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The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia)

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ABSTRACT

Elateriformia consists of Dascilloidea, Buprestoidea (jewel beetles), Byrrhoidea and Elateroidea (click beetles, fireflies and relatives). Numerous elateroid lineages contain taxa with modified metamorphosis resulting in sexual maturity while retaining larval characters. Additionally, they evolved unique defensive strategies including clicking mechanism, aposematic coloration and bioluminescence. To investigate the phylogenetic position of Elateroidea within Coleoptera, we merged 1048 newly produced 18S rRNA, 28S rRNA, *rrnL* mtDNA, and *cox1* mtDNA sequences for ~300 elateriform taxa with data from GenBank. The 975-taxa dataset aligned in BlastAlign was analyzed under maximum likelihood criterion. The results agreed in most aspects with the current morphology-based classification and results of molecular studies. Elateriformia were monophyletic and Elateroidea were sister to Byrrhoidea. Further, we analyzed all-data (513 elateriform taxa) and pruned matrix (417 elateriform taxa, all fragments present) using parsimony and maximum likelihood methods to reveal the phylogenetic relationships among elateroid lineages and examine the evolution of soft-bodiedness, neoteny and bioluminescence. We confirmed the monophyly of Elateroidea *sensu lato* and most of the families, with Telegeusidae inferred in most trees within paraphyletic Omethidae. The clade Artematopodidae + Telegeusidae + Omethidae was a sister to remaining elateroids. All topologies reject the relationships of hard-bodied Elateridae, Eucnemidae, Throscidae and Cerophytidae, formerly supposed to be a monophylum. Eucnemidae and Throscidae formed independent lineages and the position of Cerophytidae was variable – either a sister to Throscidae, or an independent lineage. The Lampyridae + Cantharidae clade was in most trees sister to Phengodidae + Rhagophthalmidae + Omalisidae + Elateridae. Molecular phylogeny of Elateroidea confirmed the multiple origins of soft-bodied, neotenic and light emiting lineages. On the basis of our molecular phylogeny, we place former Telegeusidae as a subfamily in Omethidae.

1. Introduction

The Elateroidea with ~24,000 described species form a substantial part of the series Elateriformia and belong to major and oldest Polyphagan lineages (Ponomarenko, 1995; Bocak et al., 2014). The extraordinary morphological diversity of elateroids resulted in delineation of polyphyletic taxa based on superficial resemblance, such as Cantharoidea (e.g., Crowson, 1972). The elateroid beetles are interesting from the evolutionary point of view because of bioluminescence, neoteny and mimicry present in distantly related lineages (Viviani, 2002; Bocakova et al., 2007; Bocak and Yagi, 2010). Despite species richness and evolutionary importance, the formal classification of Elateriformia is unstable and the relationships among elateroid families remain unresolved (Lawrence and Newton, 1995; Lawrence et al., 2011; Bocak et al., 2014). Elateriformia were merged with the now separate series Scarabaeiformia and Scirtiformia (Lawrence and Newton, 1982) or with Scirtiformia (Lawrence and Newton, 1995; Beutel and Leschen, 2005; Bouchard et al., 2011). Lawrence et al. (2011) defined Scarabaeiformia and Scirtiformia and restricted Elateriformia to superfamilies Dascilloidea, Buprestoidea, Byrrhoidea and Elateroidea. Conflicting hypotheses were proposed for the relationships among superfamilies (Beutel and Leschen, 2005; Timmermans and Vogler, 2012) and various sister taxa to Elateroidea were proposed: Dascilloidea (Caterino et al., 2005; Hunt et al., 2007; Anton and Beutel, 2012), a part of the dryopoid lineages (Böving and Craighead, 1931; Beutel, 1995), Psephenoidea *sensu* Lawrence, 1988 (Lawrence et al., 2011), Byrrhoidea incl. Buprestoidea (Bocak et al., 2014), a

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clade containing Dascilloidea, Byrrhidae and Nosodendridae (McKenna and Farrell, 2009) or a clade containing Dascilloidea, Buprestoidea and dryopoid lineages (Bocakova et al., 2007).

Lineages currently classified in Elateroidea (Bouchard et al., 2011) were originally placed into three different superfamilies – Artematopoidea, Elateroidea *sensu stricto* and Cantharoidea (e.g., Lawrence and Newton, 1982). Crowson (1955) first mentioned that Elateroidea should be merged with Cantharoidea and possibly Artematopoidea due to the similar wing venation and shape of metendosternite. Lawrence and Newton (1982) added several larval and adult characters supporting their relationships, and Lawrence (1988) formally proposed the superfamily Elateroidea *sensu lato* as consisting of former Artematopoidea, Elateroidea and Cantharoidea. Such broad elateroid concept was adopted by Lawrence and Newton (1995), although subsequent authors studied cantharoid and elateroid lineages separately (Muona, 1995; Branham and Wenzel, 2001). Molecular study based on 18S rRNA (Sagegami-Oba et al., 2007) showed both elateroids and cantharoids as paraphyletic lineages, but this single-gene study rejected broadly defined Elateroidea. Bocakova et al. (2007) used four molecular markers and confirmed monophyly of Elateroidea *sensu lato*, multiple origins of bioluminescence, neoteny and soft-bodiedness. Although better sampled than previous datasets, some species-rich lineages (e.g., Elateridae) were poorly represented. Kundrata and Bocak (2011) included 180 taxa representing 11 elateroid families in the largest molecular phylogeny of Elateroidea to date. Elateroidea *sensu stricto* and cantharoid lineages were paraphyletic. Telegeusidae, Omethidae, Eucnemidae and Throscidae formed the basal elateroid lineages, but their precise relationships remained unresolved due to inadequate taxon sampling. Species-rich soft-bodied families Lycidae, Lampyridae and Cantharidae formed either a single clade, or Lycidae were in paraphyletic position to Lampyridae and Cantharidae. Elateridae consistently formed a clade with soft-bodied Phengodidae, Rhagophthalmidae, Omalisidae and Drilidae, supporting the results of previous molecular-based studies (Bocakova et al., 2007; Sagegami-Oba et al., 2007), as well as larval morphology (Pototskaja, 1983), but in deep contrast with adult morphology (Lawrence et al., 2011). In all analyses, Drilidae were inferred as one of the terminal lineages in Agrypninae (Elateridae) and their rank was lowered to tribe (Kundrata and Bocak, 2011). Kundrata et al. (2013) investigated a position of Artematopodidae and recovered them as one of the deepest lineages of Elateroidea.

