COMPREHENSIVE PHYLOGENETICS, SYSTEMATICS, AND EVOLUTION OF NEOTENY OF LAMPYRIDAE (INSECTA: COLEOPTERA)

BY

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Abstract

A comprehensive phylogenetic study of Lampyridae covering nearly 80% of documented genera was conducted. A total of 410 male characters explored from 220 species of ten families were selected and coded. The outgroup relationships were largely congruent with previous morphological phylogenies and considerably different from recent molecular studies. A relationship of (Artematopodidae + (Brachypsectridae + (Drilidae + (Omalisidae + ((Lycidae + Omethidae) + (((Phengodidae–Telegeusidae) + Rhagophthalmidae) + Lampyridae))))))) was revealed. The definition of Lampyridae *sensu* Crowson was supported. Eight monophyletic subfamilies; Pterotinae, Cyphonocerinae Luciolinae, Photurinae, Cheguevarinae [replacement name for Megalophthalminae], Amydetinae, Psilocladinae, and Lampyrinae; were recognized. A taxonomic solution for the paraphyletic Ototretinae–Ototretadrilinae complex was discussed. McDermott's tribal classification was not supported and should be abandoned. Paedomorphosis in Elateroidea was investigated, with emphasis on Lampyridae. Its differentiation, taxonomic distribution, ontogenetic origin, evolution, and other heterochronic questions were thoroughly evaluated.

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Chapter I. Introduction and a Brief Historical Review

The taxonomy of Lampyridae celebrated its 250th anniversary this year. Linnaeus (1758) described the first firefly species, *Lampyris noctiluca* (in *Cantharis* at that time) in the 10th edition of his *Systema Naturae*. The family-group classification was initiated over a half-century later and refined by several naturalists and entomologists, including Laporte de Castelnau (1833), Melsheimer (1846), Motschulsky (1852, 1853a, b, 1854), LeConte (1851, 1862, 1881), Lacordaire (1857), Olivier (1885a, b, 1886, 1888, 1907, 1910a, 1911), Gorham (1880, 1880–1886), Leng and Mutchler (1922), Green (1948, 1959), McDermott (1964, 1966) and Crowson (1955, 1972), among several others. The classification kept adapting to meet the contemporary standards, and continues to this day. Unfortunately, the classification remains quite controversial and a revise system is desperately needed.

The modern classification of Lampyridae was essentially built on the synthetic works of Olivier (1907, 1910a). Olivier (1907) published the first edition of the world lampyrid catalog in which he constructed a nine-subfamily system to accommodate 1002 species and 48 genera. The subfamilies were largely differentiated according to the morphology of the antennae and head. Meanwhile, Rhagophthalmidae were established for thee Asiatic genera. An updated catalogue was released later, including 1109 species and 58 genera (Olivier 1910a). Considering the highly homoplastic nature of antennal morphology, Green (1948, 1959) made significant changes to Olivier's classification, especially within Lampyrinae. Green introduced a tribal/subtribal system and demoted several of Olivier's subfamilies to subordinate units of Lampyrinae, mainly according to the morphology of mouthparts, abdominal spiracles, and tarsi. LeConte's (1881) Matheteini were raised to a subfamily and placed in Lampyridae (Green 1948). Green's tribal classification was further expanded by McDermott (1964) and applied to the whole family. McDermott built a seven-subfamily system and provided the most recent comprehensive account on the family-group definition and composition. Later, McDermott (1966) published the second edition of the world lampyrid catalog, listing 1892 species and 92 genera within 15 tribes/subtribes of seven subfamilies. In this catalogue he reduced Ototretinae to a lucioline tribe and elevated the lampyrine Amydetini to an independent subfamily in comparison with his previous classification. Crowson's (1955) placement of Rhagophthalminae and Pterotinae in

Lampyridae was followed by McDermott (1964, 1966). However, Crowson (1972) removed Rhagophthalminae and Matheteinae from Lampyridae *sensu* McDermott to Phengodidae and Omethidae, respectively. In addition, he revived the subfamilial status of Ototretinae, suspended Green/McDermott's tribal classification, and replaced this with a new eight-subfamily system. He described another two lampyrid subfamilies, Cyphonocerinae and Ototretadrilinae, and transferred several drilid genera to them as well as to Ototretinae. The three classifications by Olivier, McDermott, and Crowson are summarized in Table 1. In total, 22 family-group taxa based on different types have been proposed across the three major classifications. Another two were added by subsequent authors (see Jeng et al. 2007a).

The currently prevailing higher classification of Lampyridae is fundamentally a mix of McDermott's and Crowson's systems to different extents (Jeng et al. 2007a). There are three major variants. Subsequent authors either accepted Crowson's subfamilial system and followed McDermott's generic composition of each subfamily (e.g. Newton and Lawrence 1995, Lai et al. 1998), retained McDermott's tribal classification under Crowson's subfamilies (e.g. Lloyd, 2002, Kazantsev 2006), or modified McDermott's generic composition of some groups as well as the definition or position of Crowson's subfamilies (e.g. Nakane, 1991, Jeng et al. 1998, Branham and Wenzel, 2001, Kawashima et al. 2003). None of the variants is presently more prevalent than the others. The variants appeared as a natural consequence owing to the very different properties of McDermott's and Crowson's classifications. The former was comprehensive and detailed, but the higher classification, especially the tribal system, was probably unnatural. In contrast, the latter gave loose definitions of subfamilies in which only a few exemplar genera were examined and listed, but the definition of Lampyridae looked more reasonable. Furthermore, abandonment of tribes/subtribes in Crowson's system likely also reduced the risk of non-monophyletic subordinate taxa. Nonetheless, the gaps and conflicts of three approaches require a comprehensive phylogeny, before they can be answered.

Modern phylogenetic analysis was not applied to Lampyridae until the late 1990s. Suzuki (1997) built a gene tree of selected Japanese fireflies from four lampyrid subfamilies and one rhagophthalmid genus. His neighbor-joining tree (Fig. 1A) showed that the clade of Rhagophthalminae + the ototretine *Stenocladius* was in Lampyridae, while the ototretine *Drilaster* (type genus) was the sister group to all the other lampyrids. Branham and Wenzel (2001, 2003) were the first to reconstruct a phylogeny of Lampyridae with a more global sampling. They used three rhagophthalmid genera and 37 lampyrid genera from all of Crowson's subfamilies except Ototretadrilinae for their morphological coding, and took another eight families as outgroups to determine the boundary of Lampyridae. Their phylogeny (Fig. 1B) revealed that Rhagophthalmidae were tied in a trichotomy with Lampyridae and several outgroup families as well as Pterotinae and a paraphyletic Ototretinae, while the remaining lampyrid subfamilies except Luciolinae and Photurinae were either para- or polyphyletic. Their tree suggested that the current classification of Lampyridae was on the edge of total collapse. Stanger–Hall et al. (2007) compiled a three-gene data matrix for 30 lampyrid genera of five subfamilies and one rhagophthalmid genus, and built a phylogeny implemented with maximum likelihood under Bayesian analysis. The resulting tree (Fig. 1C) largely supported Crowson's classification with minor exceptions, e.g., the clade of Pterotinae + Rhagophthalmidae remained unsolved as a quadrichotomy with Cyphonocerinae, Luciolinae, and the ototretine *Stenocladius*, whereas the ototretine *Drilaster* +

Brachylampis were the sister group to them. This large clade together with the other major lineage composed of the remaining lampyrid genera constituted Lampyridae. As part of their study on the phylogeny of Elateroidea, Sagegami–Oba et al. (2007) provided another molecular phylogeny of Lampyridae based on 18S ribosomal DNA sequences of limited taxon sampling (nine genera from six lampyrid subfamilies). Their tree (Fig. 1D) partially agreed with Stanger–Hall et al.'s in having two similar major branches in Lampyridae, but Rhagophthalminae were found grouping with Phengodidae and located distantly from Lampyridae. Bocakova et al. (2007) published their four-gene phylogenies of Elateriformia shortly after Sagegami–Oba et al's study. The analysis was performed using both parsimony and Bayesian methods with different alignments. The most parsimonious tree demonstrated two major clades in Lampyridae like previous studies, but with different compositions and patterns: Cyphonocerinae were linked with Amydetinae + Lampyrinae rather than with a paraphyletic Luciolinae + Ototretinae (Fig. 1E). A combination of the alignment from BlastAlign and Bayesian analysis yielded a very different topology (Fig. 1F) from the most parsimonious tree. The components of Lampyridae emerged in a pectinate pattern in which a paraphyletic Ototretinae + Ototretadrilinae became the most basal branch of Lampyridae, whereas Luciolinae were sister to the remaining subfamilies. An alternate tree (Fig. 1G), obtained from another alignment from ClustalX and Bayesian analysis, showed that the paraphyletic Luciolinae were the basalmost group in Lampyridae. Rhagophthalmidae were always allied to Phengodidae and distant to Lampyridae in all of Bocakova et al's topologies. The seven trees generated by Suzuki (1997), Branham and Wenzel (2001), Stanger–Hall et al. (2007), and Bocakova et al. (2007) are shown in Figure 1. Lately Hunt el al. (2007) provided a comprehensive phylogeny of beetles in which about eight genera of Luciolinae and Ototretinae were included. Their parsimonious tree with full taxon sampling supported the monophyly of both subfamilies, and Cantharidae were sister to Lampyridae. The clades of Rhagophthalmidae + Omalisidae and Phengodidae + Telegeusidae were in more basal positions in relation to Lampyridae within Elateroidea. An alternate tree produced by Bayesian analysis with reduced taxon sampling suggested a relationship of Lycidae + Lampyridae, while Cantharidae were sister to them (Figs. 7).

It is obvious that there is little agreement on the existing hypothesis of relationship to and within Lampyridae. Conflicts exist not just between morphological vs. molecular approaches, but even the same molecular data set with different alignments and analytic methods generated fairly different topologies. None of the analyses simultaneously explored all of Crowson's eight subfamilies, not to mention the other family-group taxa. The position of Ototretinae, Ototretinae, Pterotinae, and Rhagophthalminae/-idae, and thus the boundary of Lampyridae, remained controversial. In addition, a lack of consensus on the composition and definition for most of the lampyrid subfamilies has not been really solved. A critical question that needs to be answered is if the taxon sampling has been sufficient to represent the family and each subfamily in phylogenetic analysis. There has been no updated generic list of Lampyridae for the past 40 years. A number of newly described, revived, or transferred genera have been added to the Lampyridae during this same period of time (e.g. Wittmer 1979, Geisthardt 1983, 2007, Zaragoza 1995, 2000, Ballantyne and Lambkin 2000, 2006, Cicero 2006, Kazantsev 2006, Jeng et al. 2007a). Aside from these explicitly added genera, there may be a number of genera to be added to Ototretinae/ Ototretadrilinae presently considered drilids. More than 40 genera of Drilidae were listed in the latest catalogue by Wittmer (1944). Crowson (1972) transferred several of them to Lampyridae or other families, and specified three to four genera as true drilids. Lately Kundrata and Bocák (2007) revised the generic composition of Drilidae and verified six genera in the family, exclusively from the Palearctic and Ethiopian regions. This indicates that a considerable portion of Drilidae *sensu* Wittmer lacks a clear familial placement at present. Through extensive examination of specimens in several museums, I am aware that many potential lampyrid and rhagophthalmid genera remain unrecognized and misplaced in Drilidae (Jeng et al. 2007a). Based on my account, there are at least 114 documented genus-group taxa of Lampyridae *sensu* Crowson and 13 of Rhagophthalminae as of May 2008 (refer to Appendix I). This means previous phylogenetic analyses sampled merely 35% of the known genera, at most (e.g. Branham and Wenzel 2001, 2003), whereas many of them used 10–20%. The remaining 65%, including some highly heterogeneous or little known genera, remain unstudied in regard to their phylogenetic positions.

It has been extensively suggested that increasing taxon sampling may increase the probability to find more accurate topologies under parsimony (Hillis 1996, 1997, 1998, Purvis and Quicke 1997, Pollock et al. 2002, Zwickl and Hills 2002, DeBry

2005, Heath et al. 2008). Through years of effort, I was able to collect material of nearly 80% of the known lampyrid and rhagophthalmid genera. A substantial dataset with over 90,000 codings compiled from the available material was built in this study. My primary goal was to conduct a cladistic analysis to reconstruct a comprehensive phylogeny of Lampyridae and a revised, natural classification for the family. Franz (2005) showed that an increasing number of phylogenetic studies are no longer translated into classifications. He encouraged systematists to persist and strengthen the link between phylogenetics and taxonomy by defining and naming the recovered phylogenetic lineages to reflect their preexisting taxonomic history as well as new insights. In comparison with earlier studies, our study is a novel approach not just emphasizing the phylogenetic relationships, testing monophyly of groups, but also toward solving practical systematic/ taxonomic problems for the family.

Chapter II. Material and Methods

1) Taxon sampling

In total 129 genus-group taxa and 220 species from 10 families were included in the present study (Appendix II). The affinity of rhagophthalmids with Lampyridae was disputable and thence conveniently treated as a subfamily and part of the ingroup *a priori* to the analysis. Because the boundary of Lampyridae was unclear and the elateroid families, especially the cantharoids, were substantially diverse in morphology (Lawrence 1987), multiple outgroups for polarity determination were required. Among the materials 30 species of 28 genera from nine families other than Lampyridae and Rhagophthalminae were listed as explicit outgroups.

The outgroup families were composed of Dascillidae, Artematopodidae, Brachypsectridae, Drilidae, Lycidae, Omalisidae, Omethidae, Phengodidae, and Telegeusidae. The latter six have been long regarded as part of Cantharoidea (Crowson 1955, 1972, see also Lawrence et al. 1995), but some recent studies showed conflicting evidence (e.g., Bocakova et al. 2007, Hunt et al. 2007). These cantharoid families were found tied with Rhagophthalminae and Lampyridae in Branham and Wenzel's (2001) phylogeny, and thereby taken into our taxon sampling for further evaluation. Cantharidae appear to be a controversial taxon. The family is considerably derived and diverse both morphologically and ecologically (Crowson 1972). An unusual pattern in Beutel (1995) revealed that Cantharidae were allied to elateroids rather than to the other cantharoids, while Branham and Wenzel (2001) demonstrated the paraphyly of Cantharidae. Owing to these uncertainties, especially Beutel's phylogeny, as well as the highly diverse nature of Cantharidae, the family was excluded from my taxon sampling. To determine its position and monophyly would require a comprehensive phylogeny of Elateroidea, which is far beyond the scope of the present analysis. As for Artematopodidae and Brachypsectridae, Crowson (1972) postulated their close relationship and later raised the superfamily Artematopoidea for them (Crowson 1973). Lawrence's (1988) phylogenetic analysis did not support Artematopoidea, and he suggested that these primitive families like Artematopodidae and Brachypsectridae might represent a bridge between elateroids and cantharoids. Based on larval characters, Beutel (1995) presented a phylogeny of Elateriformia in which Brachypsectridae was positioned distantly from Artematopodidae and, instead, fell basal among cantharoids. The morphological variations of the two families have been examined thoroughly and in detailed by Lawrence (2005) and Costa et al. (2006). Following these studies, both families were included in my analysis. Lately Bocakova et al. (2007) argued that Telegeusidae + Omethidae, rather than Artematopodidae or the other “primitive” families, were the most basal lineage of Elateroidea. Accordingly, a taxon indisputably outside Elateroidea was needed to root my analysis. Dascilloidea, Byrrhoidea, or Dryopoidea has been proposed to be the sister group of Elateroidea (Lawrence 1987, Beutel 1995, Sagegami–Oba et al. 2007, Bocakova et al. 2007, Hunt et al. 2007). Dryopoidea are generally specialized to aquatic life (Brown 1987) and has been systematically tangled with Byrrhoidea in recent decades (Lawrence 1988, Lawrence and Newton 1995, Lawrence et al.1999). Herein I chose Dascillidae of Dascilloidea as the most distant outgroup.

The remaining taxa sampled were 180 species of 92 genera/subgenera from Lampyridae *sensu* Crowson (with two undescribed genera and species), and 10 species of nine genera from Rhagophthalminae (with one undescribed genus and species). The former alone represented 79% (90/114) of the documented genera/subgenera of Lampyridae, or 77% (98/127) if both were combined into the ingroup. These included generic taxa cover over 90% of the described species of the family/ subfamily. The unavailable genera were mostly little known, with very few species or even monotypic. They will be incorporated into further analysis wherever material becomes available.

To test the validity and composition of the 24 family-group lampyrid taxa proposed thus far, representative species from all of the nominotypical genera were included. These type genera act as nomenclatural landmarks of each family-group taxon in the phylogenetic tree. Such an attempt has never been attempted for Lampyridae. It was not my intention to verify Green/ McDermott's tribal classification. Instead, it is reasonable to anticipate that some of the demoted or invalidated groups might be revived to their original status while others become eligible as subfamilies. In addition, according to the Principle of Coordination (ICZN, 1999, Art. 36), we need to determine the priority of names for the family groups when these taxa are merged into single entities. In this sense, it is insufficient to use representatives of subfamilial taxa alone upon which to build a phylogenetic classification.

At the generic level, three points needed to be addressed. First, I included four subgenera listed in McDermott's catalogue as valid genera in our sampling. They were *Pygoluciola* Wittmer and *Hotaria* Yuasa of *Luciola* Castelnau de Laporte, *Daiphoturis* Pic of *Photuris* Dejean, and *Fenestracladodes* Pic of *Cladodes* Solier. Among them *Pygoluciola* has been reinstated to generic status by Ballantyne and Lambkin (2000), while *Hotaria* was synonymized with *Luciola* s.str by Kawashima et al. (2003). The phylogeny can test if these subgenera are really allied to their parental genera or not. Second, several invalid (synonymous) genera in McDermott (1966) like *Drilaster* Kiesenwetter of *Ototreta* Olivier, *Atyphella* Olivier of *Luciola*, *Pleotomodes* Green of *Lampyris* Geoffroy, and *Pyrocoelia* Gorham of *Lychnuris sensu* Dejean have been reinstated by subsequent authors (Satô 1968, Geisthardt 1986, Jeng et al. 1999c, Ballantyne and Lambkin 2000). *Ototreta* further became a junior synonym of *Drilaster* (Satô 1968, Branham and Wenzel 2001) and I agreed with this synonymy after examination of the type species of both genera. *Lychnuris sensu* Dejean was synonymized with *Lucidota* because the first included species of the former by Melsheimer (1846) was a species of *Lucidota,* and McDermott's subsequent designation of *Lampyris bicolor*, the type species of *Pyrocoelia*, for *Lychnuris*, was accordingly invalid (Jeng et al. 1999c). The validation of the other pairs were conveniently followed here for further testing.

Third, I used as many type species as possible when materials were available. About 80% of the included genera have their type species represented in the analysis. Species closely allied to a type species was used if the type itself was not available. This was for nomenclatural stability more than for phylogenetics because the position and validity of a genus group taxon is determined by its type species. Inclusion of type species of the putative genera is an extreme means to test the above two hypotheses in a practical taxonomy.

In addition to the type species or its similar allies, more species of a given genus were included if the genus exhibited great variation. For example, 12 species of *Luciola* were used in responding to its great diversity with nearly 300 species. At least one type-dissimilar species was added to a genus if the genus showed considerable variation and material was available. The sampling principle was applied to the genera with disjunct distributions, like *Vesta* (mainly Oriental and Neotropical, Jeng et al. 2007b) and *Diaphanes* (Ethiopian and mainly Oriental). These samplings were to test the monophyly of the genera in question.

2) Character selection and coding strategy

Kazantsev (2004) provided a thorough account on the morphology of Lycidae and related families, and we used this as a good reference to explore our character sampling. A total of 410 morphological characters of males were selected and coded from fully explored material. The characters came from all parts of the body and their appendages except the hind wings. The exact number from each part are; antennae (18); compound eyes (5); head and mouthparts (74), thoraces and elytra (120); legs (58); abdomen (76); male genitalia (59). In summary, 97 characters were selected from the head, 178 from the thorax, and 135 from the abdomen. The characters used in the present analysis are elaborated in Appendix III and the data set provided in Appendix IV. Inapplicable data were coded as "–", while unexamined characters due to rarity of specimens or missing body parts were coded as "?". Autapomorphic characters were excluded from character selection, though some unique, species-specific states were retained in multistate characters if they could not be attributed to the other states. Individual matrices for each body part were built independently for convenience of coding, and then merged into a master matrix.

To test the validity of higher taxa from genus to family, I selected characters with potential phylogenetic information of all levels rather than simply diagnostic characters of family-group taxa. This is somewhat analogous to recent molecular phylogenetic analyses which use multiple genes with different rates of change. Philosophically, I assumed no higher taxa as valid, thereby requiring the entire higher classification to be rebuilt based on the phylogeny. Scotland et al. (2003) argued that increasing the number of characters in a phylogenetic analysis also increased the ambiguous and problematic characters. Empirically this appeared true that there were very limited "unambiguous" characters in my large data set. This also reflects the low consistency index in general for characters (Appendix III) after the analysis. However, unambiguous characters were so scarce that they alone would contribute little to the resolution of trees when all problematic characters were removed. In addition, there is no justification to exclude ambiguous characters *a priori* (Jenner 2004). The "true" homology (status as synapomorphy) of a primary homology can only be determined by an analysis of congruence (De Penna 1991). Further, homoplasies were not universally hazardous to phylogenetic reconstruction (Goloboff 1991). It has been suggested that the benefit from a great number of characters to a phylogenetic tree outweighed the potential cost of including potentially homoplasic characters (Poe and Wiens

2000, Wien 2004).

The 410 characters exhibited a total of 1446 states, with 1036 derived states among them. Most of the characters were multistate, and some had 10 states in maximum. This corresponded to the tremendously diverse morphologies from a broad and dense sampling of taxa. In morphological examination I have been aware that superficially discrete states of a given character in low density of taxon sampling frequently became somewhat continuous in a denser taxon sampling. Consequently the boundary between higher taxa became ambiguous when included taxa increased, a problem taxonomists have frequently experienced. Rendering a complex character into several binary characters by nominal variable coding [(Pimentel and Riggins 1987, = present/absent coding in Pleijel (1995) or absence coding in Strong and Lipscomb (1999)] is hard to apply precisely and may cause illogical character optimizations. Instead, I tended to use composite coding by incorporating definable attributes into a multistate character, especially for complicate three dimensional shape of a structure (e.g. male genitalia, etc.). Wilkinson (1995) indicated that composite coding is justified if the different aspects of the complicated structure are not independent. I took the overall shape of a structure into consideration as one state because I was not sure if rendering it into several two-dimensional homologies was biologically meaningful or not. Occasionally I needed to break some highly variable characters into several separate characters owing to practical problems, e.g. the observed states exceeded the 10-state limitation of the cladistic program. In such situations, subjective determination of primary homologies was inevitable. For less complex characters, conventional coding was widely used in the present study.

Coding of characters in serial homology needed to be addressed. It occurred in segmented appendages like antennae and mouthparts palps. For instance, antennal flagellar articles were secondarily segmented and had a range of number from 7 to more than 30 in my material. Individual flagellar articles were therefore serially homologous to one another and should not be compared directly according to their superficial order among taxa with different numbers of flagellar articles. My coding strategy was more or less like a composite coding by denoting each state with specific conditions, like “flagellomere 2 longer than 1 if flagellum with n articles”. This coding strategy easily produced many states for a character, and may have limited phylogenetic information (Wilkinson 1995, Lee and Bryant 1999).

Since serially homologous characters were few in this study, the impact was negligible.

Female characters were not used in the present study due to both theoretical and practical difficulties. It has been well documented that neotenic or paedomorphic females are common among cantharoids, especially in Drilidae, Phengodidae, Rhagophthalminae, and many lampyrid lineages (Tiemann 1967, Crowson 1972, Cicero 1988, Ohba et al. 1996, 1997, Kawashima 1998, 1999, Jeng et al. 2000, 2001, Bocakova et al. 2007, Hunt et al. 2007). Theoretically it is questionable to compare a larval character with an adult features in determining homologies. This would also be the case if a female was really neotenic or "larviform" and preserved a larval morphology. For example, phengodid and perhaps some rhagophthalmid females have tarsunguli (unsegmented tarsus + single pretarsal claw) which is a larval morphology and not seen in normal adults (Cicero 1988). Comparing paedomorphic tarsunguli with adult tarsi was practically difficult, and requires ontogenetic evidence to specify each corresponding part. Simplifying such cases would generate questionable coding as well as lots of missing or inapplicable data. Another example with experimental evidence was the firefly lanterns. Strause et al.

(1979) demonstrated that development of adult lanterns was not affected by artificially destroyed lanterns in the larval stage of *Photuris* fireflies. This implied that larval and adult lanterns might not be homologous, at least in some *Photuris* males whose lanterns were in different abdominal segments between larvae and adults). Generally lanterns of female fireflies occurred on abdominal segment 6, 7, or 8, or in several, and with various shapes and numbers, while larval lanterns were restricted to segment 8 only, usually a pair. It is risky to argue that a better developed lantern in segment 8 of a normal female (like in female *Luciola*) was homologous with a pair of small lanterns in a neotenic female.

In addition to the above philosophical and coding problems, female material was usually more difficult to obtain than males, especially the neotenic form which was ecologically cryptic and prone to dehydration and hard to preserve intact. Approximately 63% of the genera in my material had available specimens of both sexes, and I will keep collecting material to develop a better coding strategy to perform a phylogenetic analysis incorporating females in the future.

3) Cladistic analyses

The analyses were implemented with the programs Nona (Goloboff 1999b), run within Winclada (Nixon 2002), and TNT (Goloboff et al. 2007), respectively. TNT was used to check fast, preliminary results of pretests (partition of matrix and number of steps) and Nona/Winclada was used to find a large set of trees. I employed the “New Technology Search” consisting of four algorithms (sectorial search, rachet, drift, and tree fusing: Goloboff 1999a) to search trees in TNT. The parameters for each algorithm used the default setting except increasing the number of rachet iterations to 2000 and five random addition sequences were conducted. For my full data matrix, TNT usually took about 30 minutes to complete an analysis with the above setting by a laptop computer with 1GB memory and with a 1.7GHz Centrino processor. Parsimony rachet (Nixon 1999) implemented in Nona was chosen to find trees after I evaluated its searching ability by a heuristic search which always found less parsimonious trees than did the rachet. All of the characters were unweighted and non-additive except the position of abdominal spiracles (Character 332) which showed a clear transition during metamorphosis and thus was considered additive (Cicero 2007). The resulting topologies were then collapsed into a strict consensus tree. 500 replications of Jackknifing were implemented to estimate branch support.

Three analyses were performed emphasizing different aspects. The first analysis was on the full data set to generate a comprehensive phylogeny. Most questions would be answered according to this tree, like the definition of Lampyridae, evolution of a given character and so on. I made a series of pretests to evaluate the searching ability of the rachet in Nona from 2000, 4000, 6000, 8000 to 10,000 iterations. The number of iterations was set to be 2000, with five addition sequences. By this procedure I was able to compare the results from every 2000 iterations and determined when the trees become stable (number of steps) and enough (number of trees) to stop. Usually the results in terms of steps were stable within 4000 iterations, but occasionally 6000 found more parsimonious trees with one step less, and 10000 iterations discovered the greatest set of trees of shortest lengths. Hence I set the number of iterations to 10000 with 10% random constraint level and the default setting of collapse (amb- ploy=). My pretests also suggested that the constraint level from 8, 10, 12, to 15 and a setting of collapse or polytomy had little or no effect on the result in a great number of rachet iterations. For my full size dataset, it usually took one hour for every 1000 rachet iterations under the above conditions and equipment. The resulting most parsimonious trees were then submitted to heuristic search by TBR with 10,000 trees held in maximum so that more trees of equal length could be found. A similar procedure was implemented in TNT by using New Technology Search first then submitting the trees to traditional search. The results from the two programs could be compared with each other.

In the second analysis I reduced the taxon sampling to only type species or a resembling species for each genus. Because type taxa are the basis of nomenclatural stability, I did not make nomenclatural changes or define a higher taxon unless both this and the preceding analyses showed a congruent pattern for that taxon.

In the third analysis, the matrix was further reduced to include the type species or allied species of nominotypical genera only. Such sampling is common to phylogenetic studies, especially in molecular approaches in which usually only a limited number of representative species for each higher group is sampled. To test the monophyly of the included outgroup families, multiple species were used even if there was no subfamilial classification within those families (e.g. Drilidae, Telegeusidae). More than one species of a given genus were included if I was uncertain which was most similar to their congeneric type species (e.g. *Magnoculus*). By comparing the result of this analysis with the previous two tests, I could see the behavior of various taxon numbers in a phylogeny from sparse to dense sampling, and the representation of the nominotypical genera. The fundamental topology should be the same with that of a comprehensive phylogeny if the nominotypical taxon was a suitable representative of its higher group.

Chapter III. Results

1) Full data set

The analysis implemented with 10,000 iterations of parsimony rachet found 903 most parsimonious trees (MPTs) with 7682 steps for each. Subsequent heuristic search increased the number of trees to 1008. The Consistency Index (CI) was 0.13 and Retention Index (RI) was 0.69. A strict consensus yielded a consensus tree with 19 collapsed nodes and a length of 7808 steps (Fig.2). The resolution was fairly good, with over 90% of total nodes being resolved. I used "comprehensive tree" to differentiate this tree from the others obtained by taxon-reduced data sets.

In the comprehensive tree, lineages of family level were fully revealed, and the boundary of Lampyridae was clearly delimited. Aside from the paraphyletic Phengodidae, intermingled with Telegeusidae, the other families were monophyletic. The relationships of outgroup families will be discussed in detailed in Chapter IV. As for Lampyridae, my result fundamentally supported Crowson's definition of Lampyridae. Contrary to Branham and Wenzel's (2001) morphological tree, many of Crowson's subfamilies were demonstrated to be monophyletic. The only problematic group was the Ototretinae/ Ototretadrilinae complex, which could not be easily solved. On the other hand, Green/ McDermott's classification suffered from extensive trouble in that the tribes/subtribes were not monophyletic. These problems will be discussed thoroughly in Chapter V.

2) Data set containing type species (or their equivalent) only

There were 16 characters that became uninformative when the number of taxa reduced to about 60% (137 out of 220) of the full taxon sampling. The parsimony rachet found 445 MPTs with a length of 6292 steps for each. Subsequent heuristic search raised the total number of trees to 720. The strict consensus (Fig. 4) had 15 nodes collapsed and a length of 6375 steps. The values of CI raised slightly and RI decreased in comparison with the former analysis. The resolution was about the same with that of the comprehensive tree. We termed this tree as "type-species tree" for purpose of convenience.

The branch pattern of the consensus tree did not change dramatically from that of the comprehensive tree. The phylogenetic relationships of the outgroup families remained unchanged. Among ingroup taxa, a clade including *Ototretadrilus* and another three genera in the comprehensive tree was collapsed in the type-species tree.

A polytomy mix of Photurinae, *Amydetes*, *Psilocladus*, and *Magnoculus* + *Cheguevaria* in the comprehensive tree was partially resolved in the type-species-only tree. The latter two lineages were united with the other members of Lampyrinae.

Another noticeable difference between the two trees was a “higher” clade in Lampyrinae. The generic composition largely corresponded to McDermott’s Lampyrini, Pleotomini, Lamprocerini, and Cratomorphini as a whole. The large clade were split into several smaller clades in the comprehensive tree, but became pectinate in the type-species tree.

Though there existed differences between the two analyses, the composition of each major group in Lampyridae did not deviate from each other. On this basis, we were able to establish a revised systematics of Lampyridae with maximum congruence of the two trees (see Chapter V).

3) Data set containing type species of type genera only

There were 354 informative characters remaining in the type genus data set. Six trees each with 2907 steps were found by 500 iterations of the parsimony rachet using Nona/ Winclada. Two nodes were collapsed in the strict consensus, yielding a tree length of 2918 steps. The resulting CI and RI significantly changed in relation to the previous two analyses, giving values of 0.29 and 0.55, respectively. This tree was called the "type-genera tree" for purpose of convenience.

The consensus tree of this analysis considerably deviated from the previous two. Telegeusidae were no longer intermingled with Phengodidae, making both families monophyletic. Rhagophthalmidae departed from the former clade and became the sole sister group to Lampyridae. The relationships of major lineages in Lampyridae remained about the same, but differed in low-level detailed patterns, especially in Lampyrinae.

In general, the results of the three analyses were largely consistent in terms of branching patterns and taxonomic composition of the main groups. This suggests that the type species or type genera sampled well represented their groups in most cases. Major conflicts occurred in the relationships of Rhagophthalmidae, Phengodidae, and Telegeusidae among the outgroups, and in the Ototretinae/Ototretadrilinae complex of the ingroup. These taxa appeared to be problematic to earlier studies as well (see Suzuki, 1997, Branham and Wenzel, 2001, 2003, Bocakova et al. 2007, Hunt et al. 2007, Stanger–Hall et al. 2007, Sagegami–Oba et al. 2007). Further studies with more evidence or integrated approaches would be required to solve the problem.

(4) Support of characters, trees, and branches, and other statistics

Archie (1989, 1990) indicated that the consistency index (CI) has a negative correlation with the number of taxa, and sometimes, of characters. The former correlation was observed in these analyses. In a large data set, CI is not an appropriate estimate of homoplasy (Archie 1989). The CI value for each character was quite low for most of the characters in the comprehensive tree (see Appendix III), but increased in general when the number of taxa was reduced. I made a simple statistic to examine the impact of increasing number of characters to the overall consistency and retention indices. The plots between the character/taxon ratio and overall CI values of the three analyses were in a nearly perfectly linear relationship, with a correlation coefficient of approximately 1.00. This was also true when replacing the character–taxon ratio with the value of derived states/species. It implies that either increasing characters or reducing number of taxa would increase the overall CI value in our studies. With respect to the overall retention index, its relationship with character–taxon ratios was inversely correlated, with a correlation coefficient of -0.91. Yet Wiens (2004) demonstrated no significant relationship between characters/taxa and levels of homoplasy (using RI as an estimate).

The retention indices of characters in the comprehensive analysis were much higher than CI values, but only few reached 1.00 (Appendix III). This reflected that while homoplasies were common, their level was not particularly high in the full data set. This might result fro large taxon sampling, helping to disperse homoplasies across a large tree rather than concentrate them in limited lineages (Hillis 1996). The fact that the character and overall RI values were decreased in the reduced-taxon-sampling analyses agreed with this interpretation. In contrast to Scotland et al.'s (2003) criticizing the inclusion of homoplastic characters in morphological phylogenetic studies, the largely consistent results of my three analyses demonstrates that the homoplasies at lower taxonomic levels did not have a severe impact on the higher-level phylogenetic reconstruction, provided the number of characters was great enough.

The jackknife support values for the comprehensive tree are shown in Fig. 3. All families except Lampyridae were well supported. This was owing to the weak support of Pterotinae in Lampyridae. Most of the monophyletic subfamilies of Lampyridae had jackknife support values greater than 50%, except the highly diverse Lampyrinae. Many of the internal lineages in Lampyrinae were not well supported either, further discouraging the use of Green/McDermott's tribal classification.

I tried to estimate Bremer values (Decay Index: Bremer 1994) for the comprehensive trees but the results were in vain. In a test with Nona, 50,000 trees held for five steps (Suboptimal 5) longer than the shortest trees was set. Unfortunately the number overflowed and the laptop ran out of memory then crashed after some 30 hours of running. TNT suffered form an even smaller capacity of tree saving than Nona, with only about 15,000–16,500 trees held. The setting of Suboptimal 1 found more than 11,000 trees and the set maximum number of trees held overflowed when Suboptimal 2 was employed. Since Decay Index was sensitive to the number of trees saved, limiting the number of trees in memory resulted in overestimates of support for clades (Morgan 1997). For example, Bremer values were fairly high for most of the clades when 15 extra steps were set in TNT. Predictably, the required capacity for tree saving in order to obtain reliable

Bremer values for the data set was many tens of times greater than the maximum setting. The limit of TNT for Bremer Support has been indicated by Meier and Ali (2005).

A related and interesting fact was the relationship between resolution and character/taxon ratio. The resolution for the comprehensive, type-species, and type-genera trees were 0.91, 0.89, and 0.96, respectively, whereas the characters/taxa values were 1.9, 2.9, and 7.5. It was clear that the resolution was not in a simple positive correlation with the number of characters; or alternatively, not negatively correlated with the number of taxa. Though I will never know the accuracy of my trees, the largely concordant results of the three analyses support Hillis et al.'s (2003) argument that there is no absolute or easy answer whether adding more characters or taxa is better in a phylogenetic analysis.

(5) Effect of multistate coding to phylogenetic reconstruction

It has been suggested that composite coding and unordered multistate characters discards considerable phylogenetic information, and thus limits resolution of relationships (Strong and Lipscomb 1999, Lee and Bryant 2000, Forey and Kitching 2000). Forey and Kitching (2000) further stated that binary characters would be responsible for most of the resolution in a dataset mixing binary and multistate characters. Unordered multistate characters may improve some resolution if binary characters provide only partial resolution. However, my analyses demonstrate that high resolution can be obtained from a multistate-character-dominant data set. This fact indicates that the effectiveness of multistate characters in a phylogenetic study might be more complicated than traditional empirical thought. It is likely that the number of total characters play an important role. Schulmeister (2004) used a hypothetical four-taxon case with a five-paramere model and *k*-state characters (k = 2 and greater) to investigate the conditions causing inconsistency in parsimony. One of the four general conditions increasing risk of inconsistency is a small number of character states (k). Though it is not yet known whether this is true or not for a more complicated model, Schulmeister's study provided some positive expectations for multistate coding.

Chapter IV. Phylogeny of Lampyridae and Related Families

1) Phylogenetic relationships of outgroup families

It was not my intention to reconstruct the phylogeny of cantharoid or elateroid families in the present study since the taxon sampling did not cover all families for either group. Instead, the morphological trees could serve as an independent reference for recent molecular phylogenies. Phylogenetic topologies of previous studies for Cantharoidea, Elateroidea, and Elateriformia were given in Figure 7. It should be mentioned that the Figure 1b in Bocakova et al. (2007) deviated considerably from Branham and Wenzel's original topology (cf. Fig. 7B).

