribe by Kleine (1933) and later synonymized with Macrolycini

by Bocak and Bocakova (1990). Kazantsev listed Dilophotini as a tribe in Calochrominae (Kazantsev 2005). The composition of Dilophotini needs further study.

Lycinae Laporte

Lycinae Laporte, 1836: 25.

Type genus. *Lycus* Fabricius, 1787.
Remark. Most lycid lineages are included in Lycinae. The relationships between tribes and groups of tribes remain weakly supported and only further data can bring strong support for basal branches of Lycinae. On the other hand, all tribe level lineages got high support and are well defined by both molecular and morphological characters.

Tribes Calopterini, Macrolycini, and Lycini (including *Thonalmus* classified inside Lycini) were classified in Lycinae by Bocak and Bocakova (1990). Further tribes are classified in Lycinae herein: Platerodini were independent subfamily (Miller 1997) or in Lycinae as a tribe related to Erotini (Kazantsev 2005), Erotini were a subfamily (Bocak and Bocakova 1990, Miller 1997) or a tribe within Lycinae sensu Kazantsev (2005); Conderini and Metriorrhynchini were classified in Metriorrhynchinae (Bocak 2002b) and they got the position of independent tribes within Lycinae and Calochrominae, respectively (Kazantsev 2005), Calochromini were classified as a subfamily (Bocak and Bocakova 1990, Kazantsev 2005), Eurrhacini were a subtribe of Calopterini (Bocakova 2005), Lyponiini were placed in Platerodini (Bocak and Bocakova 1990) or in Calochrominae (Kazantsev 2005), Leptolycini were considered to be a subfamily by Bocak and Bocakova (1990) and Kazantsev (2005). Thonalmini Kleine, 1933 are re-instated and Dihammatini trib. nov. is proposed.

Lycini Laporte

Lycusites Laporte, 1836: 25.
Lycinae: Kleine 1928: 222.

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. Elytra slightly widened posteriorly to hemispherically expanded, each elytron with four longitudinal costae, reticulate costae reduced, irregular. Male genitalia with long slender aedeagus, paramerae short, rarely reaching half of phallic 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, prementum 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.

Genera and distribution. E.g., *Lycostomus* Motschoulsky, 1861, *Lycus* Fabricius, 1787. Afrotropical, Nearctic, Oriental, and Palaearctic regions.

Remark. Lycini show close affinities with Calopterini. With several hundreds of species described in *Lycostomus* Motschoulsky, 1861 and *Lycus* Fabricius 1787 by French entomologists in late 19th and early 20th century and no revisionary study available, the species level taxonomy of the tribe is in complete chaos.

Calopterini Green

Calopterini Green, 1949: 56 (nec Kleine 1933): Bocak 1998a: 247.

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. Maxillary palpi four-segmented, labial palpi three-segmented. Pronotum with median longitudinal carina sometimes forming longitudinal areola posteriorly; transverse pronotal carinae absent. Anterior thoracic spiracles mostly tubular. Elytra with 3–4 primary costae, secondary costae sometimes absent, reticulate cells mostly distinct, sometimes irregular. Female terminal sternum with short spiculum ventrale. Male genitalia with phallus ventrobasally emarginate, paramerae 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).

Genera and distribution. *Acroleptus* Bourgeois, 1886, *Caenia* Newman, 1838, *Calopteron* Castelnau, 1838, *Cartagonum* Pic, 1922, *Cephalolycus* Pic, 1926, *Ceratopriomorphus* Pic, 1922, *Cyrtopteron* Bourgeois, 1905, *Falsocaenia* Pic, 1922, *Flabellocaenia* Pic, 1929, *Idiopteron* Bourgeois, 1905, *Leptoceletes* Green, 1952, *Lycinella* Gorham, 1884, *Lycomorphon* Pic, 1922, *Macrolycinella* Pic, 1922, *Mesopteron* Bourgeois, 1905, *Metapteron* Bourgeois, 1905,

Pseudacroleptus Pic, 1911. Neotropical and Nearctic regions.