Here, we present the largest molecular phylogeny of Elateroidea to date. We concatenated four markers of representatives of all main lineages of Coleoptera and substantially improved sampling of Elateroidea (a) to examine the position of Elateriformia and Elateroidea in Coleoptera, (b) test the monophyly of Elateroidea *sensu* Lawrence (1988), (c) infer robust support for phylogenetic relationships among elateroid lineages, and (d) investigate the evolution of soft-bodiedness, neoteny and bioluminescence on the basis of this revised phylogenetic hypothesis. The study aims to deal with the shortcomings of previous analyses which relied on a very sparse sampling of many lineages, such as Throscidae, Eucnemidae, or omitted some families and subfamilies that time unavailable for the DNA extraction.

2. Materials and methods

2.1. Taxon sampling, DNA extraction, amplification and sequencing

Our sampling comprised ~260 species belonging to 13 families of Elateroidea and 31 species of other Polyphaga: Byrrhoidea (14 taxa), Scirtoidea (12), Dascilloidea (2), Bostrichoidea (1), Tenebrionoidea (1), and Chrysomeloidea (1) (Table S1). Material was fixed in 96% alcohol in the field and subsequently stored in −20 °C. Voucher specimens are deposited in the collection of Laboratory of Molecular Phylogenetics, UP Olomouc (Table S1). Whole genomic DNA was extracted using DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany) and Wizard SV96 Purification System kit (Promega Corp., Madison, WI) following standard protocols. The PCR and cycle sequencing conditions followed Kundrata and Bocak (2011). Four molecular markers were amplified – 18S rRNA (SSU; ~1900 bp; 272 taxa) and fragments of 28S rRNA (LSU; ~650 bp; 254 taxa), *rrnL* mtDNA (~525 bp; 255 taxa), and *cox1–3′* mtDNA (723 bp; 267 taxa). The primers are listed in Table S3. PCR products were purified using PCRμ96 plates (Millipore Corp., Bedford, MA) and sequenced by ABI 3130 Genetic Analyzer using Big Dye Terminator 1.1 Cycle Sequencing kit. GenBank accession numbers of newly produced sequences are listed in Table S1.

2.2. Dataset assembling and alignment procedures

Sequences were edited using Sequencher 4.7 (Gene Codes Corp., Ann Arbor, MI, USA). We aligned newly produced elateriform sequences with previously published data (Table S2; Bocakova et al., 2007; Kundrata and Bocak, 2011) to investigate the phylogeny of Elateroidea. The Scirtoidea, Staphyliniformia, Scarabaeoidea, Byrrhoidea and Buprestoidea were used as an outgroup (Hunt et al., 2007) and phylogenetic trees were rooted by *Declinia versicolor* or *Cyphon hilaris* (Scirtoidea), as these are treated as basal splits of Polyphaga (Hunt et al., 2007; Bocak et al., 2014). Dascilloidea, whose position was inferred in analysis of the Coleoptera dataset (see below), were omitted from outgroup due to their unstable position. We assembled the all-taxa dataset containing terminals for which at least two markers were available (555 taxa) and the pruned dataset with terminals represented by all four fragments (448 taxa). Length invariable protein-coding *cox1* sequences were aligned by ClustalW 1.83 (Thompson et al., 1994) and checked by amino acid translation. Length variable sequences were aligned separately using ClustalW 1.83 (parameters: 22.5 for gap opening and 0.83 for gap extension), Mafft 6.822 (default parameters; Katoh et al., 2002; implemented in CIPRES portal; www.phylo.org; Miller et al., 2010), and BlastAlign 1.2 (default parameters; Belshaw and Katzourakis, 2005). Alignments produced by ClustalW and Mafft algorithms were manually edited at beginnings and ends of sequences where apparent misalignments were observed. All-taxa (555 taxa) and pruned (448) datasets aligned by ClustalW and Mafft were analyzed either in full length or with loop regions excluded (18S and 28S only, as described by Kundrata and Bocak, 2011). Futher, the hypervariable regions were removed by Gblocks 0.91b (Castresana, 2000), but despite the conservative parameter settings (b5 = a, b4 = 3; see Jordan and Goldman, 2012), a substantial part of information was lost (Dessimoz and Gil, 2010; Jordan and Goldman, 2012). We did not consider different setting for GBlocks or subsequent re-alignment of the dataset after the GBlocks procedure since the application of the conservative parameters resulted in the loss of phylogenetic signal and removed almost completely the length variability. Instead, we manually removed only apparently ambiguously aligned regions in Se–Al (Rambaut, 1996) and used BlastAlign, which omits parts of the length variable regions when reliable alignment cannot be inferred. The structural alignment was not used here as this approach is suitable for a global alignment of highly diverged rRNA sequences (i.e., datasets with the identity of sequences <~80%; Sahraeian and Yoon, 2011). For the relatively conserved 18S and 28S rRNA, the advantage of this method is small (Mafft manual, Katoh and Toh, 2008), especially considering the limited length variation in sequences representing a single superfamily. Additionally, the manual for Mafft recommends the structural alignment methods for datasets of 50–200 sequences and 1000 bp and our dataset is more than 10times larger.