Like the inconsistency among lampyrid topologies by different studies (Fig. 1), the incongruity among the existing phylogenetics of cantharoid/ elateroid families is substantial. Some molecular trees (e.g., Bocakova et al 2007, Hunt et al. 2007) exhibited very different topologies from those of morphological studies (e.g., Crowson 1972, Kasap and Crowson 1975, Lawrence 1987, Beutel 1995, Branham and Wenzel 2003, Lawrence et al. 2007). For instance, a clade incorporating Telegeusidae and Driloniinae (Omethidae) was shown to be the basalmost lineage of Elateroidea in both molecular studies mentioned (Figs. 7F–G). The other cantharoid families were either scattered across Elateridae or formed separate lineages. Yet the molecular studies were not controversial-free among each other or within a single study. For example, Hunt et al.'s full taxon tree generated by parsimony differed considerably from their reduced-taxon tree performed by Bayesian analysis in detailed patterns (Fig. 7G, H). In the former, Driloniinae were grouped with Scymaenidae of Staphyliniformia, while Phengodidae and Telegeusidae together became a clade sister to Elateridae and the other cantharoid families. Additionally, Lycidae were in a fairly basal position in Elateroidea in the full taxon analysis but sister to Lampyridae in the taxon-reduced tree. The molecular phylogenetics conducted by Sagegami–Oba et al. (2007, Fig. 7I) partially agreed on the topologies of Bocakova et al. and taxon-reduced tree of Hunt et al. (2007) in having a Lycidae–Cantharidae–Lampyridae lineage, but the remaining cantharoid families were intermingled with members from Dascilloidea, Dryopoidea (Byrrhoidea), Buprestoidea, and Elateroidea (i.e., none of the superfamilies were monophyletic). Furthermore, Sagegami–Oba et al. (2007) asserted that the sister relationship between Cantharidae and Lampyridae in their tree was likely artificial owing to long-branch attraction.

In relation to the existing phylogenies, my results (Figs. 2, 4, and 6) are concordant with various morphological approaches to different extents. The families Artematopodidae and Brachypsectridae represent the basal lineages of Elateroidea in my analyses. This is supported by Lawrence (1987, his Fig.30 = Fig. 7C in this study) and Lawrence et al. (2007) which employed multiple sources of evidence in their phylogenetic analysis. Our result fundamentally agrees with Beutel (1995, Fig. 7D) in the section of cantharoid phylogeny based on larval characters, except for Cantharidae which were not included in my analysis. With respect to Crowson's (1972) inferred phylogeny of Cantharoidea (Fig. 7A), my trees share with it that Phengodidae (including Rhagophthalminae) and Telegeusidae group together as the sister clade of Lampyridae.

As indicated by Bocakova et al. (2007), the possibility of Telegeusidae + Driloniinae being the basalmost elateroids could be logically determined only by employing an outgroup outside Elateroidea. During the final stage of the study I changed the root from the elateroid Brachypsectridae to the dascilloid Dascillidae to test this hypothesis. The result appeared to be more concordant with the conventional view than that proposed by Bocakova et al. (2007) and Hunt et al.

(2007). Actually, the phylogenetic positions of these two groups and the others did not dramatically change when using Brachypsectridae as the root (Jeng, unpublished). Therefore it is not likely a deviation owing to long-branch attraction (see Bergsten 2007).

Some unique patterns appear in the present phylogeny. For example, the sister relationship of Omethidae and Lycidae is new relative to previous studies. Omethidae were usually considered allied to Cantharidae (Crowson 1972). Branham and Wenzel (2001, 2003) showed the family intermingled among the paraphyletic Cantharidae (Fig. 7B). This might be an explanation for the Lycidae–Omethidae clade since Cantharidae, Lycidae, and Lampyridae were thought to be closely related as mentioned above and Cantharidae were not included in my analysis. Inclusion of cantharid representatives in the future I will be critical to answer this question.

The family Telegeusidae was grouped with Mastinocerinae, resulting in a paraphyletic Phengodidae in the comprehensive and type-species trees (Figs. 2, 4). Yet this tangle did not appear in the type-genera tree (Fig. 6) in which both families were monophyletic. Telegeusidae are a small family comprising three documented genera currently (Miller 2002b), but the potential diversity would be higher according to our examination of museum collections. Telegeusids are morphologically similar to small phengodids (Mastinocerinae) but never confused with each other. The former family is universally characterized by elongate, lobed terminal article of maxillary palpi (state 1, Character 82), while the 14-articled, bipectinate antennae and presence of the genital whip (see discussion under Rhagophthalmidae in the next section) in the male genitalia make Phengodidae another distinctive family. However, the Mastinocerinae are highly diverse taxonomically and morphologically (Wittmer 1976, O'Keefe 2002). In addition, a poorly known phengodid subfamily, Penicillophorinae, which has 11-articled and serrate antennae in males, has never been evaluated phylogenetically (Wittmer 1976, Lawrence et al. 1999). The monophyly of Phengodidae needs further investigation.

With respect to Drilidae, Crowson (1972) transferred many of their genera to Lampyridae, Phengodidae, Omethidae, and Lycidae and denoted that *Drilus*, *Malacogaster*, *Selasia*, and perhaps *Pseudeuanoma* Pic were true drilids. This is largely supported by my results except the problematic *Selasia decipiens* Guérin–Méneville fell within Lampyridae. *Selasia decipiens* shares similar aedeagal morphology and many other characters with *Stenocladius rufithorax* Wittmer of the so-called "Ototretinae". The former species was likely assigned to *Selasia* on the basis of its fan-like antennae and drilid appearance rather than specific synapomorphic characters (e.g., tergite 9 covering near-body-half of sternite 9, state 1 of Character 347). Lately, Kundrata and Bocák (2007) revised the generic composition of Drilidae and added *Paradrilus* Kiesenwetter, *Euanoma* Reitter, and *Pseudeuanoma* (latter two transferred from Omalisidae) to Drilidae. All six genera except *Selasia* are confined to Europe, Africa, and the Middle East, and the distribution of *Selasia* in the Orient was suspicious. According to this study and examination of museum collections, some, if not many or all, of the Oriental *Selasia* species are actually allied to ototretine genera rather than to typical *Selasia* which is otherwise an African taxon.

The phylogenetic position of Omalisidae shares less consensus with previous studies. The taxon has been long treated as part of Lycidae (Bertkau 1891, Kleine 1933, Winkler 1952) until Crowson (1972) raised it as a family, following by various subsequent authors (Burakowski, 1988, Bocák and Bocákova 1990, Lawrence 1991, Beutel 1995, Lawrence and Newton 1995, Lawrence et al. 1999, Branham and Wenzel 2001, 2003, Bocakova et al. 2007). In recent phylogenetic analyses, the family is either a fairly basal lineage of Elateroidea (e.g., Sagegami–Oba et al. 2007), the sister group of the Cantharidae–Lampyridae–Lycidae lineage (e.g., Hunt et al. 2007), or a subordinate elaterid taxon allied to Drilidae (e.g., Bocakova et al. 2007), aside from several other proposed positions. My results (Figs. 2 and 4) somewhat agree with Branham and Wenzel (2001, 2003) in that Omalisidae are located between Drilidae and the other cantharoid families. In relation to the other cantharoid families, Omalisidae bear several elaterid-like structures, especially in the prosternum and mesosternum, such as the large prosternum (states 0 and 1, Character 147), complete intercoxal process (states 0 and 1, Character 152), reception grooves for the prosternal process and precoxae in mesosternum (state 0, Character 196), and a well defined mesocoxal fossa in the metasternum (state 0, Character 212), etc. These characters also appears in the basal lineages such as Artematopodidae and Brachypsectridae, and are apparently plesiomorphic to omalisids.

Beetles are one of the insect orders with a rich and well-documented fossil record (Grimaldi and Engel 2005). Scientists benefit greatly by gaining a solid understanding of the evolutionary history of Coleoptera, especially in its early stages (Eskov 2002). The higher taxa of fossil beetles and their geological distribution have been comprehensively organized by Handlirsch (1906–1908), Carpenter (1992), and Ponomarenko (1995, 2002). Most of the polyphagan superfamilies, including Elateroidea, originated in the Triassic or Jurassic and no later than the Early Cretaceous (Ponomarenko 1995, 2002, Grimaldi and Engel 2005). The family Elateridae emerged as early as the Late Triassic, becoming common by the Early Jurassic, and exhibiting great diversity already in the Late Jurassic (Dolin 1973, 1975, 1978, Lawrence 1987, Ponomarenko 1995, 2002). Discovered from the Triassic Madygen Formation, the oldest fossil of Artematopodidae or a stem-group form had about the same age with stem-group Elateridae (Ponomarenko 2002). These are the oldest representatives of Elateroidea known thus far, empirically corresponding to my phylogeny with a descent stratigraphic–clade rank correlation. On the other hand, based on the absence of cantharoid fossils in Canadian amber or older formations, Crowson (1972) believed that Cantharoidea were younger than other beetle superfamilies. He inferred an origin of Cantharoidea in the late Cretaceous after the major landmasses had already broken into several continents.

Based on this inference he further postulated that the global distribution of Cantharidae and some other families such as Lycidae and Lampyridae were the result of their fast dispersal owing to their flight capability. In contrast, several small families like Drilidae and Omalisidae were said to be geologically restricted by the low mobility of their flightless females. Recently a fossil cantharid from Burmese amber (Early Crustaceous, 100–105 MYA) was discovered (Poinar et al. 2007). This ancient soldier beetle demonstrated the early existence of the family and suggests an earlier origin, perhaps in the middle or Late Jurassic. The worldwide distribution of cantharids and likely the other cantharoid families can have broader plausible explanations than constrained by dispersal models.

As for the other cantharoid families, Lycidae have more abundant fossils known from several geological formations, including Baltic amber (e.g. Winkler 1987b, Kasantsev 1997). A fossil family, Berendtimiridae from Baltic amber, was inferred to be closely related to Omalisidae (Winkler 1987a), and may simply e an enigmatic form with that family. Lampyridae have several unauthenticated fossils and will be discussed later. The other families such as Phengodidae, Telegeusidae, Drilidae, Omethidae, etc. still lack known fossils and thus provide no evidence about their geological origins.

2) Boundary of Lampyridae

My results essentially support Crowson's (1972) composition of Lampyridae in that Pterotinae, "Ototretadrilinae", "Ototretinae", and Cyphonocerinae are basal groups of Lampyridae. In contrast to McDermott's classification, the inclusion of Matheteinae and Rhagophthalminae in Lampyridae was not supported.

The tribe Matheteini (originally spelled as Mathetei) was established by LeConte (1881) under Lampyridae *s. lat.* (composed of lycids, lampyrids, and cantharids in his system) for North American *Matheteus* and *Pollaclasis*. Green (1948) raised it as a lampyrid subfamily, removed *Pollaclasis* and added *Ginglymocladus* to it. The subfamily remained unchanged (Fender 1962, McDermott1964, 1966, Arnett 1968) until Crowson (1972) transferred it to Omethidae. Crowson's classification has been widely accepted by subsequent authors (Fender 1975, Lawrence and Newton 1995, Lawrence et al. 1999). However, Ramsdale (2002) indicated that the definition and synapomorphies of Omethidae had not been adequately authenticated and its monophyly was therefore uncertain. Though some genera of the family have been employed in earlier studies (e.g., Branham and Wenzel 2001, 2003; Bocakova et al. 2007), the present phylogenetic analysis is the only one including all three subfamilies of Omethidae. The resulting trees agree with Crowson's placement and composition of the family. Yet the monophyly of Omethinae is not supported by the comprehensive phylogeny in that the clade (*Malthomethes* + *Troglomethes*) lies separated from *Omethes*. The relationship of the three omethid subfamilies was a polytomy in the type-species tree. Obviously the definition of each subfamily needs further investigation. Synapomorphies seem to be in the structure of the male genitalia, defining at least some of the family members. The short, broad, and apically-projecting basal pieces greatly overlap with the parameres (states 1–2 of Character 357, state 5 of 360) and the median lobe or its basal apophyses reach or surpass the basal margin of the basal pieces (states 1 and 3 of Character 410). Unfortunately, this structure was not examined in all taxa owing to the rarity of some material, yielding many missing entries.

The subfamily Rhagophthalminae was grouped with Phengodidae and Telegeusidae but remained monophyletic. Some studies supported the affinity of Rhagophthalminae and Phengodidae (e.g., Bocakova et al. 2007, Sagegami–Oba et al 2007), whereas others did not (Branham and Wenzel 2001, Hunt et al. 2007). These two groups do share many rarely derived features in elateroids, like the 14-articled antennae (state 4, Character 5), prognathous head (state 1, Character 25), approximate posterior tentorial pits (states 1 and 2, Character 54), telescope-like abdominal apices (state 1, Character 335), etc. (Jeng et al. 2007a). In addition, their larvae are known to be millipede-hunters and the females are highly neotenic, and share a unique distribution of bioluminescent organs (Tiemann 1967, 1970, Crowson 1972, Ohba et al. 1996, Miller 1997, Eisner et al. 1998, O'Keefe 2002). However, these two groups also have remarkable differences in detailed morphology, such as the structure of the antennae, male genitalia, etc. Phengodid males usually have their first flagellar article (FA1) very short (state 7, Character 7), and the antennae are bipectinate from FA2–9 each with a pair of slender branches arising from the flagellar base (state 8 of Character 8, state 2 of Character 9, state 4 of Character 12) (see Wittmer 1975, 1976). Male antennae of rhagophthalmids have three major variants: serrate, unipectinate, and bipectinate (states 0, 7 and 8, Character 8). The FA1 is usually longer than FA2 (states 5 and 6, Character 7), and the antennae are branched from FA1 to FA9 if bipectinate. In addition, the branches are somewhat compressed, rigid, and short in rhagophthalmids (states 1 and 3, Character 9) in relation to those of Phengodidae. The material of Phengodidae examined exclusively has a compressed, long, whip-like structure arising from the subapex of the median lobe (state 1 of Character 406). This rarely derived character is absent in Rhagophthalmidae and Telegeusidae, and appears as an unambiguous synapomorphy of Phengodidae. However, Phengodidae are a highly diverse taxon and examination of more genera will be necessary to determine whether this holds under further scrutiny.

Zoogeographically Phengodidae are a western taxon while Rhagophthalminae are distributed in the Oriental Region and Palearctic of East Asia. Between the disjunct distributions exists a related genus, *Cydistus* Bourgeois, in the Middle East. Owing to its aberrant morphology *Cydistus* has been placed in Drilidae (Olivier 1910b, Wittmer 1944), Rhagophthalminae/ Phengodidae (Crowson 1972, Lawrence and Newton 1995), Karumiidae (Pic 1927b, Paulus 1972) or *incertate sedis* in Elateriformia (Lawrence et al.1999). Six species of the genus are known (Wittmer 1944). At least the type species *C. reitteri* Bourgeois has bipectinate, 12-articled antennae branching from FA2–9 (Bourgeois 1885a, b, Lawrence et al. 1999). To determine the phylogenetic position of *Cydistus* would require a broader taxonomic sampling, at least covering the family Karumiidae of Dascilloidea and an even more distant outgroup than Dascillidae.

There is no explicit reason to keep Rhagophthalminae as a subfamily. Its monophyly is verified and does not make the other groups paraphyletic in the analyses. The legitimate condition to retain Rhagophthalminae in Phengodidae *sensu* Crowson occurs only if *Cydistus* belongs to Phengodidae and separation of Rhagophthalminae from Phengodidae makes the latter paraphyletic. However, this can be solved in alternative ways, e.g., modifying the definition of one subfamily to include *Cydistus* and keep monophyly simultaneously, or raising a new family based on *Cydistus* to maintain Phengodidae and Rhagophthalmidae separately, depending on different situations. It is unfounded to discuss such hypothetical conditions in the absence of evidence. As mentioned above, not all earlier studies agreed with the sisterhood of Phengodidae and Rhagophthalmidae. In a conservative view, I agree with Lawrence et al. (1999) to treat rhagophthalmids as an independent family to avoid unverified subordinate relationship with the other families. The systematics and morphology of Rhagophthalmidae will be discussed in detail elsewhere.

A recent discovery about the formation of a spherical germ rudiment in the embryos of Rhagophthalmidae suggests a close affinity with Lampyridae (Kobayashi et al. 2001, 2002), but the study is lacking in the other cantharoid or elateroid families except Cantharidae, and consequently has limited phylogenetic utility at present.

3) Phylogeny of Lampyridae

Among those analyses ever conducted for Lampyridae, my comprehensive tree is most similar to those of Stanger–Hall et al. (2007) [abbreviated as SHLH, Fig. 1C] and Sagegami–Oba et al. (2007) [abbreviated as SOTO, Fig. 1D] than with any others. Generally, the clades with high Bayesian posterior probabilities in SHLH were recovered in the comprehensive phylogeny. Coincidentally some of the discordant branches between SHLH and my results have lower posterior probabilities (0.75 and below) in SHLH or jackknife support (lower than 0.5) in mine.

A clear incongruence between SHLH and my phylogenies is the relationship between Luciolinae and the basal groups (Pterotinae, “Ototretinae”, “Ototretadrilinae”, and Cyphonocerinae). They are clustered together into a large clade in SHLH but exhibit a pectinate pattern in mine. The typical “Ototretinae” (*Drilaster* + *Brachylampis*) become the sister group of the others, and Rhagophthalmidae fall within Lampyridae in SHLH. In the comprehensive tree Pterotinae are the basalmost lineage of Lampyridae, and the typical “Ototretinae” are sister to (Cyphonocerinae + ”higher” lampyrids). In SHLH the lineage of (basal groups + Luciolinae + Rhagophthalminae) has a lower Bayesian posterior probability. The probability decreased from 0.91 to 0.75 when Luciolinae and some other Asiatic genera were added into the analysis originally dedicated only to North American genera. The placement of Pterotinae in Lampyridae in my comprehensive trees was not well supported in terms of jackknife values, but the pattern appears in all three analyses and the value is higher in taxon-reduced trees.

Another noticeable discordance occurs in the position of *Phausis* and *Lamprohiza*. In SHLH *Phausis* is sister to the clade of (Photurinae + Lampyrinae *s. lat.*) and *Lamprohiza* is in the *Lucidina–Lucidota–Phosphaenus* lineage. The posterior probability in the Bayesian analysis for (*Phausis* + (Photurinae + Lampyrinae)) is quite low (0.57), but that for the *Lamprohiza–Phosphaenus* relationship is nearly 1.0 in SHLH. In contrast, *Phausis* and *Lamprohiza* form a clade located in the typical Lampyrinae (the group includes *Lampyris* and related genera) in my comprehensive trees, with a jackknife value of 0.58. These two genera; known from North America and Europe, respectively; were once suggested as synonyms (Arnett 1963, Fender 1966). My examination of the type species of both genera also recognized their extremely similar morphology. They were placed in Photinini by Green (1948, 1959) and McDermott (1964, 1966) mainly according to the unmodified mandibles (*sensu* Green 1959) and simple antennae. Though their general morphology considerably resembles those of typical Lampyrinae, they deviate from the latter by having unmodified mandibles *sensu* Green (1949) (other than states 5, 7, and 8, Character 72), dorsal abdominal spiracles (state 1, Character 332), and a symmetrical aedeagal sheath (state 0, Character 339) (all plesiomorphic to Lampyrinae). They are a heterogeneous group (together with *Lamprigera*) within the fairly homogeneous typical Lampyrinae. The females of the two genera are neotenic, a common trait of typical Lampyrinae but with higher (more larval like) degrees than those occurring in “Photinini” (Cicero 1988, see also Appendix 5). Considering these inconsistent facts, the phylogenetic position of these three genera needs a further confirmation.

Finally, a minor inconsistency exists in the position of *Pyractomena*. The genus is sister to “Photinini” + (“Cratomorphini” + “Lampyrini”) (*sensu* McDermott 1966) in SHLH, whereas it falls within the *Photinus*–allied lineage of Lampyrinae in my tree. This difference does not affect the taxonomic content of Lampyrinae but alters hypotheses concerning the evolution of flashing behavior. This issue will be discussed elsewhere.

On the other hand, the following lineages are supported by both SHLH and my trees: the monophyly of Luciolinae (including *Pristolycus*), Cyphonocerinae, Photurinae, typical “Ototretinae”, and typical Lampyrinae. Aside from those disputed genera (*Phausis*, *Lamprohiza*, and *Pyractomena*), the general branching pattern and taxonomic composition from Photurinae to typical Lampyrinae are largely identical in both studies. The position of “Amydetinae” in SOTO (represented by the genus *Vesta*) implicitly agrees with my trees. In SHLH several of Green and McDermott’s tribes or subtribes retain their monophyly, especially within the subfamily Lampyrinae. While they are reveled to be para- or polyphyletic in my analysis with a much denser taxonomic sampling. For example, the former members of Amydetinae are scattered in basal positions of Lampyrinae in my tree; and subordinate lampyrine groups like Photinini, Cratomorphini, Pleotomotini, and Lucidotina, among several others, are collapsed. In this sense the tribal/subtribal system should be abandoned and Crowson's subfamilial classification is a better alternative. I will develop a new phylogenetic classification of Lampyridae in the next chapter.

It is worthy to mention the fossil lampyrids. Actually most of the documented fossils have not been well authenticated. Brodie (1873) reported a lampyrid from the Rhaetic Formation of Early Jurassic (Liassic), England. This beetle was ignored by subsequent researchers except Handlirsch (1906–08), mentioning it in his fossil catalogue. It is hard to tell if it is a true lampyrid because the beetle was never formally described and the concept of Lampyridae at that time was different from author to author. Aside from this vague record, the next oldest fossils are a few *Luciola*, *Lampyris* and unidentified species in middle Eocene Baltic amber (55–38 MYA) (Berendt 1845, Menge 1856, Helm 1896, Klebs 1910). Unfortunately, none of them were named or fully described either. The species *Luciola extincta* Heyden (1862) from the Oligocene, possessing pectinate antennae, apparently does not match its present placement, or is not a lampyrid at all. *Miocaenia pectinicornis* Wickham from the Florissant beds (Eocene–Oligocene), listed as a fossil lampyrid by McDermott (1966), is now recognized as a lycid (Carpenter 1992, Ponomarenko 2002). There have been several fossil lampyrids in Dominican amber (Early Miocene) or Columbian copal (Holocene) appearing in market auctions in the recent years. To my knowledge these fairly young fossils represent some extant genera from the Neotropical region. A thorough review on lampyrid fossils is in preparation by M.A. Branham (personal communication).

Chapter V. Phylogenetic Classification of Lampyridae

In this chapter I attempt to revise the current classification of Lampyridae in accordance with the phylogenetic analyses. Three principles are followed to develop the new family-group classification. First of all, nomenclatural stability based on priority and type taxa was the primary concern. I emphasize more on re-delimitation of existing taxa than to create or change names. Establishment of new higher taxa is avoided whenever there are one or several available names applicable to a redefined taxon. Nomenclatural changes are made only if necessary under the current ICZN regulations. Secondly, monophyly is used as a fundamental but not obligate criterion for classification, especially when nomenclatural stability is threatened. The exceptional situation happens when pectinate configurations of a topology yield paraphyletic taxa, especially in basal positions. It is impractical to lump the majority of the monophyletic groups together with these paraphyletic lineages into a "super-sized" clade, or to create numerous monobasic higher taxa for each side branch within a pectinate topology. Instead I suggest giving such a paraphyletic group an informal name, or retaining its original name but adding remarks or in equivalent representation so that the non-monophyletic nature can be noted and future studies encouraged to further resolve. The solution is a compromise between enhancing nomenclatural stability and a consideration of monophyly, and differs from the philosophy of evolutionary classification's acceptance and encouragement of paraphyletic groups (i.e., their "monophyly") (Wiley 1981, Mayr and Ashlock 1991). Thirdly, a major clade is treated as a subdivision-absent group whenever it was composed of both crown groups (monophyletic) and stem groups (paraphyletic).

With maximum congruence in the topologies produced by the full data set and the type-species-only matrix (Figs. 2 and 4), nine major groups of Lampyridae are recognized. They are Pterotinae, Cyphonocerinae, Luciolinae, Amydetinae, Photurinae, Cheguevarinae (new status), Psilocladinae, Lampyrinae, and a paraphyletic "Ototretadrilinae–Ototretinae" complex. This largely agrees with Crowson's classification but with additional elements from the other systems. Additionally, the composition of some subfamilies changes remarkably, such as Amydetinae.

My trees also demonstrated that Green/McDermott's tribal/subtribal system is not in good standing because of its inadequacy to maintain the monophyly of either designated and/or non-target taxa in most cases. For instance, retaining monophyletic tribes within Lampyrinae would require establishing numerous small tribes for side branches or small clusters. Crowson made a wise choice decision to avoid such problems. I suggest virtually abandoning the tribal/subtribal classification for Lampyridae, using only subfamilies as Crowson proposed. The nine groups recognized in my tree are discussed in detail in the following sections.

Pterotinae

The subfamily is monobasic on *Pterotus* LeConte in my tree, as proposed by Crowson (1972). It is the most basal lineage of Lampyridae, and shares a somewhat phengodid-like appearance with the outgroups (McDermott 1964, 1965, Crowson 1972). However, some detailed morphologies, like the position of the posterior tentorial pits (Characters 54–55), gula (Character 59), antennal structure (Characters 7–18), abdominal 10th segment (Characters 335–336), and various aedeagal structures (Characters 406, 410) separate Pterotinae from Phengodidae and related families. Crowson's placement of this subfamily in Lampyridae was reasonable.

The subfamily was first raised as a phengodid subtribe (LeConte 1881) until

Crowson (1955) transferred it to Lampyridae. McDermott (1964) placed *Harmatelia* in this subfamily but later recognized there existed considerable similarities and differences between these two genera (McDermott 1965). McDermott admitted that this generic composition of Pterotinae was arbitrary and his placing them together intentionally reflected a transition from Phengodidae to Lampyridae. Actually, the similarities between the two genera are mainly convergent and/or symplesiomorphies. Their male genitalia are very different from each other in that *Harmatelia* has a pair of subapical angles facing inwards in the parameres (state 1 of Character 376), shared with some ototretine genera (e.g., *Gorhamia*) but absent in *Pterotus* which has bifurcate apices of the parameres (state 1 of Character 373). The placement of *Harmatelia* in Ototretinae is more reasonable than in Pterotinae, Megalophthalminae (Olivier 1907), or Amydetinae (Fender 1962) according to my tree and morphological examination.

The flightless females of *Pterotus obscuripennis* have been described by Dean (1979), Cicero (1988), and Lawrence et al (1999). The female exhibits a high degree of neoteny with the presence of a pygopodium, a typical larval structure in the abdominal apex (Cicero 1988). The larvae feed on slugs and snails in indoor experiments (Dean 1979).

Ototretadrilinae–Ototretinae complex

These two groups together are an example showing the dilemma mentioned in the second principle we applied. Their pectinate configuration in basal positions of the phylogeny makes classification based on monophyly difficult. To reveal specific questions in each group, I discuss them individually first then propose a solution later in this section.

“Ototretadrilinae”

The genus *Ototretadrilus* Pic was the only member of Ototretadrilinae when Crowson (1972) established the subfamily. He differentiated Ototretadrilinae from the other subfamilies mainly based on the position of the abdominal spiracles which are not enclosed by dorsal-folded sternites in *Ototretadrilus*. However, Jeng et al. (2007a) indicated that this character does exist in some ototretine genera, like *Stenocladius s. str.*, *Harmatelia*, *Falsophaeopterus*, and *Oculogryphus*. In the current analysis, the above genera except *Harmatelia* unify into a monophyletic group in the comprehensive phylogeny, but the clade becomes loose in the type-species-only tree. Consequently the boundaries between Ototretadrilinae and

Ototretinae are even more ambiguous.

A single species *Ototretadrilus flavoscutellaris* Wittmer was used as the representative of Ototretadrilinae in my analysis. I examined another species, *O. maai* Wittmer which has a similar morphology to that of *O. flavoscutellaris*. Both have shortened, dehiscent elytra which make the abdominal tergites partially exposed to different degrees, from 5–7 segments. Lawrence et al. (1999) showed that *O. longicornis* Wittmer has its abdomen largely covered by elytra and the text stated the number of exposed tergites from elytra to be no more than three. None of the three species examined are the originally included species [= *O. atritarsis* Pic and *O. notaticollis* Pic]. In the original description of *Ototretadrilus* Pic (1921) stated that the genus is similar to *Baolacus* Pic which has dehiscent elytra (see also the key in Jeng et al. 2007a). By this clue, the two species I examined might be closer to the originally included species. There probably exists considerable variation in the genus thereby raising uncertainty about the definition of the genus as well as the subfamily.

Males of *Stenocladius s. str.* have pectinate antennae, and are largely diurnal active flyers (Ohba et al. 1997, Kawashima 1999). Some species have shorter pectinate antennae but large, ventral-approximate compound eyes (e.g., *S. chinensis* Geisthardt, see Geisthardt 2004), imply that they use both light and chemical cues for locating mate in the night. The females of *Stenocladius s. str.*, where known, are highly neotenic, with a worm-like appearance (Ohba et al. 1997, Kawashima 1998, 1999). They are able to emit fluorescent green light weakly through the whole body in addition to a pair of brighter spots in the 7th abdominal segment, but without clear external lanterns (Chen 2003). *Oculogryphus* males have fairly large compound eyes, short antennae, and similar aedeagal morphology to that of *Stenocladius*, and the genus displays a close relationship to *Stenocladius* in my tree. The females of *Oculogryphus* are probably neotenic as well but remain unknown such is also the case for females of *Ototretadrilus* and *Falsophaeopterus*.

"Ototretinae"

When he established the subfamily, Crowson (1972) recognized that Ototretinae were probably heterogeneously assembled and the definition was unsatisfactory. This is confirmed by most of the previous phylogenetic studies and my analysis.

With the exclusion of *Baolacus*, *Falsophaeopterus*, *Oculogryphus*, and

Stenocladius which are clustered with *Ototretadrilus*, Ototretinae contain at least 12 genera worldwide, mainly from the Oriental realm. Likely there are more misplaced in the family Drilidae. This subfamily is not only poorly defined for itself, most of its included genera are also problematic. Many of the genera were described by Pic in the 1910s–1930s. His brief descriptions of numerous insect taxa across several orders without taxonomic organization make subsequent tracing very difficult. Jeng et al. (2007a) made a preliminary attempt to differentiate the ototretine genera according to their observation on available material. Further improvement based on a more thorough taxon sampling will be required.

Nine documented genera were included in my analyses. All but *Harmatelia* have their abdominal spiracles enclosed by dorsal-folded sternites. They are spread in a pectinate configuration, some are monobasic while many others are in small clusters except a larger clade constituted by *Brachylampis* Van Dyke, *Drilaster* Kiesenwetter [= *Ototreta* Olivier], *Flabellotreta* Pic, *Mimophaeopterus* Pic, and *Picodrilus* Wittmer. They share great resemblance in male morphology and at least *Brachylampis*, *Drilaster*, and *Flabellotreta* have alate females. Information of females is helpful to define the subfamily. Unfortunately, nothing is known about the females or larvae of the other genera (Lawrence et al. 1999) and I did not find female material for them. Crowson (1972) stated that the females of *Harmatelia* are “apterous and larviform” referring to Green (1912) as the source. Yet Green (1912) did not make any similar statement, or more precisely, he said he had no clue about the females of *Harmatelia*. It is likely that Green’s figure 2 was mistaken for a *Harmatelia* female by Crowson, but is actually a male of *Dioptoma adamsi*. This error has been indicated by Lawrence et al. (1999) and Branham and Wenzel (2001). The assignment of an origin of neoteny for Ototretinae–Ototretadrilinae by Bocakova et al. (2007) was probably misled by the females of *Stenocladius s. str.* or Crowson’s description of *Harmatelia*.

As one of the origins of confusion in Ototretinae, the identity of *Stenocladius* should be addressed. This genus was described by Fairmaire (1878) based on *S. davidis* Fairmaire from China. *Stenocladius bicoloripes* Pic from Taiwan, a species I examined and used in the analysis, is confirmed to be a similar species after I compared the type material of both species. All Japanese species are typical *Stenocladius* (see Kawashima 1999). These species are more allied to Ototretadrilinae than to Ototretinae according to my tree. However, many subsequently added species are not really allied to *Stenocladius s. str.* They were probably ascribed to this genus on the basis of pectinate antennae and overall similarity (mostly plesiomorphic). For example, *S. ruficollis* Wittmer, the other species I used in the analysis, shows a close relationship with *Selasia decipiens* Guérin–Méneville of Drilidae. They resemble each other not only in general morphology but also in specific traits like the male genitalia and the aedeagal sheath (see Wittmer 1979). It is likely that many, if not all, of the Oriental *Selasia* do not belong to *Selasia s. str.* from Africa but are allied to some other Oriental ototretines. Furthermore, *Stenocladius basalis* Pic, the only species of the genus examined by Crowson (1972) and now a synonym of *S. horni* (Bourgeois) according to Wittmer (1979), is actually allied to *S. ruficollis* rather than to *Stenocladius* s.str according to my examination. Crowson's interpretation is likely the origin for subsequent authors who regarded *Stenocladius* as an ototretine genus but did not doubt its identity. Examination of type species proved to be critical for the higher classification and phylogeny.

Solution for Ototretadrilinae–Ototretinae complex

There are several options to deal with the problem under the guidelines of the above principles, especially the first two.

Option 1: Keeping Ototretadrilinae monophyletic and Ototretinae paraphyletic. This is congruent with my comprehensive tree in which *Ototretadrilus*, *Falsophaeopterus*, *Stenocladius s. str.*, *Oculogryphus*, and probably *Baolacus* form the Ototretadrilinae. The other genera are lumped into a so-called "Ototretinae", consisting of the ototretine group, the *Harmatelia–Drilaster* group, the drilid-like group, or other informal names. The drawback is that the above delimitation of Ototretadrilinae is not explicitly supported by my type-species tree and consequently weakens the classification and nomenclatural stability.

Option 2: Keeping Ototretinae monophyletic and paraphyletic for Ototretadrilinae. This solution confines Ototretinae to the core subgroup only, i.e., the *Drilaster*-genus-complex. These five genera form a monophyletic group in both of my analyses, and the type genus of Ototretinae is included in the clade. Accordingly, Ototretinae have a better standing in both classification and nomenclature in relation to Ototretadrilinae in Option 1. The newly defined Ototretinae become the sister group of the remaining "higher" subfamilies, while the other ototretine genera and *Ototretadrilus* are combined into a paraphyletic

Ototretadrilinae. Similar informal nomenclature and rank should be applied to the latter group as in Option 1. A potential impact is that it dramatically changes the concepts of both subfamilies.

Option 3: Keeping both subfamilies monophyletic and treat intermediate side branches as a paraphyletic group. This solution suffers from both uncertainty in Option 1 and 2, and it needs to create a new concept or name for the intermediate branches. This is the least satisfactory alternative.

Option 4: Using Ototretinae to represent whole group. This is to accept Ototretadrilinae + Ototretinae status quo as a paraphyletic group and assign an informal name to it. The advantage is that it makes minimum change to the current classification except merging the monobasic Ototretadrilinae *sensu* Crowson into Ototretinae. Simultaneously this means a loss of significant phylogenetic information, especially when considering the substantial differences in female morphology such as neotenic *Stenocladius* vs. alate *Drilaster*.

On the evidence of current phylogenetics and taxonomic concern, the second option appears more plausible than the others. The newly defined Ototretinae, with a clear relationship and known females, should be reflected in the phylogenetic classification. However, the uncertainty, especially the unknown females for most of the genera, may increase the risk for such an explicit determination. Before further important evolutionary/phylogenetic information becomes available, I advocate using a compromise solution by calling the *Drilaster*-genus-complex as nuclear (core, typical) Ototretinae while the other branches as “pan ototretine”, “former drilid branches”, etc. The former could be recognized as either a valid name or a concept and subject to future changes to “Ototretinae”, while the latter is not valid in nomenclature but bears considerable phylogenetic/taxonomic meanings by its vernacular name.

Cyphonocerinae

The subfamily was established by Crowson (1972) for the Asiatic *Cyphonocerus* and North American *Pollaclasis*. The monophyly and generic composition of Cyphonocerinae are supported by the present phylogeny.

The taxonomic relationship of Cyphonocerinae and Psilocladinae needs to be addressed. Nakane (1991) transferred *Psilocladus* from Amydetinae *sensu* McDermott to Cyphonocerinae based on their similar body form and antennal morphology. Suzuki’s (1997) molecular tree showed a sister-group relationship between Cyphonocerinae and Lampyrinae for some selected Japanese species. Jeng et al. (1998) further advocated using Psilocladinae instead of Cyphonocerinae for the subfamily since the former has nomenclatural priority. On the above basis, Lawrence et al. (1999) synonymized Psilocladinae (and Cyphonocerinae) with Lampyrinae due to absence of unambiguous diagnostic characters of the former from the latter. These arguments were falsified by the present phylogeny. Using limited taxon sampling from Lampyridae led Jeng et al. (1998) to give a misinterpretation about the nature of their similarities.

The position of Cyphonocerinae was controversial in recent molecular phylogenies, being either closer to Luciolinae and "Ototretinae" (Stanger–Hall et al., 2007, Sagegami–Oba et al. 2007), or to Lampyrinae (Bocakova et al. 2007). From a morphological perspective, especially considering aedeagal morphology, the former is more reasonable. The aedeagal sheath and male genitalia of *Cyphonocerus* and *Pollaclasis* are always bilaterally symmetric, with a slender median lobe, apically-bifurcate parameres in most species, and a short basal piece (Jeng et al. 1998, 1999b, 2006b). The symmetry of the aedeagal sheath and genitalia is ancestral in relation to the asymmetric forms, which is dominant in

Lampyrinae, Psilocladinae, Amydetinae, Photurinae, and Luciolinae. A more basal position of Cyphonocerinae relative to the other subfamilies gives a better interpretation of this evolution.

Known females from the subfamily are similar to their corresponding males but with less developed antennae (Jeng et al. 1998, 2006b). A pair of photogenic organs on the subterminal abdominal segment is either clear or obscure among species. The first instar larvae of *Cyphonocerus ruficollis* Kiesenwetter was reported by Ohba (1976) and the mature larvae of two Japanese species were mentioned by Ohba (2004a). The black, hard sclerotized larvae live in the forest floor and hunt for snails as prey. A pair of photogenic organs is located in the lateral sides of the 8th abdominal segment. Unfortunately, no detailed description of the larvae has been published.