Remarks. Calopterini formed a paraphylum with respect to the taxon Pseudoceratoprion (in litt.) and further study is necessary to solve relationships among Neotropical neotenic lineages and calopterines. The generic classification was revised by Bocakova (2003).

Leptolycini Leng et Mutchler, stat. nov.

Leptolycini Leng et Mutchler, 1922: 430, **stat. nov.**
Leptolycinae: Bocak and Bocakova, 1990: 637; Kazantsev 2005: 216.

Type genus. *Leptolycus* Leng et Mutchler, 1922.
Diagnosis. Adult. Body often very slender, small to medium sized. Head protruded anteriorly, mouthparts vertical, mandibles strongly reduced, labium with weakly sclerotized mentum, maxillary palpi 3- or 4-segmented. Antennae 10- or 11-segmented. Pronotum without carinae or with short median carina. Each elytron with two or three longitudinal costae, intercostal intervals irregularly punctured or with irregular reticulate cells. Male genitalia often reduced, heterogeneous in shape. Females neotenic. Larva. Numerous larvae were collected by M. Ivie (personal communication), but have not yet been described.
Genera and distribution. *Ceratoprion* Gorham, 1884, *Leptolycus* Leng et Mutchler, 1922, *Neolyrium* Kazantsev, 2005. Neotropical region.
Remarks. Leptolycini were considered to be an independent clade in Lycidae until Bocak and Bocakova (1990) combined them with Oriental and Afrotropical neotenic lineages in Leptolycinae. Kazantsev (2005, Fig. 599) hypothesized their independent position within the paraphyletic assemblage of basal lycid lineages, although all his analyses supported the clade of *Lyconeces* (Lyropaeini), *Dexoris* (Dexorini) and *Ceratoprion* (Leptolycini) as proposed by Bocak and Bocakova (1990) (Kazantsev 2005, Figs 595–598). Already Miller (1991) discussed the possibility of multiple origins of neoteny in terminal clades of Lycidae. This hypothesis is supported by molecular data. The taxon Pseudoceratoprion (*in litt.*) was regularly a member of Lycinae (Fig. 5a). Leptolycini as a terminal clade within calopterines render Calopterini to be paraphylelic. Consequently, Calopterini would have to be considered a junior synonym of Leptolycini. Considering the level of ambiguity in our analyses and insufficient sampling we do not formally synonymize Calopterini and we postpone this act until more support is obtained.

Eurrhacini Bocakova, stat. nov.

Eurrhacini Bocakova, 2006: 444.

Type genus. *Eurrhacus* Waterhouse.
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 paramerae 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.
Genera and distribution. *Calocladon* Gorham, 1881, *Emplectus* Erichson, 1847, *Eurrhacus* Waterhouse, 1879, *Linoptes* Gorham, 1884, *Lycoplateros* Pic, 1922, *Haplobothris* Bourgeois, 1879. Neotropical region.
Remarks. Eurrhacini were erected as a subtribe in Calopterini. The analysis of molecular data suggests their independent position in Lycinae and therefore the tribal position is proposed for Eurrhacini.

Platerodini Kleine

Platerodinae Kleine, 1928: 222.
Platerodi Green, 1952: 2.
Platerodini: Kleine, 1933: 84; Bocak and Bocakova 1990: 650 (in Erotinae), Kazantsev 2005: 217 (in Lycinae).
Platerodinae: Miller 1997: 11.