Altogether ten datasets were analyzed – two (555 and 448 taxa, no part of sequence manually removed) aligned by BlastAlign, four (555 and 448 taxa, with hypervariable regions kept and/or removed) aligned by ClustalW, and four (555 and 448 taxa, in full length and with hypervariable regions removed) aligned by Mafft.

To test the position of Elateriformia within Coleoptera and the rooting of Elateroidea, we merged four-fragment elateriform dataset with publicly available sequences representing main beetle lineages (540 taxa, downloaded from GenBank, April 2012; Table S2). All fragments were aligned individually – *cox1* mtDNA by ClustalX 1.81 (Thompson et al., 1997) and 18S rRNA, 28S rRNA and *rrnL* mtDNA by BlastAlign (Belshaw and Katzourakis, 2005). The concatenated dataset contained 975 terminals represented by at least three markers except *Priacma serrata*, *Prolixocupes lobiceps* (Archostemata) and *Delevea bertrandi* (Myxophaga), for which only two loci were available. We did not use members of other holometabolan orders as an outgroup because it is generally difficult to align very divergent sequences (Bocak et al., 2014). Instead, we used Archostemata for rooting the tree, in agreement with the fossil record and previous studies (Ponomarenko, 1995; Pons et al., 2010).

2.3. Phylogenetic analyses

All Elateriformia datasets were analyzed using parsimony (MP) and maximum likelihood (ML) approaches. For MP we used TNT 1.0 (Goloboff et al., 2003, 2008) with gaps treated as missing characters. The most parsimonious trees were found 25times using Sectorial Search, Tree-Drifting, Tree-Fusing (Goloboff, 1999) and Parsimony Ratchet (Nixon, 1999). Bootstrap values were calculated from 500 pseudoreplicates. Consensus trees were inferred from PAUP* 4.03b10 (Swofford, 2002). Elateriformia (555 and 448 taxa) and Coleoptera (975 taxa) datasets were partitioned by genes and codon positions, yielding a total of six partitions, and analyzed using RAxML 7.3.1 (Stamatakis, 2006) via the CIPRES web server (www.phylo.org; Miller et al., 2010). Branch supports were calculated using the Rapid Bootstrap algorithm (Stamatakis et al., 2008) with 100 bootstrap iterations. We used the GTRCAT model for the bootstrapping phase and GTRGAMMA for the final tree inference.

3. Results

3.1. Dataset parameters

The concatenated 555-taxa datasets included 5120 (BlastAlign), 4848 (ClustalW) and 5302 (Mafft) homologous positions. Pruned datasets (only taxa with all four fragments available; 448 taxa) included 5016 (BlastAlign), 4807 (ClustalW) and 5285 (Mafft) homologous positions (Table S4). Removing the 18S and 28S rRNA hypervariable regions from ClustalW and Mafft alignments by GBlocks reduced the datasets by 23% and 27% in length, respectively. This lead to the loss of resolution in topologies from both MP and ML analyses (results not shown). After manual deletion of 18S and 28S rRNA ambiguously aligned regions, matrices were 17% (ClustalW) and 25% (Mafft) shorter. The 18S rRNA alignment was reduced to 82% (ClustalW) and 77% (Mafft), and 28S to 63% (ClustalW) and 48% (Mafft) of the original length. The 975-taxa alignment (BlastAlign; all beetle superfamilies) included 5446 homologous positions (Table S4). Individual matrices contained 36–37% (BlastAlign), 46–51% (ClustalW) and 45–49% (Mafft) parsimony informative characters. Numbers of constant, variable uninformative and parsimony informative characters in various datasets are listed in Table S5. Maximum uncorrected pairwise distances among ingroup taxa varied from 22.2% in 18S to 35.0% in *cox1*.

3.2. Analysis of the Coleoptera dataset

The ML phylogenetic tree from BlastAlign alignment is given in Fig. 1. Bootstrap values of major deep splits were low and only Adephaga + Polyphaga clade obtained more than 50% (BS 57%). Basal lineages of Polyphaga were represented by scirtiform families (formerly in Elateriformia) and Derodontidae (Derodontiformia). Remaining series formed two large clades: (a) the cucujiform lineages and (b) paraphyletic Staphylinoidea and Hydrophiloidea, Scarabaeoidea, two lineages of paraphyletic Bostrichoidea, and monophyletic Elateriformia, barring apparently incorrect position of *Nosodendron* (Derodontoidea: Nosodendridae) (Fig. 1). The Elateriformia and the clade containing Elateriformia + Bostrichiformia obtained low bootstrap support. Dascilloidea marked a basal split in the elateriform lineage. Byrrhoidea (incl. Buprestidae) were sister to Elateroidea + *Nosodendron* with Throscidae + Cerophytidae clade inferred as separate lineage (Fig. 1) among deep elateroid splits. The 'higher elateroids' clade containing Lycidae ((Lampyridae, Cantharidae) (Phengodidae, Rhagophthalmidae, Omalisidae, Elateridae)) obtained robust support (BS 93%). All families except Omethidae were monophyletic. Telegeusidae represented a single lineage with Omethinae and Matheteinae, making Omethidae paraphyletic (Fig. 1).