Luciolinae

Luciolinae were usually regarded as one of the few good subfamilies in Lampyridae due to its distinctive abdominal segmentation. Males of the subfamily exclusively have six ventrites while females have seven. Photogenic organs are usually well developed in males, located on sternites VI and VII, and also on V in some species groups. Females have their lanterns mostly on S–VIII. However, the delimitation of Luciolinae becomes disputable when *Pristolycus* Gorham is taken into consideration. *Pristolycus* was established as a lycid genus probably owing to its brightly pinkish coloration, well developed costae, long and serrate antennae, etc., but Gorham expressed his hesitation about this placement. Winker (1952) raised the tribe Pristolycini for the genus but this name has been rarely cited since. Olivier (1911) correctly placed the genus in Lampyridae, but this classification was not widely adopted until McDermott (1964, 1966). The genus has been assigned to Lucidotinae/Lucidotina by Olivier and McDermott, or implicitly to Lampyrinae by Crowson (1972) and followed by subsequent authors (Ohba et al. 1983, Nakane 1991, Lawrence et al. 1995, 1999, Lai et al. 1998, Kawashima et al. 2003). Suzuki (1997) was the first to notice that the placement was doubtful. *Pristolycus* was found within Luciolinae in his molecular phylogeny. Branham and Wenzel's (2001, 2003) morphological tree did not support the relationship. Jeng et al. (2002) discussed the *Pristolycus*–Luciolinae morphology and verified that these two taxa were the very few lampyrids with that unique abdominal segmentation. Jeng et al., however, did not make taxonomic changes owing to limited taxon sampling. Lately, Stanger–Hall et al.'s (2007) molecular trees showed support for the *Pristolycus*–Luciolinae relationship once again, though not with a high posterior probability in their Bayesian analysis. In my analysis, an undescribed genus/species resembling *Pristolycus* but with two pairs of photogenic organs, was grouped with the latter into a clade sister to Luciolinae. I also discovered that the six-ventrite males, with exposed sternite II–VII, only exist in these lampyrid taxa and the rhagophthalmid *Dioptoma adamsi* among material examined. This is an excellent synapomorphy of Luciolinae, as suggested by Ballantyne and Lambkin (2000). Further, the modification of the aedeagal sheath of *Pristolycus* and the undescribed genus/species (state 1 of Character 339, state 0 of 341, state 1 of 342) could be found in some Luciolinae but not in the other lampyrid subfamilies. Accordingly, I agree with their close relationship and put the two genera into Luciolinae. I do not think preserving the name Pristolycini or raising it to subfamily necessary, but using informal "pristolycine lineage" or other similar expressions for purpose of convenience is acceptable, especially when considering the great diversity of Luciolinae. The new genus will be described in a separate paper (Jeng et al. in prep.).

As for Luciolinae, they are the only lampyrid subfamily with individual phylogenetic studies. Ballantyne and her colleagues made substantial contributions to this in the last decade (Ballantyne and Lambkin 2000, 2001, 2006). In McDermott's (1966) classification, Luciolinae were further split into three tribes: Luciolini, Curtosini, and Ototretini. Ballantyne and Lambkin (2000, 2001, 2006) demonstrated that there existed more lineages such as the *Atyphella* lineage, *Pteroptyx–Colophotia–Pyrophanes* lineage (including several oriental *Luciola* species), *Luciola s. str.* lineage, and "Curtosini" lineage which is ambiguous in phylogenetic position. My phylogeny basically supports Ballantyne and Lambkin's tree in several lineages, though not exactly in the same composition or position. A further phylogenetic analysis based on a broader spectrum of taxa as well as characters from both sexes and larvae are being prepared by Ballantyne and Lambkin (Ballantyne, personal communication). It is expected to reveal more lineages and different patterns, and could provide even better resolution of Luciolinae in correspondence to its diversity. However, the extensive heterogeneity of *Luciola* and elaborated abdominal modifications shaped by sexual selection in several lineages may cause problems to the reconstruction of a reasonable phylogeny. Unless a comprehensive phylogeny could be done at the whole-genus (*Luciola*) scale by including representatives of all possible lineages worldwide, nomenclatural changes in the family-group classification would be risky. As expected, there would be always some pectinate, side-branched taxa left outside the major clades in a highly diverse group. Using informal names, like XX lineage, XX species group, XX genus group rather than preserving a tribe/subtribe classification appears a reasonable solution.

About the generic validity, *Luciola* demonstrated to be para- or polyphyletic taxon as suggested by Ballantyne and Lambkin's studies. *Luciola s. str.* is based on an European species, but several Asiatic species do share great similarity in general morphology and male genitalia (such as *L. kagiana* Matsumura, *L. satoi* Jeng et Yang, *Hotaria parvulus* Kiesenwetter). The other *Luciola* species are scattered across the Luciolinae, showing affinity with different subgroups. Regarding the other genera, the validity of *Atyphella* and *Pygoluciola* is implicitly supported by my tree, at least they are independent from *Luciola s. str.* as McDermott suggested. The position of *Hotaria* and *Lampyroidea* is similar but not identical in the two analyses, thereby making it hard to determine the validity of *Hotaria*.

Known females of Luciolinae are either fully alate (for most lineages), or with reduced hind wings (in *Luciola s. str.* and *Hotaria*), or of a physogastrous, elytra-reduced type (e.g., *Lampyroidea*, some *Atyphella* and *Luciola*), but the elytra always appear. The larvae exhibit great diversity in morphology (see Ballantyne and Lambkin 2000, Chen 2003) and ecology. Several species have truly aquatic larvae with gills, while the others have apneustic larvae exchanging air from the water surface (Annandale 1900, 1906, Blair 1927, Okada 1928, Bertrand 1965, 1972, Chang 1995, Ho 1997b, 1998, Jeng et al. 2003, Fu et al. 2005, Fu and Ballantyne 2006, Thancharoen et al. 2007). Facultatively aquatic larvae were reported in *Pristolycus* and some *Pygoluciola* species (Ohba and Goto 1991, Chen 2003, Fu and Ballantyne, 2008). *Atyphella aphrogeneia* (Ballantyne and Buck) is a surf species living on coral reefs in Papua New Guinea (Ballantyne and Buck 1979).

Based on the figure of pectinate antennae in the original description, the fossil species *Luciola extincta* Heyden is not likely a *Luciola*, and its attribution to Lampyridae is suspicious.

Psilocladinae

This taxon was established as a subtribe of Amydetini by McDermott (1964) to include *Psilocladus*, *Ethra*, *Scissicauda*, *Pollaclasis*, and *Photoctus*. From a perspective of general morphology, it seems that McDermott placed those genera with slender, hairy antennal branches, either uni- or biramous, in the subtribe. The present phylogeny does not support the composition with the exception of *Photoctus* which was not included in the analysis. Instead, *Psilocladus* becomes the sole member of the subfamily. Its biramous antennae with slender and hairy branches (Characters 8–15, especially 9) are unique to the other related lampyrid groups, and therefore a set of good synapomorphies. However, the validity of Psilocladinae as a monotypic subfamily is arguable. The taxon is tied with the other groups in a polytomy in the comprehensive phylogeny but sister to Lampyrinae in the type-species-only phylogeny. Consequently it is a conservative treatment to keep Psilocladinae from Lampyrinae as an independent subfamily at the present. It would be rational to integrate both groups into one subfamily than to keep them separate as two extraordinarily asymmetric subfamilies if future analysis supports their monophyly with more evidence.

The mismatch of Psilocladinae and Cyphonocerinae was already clarified in the section of Cyphonocerinae. Morphologically I agree with Lawrence et al. (1999)

that the differences between Psilocladinae and Lampyrinae are few, except the hairy bipectinate antennae of the former. The asymmetry of aedeagal sheath and basal piece of *Psilocladus* suggests affinity to some groups of Lampyrinae. A small, transverse photogenic organ is located centrally in sternite VI in males when present (state 3 of Character 309). This is similar to some lampyrid genera but different from those of *Cyphonocerus* whose lanterns are in the lateral sides of S8.

Females of *Psilocladus* are of the typical adult type, with less-developed branched antennae. A fossil female of *Psilocladus* from Colombian copal once surfaced in an auction in recent years.

Cheguevarinae [=Megalophthalminae, unavailable name]

Olivier (1907) created Megalophthalminae for *Megalophthalmus* Gray and *Harmatelia*, but the subfamily was later abandoned by McDermott (1964) who replaced *Megalophthalmus* with *Magnoculus* McDermott due to homonymy, and moved the genus to Amydetini. The comprehensive phylogeny did not explicitly support or reject the relationship proposed by McDermott because of a polytomy. On the other hand, *Cheguevaria* Kazantsev was clustered with *Magnoculus* in both the comprehensive and type-species phylogenies.

Kazantsev (2006) raised the tribe Cheguevarini for *Cheguevaria* from the Caribbean. He placed the tribe as *incertae sedis* in Lampyridae because of its peculiar morphology, particully the phengodid-like head. The head is prognathous, with a long ventral closure (state 3 of Character 32), a gular suture (state 5 of Character 59), a pair of large mandibles which are bent inward and downward (state 3 of Character 72), small and laterally protruding compound eyes (state 1 of Character 19), a long postgena (state 5 of Character 28), a wide open mouthpart cavity (state 1 & 2 of Character 53), a small labium, etc. The other rarely seen characters of the genus are well-developed elytral humeral costae (state 1, Character 202), and very narrow and short elytral epipleuron (state 3 of Characters 173, 0 of 174). Among the lampyrid genera we examined, only some *Magnoculus* species share most of these peculiar, derived traits, especially the phengodid-like head. However, these two genera are radically different in antennal morphology in that *Magnoculus* has fan-like antennae with long and compressed branches and short flagellomeres, while *Cheguevaria* has a more or less serrate form. In addition, *Magnoculus* usually has a pair of pronotal tubercles and elongate elliptical elytra whereas *Cheguevaria* has a flat pronotal disc and somewhat narrow elytra tapering toward the apex. The aedeagal sheath of *Cheguevaria* is not exactly symmetric as described by Kazantsev (2006). Rather, its tergite has a better connection to one side with the sternite than the other side, resulting in a weakly asymmetrical sternite as seen in many lampyrids but not the basal subfamilies and Luciolinae. The aedeagal sheath of *Magnoculus* is similar with that of *Cheguevaria* but has a clearly asymmetrical sternite. The similarities of these genera with Phengodidae in the head are hard to explain as purely convergent due to adaptation because it is a suite of attributes rather than individual characters. The Lampyridae, Phengodidae, and several other families may share some basic gene genetic blueprint in this regard but express it in various ontogenetic manners under different regulatory mechanisms.

Because of the junior homonymy of the lampyrid *Megalophthalmus* to a crustacean taxon, the name Megalophthalminae must be replaced with the next available synonym (Article 39, ICZN 1999, 4th edition). Therefore the name Megalophthalminae is replaced with Cheguevarinae for *Magnoculus* and *Cheguevaria*. The subfamily can be readily defined by those phengodid-like characters.

Amydetinae

Olivier (1907) established this monotypic taxon based on *Amydetes*. The subfamily was expanded by McDermott (1964, 1966) to include several additional genera with fan-like or pectinate antennae. McDermott further differentiated Amydetinae into Psilocladini and Vestini in addition to the nominotypical tribe. The former two are revealed as separate lineages outside Amydetinae, and Amydetini reverted to its monotypic composition in my study.

The asymmetry of the aedeagal sheath of *Amydetes* implies a “higher” position in Lampyridae, but its exact affinity is not clearly revealed in my trees. The subfamily is roughly located among Photurinae, Psilocladinae, and Lampyrinae. The genus as well as the subfamily is characterized by its fan-like antennae possessing over 30 flagellar articles (state 3 of Character 5). This peculiar, derived feature together with the associated traits (states 8 of Characters 6–7, 6 of 14) are a set of unambiguous synapomorphies of the subfamily. In addition, the genus shows simultaneous possession of well-developed antennae and large lanterns which occupy the whole sternites VI–VII in males. This combination is unique to the subfamily. Their compound eyes are generally larger than those of diurnal fireflies but not as large as in typical nocturnal groups. The males probably exploit chemical and light signals simultaneously or alternatively for locating mates. Continuous glowing by flying males in the night in a tropical forest was reported by Viviani (2001) and indicated a nocturnal habit. Unfortunately, nothing about their females is known.

Photurinae

Photurinae are another "good' lampyrid subfamily in addition to Luciolinae as suggested by Branham and Wenzel (2001). This is supported by the present phylogenies as well. However, the morphological diversity is higher than McDermott (1964) described.

Three generic taxa in Photurinae need more attention. Pic (1914, 1926, 1927a) raised the genera *Photurocantharis* and *Daiphoturis*, and the subgenus *Cephalophoturis* of *Photuris* Laporte de Castelnau from South America, respectively. McDermott (1964, 1966) listed the latter two as subgenera of *Photuris*, whereas Crowson (1972) transferred *Photurocantharis* from Cantharidae to Photurinae. I examined several representative specimens of the three genera and found great similarities among them. All shared a similar orange-black pattern of coloration, thicker antennae, and well-developed lanterns in available male specimens. Only female material was available for *Cephalophoturis excavaticeps* Pic and therefore the species was not included in my analysis. Its males are likely similar to the females, analogous to the other genera. The females of the three generic taxa each have a central spot of lanterns on sternite VI or VI–VII.

The subordinate relationship of *Daiphoturis* (and likely *Cephalophoturis*) to *Photuris* is not supported by my analyses. Rather, the two orange-black colored generic taxa are tangled with *Pyrogaster* Motschulsky. From the perspective of female morphology, this appears reasonable because they share central, dot-like lanterns but not large, piece-like lanterns as in *Photuris* or *Bicellonychnia*. In addition, the *Photuris* male has a pair of slender, tentacle-like appendages arising from the basal piece of the male genitalia (state 1 of Character 366, see also McDermott 1962), whereas the other photurine genera do not share this feature. The problem is that *Pyrogaster* itself is considerably heterogeneous. Some of the species have well developed lanterns in males like most photurine genera (e.g., *P. lunifer* Eschesch., and *P. mediofasciatus* Pic), while others have a much reduced form, with small central dots in sternite VI–VII (state 4 of Characters 309 and 312, in *P. coxalis* Olivier and *P. malepictus* Olivier), as seen in the females mentioned above. Unfortunately, I was not able to obtain available specimens of the type species, *P. grylloides* Motschulsky. According to the original description (Motschulsky 1853), the males have well-developed photogenic organs, a more oval body shape, and longer antennomere 3 than 2 in comparison with *Photuris*. The species with a lantern-reduced form are probably the less typical. Whether to combine them altogether into the newly defined genus *Pyrogaster*, or differentiate *Pyrogaster* into several genera, needs a thorough revision.

Species of Photurinae share a characteristic shape of the labrum which is quite large and has a small projection centroapically [state 6 of Character 69, see also Figure 3 of Crowson (1972)]. This is a rarely derived trait in Lampyridae. Some of the photurine genera have uniquely modified claws (states 1–3 of Characters 247 and 275), as shown in Lloyd (2002, Figs. 10, 12) but this is not shared by the whole subfamily.

Lampyrinae

This is the largest lampyrid subfamily including more than 50 documented genera in existing classifications (Green 1948, 1959, McDermott 1964, 1966, Crowson 1972). My tree supports previous studies but with different delimitation for the subfamily in which most of the amydetine genera are now included in the Lampyrinae.

In comparison with the comprehensive vs. type-species trees, their branching patterns are largely congruent but also show considerable detailed variation, especially for the "higher" groups. They present mainly as a pectinate configuration in the type-species tree but are clustered into several monophyletic groups in the comprehensive phylogeny. Most of the previously recognized tribes/subtribes such as Photinini, Pleotomini, Lucidotina, etc. do not match their original definition and consequently yield paraphyly for themselves or the others. Considering the difference between the two analyses and lacking a plausible way to reasonably subdivide the subfamily without making extensive nomenclatural changes, we advocate abandoning Green/McDermott's classification of tribes/subtribes. Informal names could be applied to some major lineages for purpose of convenience.

McDermott's tribes Vestini and Psilocladini are largely corresponding to the basal lineages of Lampyrinae. The genus *Vesta*, composed of eastern and western species, are not monophyletic as Jeng et al. (2007b) indicated, though the disjunctive distributions are not a radical diagnostic feature. *Lucidota bella* Gorham, a pecies similar to *Vesta thoracica* (G.A. Olivier) but with serrate instead of pectinate antennae, is grouped into the *Vesta* clade. This agreed with Jeng et al.'s (2007b) observation that pectinate antennae are shared by most but not all of the *Vesta* species. Males of the genus exclusively possess a pair of slender appendages arising from subapex of the parameres of the aedeagi (state 1 of Character 381). This character transformed into more robust struts in those of *Dilychnia* and *Callopisma*. However, the latter two genera seem to be heterogeneous in my observation and a further examination is needed.

Rufolychnia, *Erythrolychnia*, and an undescribed genus were shown as a clade in my trees. The former two were sorted as Lucidotina (or -inae)/Photinini by various authors (Leng and Mutchler 1922, McDermott 1964, 1966, Kazantsev 2006). These placement were not supported by the present analyses. Actually, the concept of Lucidotina is fairly vague and I will discuss it later. The genera *Rufolychnia* and *Erythrolychnia* produce light, whereas the lanterns in the undescribed genera are reduced or absent. All of them are recorded from the Caribbean. Description of the new genus will be done in a separate article.

The members of the *Cladodes–Dodacles–Dryptelytra–Ledocas* lineage (or, *Cladodes*-genus-group) share a similar morphology among each other. The genus *Cladodes* is not monophyletic because *Cladodes ater* (Solier) fell outside the genus in my comprehensive tree. As for the status of *Fenestracladodes*, it could be either a subgenus of *Cladodes* or a potentially valid genus for *Fenestracladodes malleri*, *Cladodes imperfectus*, and some related species. Though clustered together, *Fenestracladodes* has considerable differences from typical *Cladodes*. Females of *C. ater* and a *Ledocas* species had been reported as larviform but their generic/specific identification are not authenticated (Barber 1923, McDermott 1964, Cicero 1988).

McDermott's Lucidotina and Photinina are paraphyletic in my trees. *Lucidota* is the largest genus within Lucidotina, with some 160 species listed by McDermott (1966). Yet the genus is paraphyletic in my analyses. It appears that many of the species were placed in this genus based on the compressed or pectinate antennae, the absence or poorly-developed lanterns, and a similar body shape. For example, *Lucidota atra* (G.A. Olivier), a very common species from North America, is distant from typical *Lucidota* from the Neotropical Region but closely allied to Oriental

Lucidina. They share a similar general and detailed morphology of aedeagus, e.g., dorsal position of the parameres and a pair of sword appendage along the median lobe (state 1 of Character 372, state 1 of Character 407). The larvae of *L. atra* and *Lucidina* fairly resemble to each other as well, and are known living in decaying logs, a uncommon habitat for in Lampyridae (Branham and Archangelsky 2000, Lloyd 2002, Kaswashima and Takai 2004). Olivier (1911) noticed the difference of *L. atra* from typical *Lucidota* and thence established *Rileya* for the species, but *Rileya* was later rendered as a synonym of *Lucidota* by McDermott (1966), followed by Arnett (1968). It is likely that the North American *Lucidota* species are actually the Nearctic representatives of *Lucidina.* About the *Lucidina–Mimophotinus–Phosphaenus* lineage, their pectinate branching pattern in the comprehensive tree is not recovered in the type-species tree. Accordingly I do not make taxonomic changes herein until a lower-level phylogeny is built. In a more local level, my comprehensive tree suggests a synonymous relationship for *Lucidina* and *Lucidotopsis*, as indicated by Jeng et al. (2007a). The latter genus was established based on McDermott's believing of geological separation (for three Asiatic *Lucidota* species) rather than by specimen examination (see McDermott

1960).

The position of *Dadophora*, the only member of Dadophorina (-inae), is not inconsistent between the comprehensive and type-species trees. From a morphological aspect, the genus is not distinctive enough as a higher taxon from the other genera of “Lucidotina” or “Photinini”. None of its characters are uniquely derived in relation to the others.

There is a monophyletic group approximately corresponding to “Photinini” in both of the comprehensive and type-species trees. The included genera are *Pyropyga*, *Ellychnia*, *Photinus*, *Robopus*, *Macrolampis*, *Pyractomena*, and *Pyractonema*. *Pseudolychnuris* is likely also belonged to this group but not explicitly supported by the comprehensive tree. Some rarely derived characters, such as deeply-divided tergite 9 of the aedeagal sheath (state 1 of Character 349), and basal appendages of the median lobe (states 1–2, Character 408), occur only in this lineage but none of the characters supporting this clade share by all the included genera. It should be noticed that *Photinus*, the second largest genus of Lampyridae, is not a natural group as inferred by McDermott (1964).

Another monophyletic group appearing in my comprehensive phylogeny includes the members from “Cratomorphini” and “Lamprocerini”. However, the monophyly was not recovered in the type-species tree. Instead, those genera became a pectinate configuration together with the nuclear Lampyrinae (or Lampyrini *s.str.*) + *Calyptocephalus–Phaenolis–Roleta* group. The modified mandibles *sensu* Green (states 4–5, 7–8 of Character 72) occur only in this large group. They are either with reduced or very slender incisor to different extents, but the modifications are not shared by all genera. Another derived character uniquely evolved in this clade is the ventral location of the abdominal spiracles (states 2–3 of Character 332). The spiracles are either at the lateral edge of the ventrites, or slightly distant from the edge. The ventral spiracles are found in the members of “Lamprocerini”, *Calyptocephalus*-genus-complex, and “Lampyrini” but not “Cratomorphini” *sensu* McDermott (1966).

The *Calyptocephalus* and three allied genera, *Phaenolis*, *Ophoelis*, and *Roleta*, form a clade. These genera were placed in Pleotomini by Green (1959) and McDermott (1964, 1966) mainly by their bipectinate antennae, but this unnatural classification based on convergence has been indicated by Jeng et al. (2006a). A rarely seen character in Lampyridae, the elongate, bifurcate and bent-down abdominal apex (state 5 of Character 305), is found to be a good synapomorphic character to this group by DELTRAN optimization. The females of this lineage are unknown, though a larviform female has been doubtfully associated with *Phaenolis abdita* Olivier based on the pronotal coloration (Barber 1923). The genus *Petalacmis*, with a peculiar antennal morphology (8-articled flagellum, with highly compact basal articles and a large lobe apically), was classified in Lampyrini by Green (1959) and McDermott (1964, 1966). Its position is ambiguous in our analyses, either sister to the *Calyptocephalus*-genus-complex in the comprehensive phylogeny, or next to the typical Lampyrinae in the type-species tree. Accordingly, we do not regard it as a member of the typical Lampyrinae which includes *Lampyris* related genera.

The typical Lampyrinae largely agree with McDermott's Lampyrini except the inclusion of *Phausis–Lamprohiza–Lamprigera* (PLL) lineage and *Petalacmis*. Its traditional members include *Lampyris*, *Lampronetes*, and *Nyctophila* (Europe major, Asiatic and Ethiopian minor), Oriental and Palearctic *Pyrocoelia* and *Diaphanes* (Ethiopian minor), Nearctic *Pleotomus*, *Pleotomodes*, *Microphotus*, and *Paraphausis*, and *Afrodiaphanes* Geisthardt (2007) from Ethiopian region.

Another two American genera, *Nelsophotus* and *Prolutacea* described by Cicero (2007), are likely belonged to this group as well.

In comparison with the other lampyrine groups, the members of the typical Lampyrinae have been well studied, especially the Holarctic faunas. The genera *Lampyris*, *Nyctophila*, *Microphotus*, *Lamprohiza*, *Phausis*, *Pleotomus*, *Pleotomodes* and *Paraphausis* have been thoroughly reviewed or revised in the recent 50 years (Green 1959, Fender 1966, Geisthardt 1974, 1982, 1983, 1985, 1986, 1987, 1990, Zaragoza–Caballero 1992, Cicero, 2006). Ethiopian and oriental genera received increasing attention in recent years but their studies were mainly restricted to local level (Jeng 1999a, 2000, 2001, Geisthardt 2007). According to McDermott (1966), *Diaphanes* has over 90 species from Asia and Africa, and is the fourth diverse genus of Lampyridae. I examined several central African *Diaphanes* species and found that they show similar morphologies to that of *D. schotedeni*. It is likely that Ethiopian *Diaphanes* are misplaced in the current genus, as indicated by the position of *D. schotedeni* in my tree. I also noticed that the reduced number of the antennomeres, the diagnostic character of *Afrodiaphanes* proposed by Geisthardt (2007), may be instable in generic level. On the other hand, the Oriental

Diaphanes species are fairly heterogeneous in morphology (Jeng et al. 2001). Their monophyly is supported by my study but not others (e.g., Li et al. 2006, Stanger–Hall et al. 2007). A thorough revision and comprehensive phylogenetics are critical to the classification of *Diaphanes*.

The typical lampyrine genera, except *Lamprigera*, share a similar pronotal convexity which is somewhat like a shape of light bulb (states 3–4, Character 119). Other characters shared by all but the PLL lineage include the reduced mandibles (state 5 of Character 72), the ventral spiracles (states 2–3 of Character 332), the highly asymmetrical aedeagal sternite (states 0 and 1 from Characters 343), etc. Apparently PLL is a heterogeneous portion within a fairly homogeneous "Lampyrini". Recent molecular approaches suggest different phylogenetic locations for the PLL genera, mainly in the basal positions of Lampyrinae (Li et al. 2006, Stanger–Hall et al. 2007). Regardless, inclusion of PLL in Lampyrinae is concordant with both my morphological studies and other molecular approaches. We tentatively keep the PLL group in the typical Lampyrinae in the present classification. Further analyses with new evidence would be required to solve the incongruence.

Ecologically the typical Lampyrinae show diverse features. For example, *Pleotomode*s species lives in ant nest (Sivinski et al. 1998); occurrence of adults in late autumn to winter (or dry season in tropical area) appear in some genera such as *Pyrocoelia*, *Diaphanes*, and *Lamprigera* (Chen 2003); coexistence of diurnal and nocturnal species within a genus like *Pyrocoelia* (Jeng et al. 1999c, Chen 2003, Ohba 2004a, b). Unlike those flashing genera in Lampyrinae (*Photinus*, *Macrolampis*, *Pyractomena*, and *Aspisoma*), the genera of the typical Lampyrinae do not produce flash light signals (Lloyd 1966, 2002, Viviani 2001). Females of the typical Lampyrinae are neotenic where known, so are the PLL lineage (Cicero 1988, Jeng et al. 1999c, 2000, 2001, Jeng and Yang 2003).

Conclusion

In summary, a phylogenetic classification of Lampyridae is established based on the maximum congruence from the comprehensive and type-based phylogenetic analyses. Eight out of the nine groups recognized are monophyletic and treated as subfamilies in zoological nomenclatural standing. For the paraphyletic "Ototretadrilinae–Ototretinae" complex I suggest using informal names such as "former drilid complex" or "pan-ototretines" for the side branches, and nuclear (typical) Ototretinae for the monophyletic *Drilaster*-genus-complex. The two groups together could be termed “so-called” Ototretinae or “Ototretinae s. lato” to reflect its heterogeneous, non-monophyletic nature. The concept and classification of this combined group are waiting for future improvement, especially once data from female morphology are discovered.

Several subfamilies are modified in taxonomic composition. *Pristolycus* and an undescribed genus are incorporated into Luciolinae; Megalophthalminae are replaced with Cheguevarinae due to junior homonymy of the type genus; Amydetinae and Psilocladinae become monobasic subfamilies; the majority of the former amydetine genera are transferred to Lampyrinae. The other subfamilies (Pterotinae and Photurinae) remain unchanged from Crowson’s (1972) classification. Green and McDermott’s tribe/subtribe classification does not have good standing in the preset phylogeny and are suspending it except for informal convenience to refer to some subordinate groups within a highly diverse lineage.

The analyses provide the most comprehensive account on the generic composition for each subfamily of Lampyridae. One of the most important values of the study is that it offers a fundamental and dense enough phylogenetic framework for Lampyridae so that future analyses at local levels could be conducted in a reasonable manner and need not rely purely on the previous, traditional classification. For example, determining the position of a new genus becomes easier by including potentially allied genera and suitable out groups into an analysis. The comprehensive phylogeny also reveals the unnatural classification of several genera and identifies some questionable lineages. Incongruence between the comprehensive and type-based phylogenies needs to be resolved by additional morphological and/or molecular approaches. Future studies on the systematics of Lampyridae can be guided and improved on this new basis.

Key to the subfamilies of Lampyridae based on male characters

1. Abdominal spiracles not enclosed by back folded sternites 2

– Abdominal spiracles enclosed by back folded sternites 3

2. Ventral closure of head long, slightly shorter than dorsum; occipital foramen nearly orthogonal to head axis .... Pterotinae

– Ventral closure of head shorter than dorsal one; occipital foramen more or less oblique to head axis ....

.... pan-ototretines (part, including “Ototretadrilinae” and *Harmatelia*)

3. Abdomen with six ventrites .... Luciolinae

– Abdominal with more than six ventrites 4

4. Antennae with more than 30 articles .... Amydetinae

– Antennae with 14 articles at most 5

5. Head with long ventral closure; occipital foramen orthogonal to head axis; compound eyes small to moderate in size; subgena widely exposed and gula present as suture .... Cheguevarinae

– Head with shorter ventral closure; occipital foramen somewhat oblique relative to head axis; gula either short, broad or elongate; compound eyes large and subgena barely exposed if gula present as suture 6

6. Antennae symmetrically bipectinate, with branches either slender or somewhat thick and cylindrical, but never lobed 7

– Antennae varied; branches lobed if bipectinate 8

7. Aedeagal sheath bilaterally symmetric; antennal branches thick and short, about as long as flagellar article, with short pubescence .... Cyphonocerinae

– Aedeagal sheath bilaterally asymmetric; antennal branches slender and hairy, clearly longer than flagellar article .... Psilocladinae

8. Head partially exposed from pronotum; pronotum without clear lateral expansion 9

– Head barely or totally covered by pronotum; pronotum with clear lateral expansion 10

9. Tibial spurs usually absent, palps of mouthparts extraordinary large and lobed if tibial spurs present .... pan ototretine (part)

– Tibial spurs present; palps of mouthparts never larger than antennae ....typical Ototretinae

10. Labrum large, with a centroapical projection; claws of males bifurcate apically on one side or both sides in some genera; abdominal spiracles always in dorsal position; mandibles robust and curved; never with pronotal aerolet above compound eyes; abdominal segments never lobed .... Photurinae

– Labrum varied, but never with centroapical projection; claws not bifurcate apically; abdominal spiracles either positioned dorsally, or at ventrolateral edges or slightly distant from lateral edge ventrally; mandibles modified in some genera, either becoming abbreviated or extraordinarily slender in apical half; pronotal aerolets present in some genera; abdominal segments lobed in some genera .... Lampyrinae

Chapter VI. Evolution of Neoteny in Lampyridae and Elateroidea

Introduction

Coleoptera (beetles) is presently known as the most diverse order of organisms, composed of more than 130 families and over 300,000 species (Lawrence and Britton 1991, 1994). Thanks to their long history and myriad adaptations related to a cryptic lifestyle, beetles are thriving and successful in most extant terrestrial and freshwater ecosystems (Grimaldi and Engel 2005). This diversity has brought forth a remarkable array of morphological and ecological features. Among these are the intricate bioluminescent behaviors for sexual interaction and the "larviform" females of many species in the Elateroidea, especially within the cantharoid (former Cantharoidea) subgroup. Superficially these two traits appear unrelated or even in conflict with each other (explicit vs. cryptic lifestyles). Yet there may exist a virtual connection most exist between them (Crowson 1972, see discussion).

In insects, "larviform" is often used as a general descriptive term for holometabolous adults which have a larval appearance: worm-like, juicy, soft, slow-moving, and flightless. In a more narrow sense, it denotes the persistence of larval traits into the adult stage, or neoteny in terms of evolutionary ontogeny

(Grimaldi and Engel 2005). Neoteny is credited for playing a pivotal role in amphibian evolution (Gould 1977, Rosenkilde and Ussig 1996, Wakahara 1996, Hanken 1999). However, this term has been given more restrictive meanings across an unwieldy spectrum of traits by various authors for their own emphases, and this has led to considerable confusion in the literature (Healy 1970, Eagleson 1976, Gould 1977, Norris et al. 1977, Alberch et al. 1979, Pierce and Smith 1979, Reilly et al. 1997, Hanken 1999, Mabee 2000, Hemming 2003, Wiens et al. 2005). The confusion has generally stemmed from a dispute as to whether to recognize neoteny as an evolutionary process or pattern, and by its ambiguous application at phylogenetic vs. tokogenetic levels (Reilly et al. 1997, Hanken 1999, Hart and Wray 1999). Reilly et al. (1997) endorsed preservation of the traditional and more general definition of neoteny, and advocated an alternative terminology for heterochrony. These authors differentiate heterochronic process and pattern in different levels with distinct terminology. For example, paedomorphosis is specified as one of the three heterochronic patterns in a phylogenetic framework (neoteny fixed in species), with hypomorphosis (= terminal deletion, truncated in developmental trajectory), deceleration (retardation in development), and post-displacement (delay in ontogenetic beginning) representing the underlying mechanisms resulting in paedomorphosis. Paedogenesis is designated as intraspecific neoteny, a facultative, usually environment-induced polyphenism within a population or among metapopulations (Reilly et al. 1997). Herein I follow Reilly's definition of paedomorphosis, i.e., a synonym of neoteny in its traditional meaning. As an evolutionary pattern, a phylogenetic approach is critical to the understanding of neoteny (Reilly et al. 1997, Wiens et al. 2005).

Neoteny has been considerably cited as a major evolution process/pattern in some insect groups, especially the termites (Nalepa and Bandi 2000, Costa et al. 2004, Crosland et al. 2005, Grimaldi and Engel 2005, Kindl and Hrdy 2005). However, many of the studies were effectively restricted to documenting an intraspecific pattern (i.e., paedogenesis). At a higher level, it has been suggested that termites are essentially "juvenile roaches", and some termite families may have evolved through the retention of a juvenile roach-like appearance in the adult (Nalepa and Bandi 2000, Grimaldi and Engel 2005). Matsuda (1976) claimed that Grylloblattodea is also an apparently neotenic order. Crowson (1981) summarized the distribution of neoteny in beetles such as Staphylinidae, Cantharoidea, Melyridae, Thylodriinae, Lymexylidae, Rhipidiinae, and Histeridae. Those cases occurring in the cantharoid beetles have received particularly intensive investigation (King 1880, Riley 1887, Wenzel 1896, Gorham 1880–1886, Olivier 1907, Priske and Main 1911, Paiva 1918, Mjöberg 1925, Bruces 1941, Green 1941, 1956, Bess 1956, Fender 1970, Crowson 1972, Buschman 1977, Lloyd 1979, Wing 1984, Cicero 1988, Ohba et al. 1996, Ho 1997a, Kawashima 1997, Silvinski et al. 1998, Chen 1999, 2003, Jeng et al. 1999c, 2000, 2001, De Cock 2000, Ho and Chu 2002, Ohba 2002, Jeng and Yang 2003, Bocakova et al. 2007). Among them are the famous “trilobite larvae” from Borneo, which are actually the female adults of *Duliticola* [= *Platerodrilus*] of Lycidae (Mjöberg 1925, Kazantsev 2002). McDermott (1964) listed 25 out 92 documented genera in Lampyridae known to have flightless/ larviform females. These genera were principally concentrated in Lampyrinae, Amydetinae and Rhagophthalminae, a few in Luciolinae, some uncertain cases in Pterotinae, and were absent in Photurinae. In addition to Lycidae and Lampyridae, the other cantharoid families like Phengodidae, Drilidae, Plastoceridae, and Omalisidae also have flightless females, showing different degrees of paedomorphosis (Geisthardt 1979c, Bocakova et al. 2007).

Crowson (1972) considered the evolution of the flightless females a dilemma to the phylogeny of Cantharoidea. In his inferred phylogeny, those families with flightless females were considered older than other families which have predominantly winged females. Accordingly he favored a single-origin explanation for neoteny in cantharoids. Yet a necessity of this hypothesis was that the taxa with ordinary, adult-looking females must have evolved independently through myriad reversals or "reimaginization" from a larviform common ancestor. He believed this would be quite difficult and unlikely, but not impossible, and hence regarded the question as dilemmatic. On the other hand, he argued against the multi-origin hypothesis, i.e., repeated loss (of adult morphology) or independent "larvalisation" as Dollo's Law may suggest. Crowson adduced the discrepant geographic distributions of the taxa with alate vs. flightless females to support his single-origin explanation. He claimed that some basal lineages of Cantharoidea (e.g. Drilidae, Plastoceridae, and Omalisidae) have a longer geographical age but limited geographic ranges in relation to the lycids and lampyrids with predominantly winged females and a global distribution. Crowson inferred that this was caused by the poor dispersal ability of the flightless females in the former lineages. Lately, several phylogenetic analyses on various cantharoids have been undertaken (Branham and Wenzel 2001, 2003, Bocakova et al. 2007, Sagegami–Oba et al. 2007, Hunt et al. 2008). These phylogenies, ranging from several cantharoid families to the entire Coleoptera, uniformly support multiple origins of neoteny, either explicitly or implicitly. However, the evolution of neoteny in Elateroidea is not just a single or multi-origin question. Ignoring its nature, characteristics, underlying mechanisms, and other related information may give a misleading phylogenetic reconstruction (Wiens et al. 2005). The most fundamental question is why we believe these females are "neotenic". For example, elytra never occur in larvae, regardless of how reduced they are in a flightless female. Without ontogenetic knowledge, phylogeny can provide only a superficial answer regarding the distribution of paedomorphosis, and provides little insight into its evolution. Fortunately, Cicero (1988, 2007) provided a thorough account of the ontogeny of neoteny in cantharoid beetles and on this foundation I was able to develop my study in combination with an extensive morphological examination and phylogenetic analysis.

Cicero's Hypothesis of Gradient Paedomorphosis.

Crowson (1981) noted that the paedomorphic females of cantharoids rarely or never exhibited a uniform "larvalisation" of all characters, but instead a mosaic combination of larval- and male-like traits. Cicero (1988) provided the most comprehensive account on flightless females in cantharoid beetles, including the full spectrum of their morphological character changes. On the basis of his observations on the metamorphosis of a firefly, he believed that the extraordinary sexual dimorphism in some cantharoid beetles was a consequence of the early termination of the female pharate pupal stage relative to males (either by hypomorphosis or deceleration). Figure 10 contrasts the ontogenetic trajectories of an ordinary vs. neotenic species. Different times of termination result in different degrees of "larvalisation", and therefore constitute a gradient distribution of paedomorphosis.