Type genus. *Plateros* Bourgeois, 1879.
Diagnosis. Adult. Body small to medium sized. Head without rostrum, antennal tubercles inconspicuous, antennae slightly serrate to flabellate in males, serrate in females. Pronotal carinae absent, at most vestiges present at margins; elytra with nine longitudinal costae, usually similar in strength, reticulate cells often reduced, irregular. Male genitalia with long (*Teroplas* Gorham, 1884) to absent paramerae (*Plateros*); female genitalia, with basally widened paraproctal baculi, spiculum ventrale absent. Larva (*Plateros* spp.). Body parallel-sided, all terga 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.
Genera and distribution. E.g. *Callolycus* Gorham, 1881, *Cavoplateros* Pic, 1913, *Falsocalleros* Pic, 1933, *Microlycus* Pic, 1922, *Plateros* Bourgeois, 1879, *Sculptocalleros* Pic, 1949, *Teroplas* Gorham, 1884. All zoogeographical regions.
Remark. Platerodini are classified in Lycinae as a tribe. Their relationships with Dictyopterini as proposed by Bocak and Bocakova (1990) and Kazantsev

(2005) did not obtained any support from molecular data. The generic classification was revised by Bocakova (2001a) along with geographically restricted revisions (Bocakova 1997b, c, 1999).

Calochromini Lacordaire, stat. nov.

Calochromines Lacordaire, 1857: 301.
Calochrominae: Kazantsev 2005: 216.
= Lygistopteri Leconte, 1881: 27; Bocak and Bocakova 1990: 653.
= Lygistopterini: Kleine 1933: 102.

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. Mouthparts modified when rostrum developed. Pronotum without apparent carinae, with elevations at lateral margins. Elytra parallel-sided, seldom considerably widened posteriorly, four indistinct costae in each elytron, transverse costae absent or rudimentary. Male genitalia with asymmetrical phallobase, paramerae robust, 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.

Genera and distribution. *Adoceta* Bourgeois, 1882, *Caloptognatha* Green, 1951, *Calochromus* Guérin Méneville, 1833, *Dumbrelia* Lea, 1909, *Falsocalochromus* Pic, 1942, *Lygistopterus* Mulsant, 1838, *Lucaina* Dugès, 1879, *Macrolygistopterus* Pic, 1929. All zoogeographical regions.

Remarks. Calochrominae were treated as an independent subfamily and/or tribe since proposed and Kazantsev (2005) combined them with Metriorrhynchini, Dilophotini, Macrolycini, and Slipinskiini solely on the basis of asymmetrical phallobase and in conflict with results of majority of his analyses. The coding of an asymmetrical phallobase is affected in Kazantsev's analyses by poor sampling. The symmetrical phallobase is found in many Metriorrhynchini (Bocak 2002b) and asymmetrical in many Platerodini and Lycini (Bocak and Bocakova 1990). Our analyses of molecular data do not support close relationships of any of these taxa and Calochromini s. str. and we classify Calochromini s. str. as a tribe in Lycinae. Already Bocak and Bocakova (1990) suggested relationships between Erotini and Calochromini. The results of the present molecular analyses support their relationships. Considering their morphological divergence and

diversity of both lineages, we assign tribal status to both of them. Bocakova (1992) published the only recent study on Calochromini.

Erotini Leconte

Erotes Leconte, 1881: 23.
Erotinae: Bocak and Bocakova 1990: 649.
Erotini: Kazantsev 2005: 217 (in Lycinae).

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 closed median areola, either with simple cross-like structure or two slightly divergent carinae. Elytra with four primary and five secondary costae, reticulate cells in intercostal intervals sometimes reduced. Male genitalia with long paramerae, sometimes shortened, as long as half of phallic length. Female genitalia slender, with long paraproctal baculi, spiculum ventrale short with processes at base or shortened. Larva (*Eros*, *Lopheros*, and *Platycis*). Body sub-parallel; lateral part of epicranium well sclerotized and pigmented; terga small, transverse, undivided, pleurites indistinct, tergum A9 simply rounded, urogomphi absent.

Genera and distribution. E.g., *Eropterus* Green, 1951, *Eros* Newman, 1838, *Lopheros* Leconte, 1881, *Microcoleborus* Pic, 1913, *Platycis* Thomson, 1864. Palaearctic, Nearctic and Oriental regions.