3.3. Analysis of the Elateroidea dataset

The detailed topology of the elateroid clade was investigated using the 555 and 448-taxa datasets. An overview of inferred topologies and bootstrap values is given in Tables 1 and S6 and the ML phylogenetic hypothesis is shown in Fig. 2. Elateroidea *sensu lato* were monophyletic in all ML analyses, but most MP analyses suffered from unexpected positions of some byrrhoid families (Chelonariidae and Dryopidae) in relationships to basal Artematopodidae + Telegeusidae + Omethidae or Artematopodidae were inferred outside Elateroidea close to some byrrhoid lineages (Table 1). Monophyletic Artematopodidae, Telegeusidae, Throscidae, Lycidae, Cantharidae, Lampyridae, Rhagophthalmidae and Phengodidae were supported with average bootstrap values over 90% across all analyses, while lower supports were inferred for Eucnemidae *incl.* Anischiinae (70%) and Omalisidae *sensu* Kundrata and Bocak (2011; 65%). Monophyletic Elateridae obtained bootstrap supports lower than 50%. The Artematopodidae + Telegeusidae + Omethidae clade was presented in most topologies showing Artematopodidae sister to Telegeusidae + Omethidae (Table 1). Omethidae were paraphyletic in majority of trees inferred from analyses of the BlastAlign and ClustalW alignments and monophyletic in most Mafft alignments although with low support (Table S6). Driloniinae were frequently found as a sister to Telegeusidae + Omethinae + Matheteinae. The bulk of Elateroidea (excluding species-poor basal lineages as Artematopodidae, Telegeusidae, and Omethidae) were monophyletic in all analyses (lower support in MP; higher in ML analyses, BS 86–100%; Table 1). The Eucnemidae + Throscidae + Cerophytidae clade was not supported by the analyzed data. *Cerophytum* formed a clade with Throscidae in most analyses but in some trees it was a sister to higher elateroids. The clade of higher elateroids was present in almost all trees and obtained strong BS support in ML analyses (Figs. 1 and 2, Table 1). In most analyses, Lycidae formed a sister lineage to all other groups in the clade, while other topologies showed lycids as a monophylum with Lampyridae and Cantharidae (Table 1). Lampyridae were regularly a sister to Cantharidae. The clade Omalisidae + Rhagophthalmidae + Phengodidae + Elateridae with its subclade Omalisidae + Rhagophthalmidae + Phengodidae was inferred in most topologies (Fig. 2), but without high bootstrap support. The position of species-poor neotenic families, i.e., Omalisidae, Phengodidae and Rhagophthalmidae, was unstable and all or some of them were nested in Elateridae in

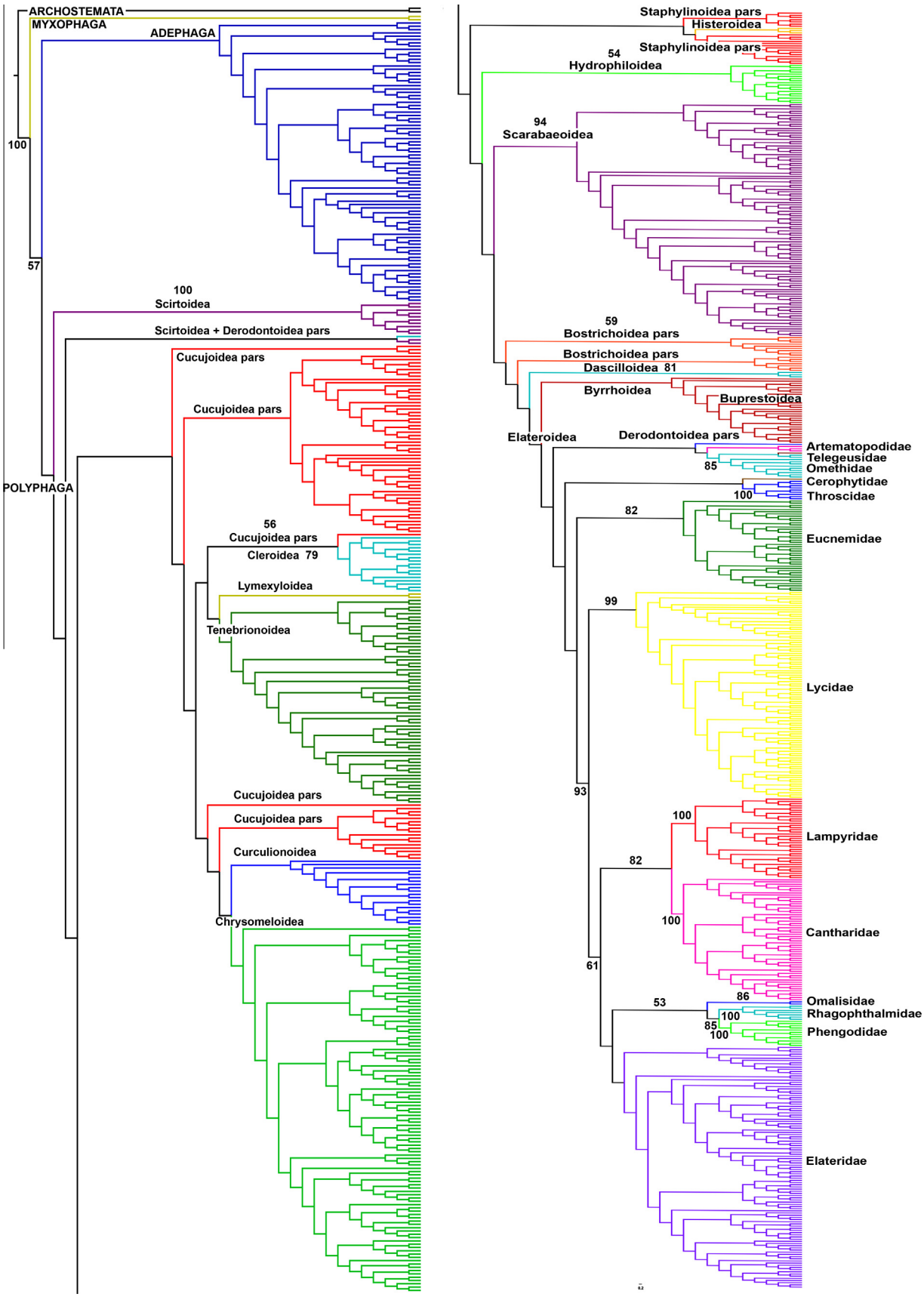

Fig. 1. The ML Coleoptera phylogenetic tree of 975 taxa aligned by BlastAlign. Values at selected branches indicate bootstrap support.