By examination of a broad spectrum of taxa, Cicero (1988) asserted that there did exist such a gradient among flightless females across the cantharoid families. He hierarchically categorized flightless females into levels from one to ten, according to an accumulative set of larval characters. The degree of "larvalisation" increases along with the level number. A higher level has extra larval characters in addition to what its lower level has (an accumulative set). Normal females were categorized as level 0, or “fully imaginal”. The morphological changes show a rough order from most common to rarest: hind wing and elytral reduction first, sometimes accompanied by a physogastrous abdomen, then incomplete pigmentation, followed by modifications of the thoracic and abdominal sclerites, as well as head appendages and legs, and finally presence of larval-structures like a pygopodium and tarsunguli. The hierarchy demonstrates that Phengodidae and phengodid-like *Pterotus* have the highest degree of paedomorphosis, while Lampyridae exhibit variable degrees. Based on his observation and a modified phylogeny of Cantharoidea from that of Crowson, Cicero claimed that extreme paedomorphosis was primitive to cantharoids and a fully imaginal morphology was later regained piece by piece in some groups. He accepted the reversibility of neotenic evolution, i.e., contrary to Dollo’s Law. Meanwhile, he did not rule out the possibility of jumping among levels, rather than a progressive shift through the various levels of larvalisation.

From an ontogenetic prospective, Cicero’s observation on the metamorphosis of a *Photinus* firefly was critical to the understanding of neoteny because he noticed that the major changes occurred in a short period of time in pharate pupae rather than in a regular larval or the pupal stage. Ignorance of this ontogenetic window loses the morphological connection between a larva and an adult, and the application of "neoteny" in this situation would be potentially misleading. It was possible to denote the reduced elytra as a neotenic character when their existence in the pharate pupae was seen as as a sequential change from wingless larvae to winged pupae. Furthermore, it was possible to determine which heterochronic process was involved. Herein I apply such an understanding of neoteny to a broad phylogeny of Lampyridae and related cantharoid families.

Material and Methods

1) Available female specimens and their coding of neotenic elaboration

Among the 220 species used in our comprehensive analysis of Lampyridae and related families, 140 have available female specimens. In addition, I sampled several species that, while not examined, were explicitly accounted for by Cicero (1988) or other sources. In total, 150 females had definable states for comparison and analysis. Appendix 5 summarizes the species I studied and their "neotenic state" as defined by Cicero (1988).

Chapter II addressed the reason why I did not construct and integrate a female matrix into my male matrix. Further, I was interested in the phylogenetic distribution of the different neotenic degrees rather than the evolution of individual paedomorphic characters. Therefore, different types of females were coded as individual states in accordance with Cicero's classification. According to this classification, the following genera were explicitly assigned to the level(s) noted in the parenthesis: *Photinus* (level 1, 2), *Ellychnia* (1), *Pseudolychnuris* (1), *Macrolampis* (1), *Pleotomus* (3), *Pleotomodes* (3), *Lucidota* (3), *Lampyris* (4), *Phausis* (5), *Ledocas* (5), an African genus (probably *Lampyris* or *Afrodiaphanes*, 6), *Microphotus* (7), *Phaenolis* (8), *Pterotus* (9), and *Zarhipis* (Phengodidae, 10).

Cicero's classification was slightly modified owing to new information on the morphology of Lampyridae and Rhagophthalmidae. First, Level 8 was omitted because I did not have species exhibiting the described morphology (see discussion). Second, I found that the index character of level 7, the unifaceted eyes, was not present in some taxa in higher neotenic levels. For example, a large rhagophthalmid female, probably *Menghuoius kusakabei* Kawashima from Myanmar, was found to have tarsunguli [of the highest neotenic level in Cicero (1988)] but clearly multifaceted eyes. The other females of the family such as *Rhagophthalmus* and *Diplocladon* shared very similar morphology (e.g. Ohba et al. 1996, Lau and Meyer–Rochow 2003) except the reduced number of tarsomeres (to 2 segments) in place of tarsunguli. Though a highly reduced number of tarsomeres also appears in level 7, the complete abdominal epipleurites in all segments of Rhagophthalmidae suggests a higher neotenic level (9). Accordingly I combined level 6 and 7 into one category (as level 6), and degraded Cicero's levels 9 and 10 into 7 and 8, respectively. In short, there were nine states in our coding, from fully imaginal (0) to maximally neotenic (8).

2) Phylogenetic distribution of neoteny

My full data set (220X410) of males was used as the master matrix. The coding of females was integrated into it, and then analyzed using the parsimony rachet then heuristic search as described in Chapter 2. The female character was set as either additive or non-additive to compare the results, particularly since Cicero's (1988) gradient hypothesis suggested a directional or accumulative change.

Our reasoning for employing a non-additive coding was to see if, without assuming an ontogenetic order, the topology would be dramatically altered. Ultimately, I address the following questions: first, is the overall pattern of evolution in the tree directional, either gradual loss due to paedomorphosis or gradual reacquisition from paedomorphosis, or a homoplastic pattern; and second, does a directional evolutionary pattern occur in some particular subgroup.

Results

The two approaches found 1008 equally parsimonious trees, respectively. The tress resulting from the additive coding for the neotenic character each had a length of 7734 steps. The strict consensus tree had 19 nodes collapsed and the number of steps increased to 7860 (Figs. 12–14); the branch support is shown in Fig. 11. The data set with non-additive coding produced trees of 7706 steps, with the strict consensus having 7832 steps (Figs. 15–17). The consensus trees obtained from the analyses shared identical topologies except different tree length, and this is true to the trees obtained from the male matrix.

Since different analyses settings did not yield different topologies, the distribution of neotenic females on the tree was exactly the same for the two analyses. Among the outgroups (families aside from Lampyridae), minor and moderate neoteny were spread across Omalisidae and Drilidae, respectively. Highly neotenic females occur in the sister groups of Lampyridae (Phengodidae, Rhagophthalmidae, and perhaps Telegeusidae) as well as the basal lampyrid lineages (Pterotinae and *Stenocladius*). The females of most of the ototretine genera were unknown, but neoteny at least did not appear in the typical Ototretinae (*Drilaster* and another four allied genera). From there, neoteny had originated independently in several lineages, like Luciolinae and *Photinus*-related genera of Lampyrinae, but to much less degrees (1 to 3, except *Macolampis perelegans* (Gorham) as 4). Finally, neoteny extensively evolved again in the clade composed of *Lampyris* and related genera, from moderate (e.g., *Diaphanes*, *Lamprohiza*, *Lampyris*, *Lampronetes*, *Nyctophila*, *Pleotomodes*, *Pleotomus*, and *Pyrocoelia*) to an advanced degree (e.g., *Microphotus*, *Phausis*, *Lamprigera*). Although shown as unknown in many of my taxa, females of particular genera were not totally unknown (explained below).

Because the identical consensus topologies were generated by both analyses, only the optimization of female neotenic states mattered. I used accelerated transformation (ACCTRAN, fast), delayed transformation (DELTRAN, slow), and unambiguous optimizations to compare the changes of neotenic differentiations across the branches in the tree. As a general pattern, additive coding had fewer origins of neoteny in relation to those of non-additive coding, especially in the outgroup families. The former usually placed lower coding in the ancestral branch of a clade with that coding or higher, and reversals to lower coding from higher ancestral coding also occurred frequently (Figs. 12–14). The detailed patterns were considerably different from one another by different optimization criteria. This is discussed below.

In summary, my result revealed non-directional evolution and multiple origins of neoteny in Elateroidea. Yet there were some clades, particularly Lampyrinae (*Lampyris* and allied genera) possessing exclusively neotenic females, such that this trait did perform well at more localized levels

Discussion

1) Neoteny in Elateroidea

Taxonomically, paedomorphosis, of course, is not limited to the taxa we used in the study. Plastoceridae, Cebrioninae of Elateridae, and Duliticolinae of Lycidae are also known to have flightless females (Mulsant and Rey 1863–64, Crowson 1955, Lawrence et al. 1999, Bocakova et al. 2007). The neotenic level of the former two is low, basically just brachelytral forms, while the duliticoline lycids (“trilobite larvae”) are highly paedomorphic (Mjöberg 1925, Crowson 1972, Wong 1996, Miller 2002a). Among the families I used, it is likely that all genera of Phengodidae, Rhagophthalmidae, and Drilidae are neotenic in their females (Crowson 1995, O’Keefe 2002). The females of Telegeusidae were also inferred to be larviform, but no published evidence yet exists for the family. A suspicious genus, *Astraptor* Barber, was inferred to represent telegeusid females by Crowson (1972), but Miller (2002b) indicated that it might be a group of phengodid Mastinocerinae.

Dioptoma adamsi Pascoe of Rhagophthalmidae, *Cladodes ater* Solier and *Vesta cincticollis* Blanchard from Lampyridae have known larviform females (Barber 1923, McDermott 1964), yet I was not able to determine their neotenic level because of a lack of available specimens or further information. According to my tree it is clear that the latter two lampyrid species do not belong to the genera in which they are currently placed. Typical *Vesta* species have winged females, at most weakly physogastrous. Based on my examination of specimens, McDermott's (1964) placement of *cincticollis*, probably also *latastei* Olivier and *melanura* Laporte de Castelnau in *Vesta* was not natural. I did not find any female material of them in several collections, and probably they are all flightless and cryptic ecologically. Among genus-group taxa, flightless females have been documented in the following genera, but either for unknown specific identity or based on species not included in my analysis: *Selasia* of Drilidae; *Phrixothrix* ("railroad worm") of Phengodidae; *Diplocladon* ("star worm") of Rhagophthalmidae; *Cratomorphus*, *Ellychnia*, *Jamphotus, Ledocas*, *Lucidina*, *Lucidota*, *Phaenolis*, and *Pyropyga* of Lampyridae (Barber 1923, 1941, Harvey 1952, McDermott 1959, 1964, Barker 1969, Cicero 1988, Bohórquez 1993, Lloyd 1999, Ohba 2004a, Kawashima and Takai 2004, 2005). Among these genera, *Selasia* likely shares a similar neotenic level with its relatives (Barker 1969), and the same is true for the phengodid and rhagophthalmid genera (Harvey 1952, Ohba 2004a). Cases of minor neoteny (levels 1–2) were reported from *Cratomorphus*, *Ellychnia*, *Lucidina*, and *Lucidota*, though most of their congeneric species have winged females (Cicero 1988, Bohórquez 1993, Kawashima and Takai 2004, 2005). Lloyd (1999) demonstrated that brachypterous females and males exist within and among some populations of *Pyropyga nigricans* Say, especially for riparian dwellers. *Ledocas* has quite elaborate larviform females (level 6) (Cicero 1988), and it is possible that the allied genera, *Cladodes*, *Dryptelytra*, *Dodacles*, share a similar or identical degree of neoteny in their females. *Phaenolis abditus* Olivier is the only species with documented females for the genus, but it is highly suspicious because the identity of the female was inferred by a similar coloration pattern shared with the male (Barber 1923, see also McDermott 1956, Cicero 1988). Since the *Phaenolis* females have never been reported except for this disputable case, it is likely that *Phaenolis* and its allied genera (*Calyptocephalus*, *Ophoelis*, *Roleta*, and probably also *Petalacmis*) have flightless and cryptic females (Jeng et al. 2006a, Cicero 2007). The monotypic genus *Jamphotus* was known from a single physogastrous female (level 1) from Jamaica (Barber 1941, McDermott 1959, 1964). This female likely belongs to some other genus rather than as a separate taxon. The females of *Harmatelia bilinea* Walker were reported to be larviform by Crowson (1972), but this might be his mistaking of

Green’s (1912) figure of *D. adamsi* for the former which is actually not yet known.

The following species/genera, which were excluded from my matrix owing to lack of male material, are confirmed to have ordinary, alate females: *Cephalophoturis* (Photurinae), *Calotrachelum*, and *Oliviereus* (Lampyrinae).

Many adjectives have been used to describe neotenic females, such as larviform, brachypterous, apterous, wingless, brachelytral, anelytrous, physogastrous, etc. As implied by their etymology, these terms were at first dedicated to differentiate different types of neotenic females according to the wing/ elytral/ abdominal morphology and the resemblance between the females and their larvae. Yet these terms lack clear definitions or strict application, and cause confusion in the literature (e.g. McDermott 1964). I advocate developing a suite of standard terminology based on the neotenic levels or their index characteristics to replace or redefine these arbitrary terms.

2) Plausible physiological mechanism of neoteny in Lampyridae

Cicero (1988) suggested that it was a change in metamorphosis rather than accumulative genetic mutations that produced neoteny in Elateroidea. This hypothesis is probably accurate. Naisse (1966a, b) claimed that the European glowworm firefly (larviform female of *Lampyris noctiluca* (L.) could be fully masculized by transplanting male gonads to her in the larval stage. Androgenic hormone was therefore thought to be the factor responsible for the masculization or reimaginization in Naisse’s experiment. Yet, the masculization of females could not be repeated in a recent study, but instead, the sex of the recipient always matched that of its own gonads (Maas and Dern 2005). Maas and Dern concluded that sexing of larvae was not possible and androgenic hormone was not synthesized in the larval testes, and thus irrelevant to the formation of extreme sexual dimorphism. On the other hand, in the endocrine control of metamorphosis, juvenile hormone (JH) may play a critical role in the formation of neoteny (Matsuda 1976, Vogel et al. 1976). It has been demonstrated that changes in JH level during critical periods in development are responsible for the occurrence of dispersal polyphenisms (i.e., wing polymorphism, Harrison 1980, Roff 1986, 1990, Zera and Denno 1997, Chapman 1998, Nijhout 1999, Zera 2004). Matsuda (1976) asserted that wing polymorphism preceded the origins of some apterous taxa. For metamorphosis, a “status quo” model of JH action has been suggested and the hypothesis states that the only function of JH during metamorphosis is to maintain the current state of gene expression (Williams 1961, Riddiford 1972, 1996, Nijhout 1999). This action, making the developmental protocol pause or stop at a given point, perfectly matches the definition of hypomorphosis ("terminal deletion") in the sense of heterochrony if JH is the key factor involved in neoteny (paedomorphosis) (see Reilly et al. 1997). For a typical holometabolous insect, its pupal program is triggered in the final instar larva when ecdysteroids are produced in the absence of JH. JH is present again in the very latest stage of the larva to prevent the premature development of imaginal discs, and then is absent in a pupal stage until emergence (Chapman 1998). In the classic model of endocrine control for wing polymorphism, a reduced titer of ecdysteroids before molting and/or extended effect of JH in some sensitive period were inferred to be the cause of short-winged morphs (Zera 2004). This model predicts also that JH shall have a higher titer in flightless females than the macropterous morph and accordingly lead to early sexual maturation and high fecundity. Recent experimental evidence from crickets (*Gryllus*) was largely consistent with the classical model in the first prediction, whereas the variation of JH titer in different morphs of adults was more complicated than what the model predicted (Zera 2004). In addition, it was found that differences in the hemolymph JH titer between morphs result from differences in JH esterase (JHE) activity (Zera and Huang 1999). In this sense, flightlessness in insects would serve as a putative indicator of paedomorphosis (Matsuda 1976).

Though the endocrine regulation is not clear in lampyrids or cantharoids, it is at least theoretically possible that neotenic adults could be a consequence of mutations in control genes which caused JH production to continue and/or altered the sensitivity periods of particular organs. During metamorphosis, the presence of JH either at any given brief period of time or in low concentration will produce a mosaic morphology (Cymborowski 1992, Nijhout 1999, Konopova and Jindra 2007). The effect results from the augmented sensitivity threshold and time period for particular tissues or organs. Some are “frozen” as status quo by JH while the others keep transforming. This is pretty much close to the morphology we observed in most of the neotenic females in Elateroidea. Usually the neotenic females are hard to link with their larvae or males without ecological or molecular evidence because of their mosaic, and sometimes, unique morphology (e.g., the head of some *Diaphanes* females, Jeng et al. 2001, Jeng and Yang 2003). Maas and Dorn’s (2003) finding of an abnormal female of *L. noctiluca* provided indirect support for the JH hypothesis. The female had a mosaic appearance with a wing and an elytron on the left side but was totally wingless on the right. Also, the number of eggs in the ovaries and the volume of the corpus allatum (CA) differed remarkably for the two sides: CA in the right side was about one-third larger. No evidence of gynandomorphy was found in this female and thus the mutation was not due to altered sex hormones. These authors suggested that aptery was affected by the activity of the CA, i.e., augmented JH production. Yet it was not clear why only one side was affected by JH. Short life or low dosage of JH and thus limited range of JH action was inferred to explain this anomaly (Maas and Dern 2005).

3) Origins and evolution of neoteny in Elateroidea and Lampyridae

As suggested by my and several previous studies, neoteny has arisen multiple times in Elateroidea. The phylogenetic distribution of neoteny in our phylogeny did not show any directional evolution across the tree. Crowson's single origin hypothesis and the gradual imaginization back to fully imaginal females could not be supported.

Yet, neoteny in Elateroidea and Lampyridae is much more than a single or multi-origin question, especially when considering their elaboration and patterns of phylogenetic distribution among the higher taxa of all categories. Rendering it to a question of presence/absence in a given taxon ignores considerable evolutionary information. For example, not all genera in the so-called “Ototretinae” of Lampyridae have neotenic females, and therefore it is tenuous to assert an origin of neoteny to the whole subfamily as Bocakova et al. (2007) proposed. Also, contrary to Bocakova et al.’s (2007) argument, our tree demonstrates that neoteny in Lampyridae is not just scattered among species but also exists exclusively in large clades, at least in typical Lampyrinae, and perhaps some others. But the characteristics of the scattered and concentrated distribution are remarkably different in terms of phylogenetic composition and neotenic degrees.

Taxonomically, minor neoteny (levels 1–2) occurs in Plastoceridae, Omalisidae, Cebrioninae of Elateridae, and several lineages of Lampyridae (Crowson 1955, 1972, 1995, Geisthardt 1979a, Lawrence et al. 1999, Bocakova et al. 2007). Moderate and high degrees of elaboration (levels 3–4 and 5–6, respectively) are found in Drilidae and some of the lampyrine genera, while the ultimate forms of paedomorphism (levels 7–8) are restricted to Phengodidae, Rhagophthalmidae, Duliticolinae of Lycidae, some basal lineages of Lampyridae, and perhaps

Telegeusidae. Among the four major groups, taxa exhibiting minor neoteny generally have a slightly less correlated distribution than do the other neotenic classes. The former frequently occurred within a genus (e.g., *Atyphella*, *Photinus*, *Robopus*) or subfamily (e.g., Luciolinae), and as a mix of ordinary and flightless females. In Lampyridae, *Lampyroidea* of Luciolinae is probably the only genus with exclusively flightless females that have minor neoteny. Minor paedomorphosis is also found in some species groups, like a group composed of *Luciola filiformis* Olivier, *L. yayeyamana* Matsumura and some Southeast Asian species. Because minor neoteny usually exists within groups comprised predominantly of females, independent origins in different genera are very likely. On the contrary, genera with paedomorphic females of moderate or higher levels never have ordinary, male-looking females among them. Several genera simultaneously possess two adjacent levels in the same category (e.g., levels 3 and 4 in *Diaphanes* and *Pyrocoelia*), suggesting some degree of ontogenetic plasticity but not great enough to shift back to a normal adult morphology. This seems to be the case for the clade composed of *Lampyris* and its related genera (= typical Lampyrinae, including *Afrodiaphanes*, *Diaphanes*, *Lampronetes*, *Lamprohiza*, *Lamprigera*, *Lampyris*, *Microdiphot*, *Nyctophila*, *Phausis*, *Paraphausis*, *Pleotomodes*, *Pleotomus*, and *Pyrocoelia*). This lineage exclusively has paedomorphic females where known, and its members may have evolved back (terminal extension from a neotenic ancestor; also known as hypermorphosis for a process and peramorphosis for an interspecific pattern; Reilly et al. 1997) and forth (with even more terminal deletions, or hypomorphosis, resulting in further paedomorphosis) among neighboring levels according to their distribution in our tree (Figs. 12–17). In a strict sense of heterochrony, once a female is less neotenic than her ancestor, she is no longer paedomorphic, but peramorphic. While I use neoteny/paedomorphosis for those flightless females throughout this paper to avoid confusion, readers should keep in mind that a heterochronic pattern should be determined in a comparative framework of ancestor–descendent relationship, not solely as a static or morphological mode.

The occurrence of ultimate paedomorphism in the sister group and basal lineages of Lampyridae is indeed more or less dilemmatic as Crowson (1972) surmised. If they shared a single origin of neoteny, a reversal to ordinary females in later "higher" levels of lampyrids would be an inevitable conclusion. This is approximately corresponding to the trees resulted from our additive coding. Like the taxa with moderate and high neoteny, the families and genera with ultimate paedomorphosis appear exclusive, not coexisting with male-looking or even moderately/highly neotenic members. This implies that a reversal (hypermorphosis) to a fully imaginal female from an ultimately paedomorphic form is not likely. Alternatively, a corresponding question would be if it was easy to evolve. Though ultimate neoteny is not common nor widely distribution across the elateroid beetles, it may be not that difficult to occur if modification of endocrine regulation in metamorphosis is the underlying mechanism. Evidence from endocrine experiments on *Blattaria* species demonstrated that different degrees of wing reduction could be induced by implantation of corpora allata or allatectomy during different instars of nymphs, but a reversal from a brachy- or apterous species to macroptery by the same treatments could not be achieved (Lefeuvre 1971). The experiments in Lampyridae yielded incongruent results and it is not conclusive if a reversal to macroptery from moderate or high levels of neoteny possible (Naisse 1966a, b, Mass and Dorn 2005). However, Mass and Dorn's (2003) discovery of an abnormal *Lampyris* female suggests that the wing gene(s) still exist but are silenced in typical females. Repeated reacquisitions of wings from winglessness ancestors have been suggested by phylogenetic patterns among stick insects (Phasmatodea) and water striders (Gerridae) (Anderson 1997, Whiting et al. 2003), though ontological evidence was lacking (see also Truemann et al. 2004, Whiting and Whiting 2004). In this sense, the slow or unambiguous optimizations on the trees of nonadditive coding (Figs. 15, 17) provided a more convincing account on the evolution of neoteny in elateroids/ cantharoids than fast optimization and additive coding performed.

According to our phylogeny, there are two equally parsimonious scenarios for the evolution of neoteny in these basal clades. There has been either three independent origins occurring in the Phengodidae–Telegeusidae–Rhagophthalmidae clade, Pterotinae, and *Stenocladius*, respectively (Fig. 17), or two gains of neoteny in the former two groups and *Stenocladius*, and one reversal to macroptery in lampyrids “higher” than Pterotinae (not shown, but applicable to Fig. 15). Unfortunately, females of the so-called “Ototretinae” (paraphyletic, including “Ototretadrilinae”), which are critical to the optimization of neoteny, are unknown and thereby retard a full resolution of this problem.

On the basis of the above reasoning and current data, I prefer the first hypothesis, i.e., accept macroptery as the ancestral state in Lampyridae. Each of the three optimizations on the trees obtained from the nonadditive coding (Figs. 15–17) is of pertinence to our hypothesis to some extent. This hypothesis needs to be reevaluated when those unknown ototretine and otatretadriline females are found and new ontogenetic evidence is available.

4) Heterochrony in evolution of Elateroidea and some ecological issues

I have analyzed the origins and evolution of the larviform females with different levels of neotenic elaboration in elateroid and lampyrid beetles. But neoteny is not only known in females. Though very rare in Lampyridae, flightless males (level 1) are known in the European *Phosphaenus hemipterus* Fourcroy, whose females do not have elytral rudiments (McDermott 1964, Geisthardt 1979b). Interestingly, another poorly known genus, *Phosphaenopterus*, based on *P. metzeneri* Schaufuss and with ordinary males, was found to be the sister group to *Phosphaenus*. Their distributions are partially overlapping with each other and the females of *Phosphaenopterus* are unknown (McDermott 1966). As suggested by their morphological resemblance, it appears to us that these two genera are actually a single group composed of two species complexes with elytral/ wing polymorphism. This pair of genera shall provide an ideal example to study changes in the ontogenetic protocol as well as endocrine control during metamorphosis.

Neoteny may have played a significant role in the evolution of males in Elateroidea, but was overshadowed by the presence of elytra and therefore often ignored. For instance, the ventral spiracles and rudimentary depression of the pleurosternal sulcus in the abdomen of both sexes in some lampyrid lineages are probably neotenic traits caused by either hypomorphosis or deceleration in relation to the dorsal spiracles and complete fusion of the pleurites and sternites (see Cicero 2007). Even more fundamentally, the hologastrous abdomen (Richards and Davis 1977), a traditionally recognized character of Cantharoidea, is also likely a set of paedomorphic traits. A recent discovery of photogenic organs in males of *Rhagophthalmus ohbai* Wittmer (Rhagophthalmidae) demonstrates that they share a similar, peculiar distribution (i.e., a series of one dorsal central spot and two laterals per segment) with those of the larvae and females, but are much weaker in brightness (Chen 2003). It has been suggested that the paired lantern on the 8th abdominal segments of some lampyrid adults are retained from their larvae (Barber

1941, McDermott 1964, Branham and Wenzel 2003). Wang et al. (2007) showed that the larval lanterns did not cease glowing in both sexes of *Pyrocoelia pectoralis* Olivier (Lampyridae) until 3–4 hours after emergence. These facts are supportive of the neotenic nature of the hologastrous abdomen at least in Lampyridae and Rhagophthalmidae. In this sense, ordinary winged cantharoids, either male or female, are neotenic in comparison with other elaterids which have fewer, rigidly articulated abdominal ventrites.

Though not explicit or conclusive, fossils provided some insightful clues about the origin of the hologastrous abdomen. The oldest elaterid beetles are known from Late Triassic (Ponomarenko 2002), suggestive of an early origin of Elateroidea, and the rigid and abbreviated abdomen is assuredly ancestral to the group. Crowson (1972) believed that there was no fossil of cantharoid beetles older than Baltic amber (Middle Eocene, ca. 45 MYA), and he argued for a younger history of Cantharoidea in relation to other beetle superfamilies (an error followed by Grimaldi and Engel 2005). Recently, a fossil cantharid was discovered in Early Cretaceous Burmese amber (about 100–105 MYA), representing the oldest fossil of cantharoid families. This ancient solider beetle had a hologastrous abdomen bearing six pairs of cuticular vesicles with repellent glands extruding from the abdominal sides (Poinar et al. 2007). Such a form of eversible defense glands is still preserved in extant cantharid adults as well as in the larvae of Cantharidae and Lampyridae (Okada 1928, Šulč 1949, Crowson 1981, Dettner 1987, Lawrence et al. 1999, Tyler 2001, Tyler and Trice 2001, Ho and Chu 2002, Chen 2003, Trice 2004, Fu et al. 2007). On the basis of these facts, it is legitimate to presume that selection favoring persistence of some advantageous traits of larvae into the adult resulted in the hologastrous abdomen in cantharoid beetles, and that the cantharoid lineage is of at least Early Cretaceous age.

Actually a similar hypothesis has been proposed for the evolution of bioluminescence in connection with the origin of neoteny of cantharoids (Crowson 1972). It has been widely accepted that bioluminescence originated in the larvae and served as a warning signal to nocturnal predators, analogous to the use of aposematic coloration against diurnal enemies (Crowson 1972, Underwood et al. 1997, De Cock and Matthysen 1999, 2003, Bocakova et al. 2007). In Crowson's scenario flightless, larviform females presumably originated through selection favoring the retention of the larval lanterns. Yet this inference is hampered by the initial presence of bioluminescence in neotenic females rather than in both sexes if bioluminescence was at first a warning signal and not for sexual display. In contrast, neoteny takes place more frequently in females than in males and might be an adaptation for a different reproductive strategy, i.e., K-selection, as Gould (1977) suggested. These flightless females usually have a physogastrous abdomen full of large eggs relative to the winged females in different species (Ho 2002). In addition, it has been suggested that the production of nuptial gifts was lost several times in the taxa which have large, flightless females among Lampyridae and Rhagophthalmidae (Wing et al. 1983, Reijden et al. 1997, Hayashi and Suzuki 2003, Lewis et al. 2004, Demary and Lewis 2007b, Lewis and Cratsley 2008). A reasonable inference is that the contribution of male-derived nutrition to female reproduction was relatively small compared to the females' own reserve of nutrients (Hayashi and Suzuki 2003, Lewis and Cratsley 2008). Furthermore, rhagophthalmid females exhibit clear maternal care by curling their glowing body over the eggs (Ho 2002, Ho and Chu 2002, Chen 2003, Ohba 2004a).

A hypothesis not formally tested in my study is the correlation between flightlessness and overwintering ecology. For some insects, low temperature and short photoperiodic environment are correlated with flightlessness (Harrison 1980). In forest macrolepidoptera, overwintering strategy has been suggested as a selection force for flightless females (Hackman 1966, Roff 1986, 1990, 1944a, b, Barbosa et al. 1989, Hunter 1994, Snäll et al. 2007). These adaptations include active adults in winter, large and diapause eggs for overwintering, spring and polyphagous feeding of larvae, etc. Hunter's (1995) and Snäll et al.'s (2007) phylogenentic approaches both demonstrated that flightlessness in females of moths only occurs in spring-feeding lineages (i.e., with winter-active adults and diapause eggs) and has multiple origins. In Lampyridae and Rhagophthalmidae there do exist winter-active species with neotenic females. There are two explanations for the phenomenon: adaptation and historical inertia. Larvae of these families are predaceous and their adults usually do not feed or simply consume nectar. Nutrition acquisition in the larval stage is therefore critical to reproductive success in adults (Rooney and Lewis 1999, 2000, 2002). From an adaptationist point of view, it is reasonable to infer that the occurrence of adults in late autumn or winter is a benefit owing to fewer natural enemies and, more importantly, a longer active larval duration. These taxa overwinter as adults or eggs, while spring-summer species do so as larvae. In winter (or dry season in tropical areas) prey are scarce or inactive due to low temperature or humidity. To avoid overwintering as larvae means the larval stage largely covers the prey-abundant seasons. Moreover, winter species do not waste larval nutrition storage during winter quiescence in cold areas, or can reduce mortality because they need not hunt prey in winter/dry season in warmer areas as do spring-summer species. A trade-off is that adults need to survive the hard weather and have a shorter period of activity for finding a mate owing to low temperatures. Alternately, from a historical view, winter activity of adults may imply their persistent adaptation to cool weather since the latest ice age. Though not mutually exclusive, these two explanations do conflict with each other to some extent. The former implies a derived nature of winter activity, while the latter suggests a preserved trait.

Phylogenetically winter-active species occur in *Rhagophthalmus*, *Stenocladius*, and some genera of typical Lampyrinae whose females are all moderate to ultimately paedomorphic. None of the above genera are obligate winter lineages but instead intermingled with spring-summer (or wet season) species. The other groups with flightless females, either with minor neoteny like those in some lucioline genera, *Photinus* and allied genera, or with ultimate neoteny as in *Pterotus* (Pterotinae), do not have known winter species. Zoogeographically some well studied local fauna provide implicit cues. For example, in Taiwan, six out of the 11 genera and 16 of 60 species of Lampyridae have flightless females (Jeng et al. 1999a, Chu and Ho 2002, Chen 2003). They are distributed in *Luciola* (1, number of species) and *Curtos* (1) of Luciolinae (levels 1–2), *Lamprigera* (1), *Diaphanes* (7), and *Pyrocoelia* (5) of Lampyrinae (levels 3–5), and *Stenocladius* (1) of Ototretadrilinae (level 7). Nine of the 16 flightless species occur only from mid-autumn to winter (September to January). It is noticeable that many of the *Diaphanes* species only occur at high elevations in mountainous areas (e.g., *D. nubilus* Jeng and Lai, up to 2500 m above sea level). The remaining seven species, including two from Luciolinae, one from *Diaphanes* and three from *Pyrocoelia*, are spring-summer species, and *Pyrocoelia analis* has two peaks in spring and mid-autumn (Ho 1998, 2004, Jeng et al. 1999a, c). In *Pyrocoelia*, with the exception of the nocturnal *P. analis*, the spring-summer species are diurnal and the autumn-winter species *P. praetexta* Olivier is nocturnal (Jeng et al. 1999a). Neighboring faunas with good data, like those of the Ryukyu Archipelago and Japan, show similar phenology in genera shared with Taiwan. For instance, four of the five *Stenocladius* species and three (all nocturnal) of the eight *Pyrocoelia* species appear in late autumn and winter. The other female-flightless groups such as *Hotaria*, *Luciola yayeyamana* Matsumura, and *Lucidina okadai* Nakane and Obayashi are active in spring and summer, as are all macropterous species (Ohba 2004a). No truly winter species occur in the main islands of Japan, but many occur in the subtropical Ryukyu Islands. Label data of museum specimens I examined demonstrate that many, but not all, *Diaphanes*, *Lamprigera* and *Pyrocoelia* species from the other areas such as southern China, Vietnam, Myanmar, Himalayas, India, Indonesia, etc., also appear in winter (or dry season) at least. In Australia the lampyrid fauna is restricted to Luciolinae. There is no true winter species regardless of flight capability, but some genera have quite long periods of activity, from spring to late autumn (Ballantyne and Lambkin 2000). A study on the lampyrid fauna from southeastern Brazil revealed that only one (a *Photinus*) out of the 26 species had been seen active in winter (Viviani 2001). But its female morphology was not described. In contrast, none of the lampyrid species in North America have been reported to be active in winter, though a daytime-flying species, *Ellychnia corrusca* (L.), has overwintering adults (Marvin 1965, Rooney and Lewis 1999, 2000). European species are active from summer to mid-autumn regardless of macroptery or flightlessness (Geisthardt 1979b, De Cock 2000). In Rhagophthalmidae females of *Rhagophthalmus ohbai* Wittmer in the Ryukyu Archipelago was found glowing in winter (Ohba et al. 1996, Ohba 2004a), but their phenology in Taiwan varied from spring to summer for different populations (Jeng, unpublished). Males of the other rhagophthalmid genera could be found in summer or wet season, and a female of *Menghuoius* was also collected in June from Myanmar (Jeng, unpublished; see also Kawashima 2002). Recently a resembling giant larviform female was identified as *Diplocladon* from Yunnan, China, by Li and Liang (2008). Actually the female is likely of *M. giganteus* (Fairmaire) or the other related species described from there. The other neotenic groups such as Omalisidae, elaterid Cebrioninae, Drilidae and Plastoceridae, mostly from the Palearctic and Nearctic regions, are all spring-summer lineages (Crawshay 1903, Geisthardt 1979a, c).

The winter occurrence of adults is apparently not a global phenomenon, but instead, quite rare in relation to the whole superfamily and restricted regionally.

This does not support the adaptationist hypothesis as it would predict a convergent distribution regardless of phylogeny and region. Based on our phylogeny and currently available data of phenology, the most parsimonious scenario takes six steps for the evolution of the winter groups in the tree (Fig. 18; five gains in *R. ohbai*, *Stenocladius bicoloripes* Pic, *P. praetexta*, *Diaphanes*, and *Lamprigera*, respectively, one loss in *D. formosus* Olivier). However, such an approach suffers from technical and theoretical flaws. First, none of the genera are obligate winter lineages and the species sampling in an analysis will affect the reconstruction of ancestral states. Second, unlike morphological characters, how to define ancestry to a lineage in terms of phenology is controversial (but see Miller and Wenzel 1995). The duration of a species in insects is generally much longer than Milankovitch cycles which brought dramatic global climate changes during the Quaternary (Stanley 1985, Elisa 1994). Seasonal adaptations are thus developed and shaped by dynamic climate changes. Under this notion “ancestral” should better be defined by the seasonality at the end of the latest ice age for a species or species groups, and “derived” as subsequent changes during recolonization or adaptations since that time. Legitimately, different zoogeographic zones may give different ancestral states to different species/ lineages and phylogenetic influence on phenology is subject to the changes of regional history. The above faunal cases imply that phylogeny (history) is responsible for the seasonality of neotenic elateroids in some zoogeographic regions to some degree (e.g., in Oriental, Australia), whereas climate (ecology) is likely a decisive determinant in the others, especially in temperate zones (e.g., Nearctic, Palearctic, or Palearctic main islands of Japan vs Oriental Ryukyu Islands). Probably winter weather is too harsh for firefly activities in temperate areas. An integrated study on the regional fauna and its Quaternary history, and a lower-level phylogeny (genus or species group) shall provide a more reasonable and stronger resolution than a global approach for this question.

Conclusion

Neoteny/ paedomorphosis is an interesting and significant topic in the study of the natural history of Elateroidea and Lampyridae. My study reveals that the origins, evolution, existence, and influence of neoteny are much greater than previously understood. Microscopically, not only hypomorphosis but other heterochronic processes have contributed to the evolution of Lampyridae. Macroscopically, the “cantharoid beetles” in Elateroidea could be regarded as a neotenic group in relation to other elateroid families or their allied superfamilies. Certainly our study is not an end but a new start. An integrated study with thorough morphological examination, comprehensive phylogenetic analysis, and detailed ontogenetic studies are required to answer these issues of "evodevo" in the future. In addition some ecological traits associated with neoteny can be tested based on a regional fauna and phylogenetics at the generic level.

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Table 1. Modern family-group classifications of Lampyridae

Olivier, 1907 (9 subfamilies, 48 genera)	McDermott, 1966 (7 subfamilies, 85 genera)	Crowson, 1972 (8 subfamilies)
Subfamily Lampyrinae Latreille (9)[1]	Subfamily Lampyrinae Latreille (53)	Subfamily Lampyrinae Latreille
Subfamily Lamprocerinae Olivier (14)	Tribe Lampyrini Latreille (11)	Subfamily Amydetinae Olivier
Subfamily Photininae LeConte (6)[2]	Tribe Pleotomini Green (5)	Subfamily Photurinae Lacordaire
Subfamily Lucidotinae LeConte (7)	Tribe Lamprocerini Olivier (5)	Subfamily Luciolinae Lacordaire
Subfamily Dadophorinae Olivier (1)	Tribe Cratomorphini Green (5)	Subfamily Ototretinae McDermott
Subfamily Megalophthalminae Olivier (2)	Tribe Photinini LeConte (27)	Subfamily Pterotinae LeConte
Subfamily Amydetinae Olivier (1)	Subtribe Photinina LeConte (13)	Subfamily Cyphonocerinae Crowson
Subfamily Photurinae Lacordaire (1)	Subtribe Luciodotina Lacordaire (10)	Subfamily Ototretadrilinae Crowson
Subfamily Luciolinae Lacordaire (7)	Subtribe Dadophorina Olivier (1)	
	Subtribe Phosphaeina McDermott (2)	
	Subtribe Lamprigerina McDermott (1)	
	Subfamily Amydetinae Olivier (12)	
	Tribe Amydetini Olivier (2)	
	Tribe Vestini McDermott (5)	
	Tribe Psilocladini McDermott (5)	
	Subfamily Photurinae Lacordaire (4)	
	Subfamily Luciolinae Lacordaire (9)	
	Tribe Luciolini Lacordaire (6)	
	Tribe Curtosini McDermott (1)	
	Tribe Ototretini McDermott (2)	
	Subfamily Matheteinae LeConte (2)	
	Subfamily Pterotinae LeConte (1)	
	Subfamily Rhagophthalminae Olivier (4)	

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[1] Value in parentheses indicates the number of explicitly included genera.