Remark. Erotini is a species poor lineage occurring mostly in the Holoarctic region. They were classified together with Dictyopterini, but Kazantsev (2005) supposed their paraphyly with respect to Platerodini. The relationships between these two lineages was doubted already by Bocak and Matsuda (2003) and is strongly rejected by molecular data.

Slipinskiini Bocak et Bocakova

Slipinskiina Bocak et Bocakova, 1992: 256 (in Erotini).

Type genus. *Slipinskia* Bocak and Bocakova, 1992.
Diagnosis. Adult. Body small to medium sized, antennal tubercles weakly prominent, eyes small in both sexes. Antennae almost filiform, antennomeres circular in cross section. Maxillary palpi slender, 4-segmented, terminal palpomere weakly widened distally, securiform. Labial palpi 3-segmented, terminal palpomeres strongly widened distally, labrum transverse. Pronotum provided with sharp lanceolate median longitudinal areola, and an oblique fold on each side laterally. Each elytron with nine costae, alternate four

(primary) costae conspicuously stronger, secondary costae often interrupted. Female terminal abdominal segment with spiculum ventrale shorter than the sternum. Male genitalia usually with paramerae present, sometimes paramerae reduced or mutually 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.

Genera and distribution. Flagrax Kazantsev, 1992. Afrotropical region.

Remark. Slipinskiini were represented in the dataset by *Flagrax* sp. and the analyses provided ambiguous support for the membership of this genus in Erotini. We keep Slipinskiini provisionally as incertae sedis in Lycini until more data are available.

Metriorrhynchini Kleine

Metriorrhynchinae Kleine, 1926: 97; Bocak and Bocakova 1990: 641.
Metriorrhynchini: Kazantsev 2005: 217 (in Calochrominae).
= Cladophorinae Kleine, 1928: 222 (Type genus: *Cladophorus* Guérin Méneville, 1830). Bocak and Bocakova 1990: 641.
= Dilolycinae Kleine, 1926: 186 (Type genus: *Dilolycus* Kleine, 1926); Bocak and Bocakova 1990: 641.

Type genus. Metriorrhynchus Gemminger et Harold, 1869.

Diagnosis. Adult. Body small to large, head small, sometimes with rostrum. Antennae serrate to flabellate in males, serrate in females. Pronotum always with slender median areola and lateral carinae which form up to seven pronotal areolae. Elytra with four primary longitudinal costae and five secondary costae which may be absent in some genera. Male genitalia mostly with slender phallus, internal sac often with sclerites of various shape, paramerae 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 et 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.

Genera and distribution. E.g., *Achras* Waterhouse, 1879, *Broxylus* Waterhouse, 1878, *Bulenides* Waterhouse, 1879, *Caenioxylobanus* Pic, 1922, *Cautires* Waterhouse, 1879, *Cautiromimus* Pic, 1926, *Cladophorus* Guérin-Méneville, 1830, *Ditua* Waterhouse, 1879, *Enylus* Waterhouse, 1879, *Metanoeus* Waterhouse, 1879, *Metriorrhynchus* Gemminger et Herold, 1869, *Oriomum* Bocak, 1999, *Procautires* Kleine, 1925, *Prometanoeus* Kleine, 1925, *Stadenus*

Waterhouse, 1879, *Synchonnus* Waterhouse, 1879, *Tapromenoeus* Bocak et Bocakova, 1989, *Hemiconderis* Kleine, 1926, *Diatrichalus* Kleine, 1926, *Eniclases* Waterhouse, 1879, *Kassemia* Bocak, 1998, *Leptotrichalus* Kleine, 1925, *Lobatang* Bocak, 1998, *Microtrichalus* Pic, 1921, *Trichalus* Waterhouse, 1877, *Wakarumbia* Bocak, 1999. Oriental, Afrotropical, and Australian regions.