Table 1
Recovery of selected clades with bootstrap support in maximum likelihood (ML) and maximum parsimony (MP) analyses from BlastAlign, ClustalW and Mafft alignments of total (555 taxa) and pruned (448 taxa) datasets. Only bootstrap values above 50% are shown. Datasets were analyzed either in the full length (+) or length variable regions were omitted (–).

Type of alignment	Analysis/nr. of taxa	Variable regions	ELA	ELAR	AR + OE + TE	OE + TE	TE + O + Ma	EU + TH + CE	TH + CE	CE + ELSO	ELSO	LY + LA + CA	LA + CA	PH + RH	OM + PH + RH	OM + PH + RH + EL
BlastAlign	ML 555	+	M(63)	M(86)	M(64)	M(83)	M(61)	P	P	M(50)	M(81)	P	M(85)	M(97)	M	M
BlastAlign	ML 448	+	M(65)	M(89)	M(59)	M(87)	M(77)	P	P	M	M(98)	P	M(91)	M(96)	M	M(50)
BlastAlign	MP 555	+	M	M	M	M(51)	P	P	M	P	M	M	M(68)	M	P[a]	M
BlastAlign	MP 448	+	P[b]	M	P	M	P	P	M	P	M	M	M	M(60)	P	P
ClustalW	ML 555	+	M(68)	M(98)	M(81)	M(99)	M(91)	P	M(61)	P	M(95)	P	P	M(94)	M	P
ClustalW	ML 448	+	M(72)	M(99)	M(76)	M(99)	M(92)	M	M(54)	P	M(89)	P	P	M(74)	M	P
ClustalW	ML 555	–	M(60)	M(98)	M(84)	M(98)	M(86)	P	M(57)	P	M(96)	M	P	M(90)	M	M(63)
ClustalW	ML 448	–	M(62)	M(100)	M(81)	M(92)	M(82)	P	M(75)	P	M(96)	P	M(50)	M(86)	P	M(69)
ClustalW	MP 555	+	M	M	M	M(52)	P	M	M	P	M	P	M	M	P	P
ClustalW	MP 448	+	P[c]	M	M(58)	M(73)	M(90)	P	M(91)	P	M	P	M	P	P[d]	P
ClustalW	MP 555	–	P[e]	M	M	M	M	P	M	P	M	P	M(66)	M(54)	M	M
ClustalW	MP 448	–	P[f]	M	M	M	P	P	M	P	M	M	M(71)	M(67)	P	P
Mafft	ML 555	+	M(59)	M(92)	M	M(96)	P	P	P	M	M(88)	M	M	M(97)	P	M
Mafft	ML 448	+	M(62)	M(89)	M(59)	M(99)	M	P	P	M	M(88)	P	M	M(99)	P	M
Mafft	ML 555	–	M(66)	M(95)	M(57)	M(92)	P	P	M	P	M(89)	P	M(68)	M(95)	M	P
Mafft	ML 448	–	M(51)	M(88)	M	M(87)	P	P	P	M	M(84)	M	M	M(96)	M	M
Mafft	MP 555	+	P	M	P	P	P	P	M	P	P	P	M(56)	M	M	M
Mafft	MP 448	+	P[g,h]	M	P	P	P	P	M	P	M	P	M	M(58)	M	P
Mafft	MP 555	–	M	M	M	M	P	P	P[i]	P[i]	M	M	M(65)	M	M	M
Mafft	MP 448	–	P[g,h]	M	P	P	P	P	M	P	M	P	M(54)	M	M	M

P = paraphylum; ELA = Elateroidea, ELAR = Elateroidea without Artematopodidae, Omethidae and Telegeusidae, AR = Artematopodidae, TE = Telegeusidae, OE = Omethidae, O = Omethinae, Ma = Matheteinae, EU = Eucnemidae (incl. Anischiinae), TH = Throscidae, CE = Cerophytidae, ELSO = higher elateroids: Lycidae, Lampyridae, Cantharidae, Omalisidae, Phengodidae, Rhagophthalmidae and Elateridae, LY = Lycidae, LA = Lampyridae, CA = Cantharidae, PH = Phengodidae, RH = Rhagophthalmidae, OM = Omalisidae, EL = Elateridae. The classification of Elateridae and Omalisidae follows Kundrata and Bocak (2011)

[a] PH+RH + *Pseudeuanoma*.
[b] Dryopidae + AR + OE + TE.
[c] AR + OE + TE in Byrrhoidea.
[d] OM + PH only.
[e] Dryopidae + Chelonariidae + AR + OE + TE.
[f] Chelonariidae + AR + OE + TE.
[g] AR in Byrrhoidea.
[h] Chelonariidae + TE.
[i] CE within EU.

Fig. 2. The ML Elateroidea phylogenetic tree of 555 taxa aligned by BlastAlign. Values at selected branches indicate bootstrap support.

several analyses (Table S6). Rhagophthalmidae + Phengodidae formed a clade in all but one tree and obtained robust support, mainly in ML analyses (74–99%; Table 1). All analyzed elaterid subfamilies but Denticollinae (paraphyletic in 75% of analyses) were monophyletic and supported by high BS values (Fig. 2).