[2] A homonymous name junior to a subfamilial name, Photininae Giglio-Tosi, in the Mantidae (Mantodea).

Next five pages:

Fig. 1. Comparison of existing phylogenies of Lampyridae from Suzuki (1997), Branham and Wenzel (2001), Stanger-Hall et al. (2007) and Bocakova et al. (2007).

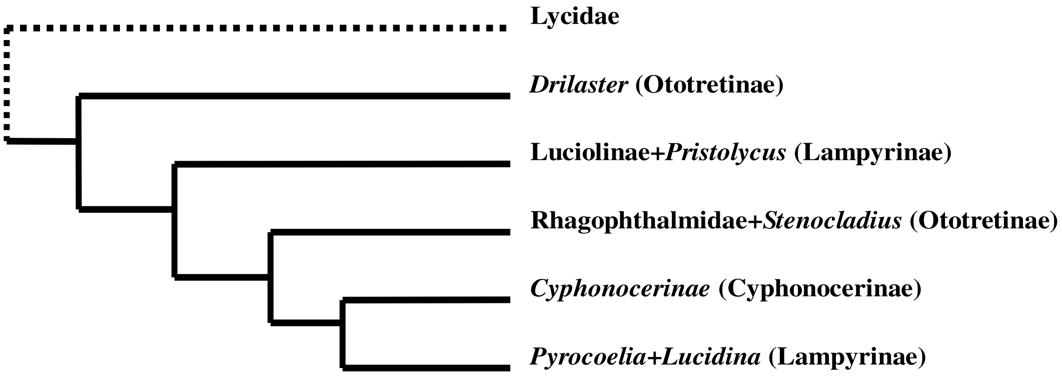


Fig. 1A. Suzuki's (1997) neighbor-joining tree based on mitochondrial 16S ribosomal RNA (16S rDNA) of 9 lampyrid genera from Japan

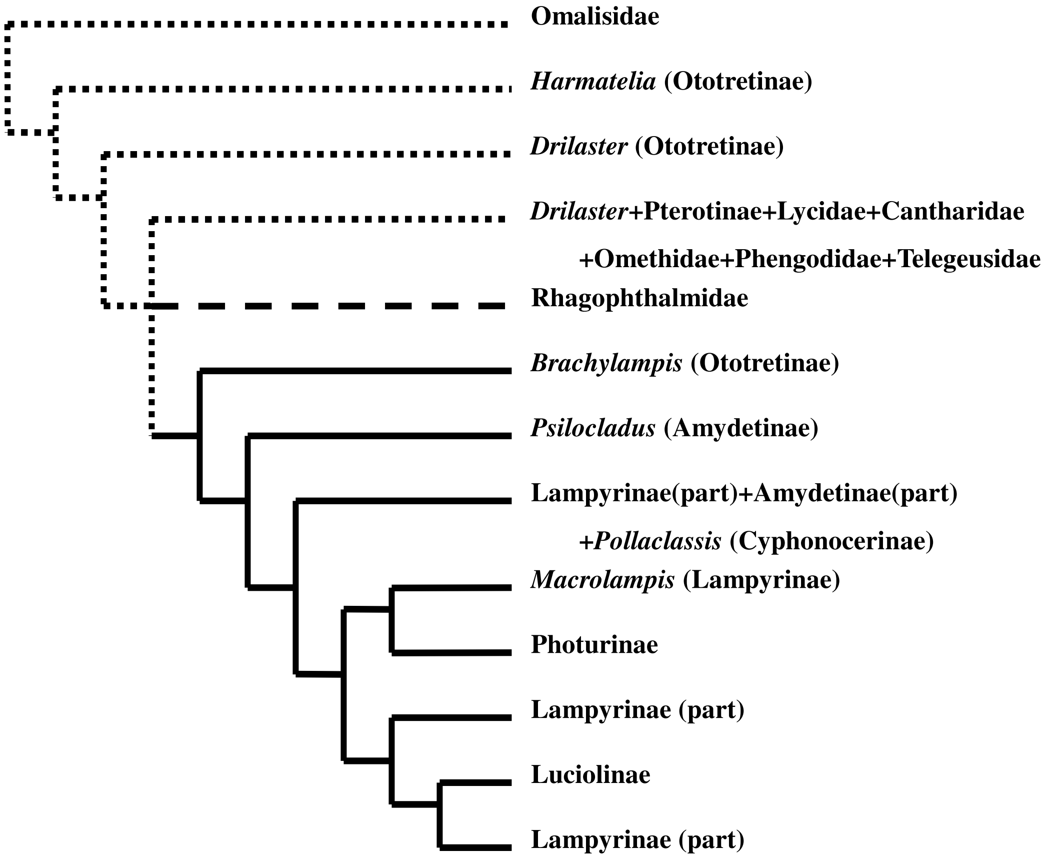


Fig. 1B. Branham and Wenzel's (2001) most parsimonious tree based on male characters of 37 lampyrid genera from global sampling

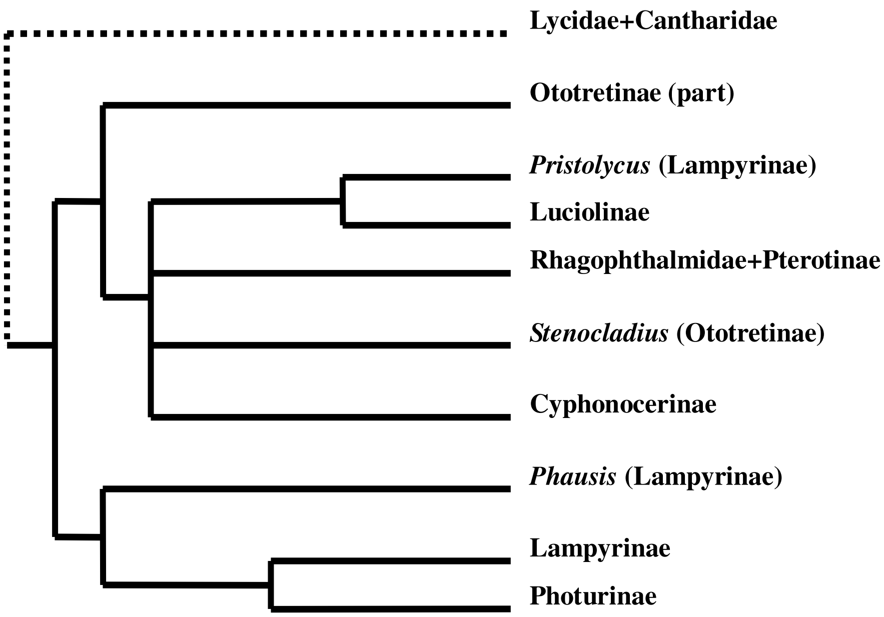


Fig. 1C. Stanger-Hall et al.'s (2007) maximum likelihood tree based on 18S rDNA, mt 16S rDNA and *COI* genes of 30 lampyrid genera from global sampling

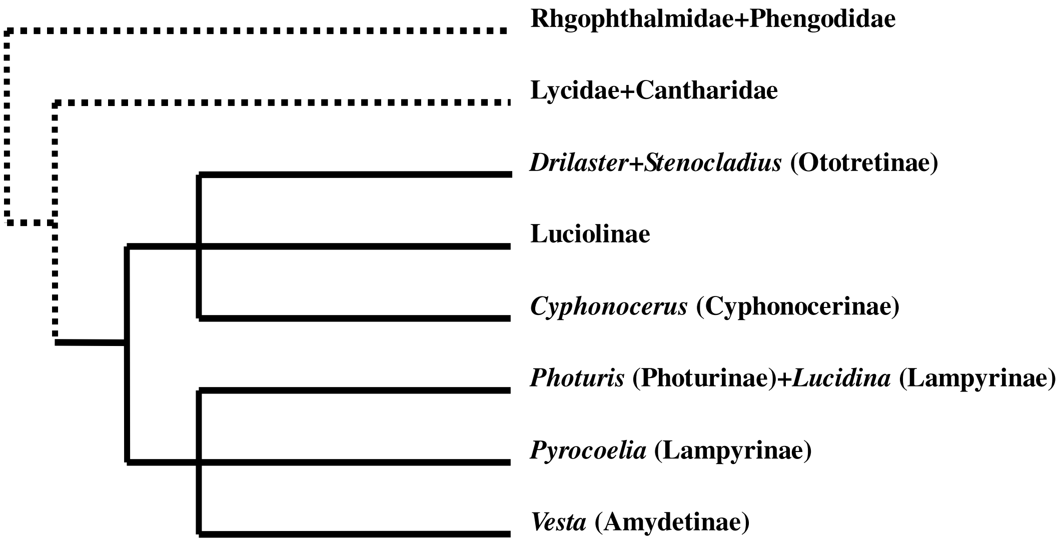


Fig. 1D. Sagegami-Oba et al.'s (2007) maximum likelihood tree based on 18S rRNA of 9 lampyrid genera from global sampling

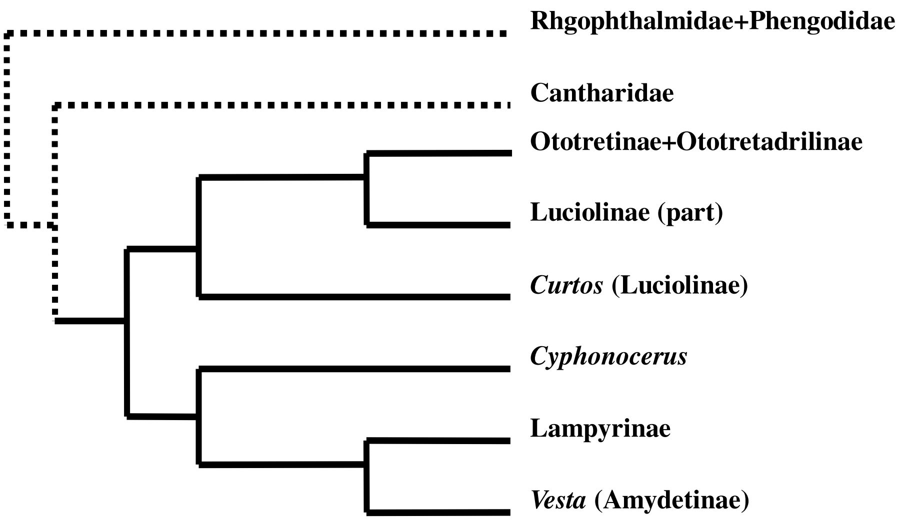


Fig. 1E. Bocakova et al.'s (2007) most parsimonious tree with ClustalX alignment of 18S rDNA, 28S rDNA, *rrnL* and *cox I* genes of 13 lampyrid genera from global sampling

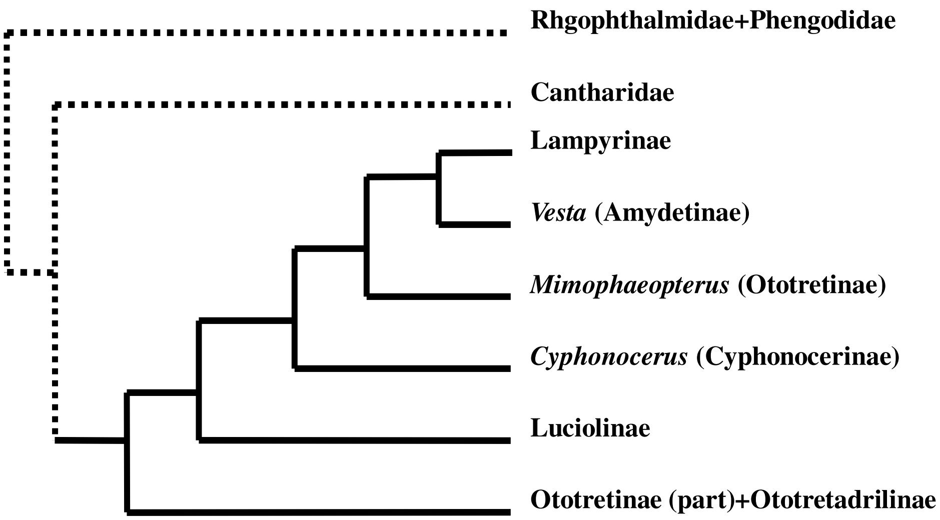


Fig. 1F. Bocakova et al.'s (2007) tree generated by Bayesian analysis with BlastAlign alignment of 18S rDNA, 28S rDNA, *rrnL* and *cox I* genes of 13 lampyrid genera from global sampling

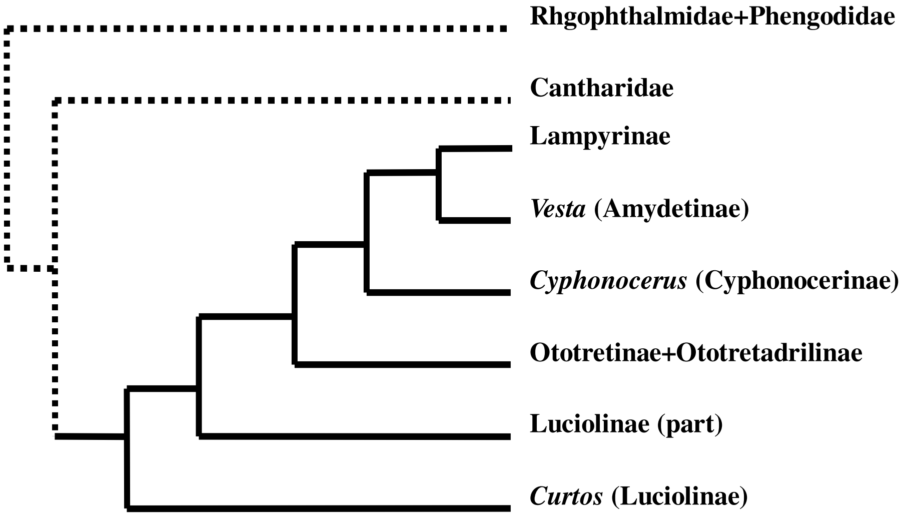


Fig. 1G. Bocakova et al.'s (2007) tree generated by Bayesian analysis with preferred ClustalX alignment of 18S rDNA, 28S rDNA, *rrnL* and *cox I* genes of 13 lampyrid genera from global sampling

Figure 1. Comparison of existing phylogenies of Lampyridae from Suzuki (1997), Branham and Wenzel (2001), Stanger-Hall et al. (2007) and Bocakova et al. (2007). Solid branches indicate Lampyridae without question; dash line for taxon with arguable placement in Lampyridae, and dot line for non-lampyrids. "Genus (subfamily)" and "genus+genus (subfamily)" mean one or two genera showing in the branch; "subfamily" refers to multiple genera of that subfamily showing in a branch; "subfamily (part)" indicates paraphyly of that subfamily in the tree; "subfamily+subfamily" and "subfamily+genus" mean several genera from different groups being mosaic in that lineage; "family+family", "family+genus" and "family+subfamily" represent to a clade with two monophyletic groups.

Next two pages:

Fig. 2. A strict consensus of 1008 most parsimonious trees obtained from 10,000 iterations of rachet and subsequent heuristic search using Nona/Winclada for a full data set of 220 species and 410 characters.


Dascillus cervinus
Macropogon testaceipennis
Brachypsectra fulva
Selasia sp
Drilus flavescens
Malacogaster passerini
Omalisus fontisbellaquei
Eropterus nothus
Lyponia delicatula
Plateros coracinus
Lycus (Neolycus) arizonensis
Lycostomus sanguineus
Cautires kazuoi
Xylobanus niger
Matheteus theveneti
Ginglymocladus luteicollis
Troglomethes leechi
Malthomethes oregonus
Drilonius striatulus
Omethes marginatus
Omethes rugiceps
Phenogodes frontalis
Zarhipis integripennis
Stenophrixothrix sp
Taximastinocerus sp
Cenophengus debilis
Distremocephalus texanus
Telegeusis nubifex
Pseudokarumia angustata
Falsophrixothrix humeralis
Monodrilus marginatus
Diplocladon hasselti
Dodecatoma bicolor
Rhagophthalminae ngen
Menghuoius ingens
Menghuoius giganteus
Dioptoma adamsi
Ochotyra semiusta
Rhagophthalmus ohbai
Pterotus obscuripennis
Falsophaeopterus fruhstorferi
Ototretadrilus flavoscutellaris
Oculogryphus fulvus
Stenocladius sp
Stenocladius bicoloripes
Stenocladius chinensis
Harmatelia bilinear
Selasia decipiens
Stenocladius rufithorax
Gorhamia krombeini
Ceylandidrilus bipartitus
Ceylandidrilus kandyanus
Lamellipalpodes annandalei
Mimophaeopterus wittmeri
Brachylampis blaisdelli
Flabellotreta fruhstorferi
Picodrilus limbellus
Drilaster auxillaris
Drilaster weyersi
Pollaclasis bifaria
Cyphonocerus ruficollis
Cyphonocerus sanguineus
Cyphonocerus sylvicola
Satolampyris dichroma
Pristolycus kanoi
Pristolycus sagulatus
Luciola cincticollis
Luciola anceyi
Pygoluciola satoi
Luciola kuroiwai
Luciola trilucida
Colophotia brevis
Colophotia praeusta
Pteroptyx fulminea
Pteroptyx cribella
Pyrophanes similis
Pyrophanes appendiculata
Luciola aquatica
Luciola substriata
Luciola ovalis
Atyphella lychnus
Atyphella carolinae
Atyphella obsoleta
Luciola peculiaris
Bougeoisia antipoda
Curtos obscuricolor
Luciola hydrophila
Luciola kagiana
Hotaria parvula
Luciola italica
Luciola lustianica
Lampyroides dispar
Lampyroides syriaca
Luciola curtithorax
Luciola filiformis
Dascillidae
Artematopodidae
Brachypsectridae
Drilidae
Omalisidae
Lycidae
Omethidae
Phengodidae
Telegeusidae
Rhagophthalmidae
Lampyridae

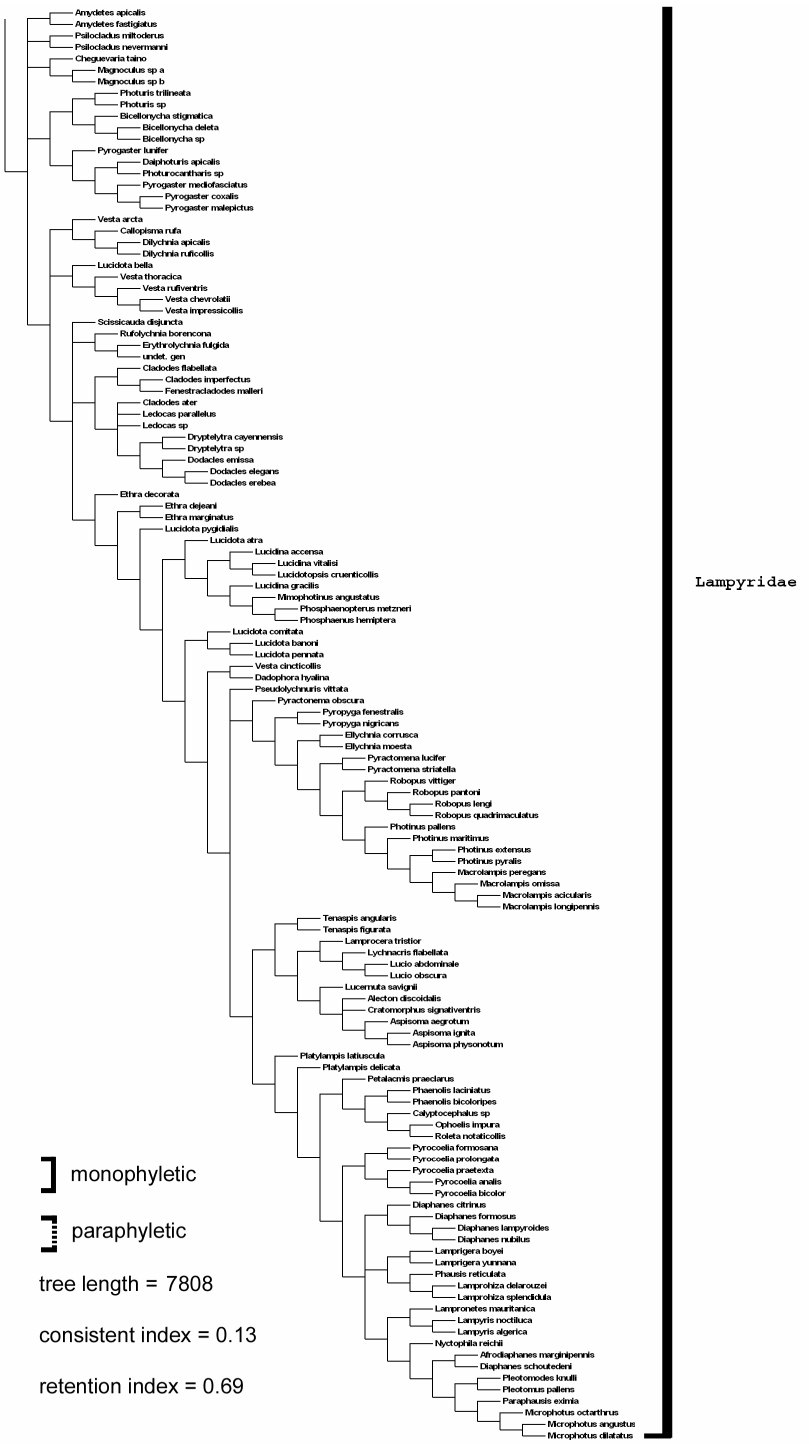
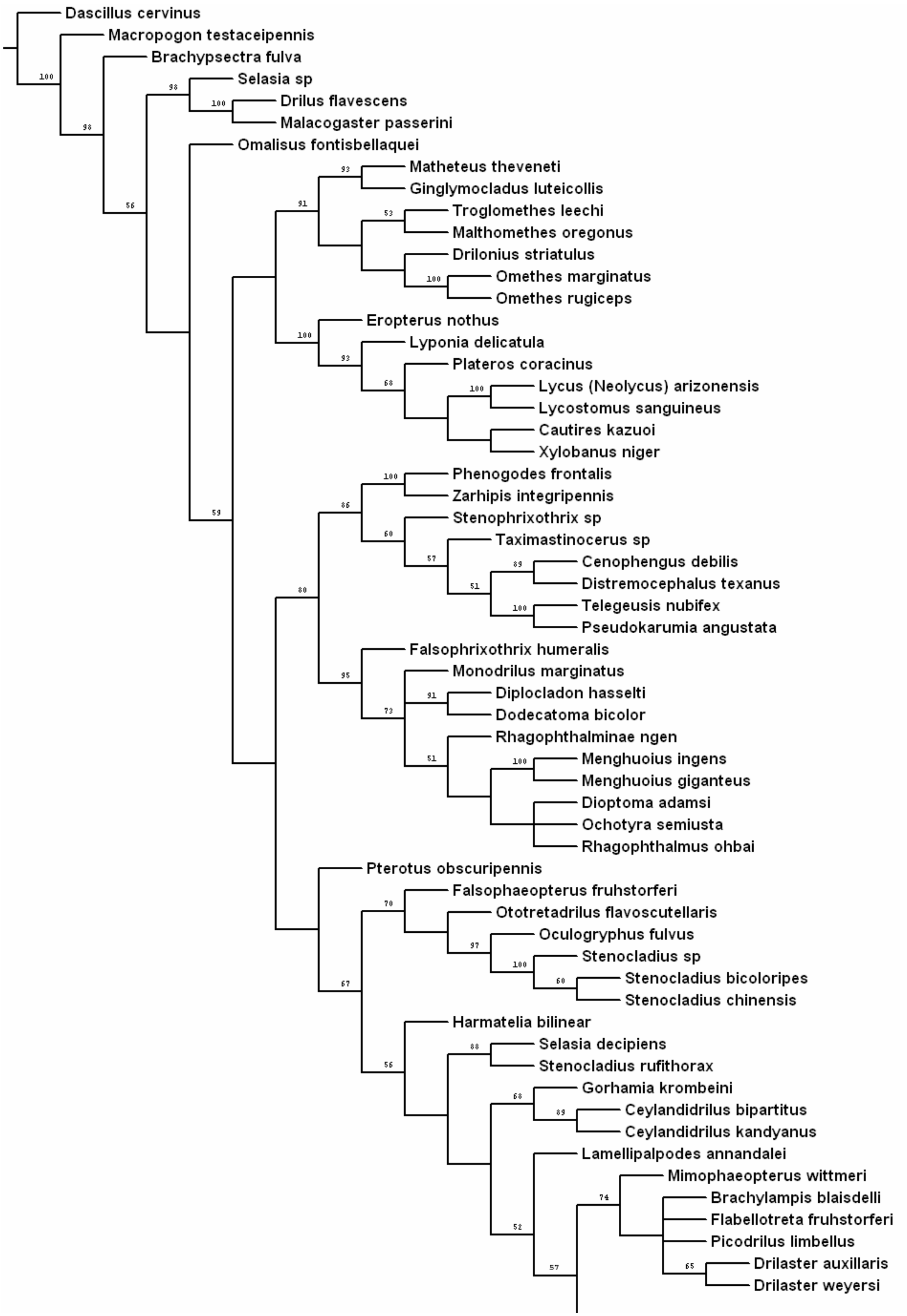


Fig. 2. A strict consensus of 1008 most parsimonious trees obtained from 10,000 iterations of rachet and subsequent heuristic search using Nona/Winclada for a full data set of 220 species and 410 characters.

Next four pages:

Fig. 3. Branch support for strict consensus tree produced by full data set; numbers above internodes are jackknife support values greater than 50% obtained from 500 replications.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Brachypsectra fulva
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Selasia sp
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Drilus flavescens
Malacogaster passerini
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Omalisus fontisbellaquei
93
Matheteus theveneti
Ginglymocladus luteicollis
91
56
53
Troglomethes leechi
Malthomethes oregonus
Drilonius striatulus
100
Omethes marginatus
Omethes rugiceps
Eropterus nothus
100
Lyponia delicatula
93
Plateros coracinus
68
100
Lycus (Neolycus) arizonensis
Lycostomus sanguineus
Cautires kazuoi
Xylobanus niger
100
Phenogodes frontalis
Zarhipis integripennis
86
59
Stenophrixothrix sp
60
Taximastinocerus sp
57
89
Cenophengus debilis
Distremocephalus texanus
51
80
100
Telegeusis nubifex
Pseudokarumia angustata
Falsophrixothrix humeralis
Monodrilus marginatus
95
91
Diplocladon hasselti
73
Dodecatoma bicolor
Rhagophthalminae ngen
51
100
Menghuoius ingens
Menghuoius giganteus
Dioptoma adamsi
Ochotyra semiusta
Rhagophthalmus ohbai
Pterotus obscuripennis
Falsophaeopterus fruhstorferi
70
Ototretadrilus flavoscutellaris
Oculogryphus fulvus
97
Stenocladius sp
100
60
Stenocladius bicoloripes
67
Stenocladius chinensis
Harmatelia bilinear
88
Selasia decipiens
56
Stenocladius rufithorax
Gorhamia krombeini
68
89
Ceylandidrilus bipartitus
Ceylandidrilus kandyanus
Lamellipalpodes annandalei
Mimophaeopterus wittmeri
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Brachylampis blaisdelli
Flabellotreta fruhstorferi
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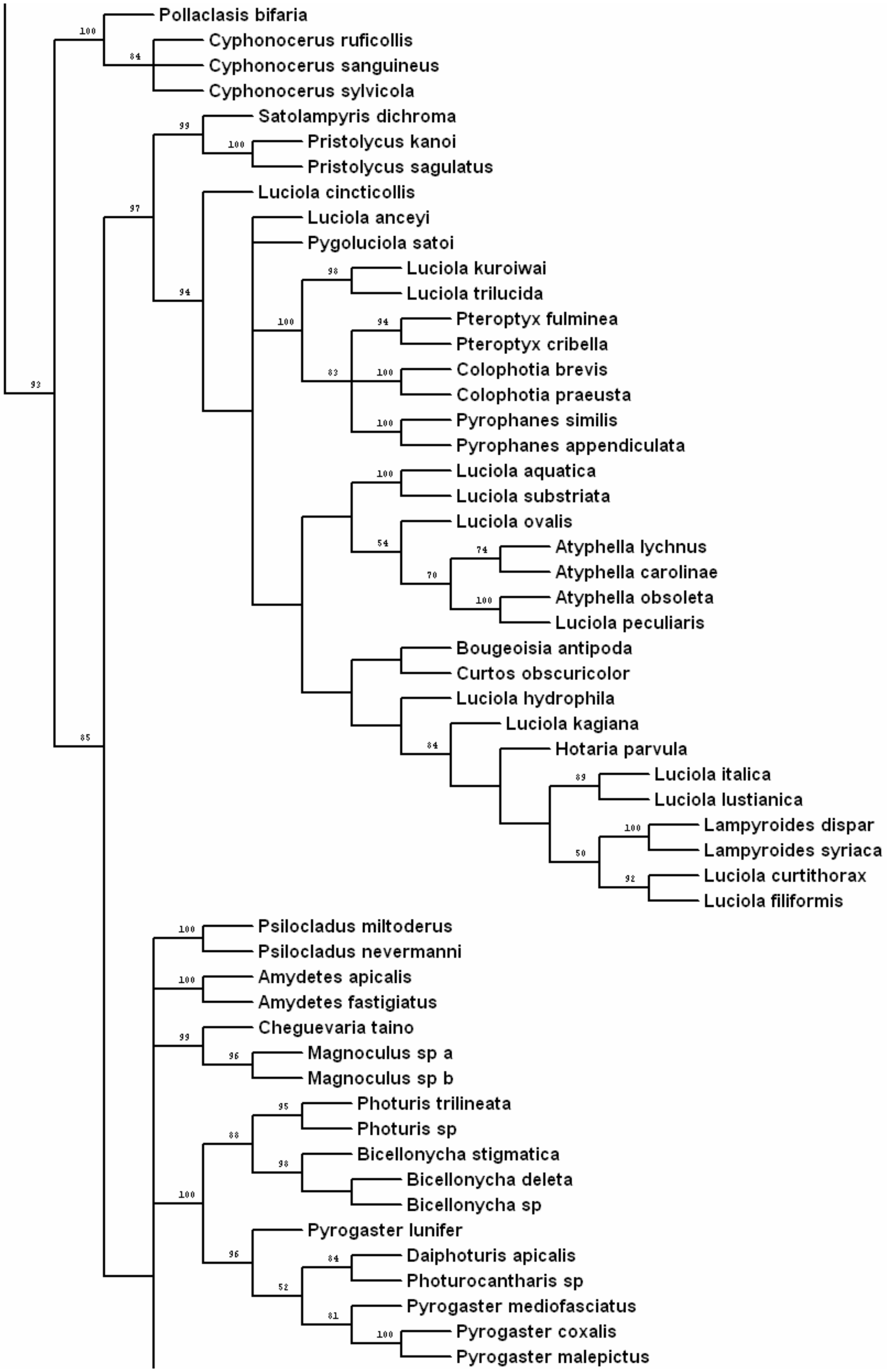
Picodrilus limbellus
65
Drilaster auxillaris
57
Drilaster weyersi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Cyphonocerus ruficollis
Cyphonocerus sanguineus
Cyphonocerus sylvicola
Satolampyris dichroma
Pristolycus kanoi
Pristolycus sagulatus
Luciola cincticollis
Luciola anceyi
Pygoluciola satoi
Luciola kuroiwai
Luciola trilucida
Pteroptyx fulminea
Pteroptyx cribella
Colophotia brevis
Colophotia praeusta
Pyrophanes similis
Pyrophanes appendiculata
Luciola aquatica
Luciola substriata
Luciola ovalis
Atyphella lychnus
Atyphella carolinae
Atyphella obsoleta
Luciola peculiaris
Bougeoisia antipoda
Curtos obscuricolor
Luciola hydrophila
Luciola kagiana
Hotaria parvula
Luciola italica
Luciola lustianica
Lampyroides dispar
Lampyroides syriaca
Luciola curtithorax
Luciola filiformis
Psilocladus miltoderus
Psilocladus nevermanni
Amydetes apicalis
Amydetes fastigiatus
Cheguevaria taino
Magnoculus sp a
Magnoculus sp b
Photuris trilineata
Photuris sp
Bicellonycha stigmatica
Bicellonycha deleta
Bicellonycha sp
Pyrogaster lunifer
Daiphoturis apicalis
Photurocantharis sp
Pyrogaster mediofasciatus
Pyrogaster coxalis
Pyrogaster malepictus
100
84
99
100
97
94
98
100
94
83
100
100
93
100
54
74
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52
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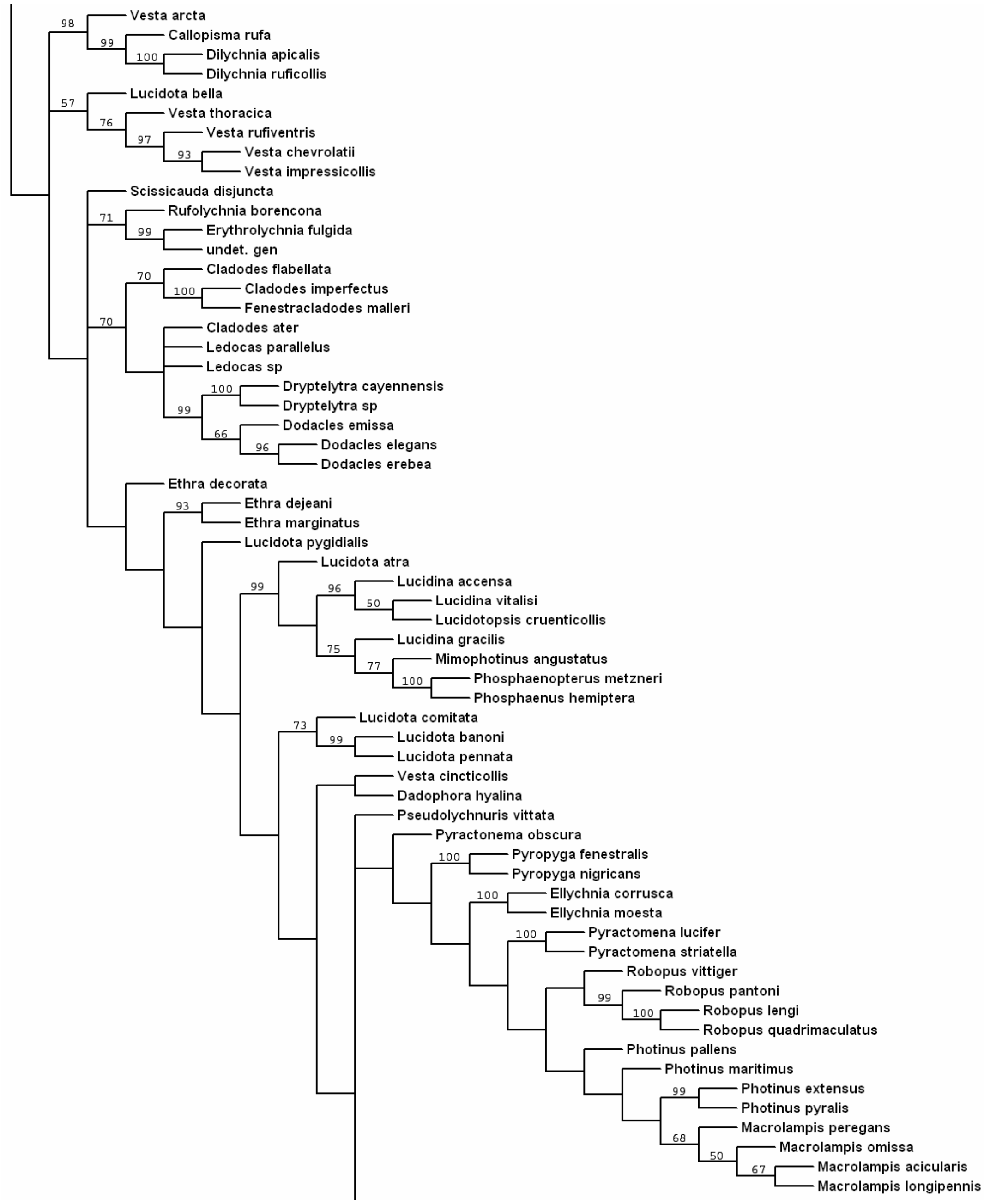
100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Vesta arcta
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Callopisma rufa
100
Dilychnia apicalis
Dilychnia ruficollis
57
Lucidota bella
76
Vesta thoracica
97
Vesta rufiventris
93
Vesta chevrolatii
Vesta impressicollis
Scissicauda disjuncta
71
Rufolychnia borencona
99
Erythrolychnia fulgida
undet. gen
70
Cladodes flabellata
100
Cladodes imperfectus
Fenestracladodes malleri
70
Cladodes ater
Ledocas parallelus
Ledocas sp
100
Dryptelytra cayennensis
99
Dryptelytra sp
66
Dodacles emissa
96
Dodacles elegans
Dodacles erebea
Ethra decorata
93
Ethra dejeani
Ethra marginatus
Lucidota pygidialis
Lucidota atra
99
96
Lucidina accensa
50
Lucidina vitalisi
Lucidotopsis cruenticollis
75
Lucidina gracilis
77
Mimophotinus angustatus
100
Phosphaenopterus metzneri
Phosphaenus hemiptera
73
Lucidota comitata
99
Lucidota banoni
Lucidota pennata
Vesta cincticollis
Dadophora hyalina
Pseudolychnuris vittata
Pyractonema obscura
100
Pyropyga fenestralis
Pyropyga nigricans
100
Ellychnia corrusca
Ellychnia moesta
100
Pyractomena lucifer
Pyractomena striatella
Robopus vittiger
99
Robopus pantoni
100
Robopus lengi
Robopus quadrimaculatus
Photinus pallens
Photinus maritimus
99
Photinus extensus
Photinus pyralis
68
Macrolampis peregans
50
Macrolampis omissa
67
Macrolampis acicularis
Macrolampis longipennis

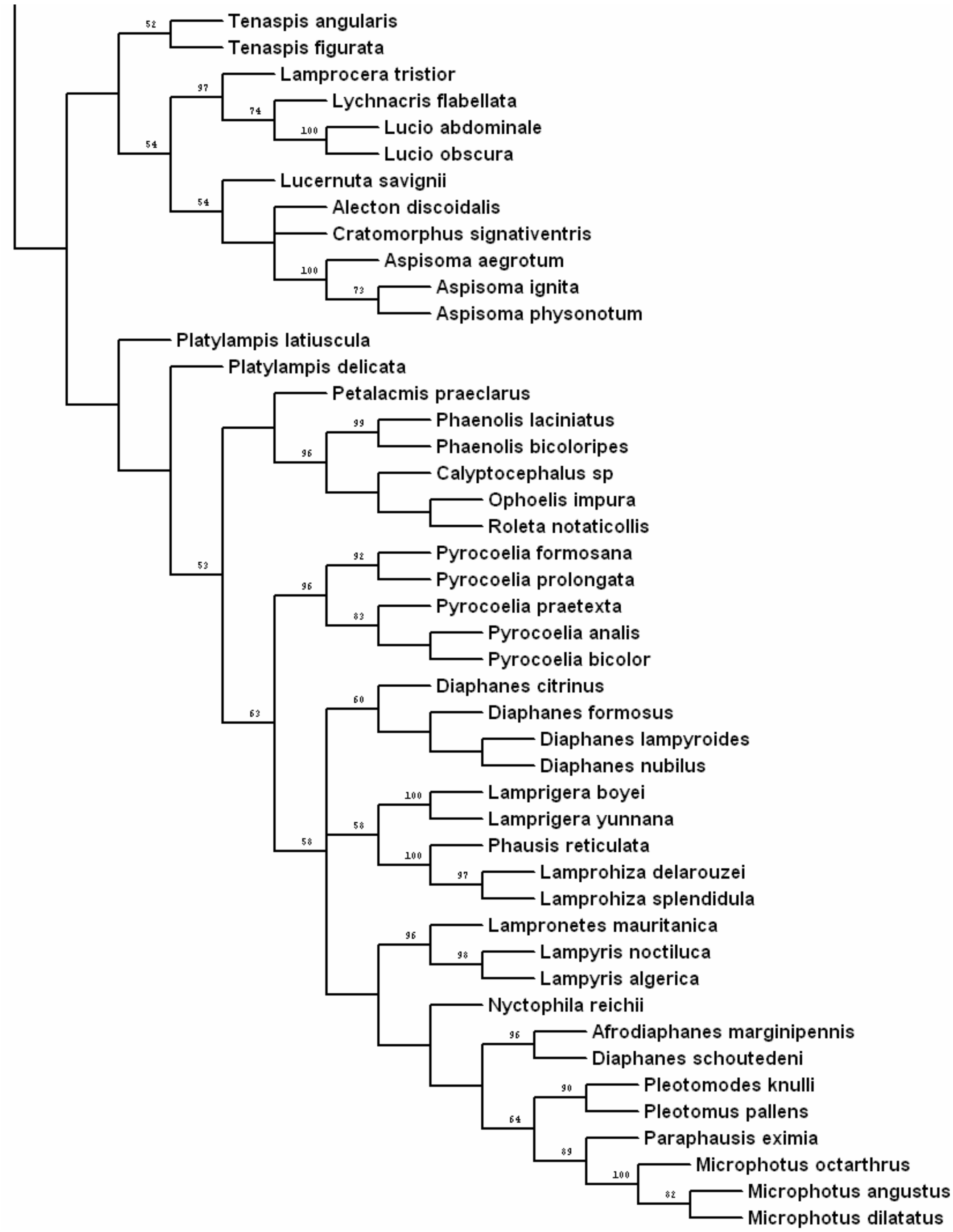


Fig. 3. Branch support for strict consensus tree produced by full data set; numbers above internodes are jackknife support values greater than 50% obtained from 500 replications.