Remark. Metriorrhynchini were redefined by Bocak and Bocakova (1990) and the generic classification was revised by Bocak (2002b). Metriorrhynchini are the most species rich lineage in Lycidae with about 1400 described species (Levkanicova and Bocak, in press) and further hundreds deposited in collections. Revisions of several genera were published by Bocak (1998b, 1999b, 2000a, b, c, 2001a, b, 2007), Bocak *et al.* (2006), and Bocak and Jass (2004).

Dihammatini trib. nov.

Type genus. Dihammatus Waterhouse, 1879.

Differential diagnosis. Dihammatini resemble externally *Plateros*, but differ in the short 3rd antennomere and the structure of both male and female genitalia (Bocakova 2001a). Unlike Platerodini, *Dihammatus* has a long phallobase and well-developed paramerae.

Description. Adult. Body small, slightly dorsoventrally flattened, subparallel-sided. Head with small eyes, antennae filiform, reaching elytral midlength. Mandibles arcuate, maxillary palpi long, 4-segmented, labial palpi short, 3-segmented. Terminal palpomere with of both palpi with distal papillae. Pronotum transverse, widest at basal margin, anterior margin produced forwards, lateral margins elevated. Scutellum weakly emarginate apically. Elytra elongate, subparallel-sided, each elytron with nine weak longitudinal costae, reticulate cells irregular. Female terminal sternum with spiculum ventrale as long as segment. Legs slender, compressed, trochanters elongate, tibial spurs small, acute, tarsomeres 2-4 lobed. Male genitalia with dorsally and sometimes also ventro-proximally fused paramerae, phallobase elongate. Female genitalia with stick-formed paraproctal baculi, coxites and paraproctal baculi separate from each other, paraprocts present, reduced. Besides proximal vaginal glands, additional pair of tubular glands joining vagina near vulva (collateral glands). Larva unknown.

Genus and distribution. Dihammatus Waterhouse, 1879. Oriental region.

Remarks. Dihammatus was classified in Platerodini for a long time and only Bocakova (2001a) transferred the genus to Libnetini on the basis of four accessory glands in female genitalia. Molecular data do not support close relationships of *Dihammatus* and *Libnetis* and we found *Dihammatus* as an independent,

frequently basal clade, in Lycinae. Therefore the tribal status is given to Dihammatini. *Dihammatus* is the only genus classified in the tribe.

Thonalmini Kleine, stat. rev.

Thonalmini Kleine, 1933: 18.

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, without 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 areole in posterior part. 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 in basal part. Male genitalia with paramerae absent, phallus slender, tubular, terminal orifice situated dorsally, phallobase small, rather hemispherical, as long as 1/6 of phallus, internal sac tubular, pigmented and sclerotized. Female genitalia with plate-like coxites, paraproctal baculi widened basally, spiculum ventrale absent. Larva unknown.
Genus and distribution. *Thonalmus* Bourgeois, 1882. Neotropical region.
Remarks. Thonalmini contain only *Thonalmus* Bourgeois. Bocak and Bocakova (1990) classified the genus in Lycini on the basis of the structure of elytral and pronotal costae. Molecular data showed independent position of *Thonalmus* with respect to Lycini and much closer relationships with Lyponiini. Therefore, we reinstate Thonalmini as a tribe within Lycinae. The authorship of the name Thonalmini Kleine, 1933 is based on the fact that although the name was not accompanied by description when proposed and it was published after 1930 (Kleine 1933), it was used as a valid name by Blackwelder (1945) (Art. 13.2, ICZN 1999).

Conderini Bocak et Bocakova

Conderini Bocak et Bocakova, 1990: 643 (in Metriorrhynchinae).