4. Discussion

This study substantially expands the data for the phylogenetic inference of elateroid relationships (Bocakova et al., 2007; Kundrata and Bocak, 2011). While only 72 and 180 elateroid terminals were presented in the previous studies, the current dataset includes almost five hundreds ingroup taxa and the analyses present the most comprehensive phylogenetic hypothesis of Elateroidea. Recently, many studies focused on clarifying the relationships within Coleoptera as well as Elateriformia (Hunt et al., 2007; McKenna and Farrell, 2009; Lawrence et al., 2011; Timmermans and Vogler, 2012; Bocak et al., 2014), however, the results still have been unequivocal and often conflicting. Therefore, we merged already published and newly produced data to compile a ~1000 terminal dataset to investigate the limits of Elateriformia and to provide a rooting for their phylogeny. The dataset has almost complete fragment representation.

4.1. Position of Elateriformia and Elateroidea in the Coleoptera tree

The comprehensive beetle topology (Fig. 1) is generally in agreement with recent molecular hypotheses using a combination of nuclear rRNA and mtDNA markers (Hunt et al., 2007; McKenna and Farrell, 2009; Bocak et al., 2014). These studies repeatedly confirmed the Adephaga + Polyphaga relationships, and supported scirtoid lineages and Derodontidae as basal Polyphagan lineages. A sister to the remaining Polyphaga can be all (McKenna and Farrell, 2009; Bocak et al., 2014) or only some (Hunt et al., 2007; Lawrence et al., 2011) staphyliniform lineages, but the current results (Fig. 1) merge Staphyliniformia, Scarabaeiformia, Bostrichiformia and Elateriformia in a single clade. Supports for these basal splits are low and their detailed relationships need further investigation. The monophyletic series Cucujiformia is inferred in all studies including this one.

We found Elateriformia as a sister to Bostrichiformia (Fig. 1) in agreement with e.g., Hunt et al. (2007) and Bocak et al. (2014). Similarly, their relationship is suggested by morphological analysis by Lawrence et al., 2011, although Scarabaeiformia were a sister to Dascilloidea in their study. The position of Nosodendridae has never been in complete agreement with their formal classification (Fig. 1; Hunt et al., 2007; McKenna and Farrell, 2009; Lawrence et al., 2011; Bocak et al., 2014), including the current, improbable position among basal splits in Elateroidea. The highly divergent and species-poor lineages are often found in unstable positions in phylogenetic trees (Bocak et al., 2014).

The Elateriformia used to include five superfamilies (Lawrence and Newton, 1995; Beutel and Leschen, 2005; Bouchard et al., 2011) but later, Lawrence et al. (2011) formally designated the scirtoid lineages as Scirtiformia. This series was found in recent analyses of molecular datasets as a part of basal Polyphagan split, always in distant relationships to Elateriformia. Until now, no analysis has demonstrated the monophyly of Scirtiformia and these families form a paraphyletic assemblage (Caterino et al., 2005; Hunt et al., 2007; McKenna and Farrell, 2009; Lawrence et al., 2011; Bocak et al., 2014, this study).

The remaining elateriform lineages i.e., Dascilloidea, Buprestoidea, Byrrhoidea and Elateroidea, formed a monophylum in all recent analyses yet no morphological synapomorphy supports this group (Beutel and Leschen, 2005). The phylogenetic relationships within Elateriformia are not congruent across recent studies (e.g., Timmermans and Vogler, 2012). The Dascilloidea are the basal elateriform lineage in current multimarker molecular analyses (Bocak et al., 2014, this study; Fig. 1), although they were proposed as a sister to Elateroidea (Caterino et al., 2005; Hunt et al., 2007; Anton and Beutel, 2012), byrrhoid lineages (Grebennikov and Scholtz, 2003; McKenna and Farrell, 2009), Buprestoidea (Lawrence et al., 1995), or Scarabaeoidea (Crowson, 1960; Lawrence et al., 2011). The position of Buprestidae in Byrrhoidea was supported by morphological and molecular analyses (Lawrence, 1988; Lawrence et al., 2011; Bocakova et al., 2007; Bocak et al., 2014, this study), but very limited sampling of Buprestidae is a problematic issue (Bocak et al., 2014). The close relationships of byrrhoid lineages and Buprestidae were assumed by Crowson (1982), Caterino et al. (2005), Hunt et al. (2007) and Timmermans and Vogler (2012), the latter two studies showing buprestids as a sister to dryopoid or byrrhoid + dryopoid clade. The Byrrhoidea are supposed to be a sister group to Elateroidea (Bocak et al., 2014, this study; Fig. 1), however, monophyly of Byrrhoidea *sensu* Lawrence and Newton (1995) remain contentious when Byrrhidae and dryopoids are frequently assumed as separate lineages (e.g., Hunt et al., 2007; Timmermans and Vogler, 2012). Increased taxon and genetic sampling is needed for future investigation of basal Elateriformia phylogeny.

4.2. Monophyly and phylogeny of Elateroidea

The current concept of Elateroidea contains several lineages previously having the superfamily rank: Elateroidea *sensu stricto* (Crowson, 1955), Cantharoidea (Crowson, 1972), Artematopoidea *sensu* Lawrence and Newton (1982), and monotypic Rhinorhipidae (Bouchard et al., 2011; Lawrence et al., 2011). These lineages are collectively accepted as a monophylum (Crowson, 1955; Lawrence, 1988; Lawrence and Newton, 1995), although some studies focused on either cantharoid (Branham and Wenzel, 2001; Stanger-Hall et al., 2007) or strictly defined elateroid lineages (Muona, 1995; Douglas, 2011). The morphology-based phylogeny confirmed monophyly of Elateroidea *minus* Rhinorhipidae (Lawrence et al., 2011), which differ in the number of Malphigian tubules and their position has been doubtful only since the description (Lawrence, 1988; Lawrence and Newton, 1995). Unfortunately, these rare beetles are not yet available for DNA extraction. The previous molecular studies confirmed the monophyly of currently defined superfamily (Bocakova et al., 2007; Hunt et al., 2007; Kundrata and Bocak, 2011; Bocak et al., 2014).