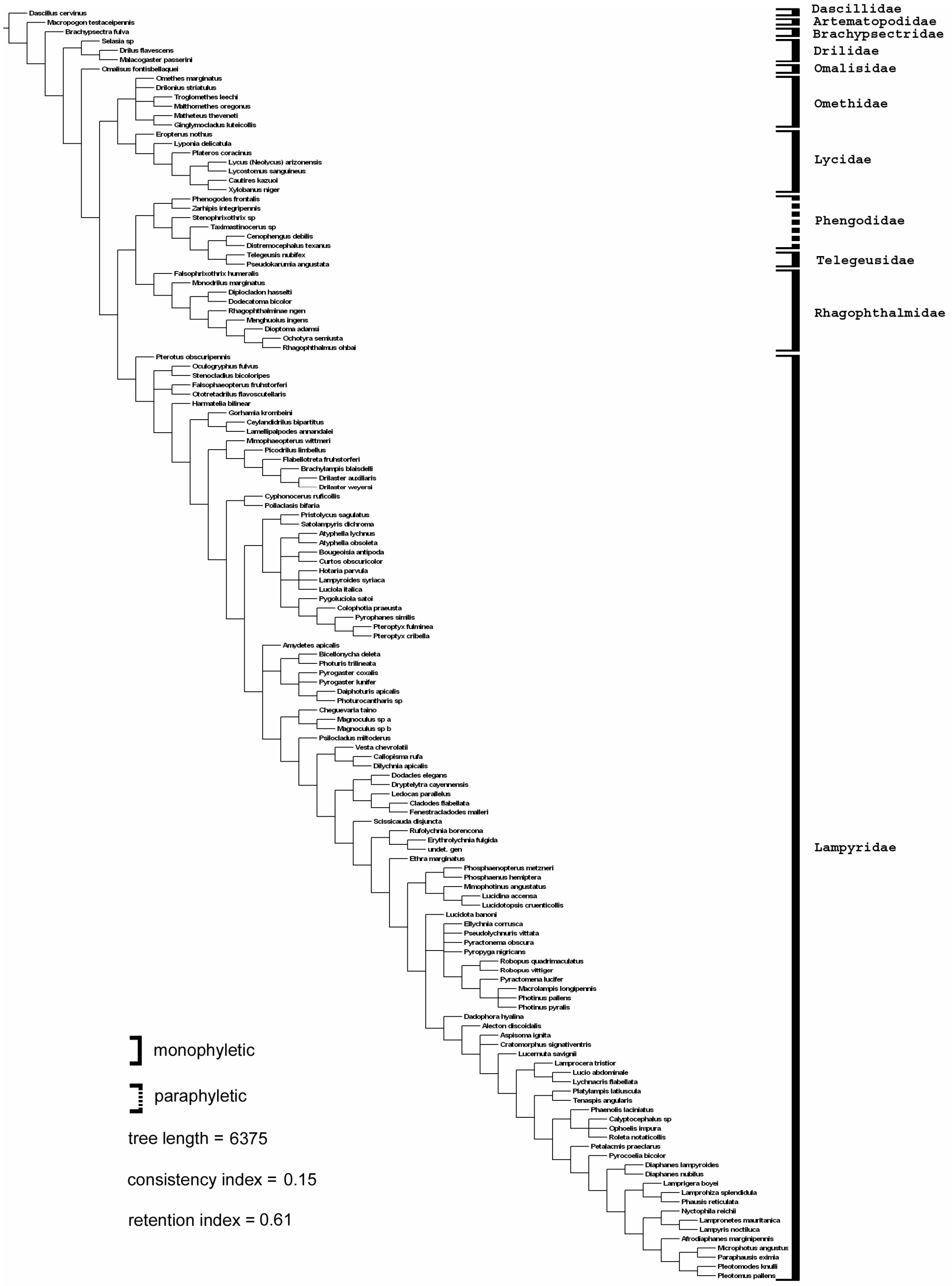
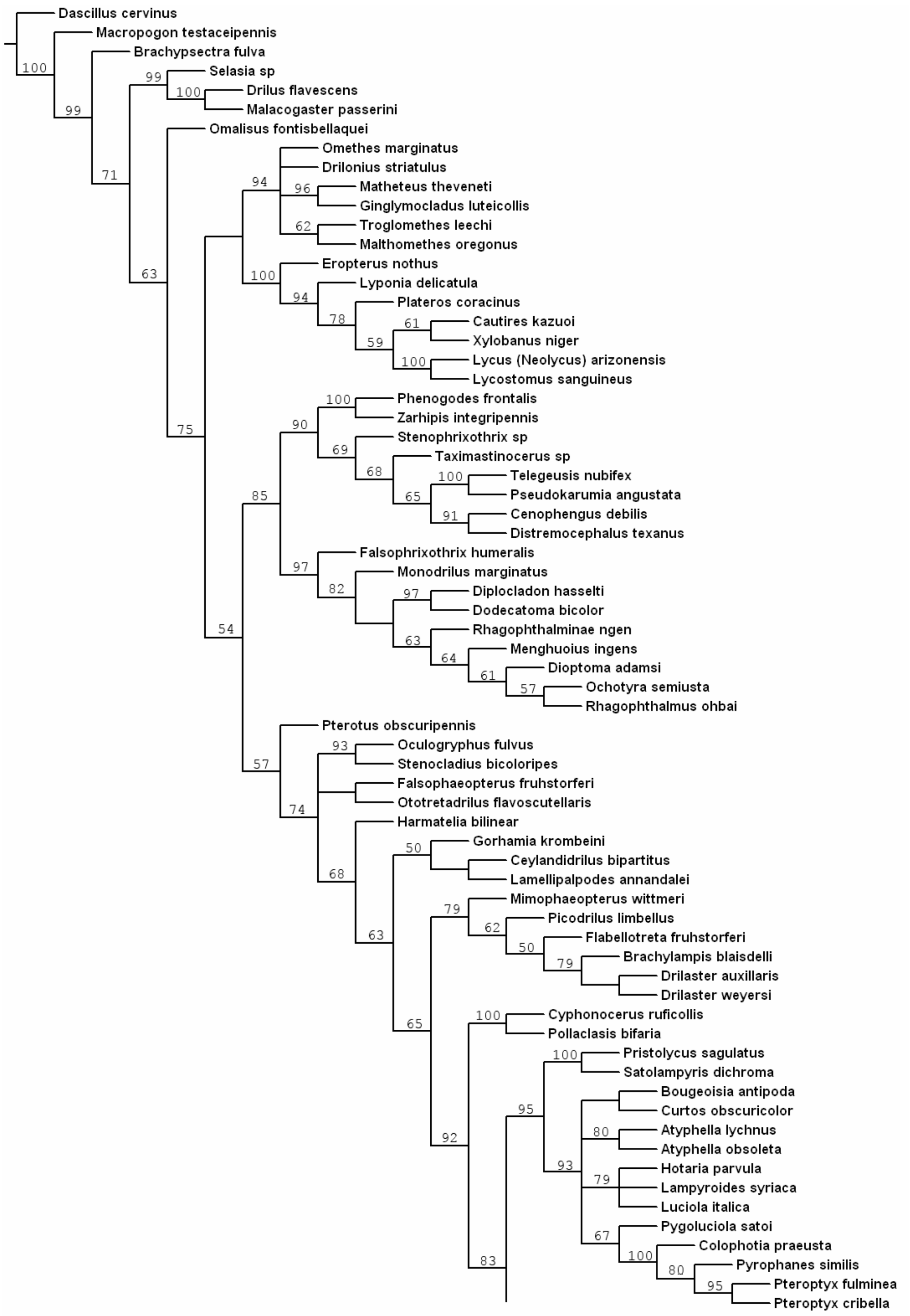


Fig. 4. A strict consensus of 720 most parsimonious trees obtained from 6,000 iterations of rachet and subsequent heuristic search using Nona/Winclada for a data set of 137 species (type species or its similar species of all genera) and 394 informative characters.

Next two pages:

Fig. 5. Branch support for strict consensus tree produced by 137 (type) species data set; numbers above internodes are jackknife support values greater than 50% obtained from 500 replications.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Macropogon testaceipennis
100
Brachypsectra fulva
99
99
Selasia sp
100
Drilus flavescens
Malacogaster passerini
71
Omalisus fontisbellaquei
Omethes marginatus
Drilonius striatulus
94
96
Matheteus theveneti
Ginglymocladus luteicollis
62
Troglomethes leechi
Malthomethes oregonus
100
Eropterus nothus
Lyponia delicatula
94
63
Plateros coracinus
78
61
Cautires kazuoi
Xylobanus niger
59
100
Lycus (Neolycus) arizonensis
Lycostomus sanguineus
100
Phenogodes frontalis
Zarhipis integripennis
90
Stenophrixothrix sp
69
75
Taximastinocerus sp
68
100
Telegeusis nubifex
Pseudokarumia angustata
65
91
Cenophengus debilis
Distremocephalus texanus
85
Falsophrixothrix humeralis
97
Monodrilus marginatus
82
97
Diplocladon hasselti
Dodecatoma bicolor
Rhagophthalminae ngen
63
Menghuoius ingens
64
54
Dioptoma adamsi
61
57
Ochotyra semiusta
Rhagophthalmus ohbai
Pterotus obscuripennis
93
Oculogryphus fulvus
Stenocladius bicoloripes
57
Falsophaeopterus fruhstorferi
74
Ototretadrilus flavoscutellaris
Harmatelia bilinear
50
Gorhamia krombeini
Ceylandidrilus bipartitus
68
Lamellipalpodes annandalei
Mimophaeopterus wittmeri
79
Picodrilus limbellus
62
Flabellotreta fruhstorferi
50
Brachylampis blaisdelli
63
79
Drilaster auxillaris
Drilaster weyersi
100
Cyphonocerus ruficollis
65
Pollaclasis bifaria
100
Pristolycus sagulatus
Satolampyris dichroma
Bougeoisia antipoda
95
Curtos obscuricolor
80
Atyphella lychnus
92
Atyphella obsoleta
Hotaria parvula
93
79
Lampyroides syriaca
Luciola italica
67
Pygoluciola satoi
Colophotia praeusta
100
Pyrophanes similis
80
83
95
Pteroptyx fulminea
Pteroptyx cribella

Fig. 5. Branch support for strict consensus tree produced by 137 (type) species data set; numbers above internodes are jackknife support values greater than 50% obtained from 500 replications.

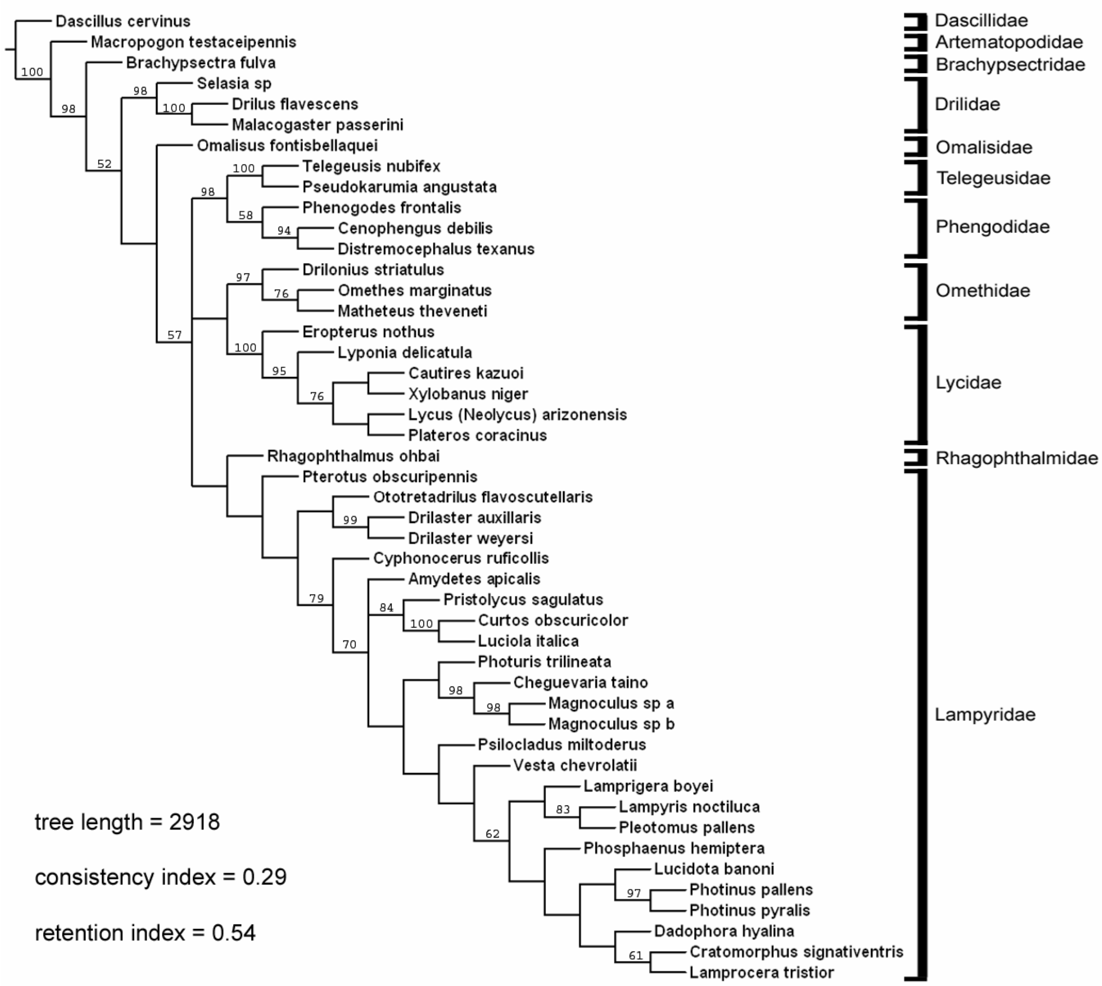


Fig. 6. A strict consensus of six most parsimonious trees obtained from 500 iterations of rachet using Nona/Winclada for a data set of 47 species (type species or its similar species of type genera) and 354 informative characters. Numbers above internodes refer to jackknife support values of 50% or more obtained from 500 replications.

Next five pages:

Fig. 7. Comparison of existing phylogenies of Cantharoidea, Elateroidea and Elateriformia by various authors.

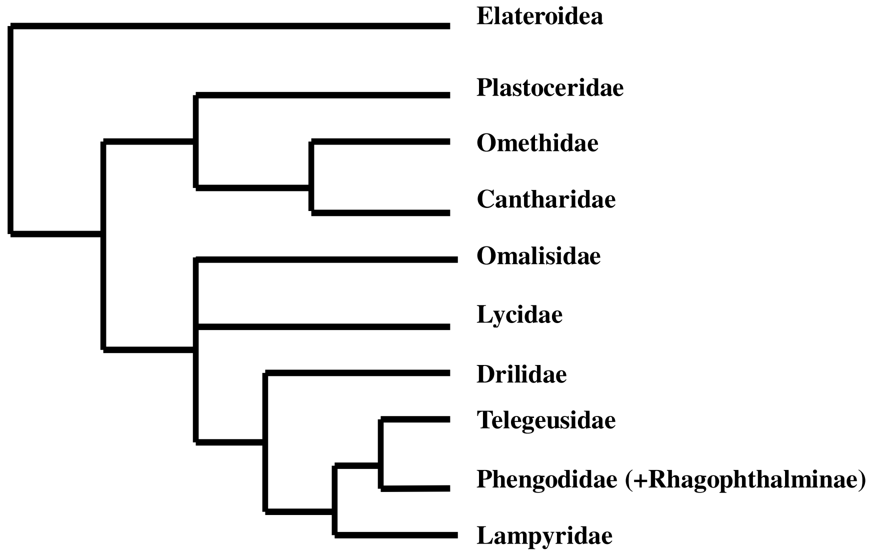


Fig. 7A. Crowson’s (1972) inferred phylogeny of Cantharoidea

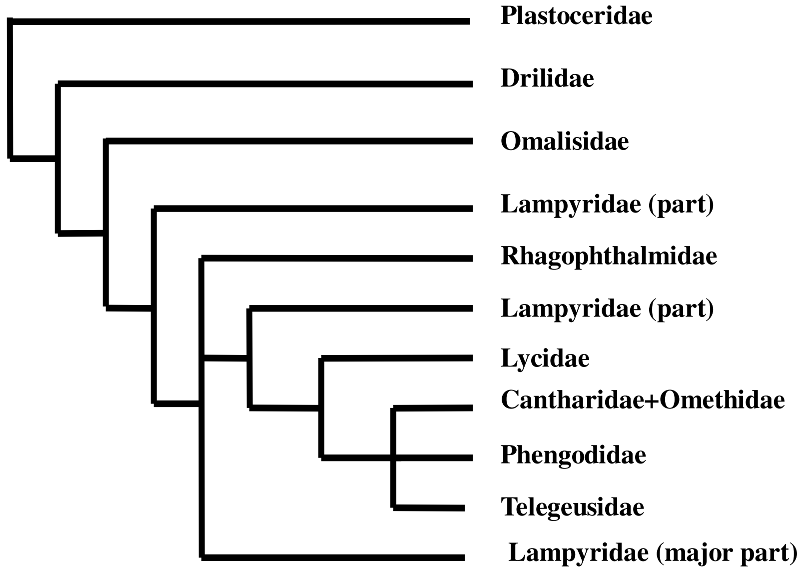


Fig. 7B. Branham and Wenzel’s (2001) parsimonious tree of cantharoid families based on morphological characters of males

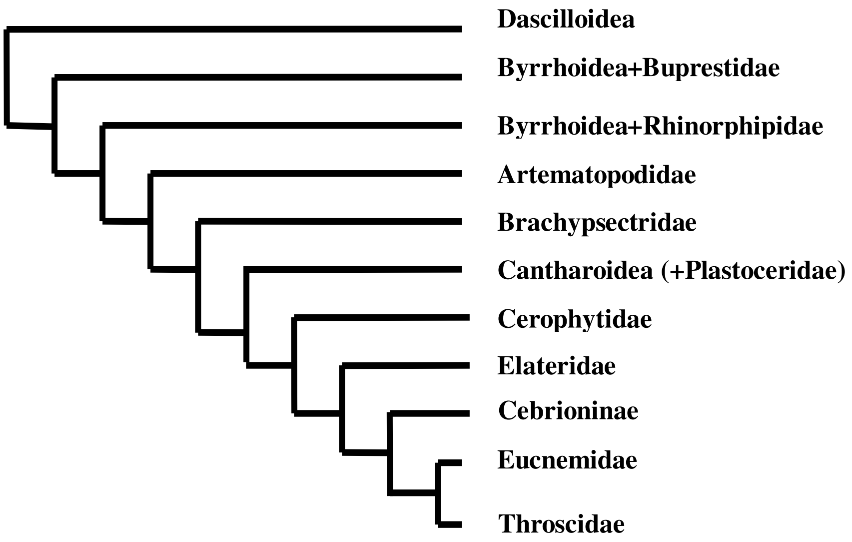


Fig. 7C. One of Lawrence's (1987) parsimonious trees of Elateroidea based on adult and larval characters

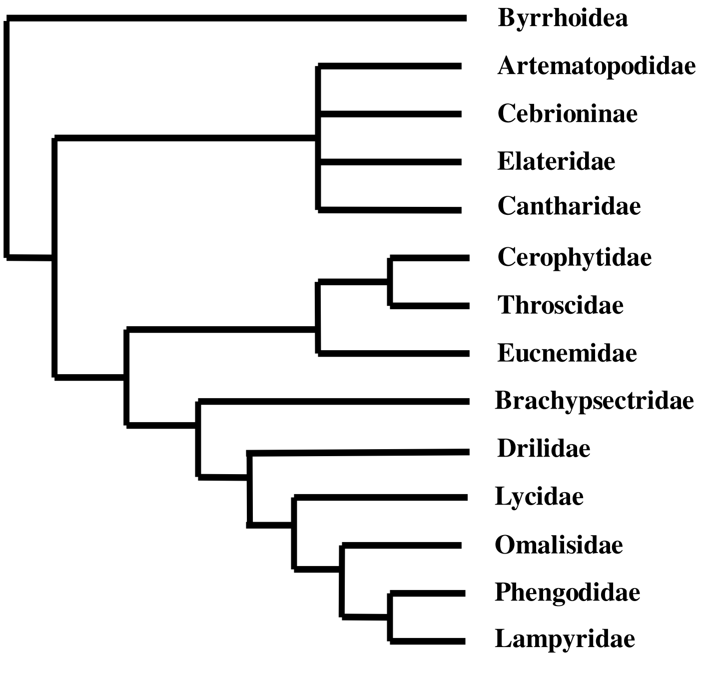


Fig. 7D. One of Beutel's (1995) most parsimonious trees of Elateroidea based on larval characters

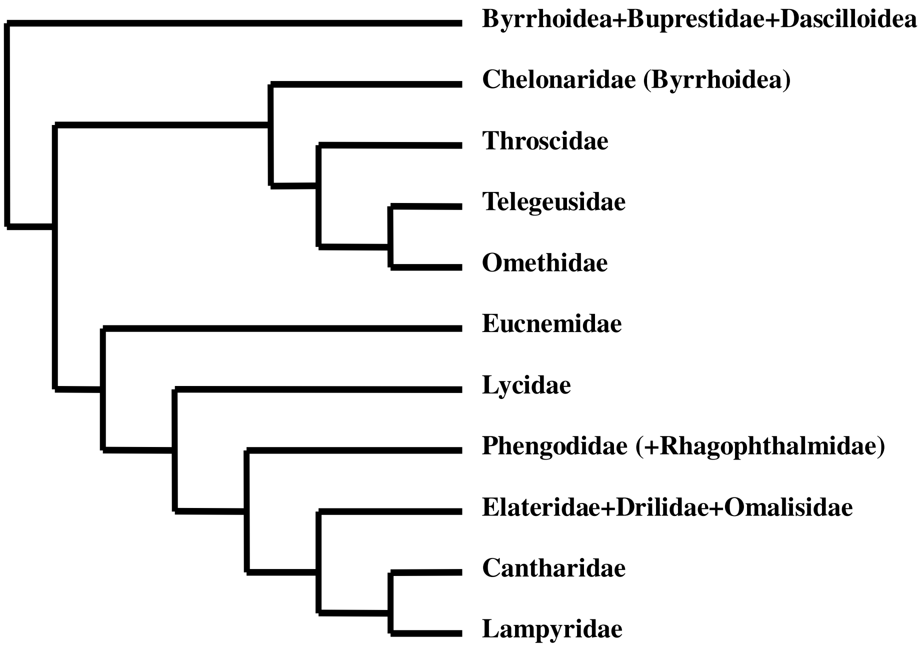


Fig. 7E. Bocakova et al.'s (2007) parsimonious tree of Elateroidea based on ClustalX alignment of four genes

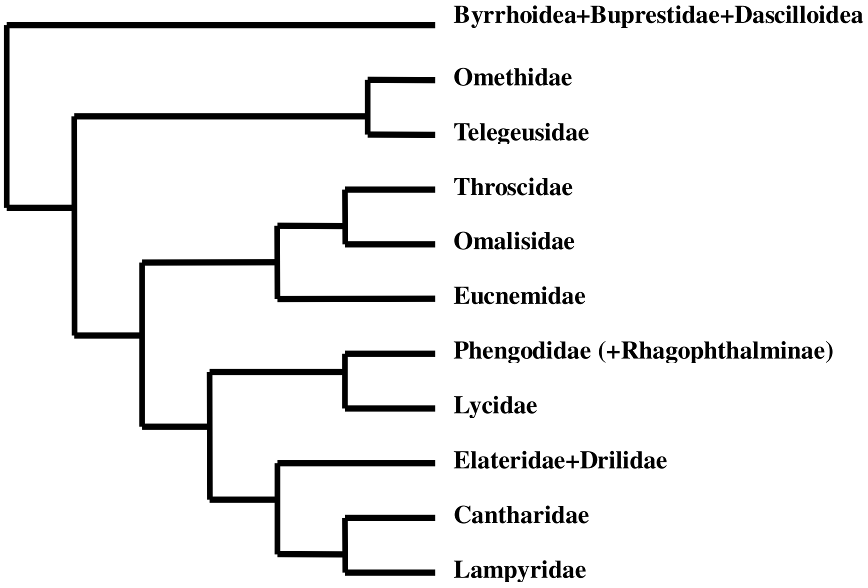


Fig. 7F. Bocakova et al.'s (2007) molecular tree of Elateroidea obtained from Bayesian analysis on BlastAlign alignment of four genes

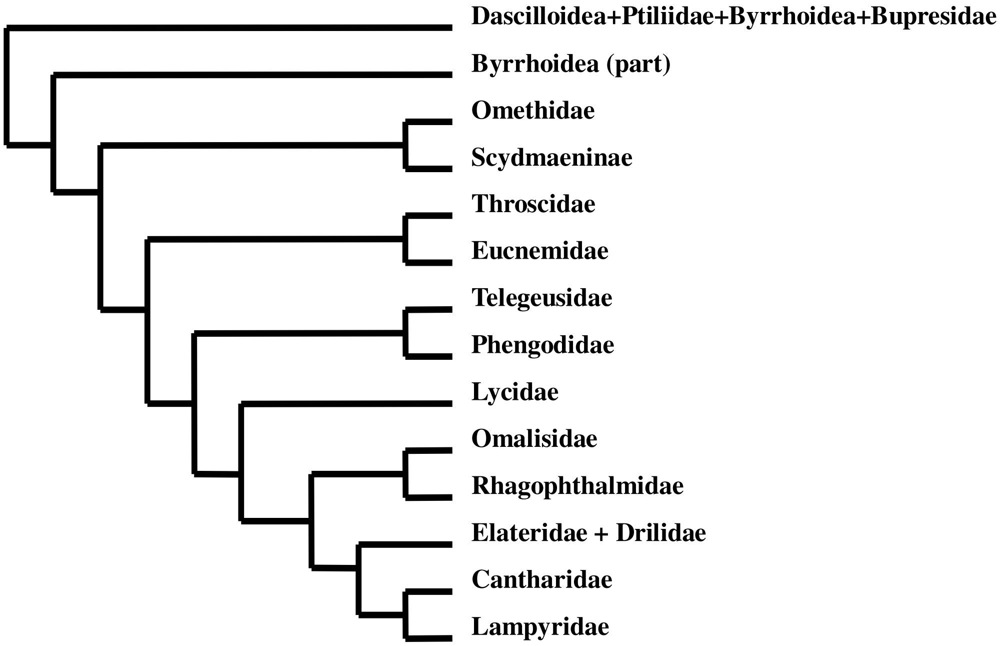


Fig. 7G. Hunt et al.'s (2007) most parsimonious tree of Elateriformia based on three genes from 1880 species

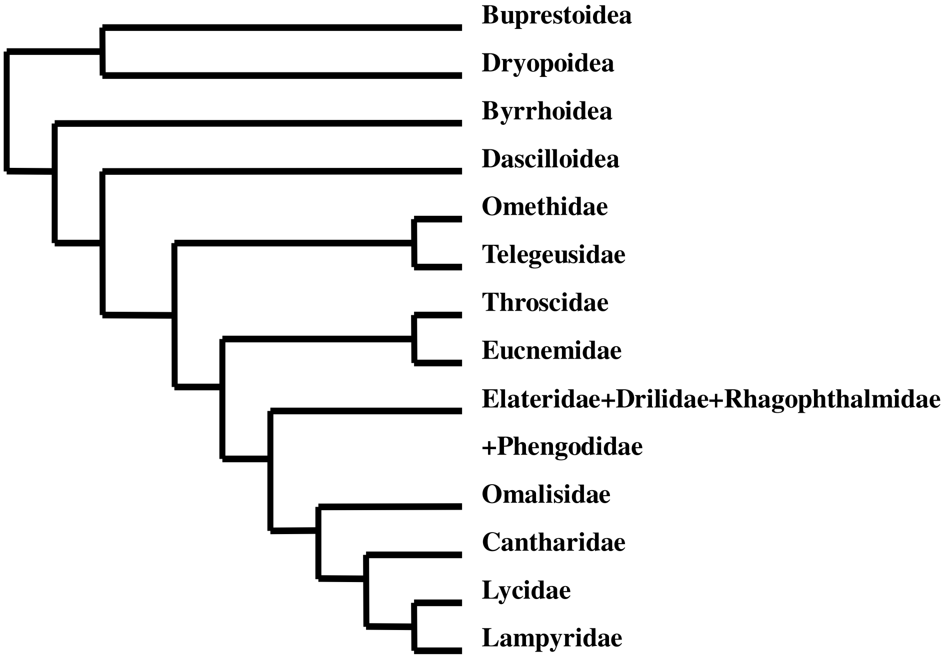


Fig. 7H. Hunt et al.'s (2007) molecular tree of Elateriformia obtained from Bayesian analysis based on three genes from 340 taxa

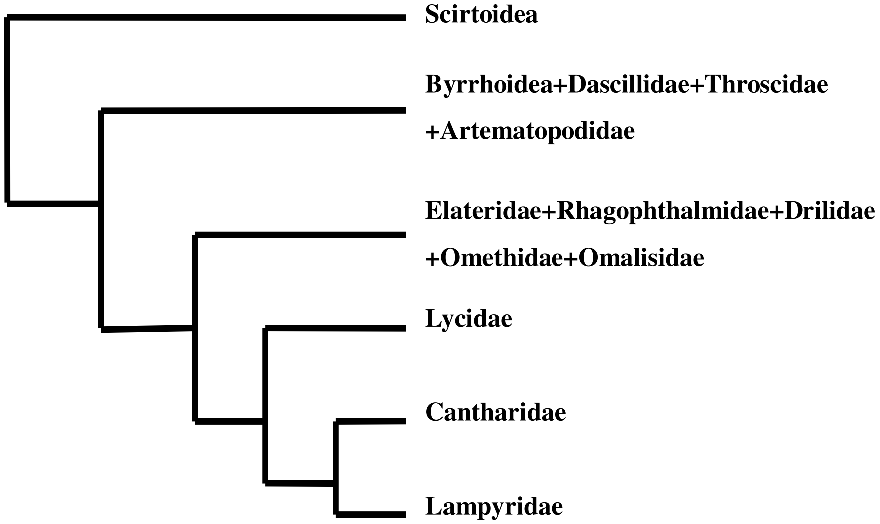
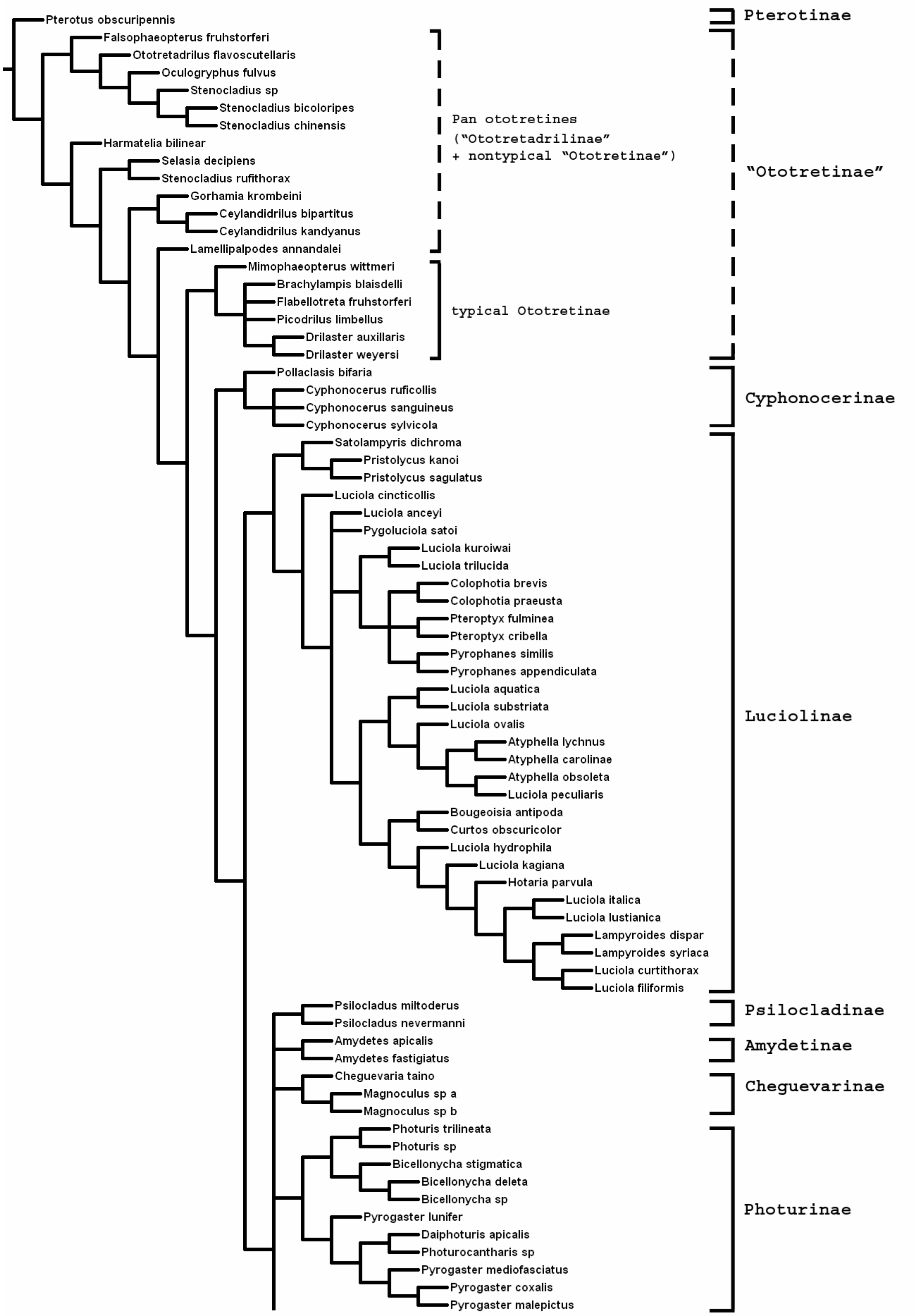


Fig. 7I. Sagegami-Oba et al.'s (2007) gene tree of Elateriformia obtained from distant method based on 18S ribosomal RNA sequences

Fig. 7. Comparison of existing phylogenies of Cantharoidea, Elateroidea and Elateriformia by various authors.