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, paramerae

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.
Genera and distribution. *Conderis* Waterhouse, 1879, *Xylobanellus* Kleine, 1930. Oriental and the Eastern part of the Palaearctic region.
Remark. Conderini is a small lineage previously classified with metriorrhynchines on the basis of circular phallobase and the shape of the median areola. The analyses support independent position of Conderini in Lycinae. These lineages differ in the structure of genitalia (presence/absence of paramerae and unpaired vaginal gland) and larval mouthparts (presence/absence of mala).

Lyponiini Bocak et Bocakova

Lyponiina Bocak et Bocakova, 1990: 652 (in Platerodini).
Lyponiini: Bocakova 2001a: 66 (in Platerodinae); Kazantsev 2005: 217 (incertae sedis in Calochrominae).

Type genus. *Lyponia* Waterhouse, 1878.
Diagnosis. Adult. Body small to medium sized. Head prognathous with characteristic foramen magnum, antennae filiform to flabellate in males, filiform to serrate in females. Pronotum subquadrate, with median line. Elytra with nine costae and well developed reticulate cells. Male genitalia without paramerae, 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 (*Lyponia*). 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.
Genus and distribution. *Lyponia* Waterhouse, 1878. Oriental and Eastern part of the Palaearctic region.
Remark. Lyponiini were classified in Platerodinae (Bocak and Bocakova 1990). Recently, Kazantsev (2005) transferred Lyponiini to Calochrominae. The tribe was revised by Bocak (1999a).

Macrolycini Kleine

Macrolycinae Kleine, 1928: 222.
Macrolycini: Kleine 1933: 5; Bocak and Bocakova 1990: 637 (in Lycinae); Kazantsev 2005: 217 (in Calochrominae).

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. Pronotum with sharp median carina in frontal part. Elytra with four longitudinal costae, intercostal intervals irregularly punctured, without reticulate cells. Claws bifid at apex. Phallus long, slender, often with processes at apex, paramerae 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.

Genera and distribution. Calcaeron Kazantsev, 2004, *Macrolycus* Waterhouse, 1878. Oriental and the Eastern part of the Palaearctic region.

Remark. Macrolycini were classified in Lycinae by Bocak and Bocakova (1990) and later they were considered as a sister group of Dilophotini and classified in Calochrominae (Kazantsev 2005).

Family-group taxa previously classified in Lycidae

Thilmaninae Kazantsev, 2005

Kazantsev (2005) transferred *Thilmanus* Gemminger, 1869 from Omalisidae to Lycidae without studying other omalisids and erected the monotypic subfamily Thilmaninae. Bocak and Brlik (2008) showed that *Thilmanus* is closely related with the omalisid genus *Phaeopterus* A. Costa, 1857 and does not belong to Lycidae.

Pristolycini Winkler, 1952

Pristolycus Gorham, 1883 is classified in Lampyridae (Crowson 1972, Nakane 1969, and Jeng *et al.* 2002).

CONCLUSIONS

The DNA sequences represent an independent source of data for the construction of lycid phylogeny and they allow us to study relationships among lineages with morphology affected by ontogenetic modifications. The data set provides support for the monophyly of Lycidae and most previously defined subfamilies and tribes (Bocak and Bocakova 1990, Bocak and Matsuda 2003). There are hypothesized five basal lineages: Libnetinae, Dictyopterinae, Lyropaeinae, Ateliinae and Lycinae. The position of dexorines remains

supported only by the male adult morphology and they are classified here tentatively as a subfamily. Lycinae are defined in a broad sense. Available molecular data do not convincingly resolve relationships among tribes of Lycinae despite sampling of all previously defined lineages and high number of markers. Nevertheless, the results clearly refuse the concept of Lycinae and Calochrominae proposed by Kazantsev (2005). The branching sequence at the base of the tree as well as tribal level relationships within Lycinae should be regarded as preliminary. The low stability of basal branches of Lycinae is caused by the fact that regularly members of a single genus or few genera represent tribes in analyses. Despite this shortcoming, the results show robustness of principal lineages across various analytical methods and parameter settings.

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