Current analyses represent the most comprehensive phylogeny of Elateroidea to date. We included all major elateroid lineages representing 13 of total 16 families. The Brachypsectridae, Plastoceridae and Rhinorhipidae were not available herein but they represent only 0.03% of elateroid diversity. The results agree in most aspects with recent molecular studies (Bocakova et al., 2007; Hunt et al., 2007; Kundrata and Bocak, 2011; Bocak et al., 2014). The monophyly of broad elateroids is strongly supported. Elateroidea can be divided into two groups of families. The first one contains basal lineages – Artematopodidae, Telegeusidae, Omethidae, Eucnemidae, Throscidae, and Cerophytidae – with weakly supported mutual positions in some cases. The second group is the strongly supported clade present in all above mentioned studies (i.e., higher elateroids; Fig. 2).

The basal-most lineage of Elateroidea is composed of Artematopodidae, Telegeusidae and Omethidae. These groups formed either a single clade or two lineages Artematopodidae and Omethidae + Telegeusidae (Kundrata et al., 2013), or independent splits (Bocak et al., 2014). Using much denser sampling, these lineages form a strongly supported clade here (Fig. 2), barring a seldom case when Artematopodidae were recovered outside Elateroidea

(Table 1). Forbes (1926) treated Artematopodidae as basal members of Elateriformia based on the primitive wing folding. Crowson (1955) placed them in Dryopoidea using larval characters, but noted similarity of adults to elateroids. All subsequent authors have kept their position in Elateroidea (e.g., Lawrence, 1988; Lawrence and Newton, 1995; Bouchard et al., 2011). Omethidae and Telegeusidae formed a clade in the most recent molecular studies, however only *Drilonius* (Omethidae) and *Telegeusis* were available and no artematopodid included. The current study recovered Telegeusidae as one of the terminal branches within the paraphyletic Omethidae *sensu* Crowson (1972) (Tables 1 and S6; Fig. 2). The clade Omethinae + Matheteinae was largely demonstrated to be the sister group of Telegeusidae, however, in some analyses we found Telegeusidae close to Driloniinae. Additionally, the terminal position of Telegeusidae within Omethidae is suggested by some morphological characters such as the similar shape of labrum (Lawrence, 2010; Ramsdale, 2010). The sister group to Telegeusidae remains unresolved, but their terminal position among omethid lineages is well supported. Therefore, we propose to synonymize Telegeusidae Leng, 1920 to Omethidae LeConte, 1861 and give them a subfamily rank.

The phylogenetic relationships of Eucnemidae, Throscidae and Cerophytidae are still to be fully resolved. The original hypothesis that they are related to Elateridae based on the presence of the similar clicking mechanism, well sclerotized body and larval morphology (Crowson, 1955; Lawrence, 1988; Beutel, 1995; Muona, 1995; Lawrence and Newton, 1995) was rejected by the first molecular studies (Bocakova et al., 2007; Sagegami-Oba et al., 2007). Eucnemidae and Throscidae have been recovered as either sister groups (Hunt et al., 2007; Bocak et al., 2014) or independent lineages (Kundrata and Bocak, 2011, this study; Table 1, Fig. 2), but always distant from Elateridae. Bocakova et al. (2007) inferred both topologies depending on the analysis method. The position of Cerophytidae is investigated with several markers for the first time and the dataset used herein contains the highest numbers of Eucnemidae and Throscidae ever analyzed. All three families are either independent lineages or Throscidae and Cerophytidae form a clade (Fig. 2). Lawrence et al. (2007) published results of their morphological and combined morphological and molecular analyses of a small number of taxa mainly from former Elateroidea *sensu stricto*. In their topologies, Throscidae + Cerophytidae were in distant position to Eucnemidae (morphological analyses) or these three groups formed a clade with Brachypsectridae (combined analysis). The association of Throscidae and Cerophytidae was already pointed out by previous authors (Lawrence, 1988; Beutel, 1995; Lawrence et al., 2007; for different opinion see Muona, 1995). However, Hlavac (1973) mentioned the fully developed propleurocoxal articulation of Cerophytidae, which separates them from remaining clicking elateroids and suggest their more distant position.

Another elateroid lineage with enigmatic position is Anischiinae (Crowson, 1955), which are inferred as a sister to Eucnemidae across current analyses in agreement with the recent morphology-based phylogeny (Fig. 2, Lawrence et al., 2007). Anischiines were classified in various elateroid families (for a review, see Lawrence et al., 2007), placed as Elateridae *incertae sedis* (Lawrence and Newton, 1995) or an independent family Anischiidae (Lawrence et al., 1999). Kundrata and Bocak (2011) reported Anischiinae as a sister to Throscidae, but a voucher check has revealed this to be based on a wrongly identified throscid specimen.

The clade of higher elateroids was well supported by Bocakova et al. (2007), Hunt et al. (2007) and others. The Lycidae are the basal-most lineage of this extensive clade (Figs. 1 and 2). Other families are grouped in two clades, which are consistently found across most recent molecular studies. The first clade contains Cantharidae + Lampyridae with robust support for their relationships suggested across various studies and analyses (Figs. 1 and 2, Table 1). The second clade contains closely related Phengodidae + Rhagophthalmidae, Omalisidae, and Elateridae. Studies, that only include a small number of Phengodidae, Rhagophthalmidae and Omalisidae taxa revealed two independent lineages Phengodidae + Rhagophthalmidae and Omalisidae within paraphyletic Elateridae (Bocakova et al., 2007; Sagegami-Oba et al., 2007; Bocak et al., 2014). However, analyses of larger datasets suggest the sister position of these three families to Elateridae (Kundrata and Bocak, 2011, this study; Table S6). The phylogenetic position of Omalisidae remains unresolved and they may be either sister to Elateridae or form the clade with Phengodidae + Rhagophthalmidae. The latter hypothesis obtained a low but consistent support (Table 1) and is suggested also by shared biology of the larvae feeding on millipedes (Burakowski, 1988; Eisner et al., 1998). According to both morphology and genetic diversity, Phengodidae and Rhagophthalmidae are closely related and sometimes treated as a single family (Lawrence and Newton, 1995; Amaral et al., 2013). The occasional placement of Phengodidae, Rhagophthalmidae and Omalisidae within Elateridae may be an artefact of the analysis.