Next two pages:

Fig. 8. A revised classification of Lampyridae on the basis of a comprehensive phylogeny including 78% of described genera and two undescribed genera.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Stenocladius chinensis
Harmatelia bilinear
Selasia decipiens
Stenocladius rufithorax
Gorhamia krombeini
Ceylandidrilus bipartitus
Ceylandidrilus kandyanus
Lamellipalpodes annandalei
Mimophaeopterus wittmeri
Brachylampis blaisdelli
Flabellotreta fruhstorferi
Picodrilus limbellus
Drilaster auxillaris
Drilaster weyersi
Pollaclasis bifaria
Cyphonocerus ruficollis
Cyphonocerus sanguineus
Cyphonocerus sylvicola
Satolampyris dichroma
Pristolycus kanoi
Pristolycus sagulatus
Luciola cincticollis
Luciola anceyi
Pygoluciola satoi
Luciola kuroiwai
Luciola trilucida
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Colophotia praeusta
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Pteroptyx cribella
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Pyrophanes appendiculata
Luciola aquatica
Luciola substriata
Luciola ovalis
Atyphella lychnus
Atyphella carolinae
Atyphella obsoleta
Luciola peculiaris
Bougeoisia antipoda
Curtos obscuricolor
Luciola hydrophila
Luciola kagiana
Hotaria parvula
Luciola italica
Luciola lustianica
Lampyroides dispar
Lampyroides syriaca
Luciola curtithorax
Luciola filiformis
Psilocladus miltoderus
Psilocladus nevermanni
Amydetes apicalis
Amydetes fastigiatus
Cheguevaria taino
Magnoculus sp a
Magnoculus sp b
Photuris trilineata
Photuris sp
Bicellonycha stigmatica
Bicellonycha deleta
Bicellonycha sp
Pyrogaster lunifer
Daiphoturis apicalis
Photurocantharis sp
Pyrogaster mediofasciatus
Pyrogaster coxalis
Pyrogaster malepictus
Pan ototretines
("Ototretadrilinae"
+ nontypical "Ototretinae")
typical Ototretinae
Pterotinae
"Ototretinae"
Cyphonocerinae
Luciolinae
Psilocladinae
Amydetinae
Cheguevarinae
Photurinae

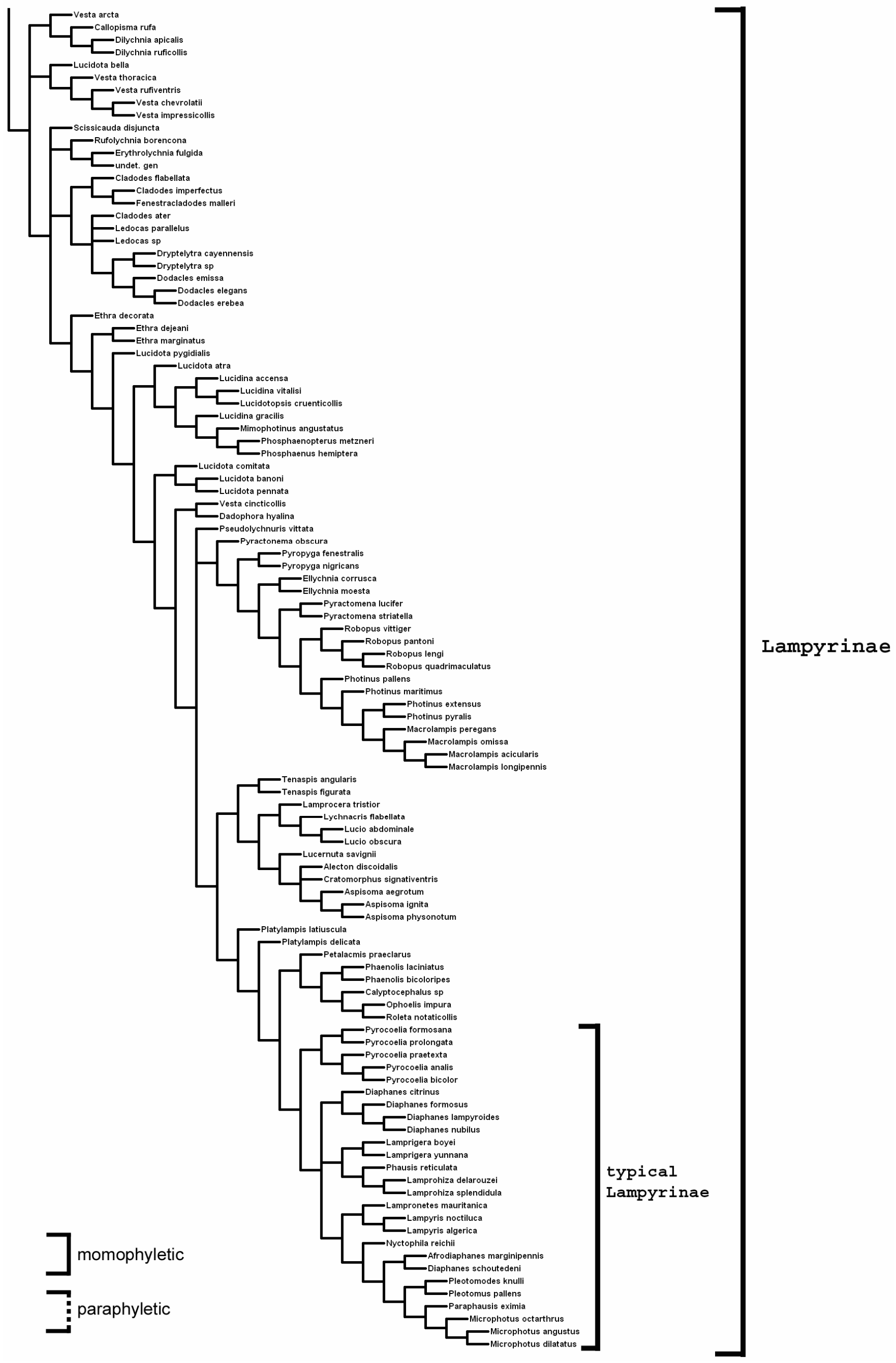


Fig. 8. A revised classification of Lampyridae on the basis of a comprehensive phylogeny including 78% of described genera and two undescribed genera.

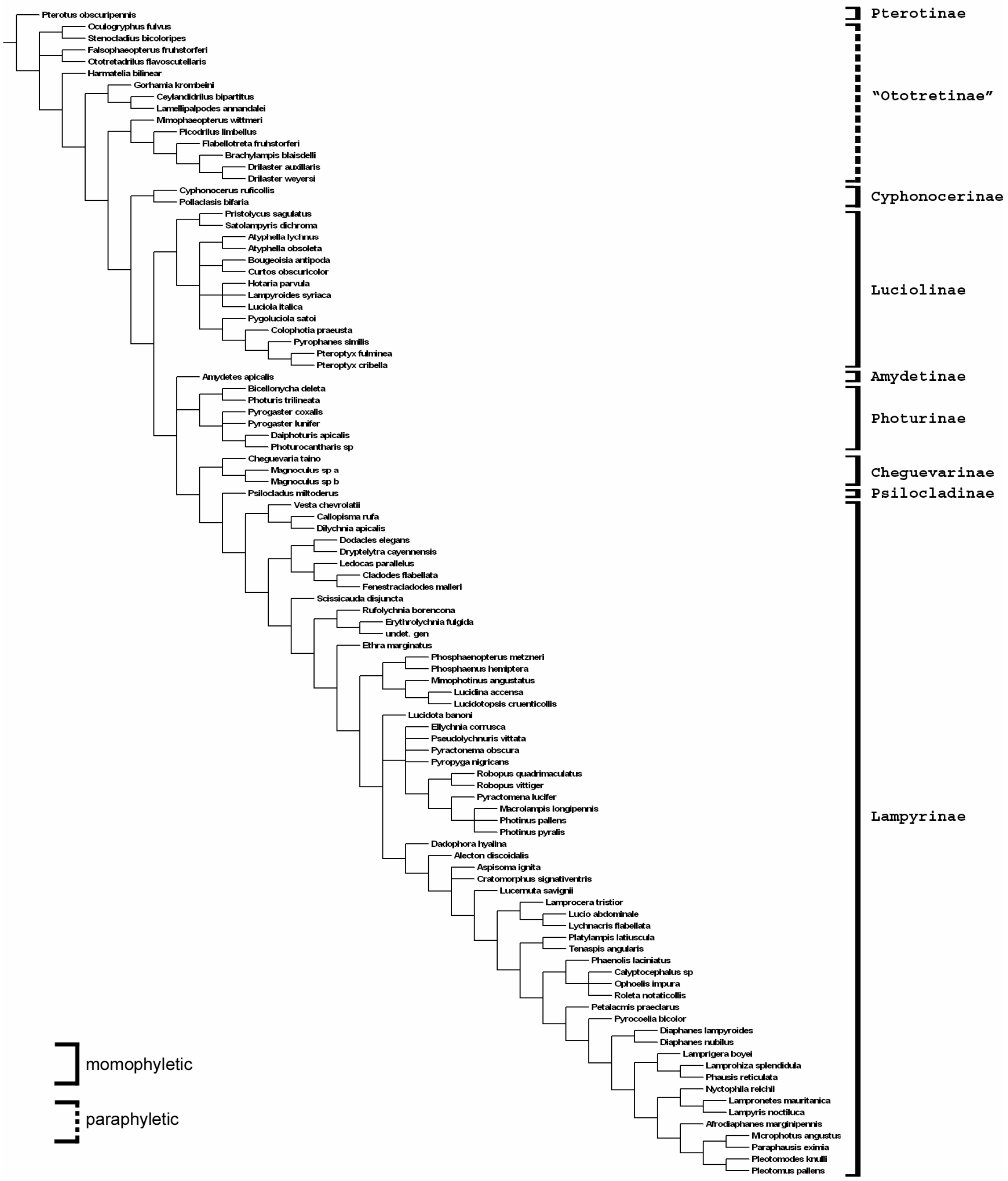


Fig. 9. Revised subfamilial classification of Lampyridae on the basis of a phylogeny including type species or their similar representative of 78% described genera and two undescribed genera.

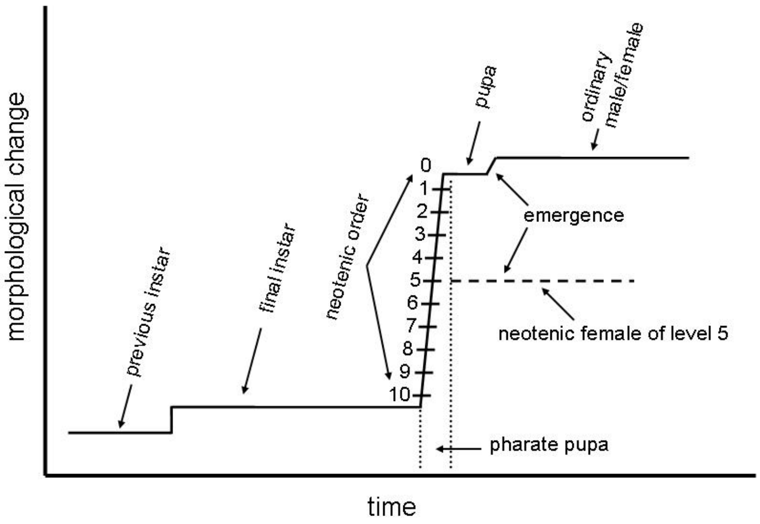
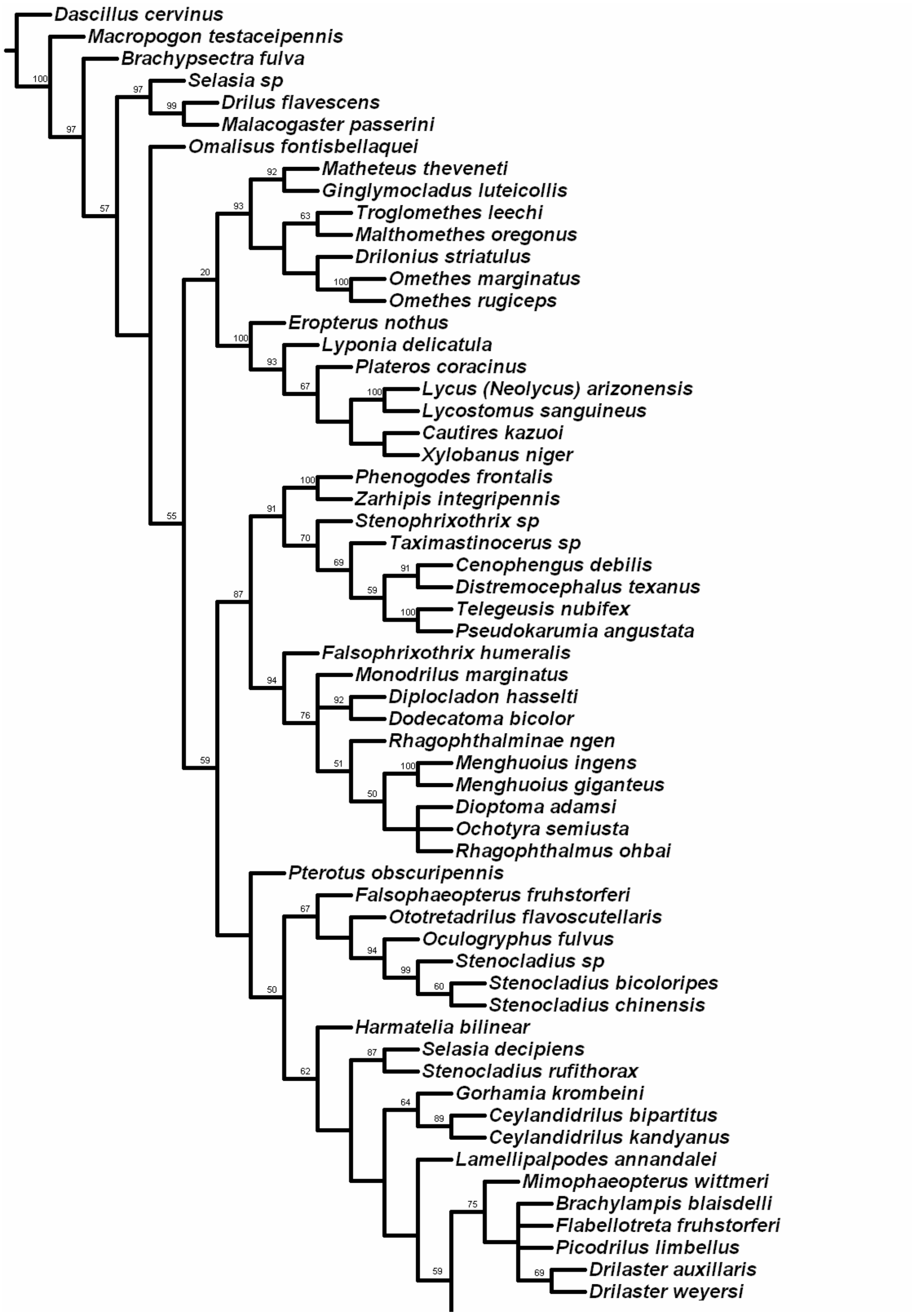


Fig.10. Ontogenetic trajectory of Cicero's (1988) hypothesis of gradient neoteny. Major transformation occurs in the pharate pupal stage and shows sequential changes in morphology. The lower the value, the fewer larval characters retained. Ordinary, fully imaginal (level 0) adults complete the whole process while neotenic females quit their transformation early in the pharate pupal stage and thus are more or less larval-like in relation to the males and ordinary females. By this concept the extraordinary dimorphism is asserted to be derived from neoteny rather than merely autapomorphic adult traits, and are able to determine the heterochronic process involved (e.g., hypomorphosis).

Next four pages:

Fig. 11. Branch support for strict consensus tree produced by data set with additive coding for the neotenic character; numbers above internodes refer to jackknife support values greater than 50% obtained from 500 replications.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Selasia sp
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Malacogaster passerini
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92
Matheteus theveneti
Ginglymocladus luteicollis
93
63
Troglomethes leechi
Malthomethes oregonus
57
Drilonius striatulus
20
100
Omethes marginatus
Omethes rugiceps
Eropterus nothus
100
Lyponia delicatula
93
Plateros coracinus
67
100
Lycus (Neolycus) arizonensis
Lycostomus sanguineus
Cautires kazuoi
Xylobanus niger
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Phenogodes frontalis
Zarhipis integripennis
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55
Stenophrixothrix sp
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Taximastinocerus sp
69
91
Cenophengus debilis
Distremocephalus texanus
59
100
Telegeusis nubifex
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Pseudokarumia angustata
Falsophrixothrix humeralis
94
Monodrilus marginatus
92
Diplocladon hasselti
76
Dodecatoma bicolor
Rhagophthalminae ngen
59
51
100
Menghuoius ingens
Menghuoius giganteus
50
Dioptoma adamsi
Ochotyra semiusta
Rhagophthalmus ohbai
Pterotus obscuripennis
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Falsophaeopterus fruhstorferi
Ototretadrilus flavoscutellaris
94
Oculogryphus fulvus
99
Stenocladius sp
60
Stenocladius bicoloripes
50
Stenocladius chinensis
Harmatelia bilinear
87
Selasia decipiens
Stenocladius rufithorax
62
64
Gorhamia krombeini
89
Ceylandidrilus bipartitus
Ceylandidrilus kandyanus
Lamellipalpodes annandalei
Mimophaeopterus wittmeri
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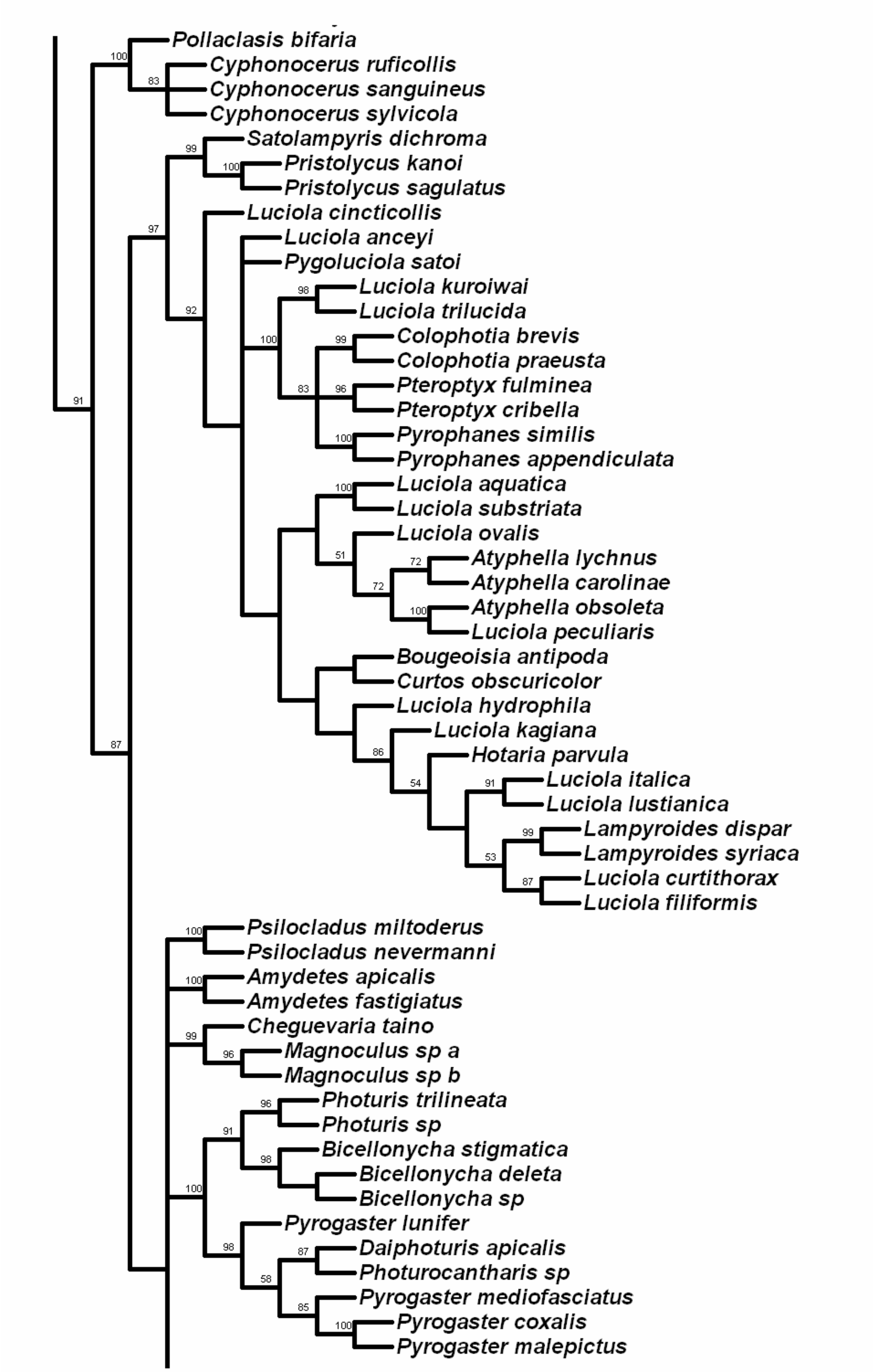
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Pristolycus kanoi
Pristolycus sagulatus
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Luciola cincticollis
Luciola anceyi
Pygoluciola satoi
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Luciola kuroiwai
Luciola trilucida
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100
99
Colophotia brevis
Colophotia praeusta
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Pyrophanes appendiculata
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Luciola substriata
Luciola ovalis
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Atyphella lychnus
Atyphella carolinae
72
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Atyphella obsoleta
Luciola peculiaris
Bougeoisia antipoda
Curtos obscuricolor
Luciola hydrophila
Luciola kagiana
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Hotaria parvula
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91
Luciola italica
Luciola lustianica
99
Lampyroides dispar
Lampyroides syriaca
53
87
Luciola curtithorax
Luciola filiformis
100
Psilocladus miltoderus
Psilocladus nevermanni
100
Amydetes apicalis
Amydetes fastigiatus
Cheguevaria taino
99
96
Magnoculus sp a
Magnoculus sp b
96
Photuris trilineata
Photuris sp
91
Bicellonycha stigmatica
98
Bicellonycha deleta
Bicellonycha sp
100
Pyrogaster lunifer
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Pyrogaster mediofasciatus
85
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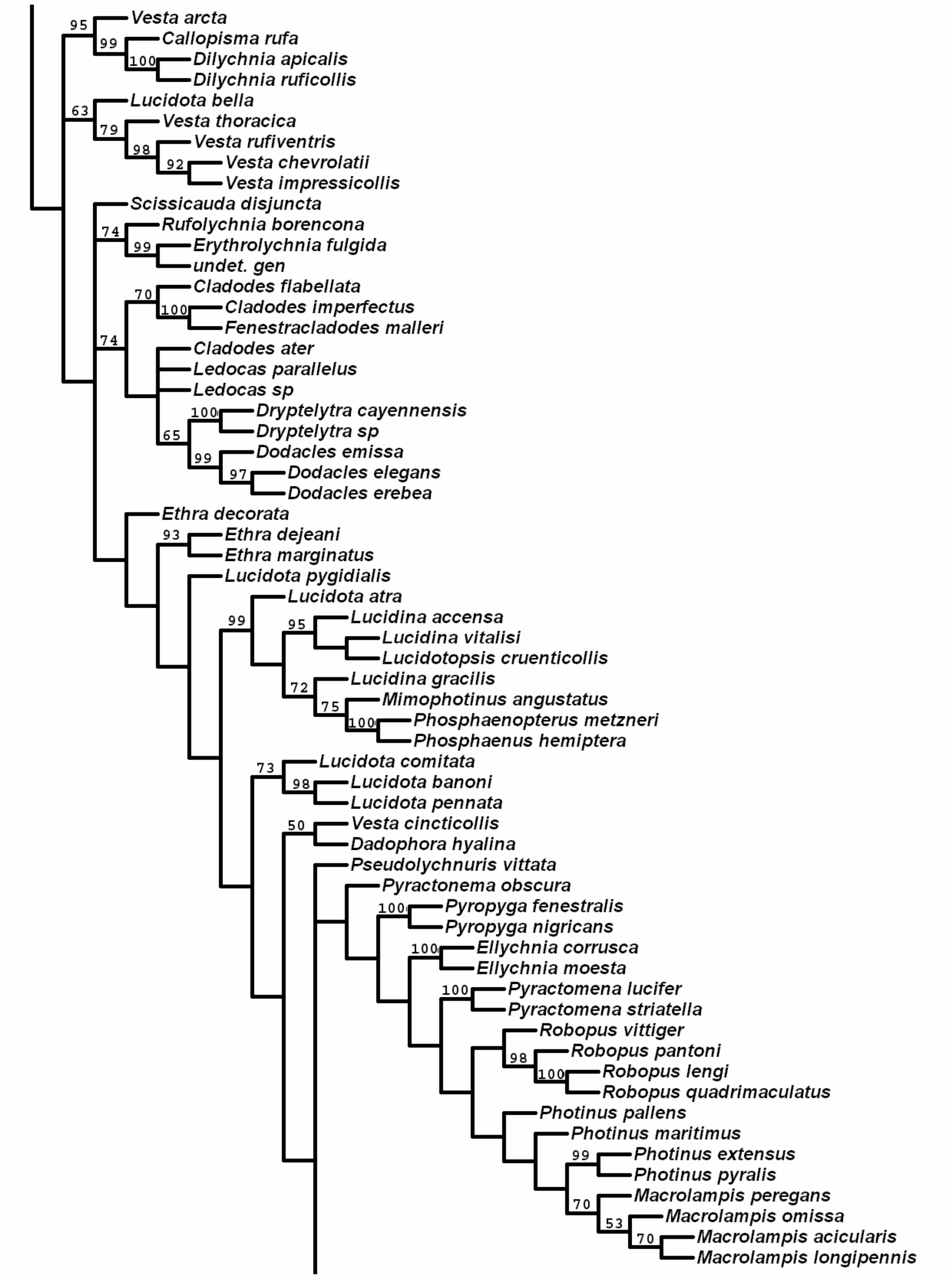
Pyrogaster malepictus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Vesta rufiventris
92
Vesta chevrolatii
Vesta impressicollis
Scissicauda disjuncta
74
Rufolychnia borencona
99
Erythrolychnia fulgida
undet. gen
70
Cladodes flabellata
100
Cladodes imperfectus
Fenestracladodes malleri
74
Cladodes ater
Ledocas parallelus
Ledocas sp
100
Dryptelytra cayennensis
Dryptelytra sp
65
Dodacles emissa
99
97
Dodacles elegans
Dodacles erebea
Ethra decorata
93
Ethra dejeani
Ethra marginatus
Lucidota pygidialis
99
Lucidota atra
95
Lucidina accensa
Lucidina vitalisi
Lucidotopsis cruenticollis
72
Lucidina gracilis
75
Mimophotinus angustatus
100
Phosphaenopterus metzneri
Phosphaenus hemiptera
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Lucidota comitata
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Lucidota banoni
Lucidota pennata
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Dadophora hyalina
Pseudolychnuris vittata
Pyractonema obscura
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Pyropyga fenestralis
Pyropyga nigricans
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Ellychnia corrusca
Ellychnia moesta
100
Pyractomena lucifer
Pyractomena striatella
Robopus vittiger
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Robopus pantoni
100
Robopus lengi
Robopus quadrimaculatus
Photinus pallens
Photinus maritimus
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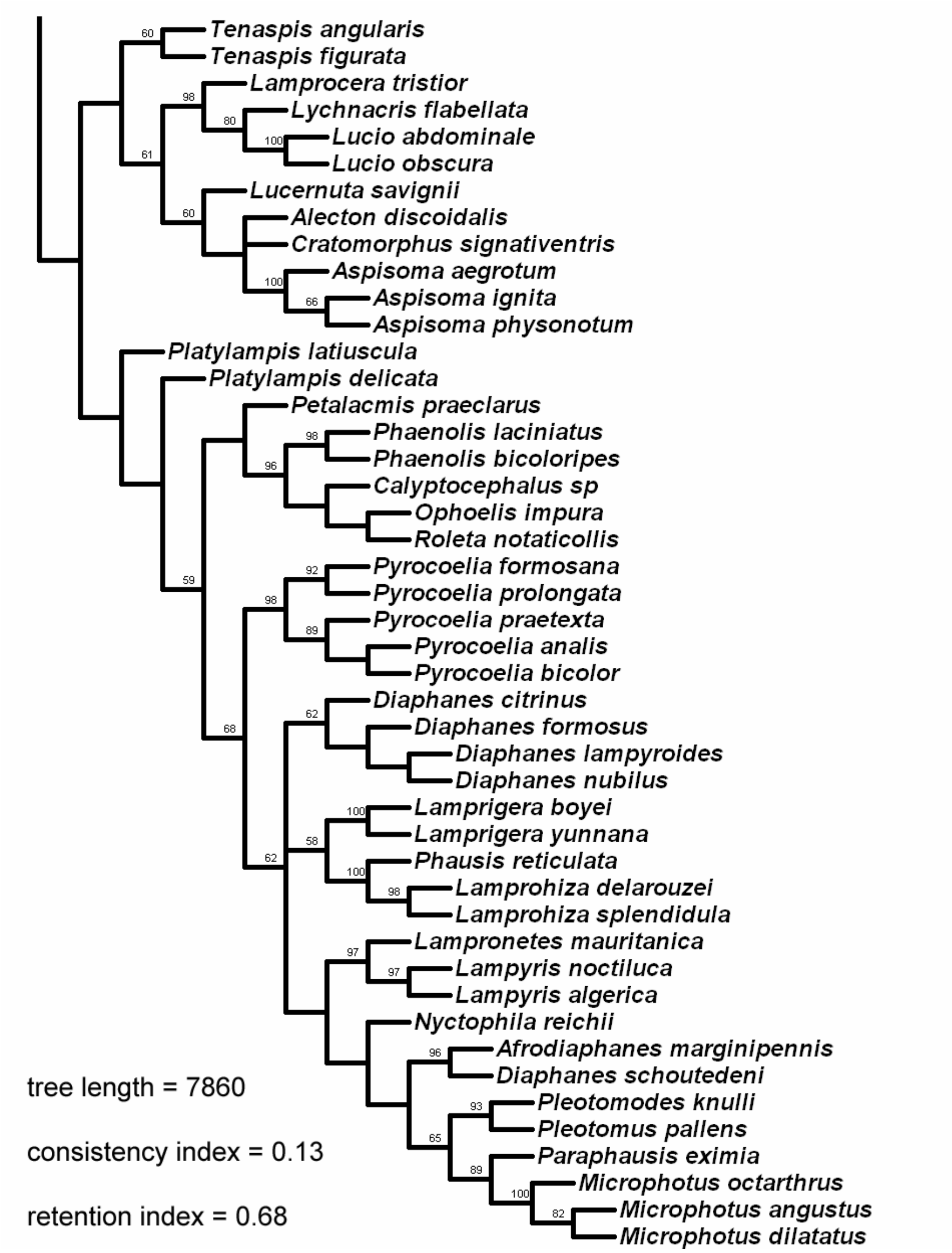
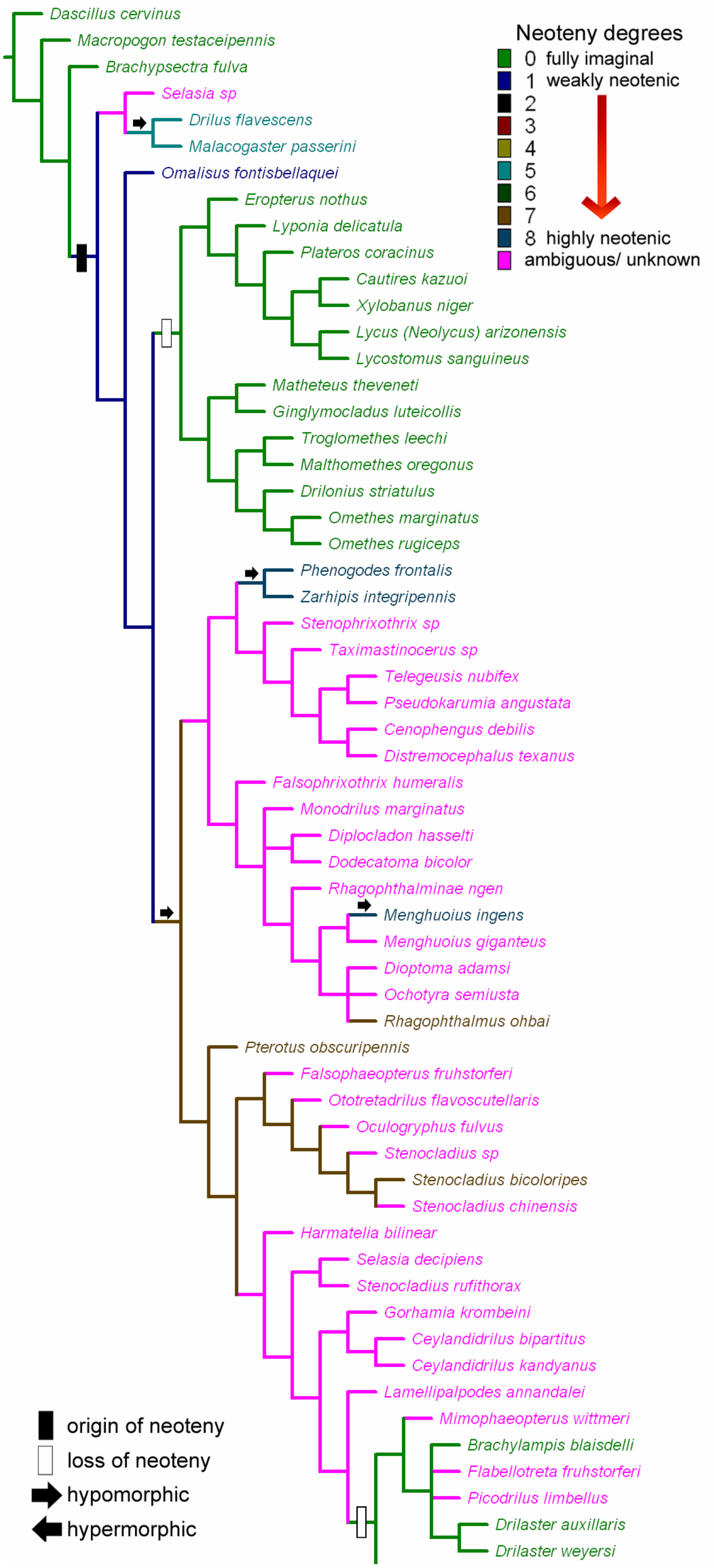


Fig. 11. Branch support for strict consensus tree produced by data set with additive coding for the neotenic character; numbers above internodes refer to jackknife support values greater than 50% obtained from 500 replications.