In the majority of analyses, Elateridae *sensu* Kundrata and Bocak (2011) were recovered as a monophylum, but with weak support similarly to previous studies (e.g., Douglas, 2011; Kundrata and Bocak, 2011; Table S6). The generally short branches of Elateridae might result in lower stability of the inferred topology (Wiens et al., 2012). Elateridae are morphologically diverse when soft-bodied drilines and divergent cebrionines are included (Kundrata and Bocak, 2011). The relationship between Elateridae and Drilini is not supported by morphology-based analyses (e.g., Lawrence et al., 2011). However, all existing molecular phylogenies consistently recover Drilini as a part of Elateridae clade and, therefore, their morphological disparity cannot be considered in the formal classification (see, e.g., Crowson, 1955; Kundrata and Bocak, 2007).

4.3. Evolution of soft-bodiedness and bioluminescence: do similar structures indicate relationships?

Several weakly sclerotized beetle lineages were placed in a single polyphyletic group Malacodermata (e.g., Gorham, 1886) and only modern systematics recognized their phylogenetic relationships. Originally, cantharoid families were placed as Cantharoidea in Elateriformia (Crowson, 1955), but later merged in a broadly defined Elateroidea (Lawrence, 1988). Despite the absence of a unique synapomorphy independent of soft-bodiedness, the cantharoid families are recovered as a monophylum in recent morphological analyses (Beutel, 1995; Lawrence et al., 2011). The current molecular phylogenies strongly reject their monophyly and suggest multiple origins of similar soft-bodied forms within Elateroidea (Kundrata and Bocak, 2011; Amaral et al., 2013). Two soft-bodied lineages, Omethidae and telegeusids, form consistently a clade and suggest only a single loss of the sclerotization among basal elateroid lineages (Bocakova et al., 2007; Kundrata and Bocak, 2011, this study). Unlike previous studies, the majority of analyses suggest a common origin of neotenic females in Omalisidae, Phengodidae and Rhagophthalmidae (Figs. 1 and 2, Table 1). On the other hand, drilines and cebrionines represent independent origins of larviform females when consistently recovered within Elateridae. The morphological divergence represents a continuous scale from weakly sclerotized body (e.g., Omethinae, most of Cantharidae) through intermediate stages of wing modifications (brachyptery, aptery; e.g., Lampyridae, Omalisidae), shortening and simplification of appendages (Elateridae: Drilini) to the larviform females (females sexually mature but retaining larval characters, e.g., some Lycidae) (Bocakova et al., 2007; Bocak et al., 2008). Additionally, similar set of modifications is found in obviously unrelated taxa (e.g., the morphological similarity of the male of *Dexoris chome* [Lycidae] and female of *Omalisus* [Omalisidae]; Bocak et al., 2013). The apparent

continuity of modifications and their similarity across Elateroidea suggest a simple mechanism in control of expression of neotenic changes; potentially the levels of juvenile hormon shorten the process of body sclerotization and expansion of wings. The incomplete sclerotization and unfinished metamorphosis affect adult morphology and consequently the outcome of the morphology-based analyses. The adult females retain characters in a state close to those in larvae – a larviform abdomen, which is much longer and wider than elytra, with extensive intersegmental membranes, absent cuticular structures as strengthened margins fitting to elytra, and incompletely sclerotized sclerites (the physogastric forms of Elateridae: Cebrionini); the absence to incomplete development of elytra and hind wings; the larval form of antennae to shortened antennae with lower number of antennomeres (Elateridae: Drilini), larviform thorax to lower ratio between the length of meta- and mesosternum in some adults (e.g., female of *Omalisus*; Bocak and Brlik, 2008). When these characters are coded in the morphological dataset, they tend to support the relationships of all soft-bodied forms. The molecular results are in deep conflict with results of morphological analyses and we need to decide which signal gets preference. There is no theoretical justification for favouring one source of data over another (Wheeler et al., 2013), but the supposed parallel origins of similar morphology due to incomplete metamorphosis should be seriously considered.

The members of Lampyridae, Phengodidae, Rhagophthalmidae and Elateridae show the ability to emit the light (i.e., bioluminescence; note that Omalisidae are not included among bioluminescent lineages, see Burakowski, 1988). All luminescent beetles (except some Staphylinidae; Costa et al., 1986) are concentrated in the higher elateroid clade (Fig. 2) and although multiple origin of bioluminescence was inferred, it is strictly limited to these closely related lineages. The molecular hypotheses consistently reject the Lampyridae + Phengodidae + Rhagophthalmidae relationship, which was considered to be supported by the presence of bioluminescence in the past (Crowson, 1972; Beutel, 1995). Pototskaja (1983) and Branham and Wenzel (2001) hypothesized, that bioluminescence originated independently in Phengodidae and Lampyridae. Branham and Wenzel (2001) even proposed a separate origin of bioluminescence in rhagophthalmids, as they rejected sister group relationships of rhagophthalmids and phengodids. Independent origins of bioluminescence in Lampyridae and Phengodidae + Rhagophthalmidae clades are also supported by current dataset, but our analyses differ in the underlying topology when we recover Phengodidae and Rhagophthalmidae in close relationships to Elateridae. The current position of Rhagophthalmidae as a sister to Phengodidae (Fig. 2) is supported not only by molecular phylogeny, but also by similar structures of luciferases (Viviani, 2002; Amaral et al., 2013).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2014.03.012.

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