Next four pages:

Fig. 12. Evolution of neoteny in elateroid/cantharoid families, with emphasis on Lampyridae. The consensus tree resulted from 1008 most parsimonious trees obtained from a 220X411 data set with additive coding of the neotenic character (see text). Unambiguous optimization was applied, showing transition of neoteny across the tree.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Lyponia delicatula
Plateros coracinus
Cautires kazuoi
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Ginglymocladus luteicollis
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Stenocladius rufithorax
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Ceylandidrilus bipartitus
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Lamellipalpodes annandalei
Mimophaeopterus wittmeri
Brachylampis blaisdelli
Flabellotreta fruhstorferi
Picodrilus limbellus
Drilaster auxillaris
Drilaster weyersi
Neoteny degrees
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2
3
4
5
6
7
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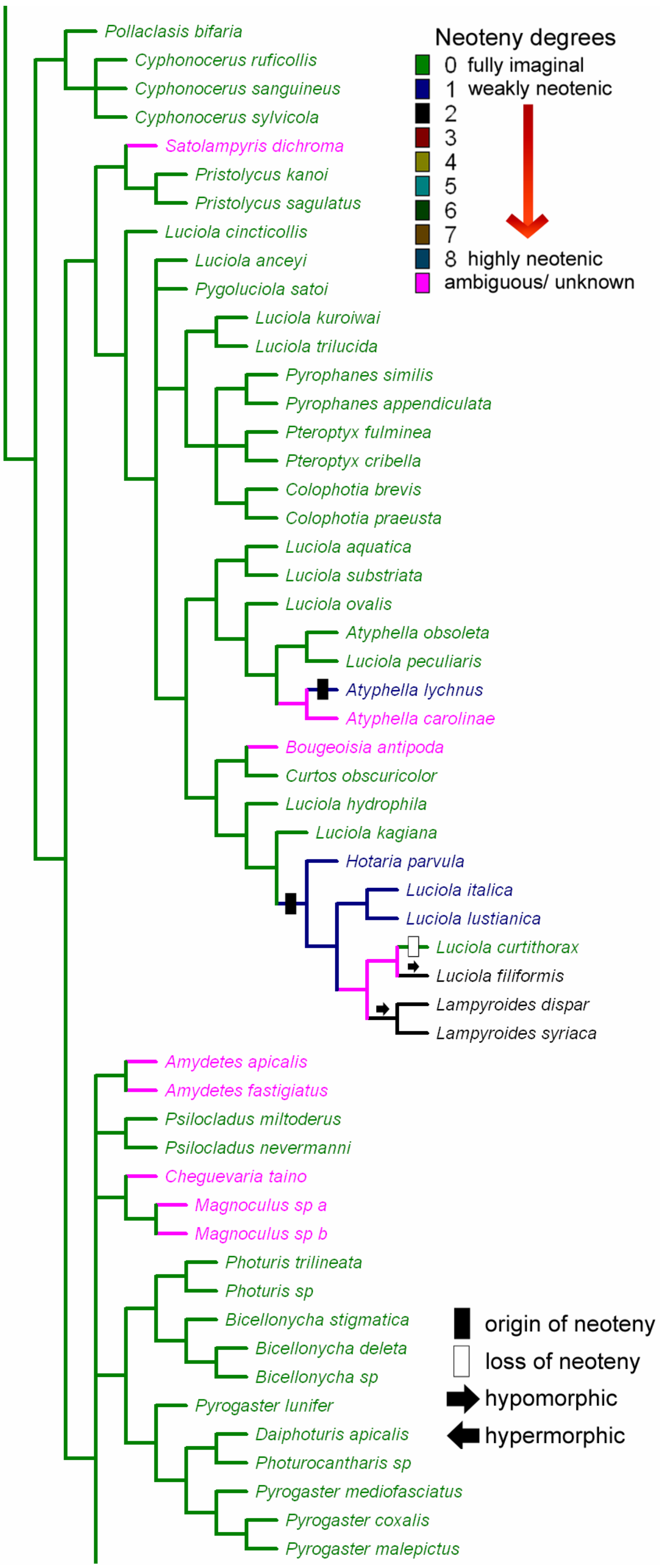
ambiguous/ unknown
origin of neoteny
loss of neoteny
hypomorphic
hypermorphic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Pyrophanes similis
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Psilocladus nevermanni
Cheguevaria taino
Magnoculus sp a
Magnoculus sp b
Photuris trilineata
Photuris sp
Bicellonycha stigmatica
Bicellonycha deleta
Bicellonycha sp
Pyrogaster lunifer
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Pyrogaster mediofasciatus
Pyrogaster coxalis
Pyrogaster malepictus
Neoteny degrees
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origin of neoteny
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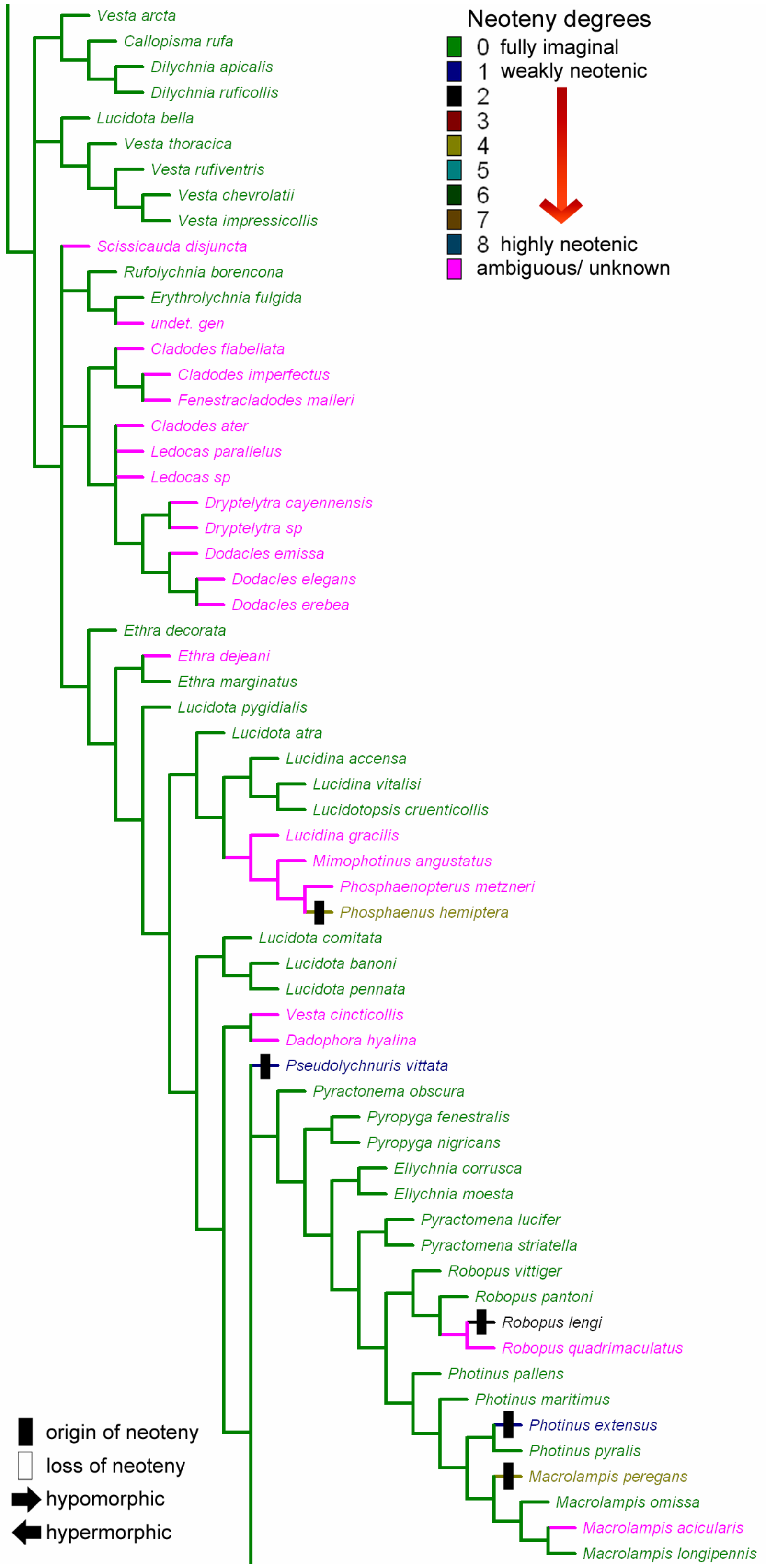
Neoteny degrees
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Vesta chevrolatii
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Erythrolychnia fulgida
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Ledocas sp
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Dryptelytra sp
Dodacles emissa
Dodacles elegans
Dodacles erebea
Ethra decorata
Ethra dejeani
Ethra marginatus
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Lucidota atra
Lucidina accensa
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Lucidotopsis cruenticollis
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Mimophotinus angustatus
Phosphaenopterus metzneri
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Lucidota comitata
Lucidota banoni
Lucidota pennata
Vesta cincticollis
Dadophora hyalina
Pseudolychnuris vittata
Pyractonema obscura
Pyropyga fenestralis
Pyropyga nigricans
Ellychnia corrusca
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Robopus vittiger
Robopus pantoni
Robopus lengi
Robopus quadrimaculatus
Photinus pallens
Photinus maritimus
Photinus extensus
Photinus pyralis
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origin of neoteny
loss of neoteny
hypomorphic
hypermorphic

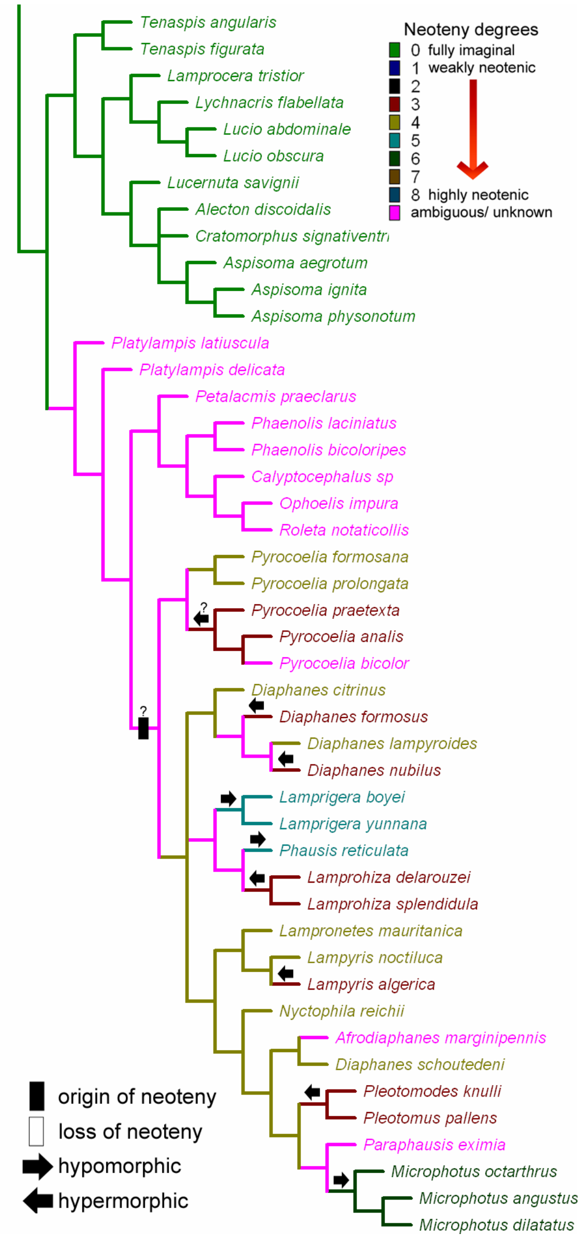

Fig. 12. Evolution of neoteny in elateroid/cantharoid families, with emphasis on Lampyridae. The consensus tree resulted from 1008 most parsimonious trees obtained from a 220X411 data set with additive coding of the neotenic character (see text). Unambiguous optimization was applied, showing transition of neoteny across the tree.

Next four pages:

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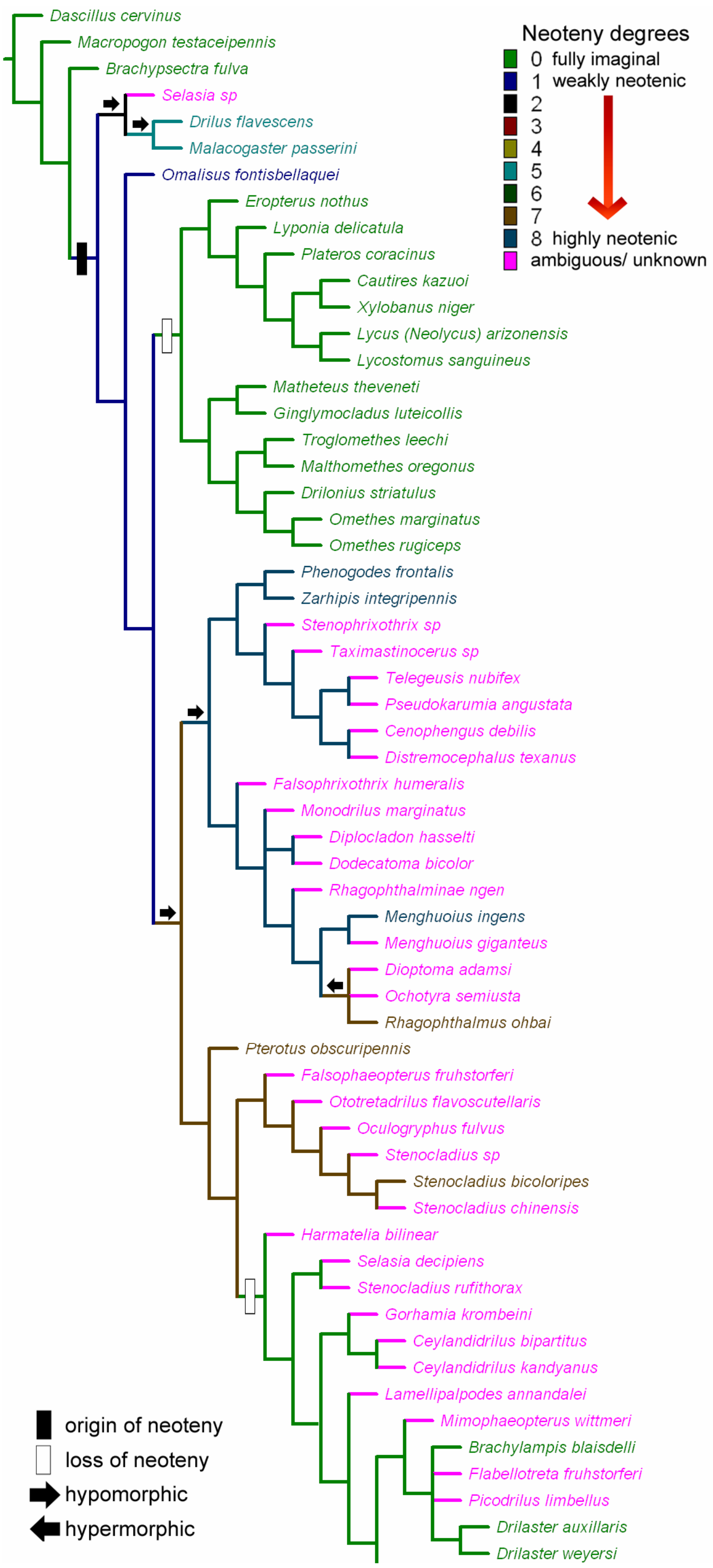
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Troglomethes leechi
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Taximastinocerus sp
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Stenocladius chinensis
Harmatelia bilinear
Selasia decipiens
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Gorhamia krombeini
Ceylandidrilus bipartitus
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Lamellipalpodes annandalei
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Brachylampis blaisdelli
Flabellotreta fruhstorferi
Picodrilus limbellus
Drilaster auxillaris
Drilaster weyersi
Neoteny degrees
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3
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7
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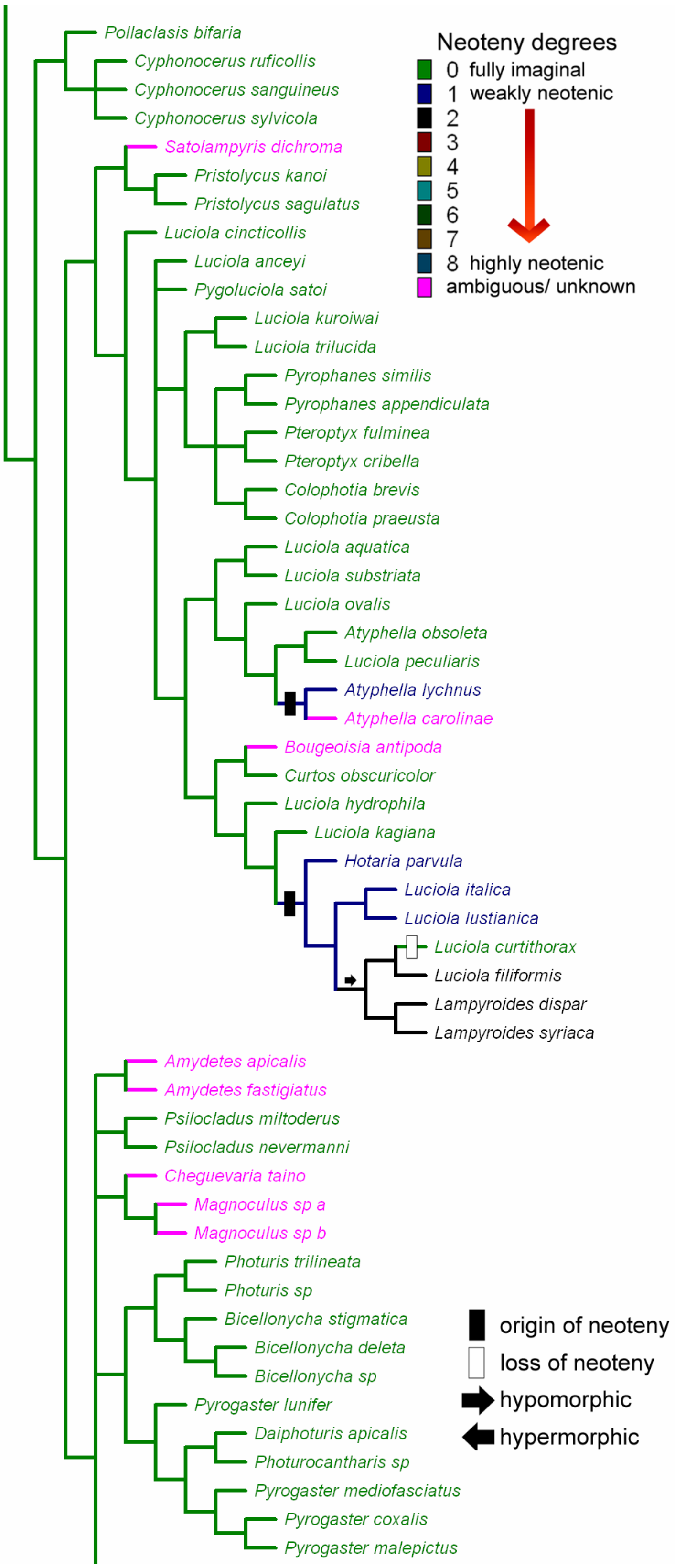
origin of neoteny
loss of neoteny
hypomorphic
hypermorphic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🟦 1 weakly neotenic
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■ 6
🟫 7
■ 8 highly neotenic
🟪 ambiguous/ unknown
Pollaclasis bifaria
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Cyphonocerus sanguineus
Cyphonocerus sylvicola
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Pristolycus kanoi
Pristolycus sagulatus
Luciola cincticollis
Luciola anceyi
Pygoluciola satoi
Luciola kuroiwai
Luciola trilucida
Pyrophanes similis
Pyrophanes appendiculata
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Atyphella obsoleta
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Hotaria parvula
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Psilocladus miltoderus
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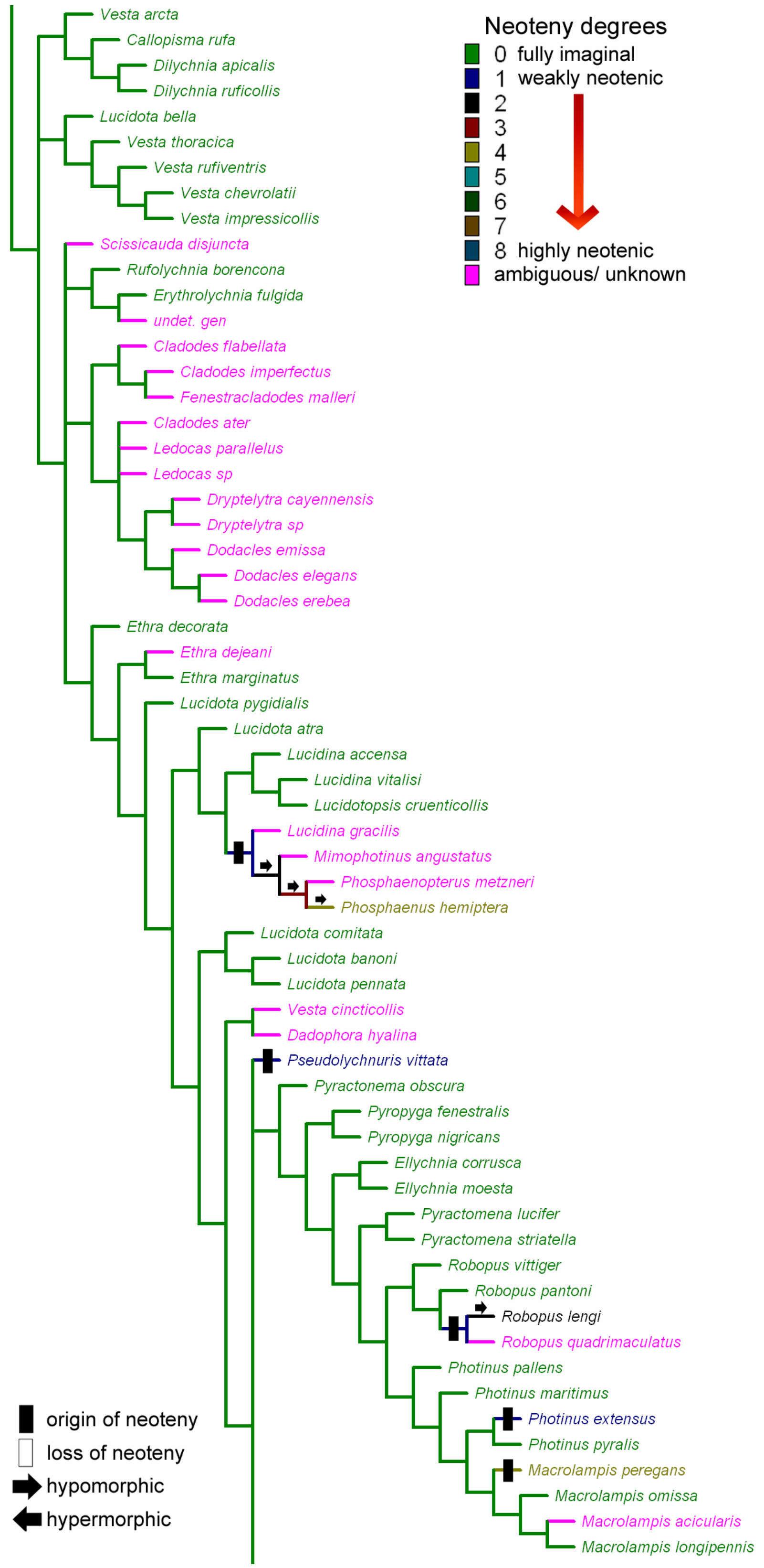
Cheguevaria taino
Magnoculus sp a
Magnoculus sp b
Photuris trilineata
Photuris sp
Bicellonycha stigmatica
Bicellonycha deleta
Bicellonycha sp
Pyrogaster lunifer
Daiphoturis apicalis
Photurocantharis sp
Pyrogaster mediofasciatus
Pyrogaster coxalis
Pyrogaster malepictus
▮ origin of neoteny
▯ loss of neoteny
➡ hypomorphic
⬅ hypermorphic


Neoteny degrees
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1 weakly neotenic
2
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4
5
6
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ambiguous/ unknown
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Callopisma rufa
Dilychnia apicalis
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Cladodes imperfectus
Fenestracladodes malleri
Cladodes ater
Ledocas parallelus
Ledocas sp
Dryptelytra cayennensis
Dryptelytra sp
Dodacles emissa
Dodacles elegans
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Ethra decorata
Ethra dejeani
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Lucidota pygidialis
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Phosphaenopterus metzneri
Phosphaenus hemiptera
Lucidota comitata
Lucidota banoni
Lucidota pennata
Vesta cincticollis
Dadophora hyalina
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Pyractonema obscura
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Pyractomena lucifer
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Robopus vittiger
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Photinus pallens
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origin of neoteny
loss of neoteny
hypomorphic
hypermorphic

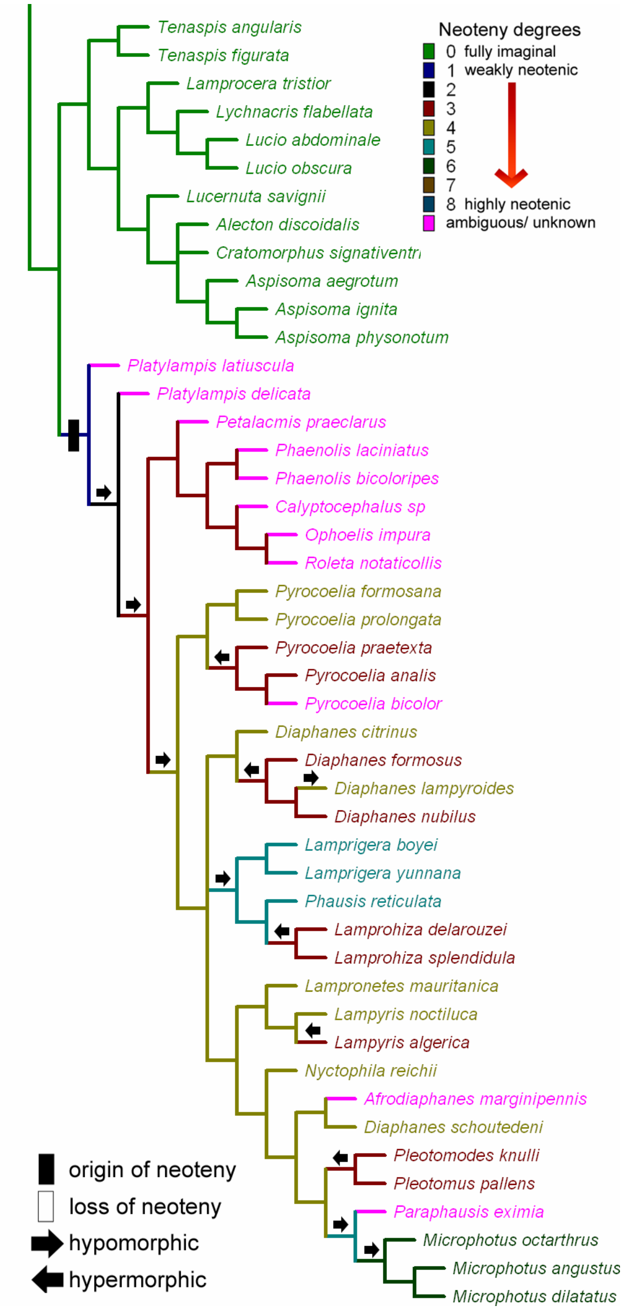
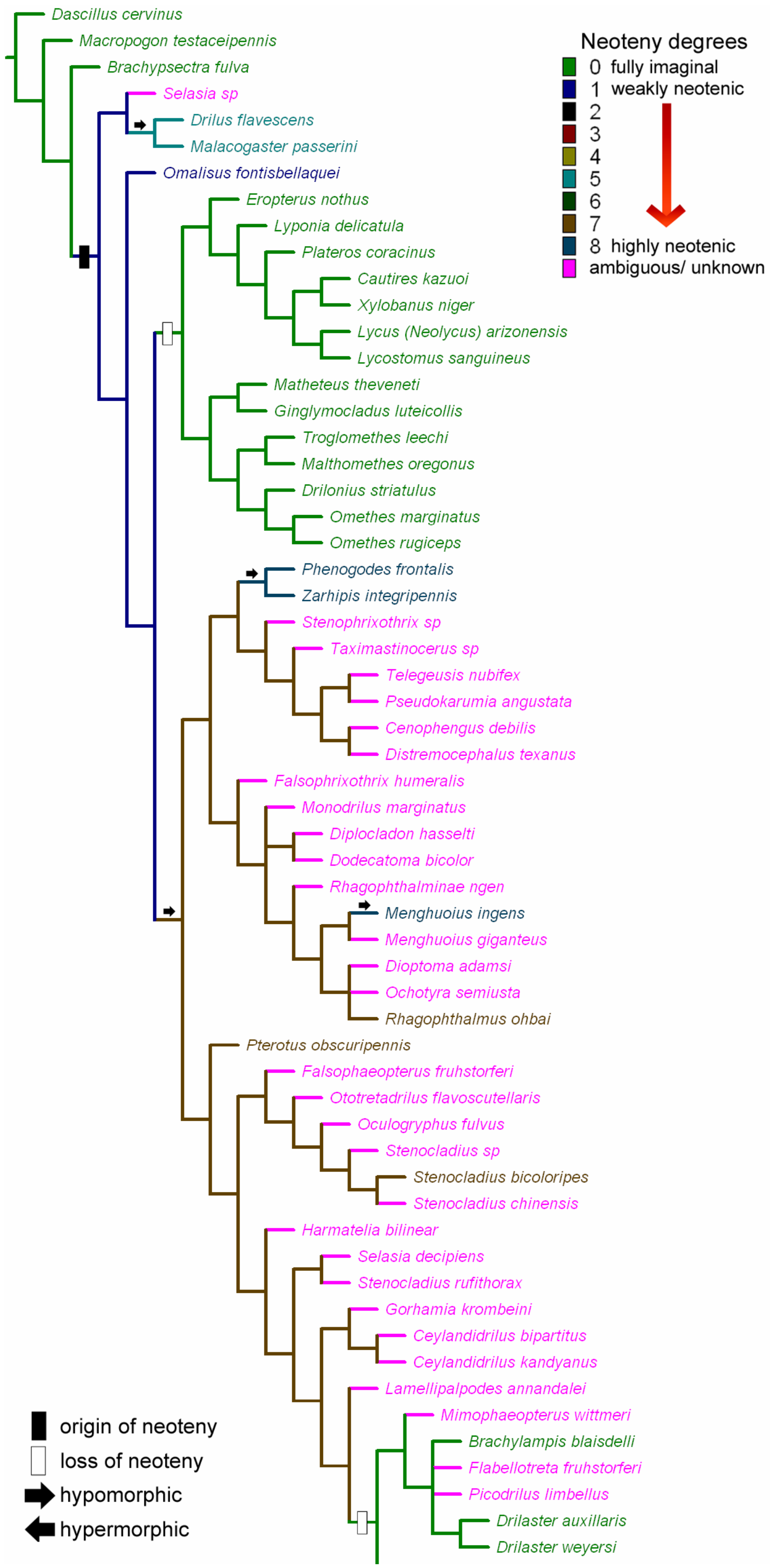


Fig. 13. Evolution of neoteny in elateroid/cantharoid families, with emphasis on Lampyridae. The consensus tree resulted from 1008 most parsimonious trees obtained from a 220X411 data set with additive coding of the neotenic character. ACCTRAN optimization was applied, showing transition of neoteny across the tree

Next four pages:

Fig. 14. Evolution of neoteny in elateroid/cantharoid families, with emphasis on Lampyridae. The consensus tree resulted from 1008 most parsimonious trees obtained from a 220X411 data set with additive coding of the neotenic character. DELTRAN optimization was applied, showing transition of neoteny across the tree.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Lyponia delicatula
Plateros coracinus
Cautires kazuoi
Xylobanus niger
Lycus (Neolycus) arizonensis
Lycostomus sanguineus
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Ginglymocladus luteicollis
Troglomethes leechi
Malthomethes oregonus
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Omethes marginatus
Omethes rugiceps
Phenogodes frontalis
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Taximastinocerus sp
Telegeusis nubifex
Pseudokarumia angustata
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Falsophrixothrix humeralis
Monodrilus marginatus
Diplocladon hasselti
Dodecatoma bicolor
Rhagophthalminae ngen
Menghuoius ingens
Menghuoius giganteus
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Ochotyra semiusta
Rhagophthalmus ohbai
Pterotus obscuripennis
Falsophaeopterus fruhstorferi
Ototretadrilus flavoscutellaris
Oculogryphus fulvus
Stenocladius sp
Stenocladius bicoloripes
Stenocladius chinensis
Harmatelia bilinear
Selasia decipiens
Stenocladius rufithorax
Gorhamia krombeini
Ceylandidrilus bipartitus
Ceylandidrilus kandyanus
Lamellipalpodes annandalei
Mimophaeopterus wittmeri
Brachylampis blaisdelli
Flabellotreta fruhstorferi
Picodrilus limbellus
Drilaster auxillaris
Drilaster weyersi
Neoteny degrees
0 fully imaginal
1 weakly neotenic
2
3
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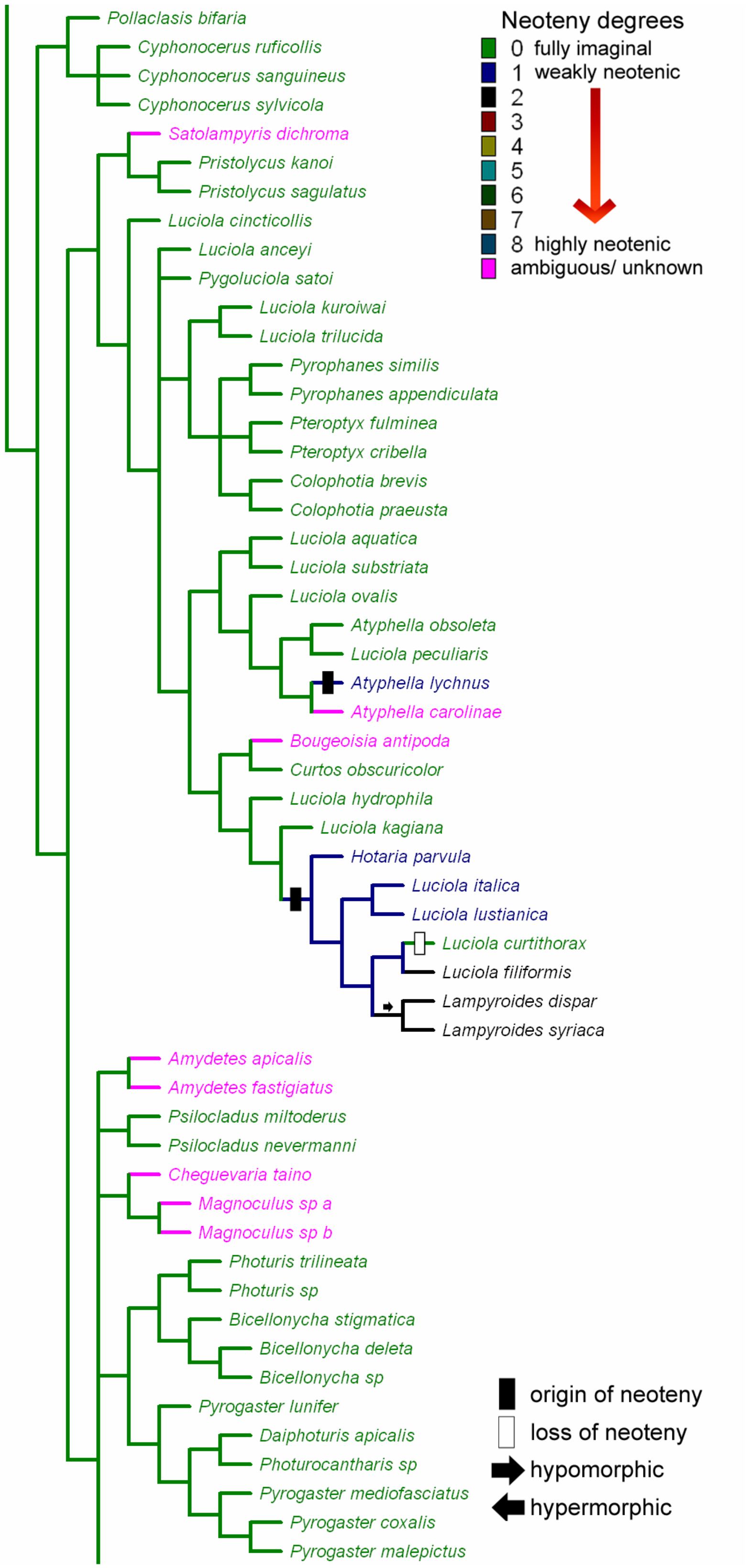
7
8 highly neotenic
ambiguous/ unknown
origin of neoteny
loss of neoteny
hypomorphic
hypermorphic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Luciola kuroiwai
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Pyrophanes appendiculata
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Pteroptyx cribella
Colophotia brevis
Colophotia praeusta
Luciola aquatica
Luciola substriata
Luciola ovalis
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Luciola peculiaris
Atyphella lychnus
Atyphella carolinae
Bougeoisia antipoda
Curtos obscuricolor
Luciola hydrophila
Luciola kagiana
Hotaria parvula
Luciola italica
Luciola lustianica
Luciola curtithorax
Luciola filiformis
Lampyroides dispar
Lampyroides syriaca
Amydetes apicalis
Amydetes fastigiatus
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Psilocladus nevermanni
Cheguevaria taino
Magnoculus sp a
Magnoculus sp b
Photuris trilineata
Photuris sp
Bicellonycha stigmatica
Bicellonycha deleta
Bicellonycha sp
Pyrogaster lunifer
Daiphoturis apicalis
Photurocantharis sp
Pyrogaster mediofasciatus
Pyrogaster coxalis
Pyrogaster malepictus
Neoteny degrees
0 fully imaginal
1 weakly neotenic
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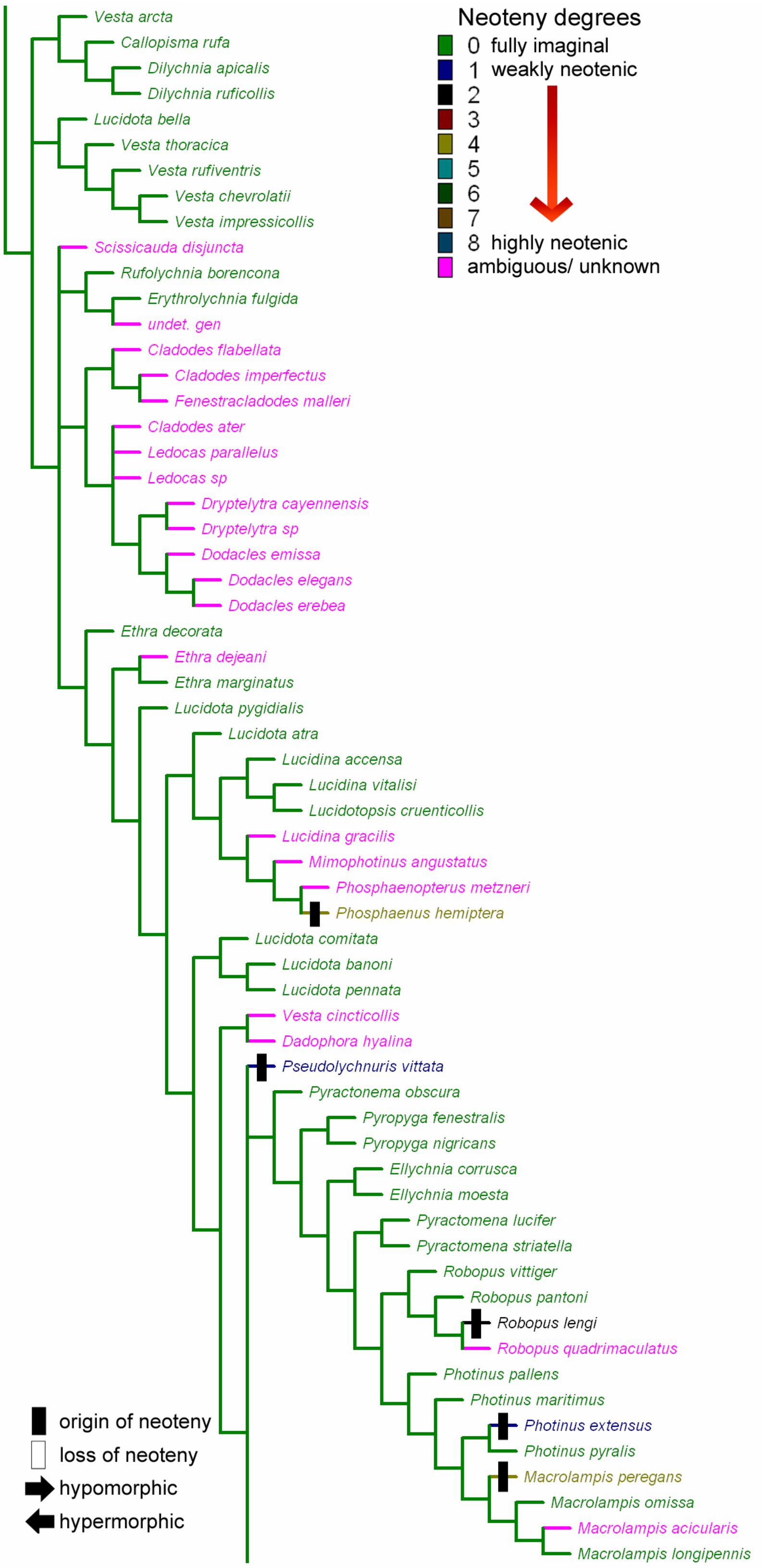
8 highly neotenic
ambiguous/ unknown
origin of neoteny
loss of neoteny
hypomorphic
hypermorphic


Neoteny degrees
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■ 1 weakly neotenic
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■ 8 highly neotenic
■ ambiguous/ unknown
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Callopisma rufa
Dilychnia apicalis
Dilychnia ruficollis
Lucidota bella
Vesta thoracica
Vesta rufiventris
Vesta chevrolatii
Vesta impressicollis
Scissicauda disjuncta
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Cladodes flabellata
Cladodes imperfectus
Fenestracladodes malleri
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Ledocas parallelus
Ledocas sp
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Dodacles emissa
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Robopus pantoni
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Photinus pallens
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origin of neoteny
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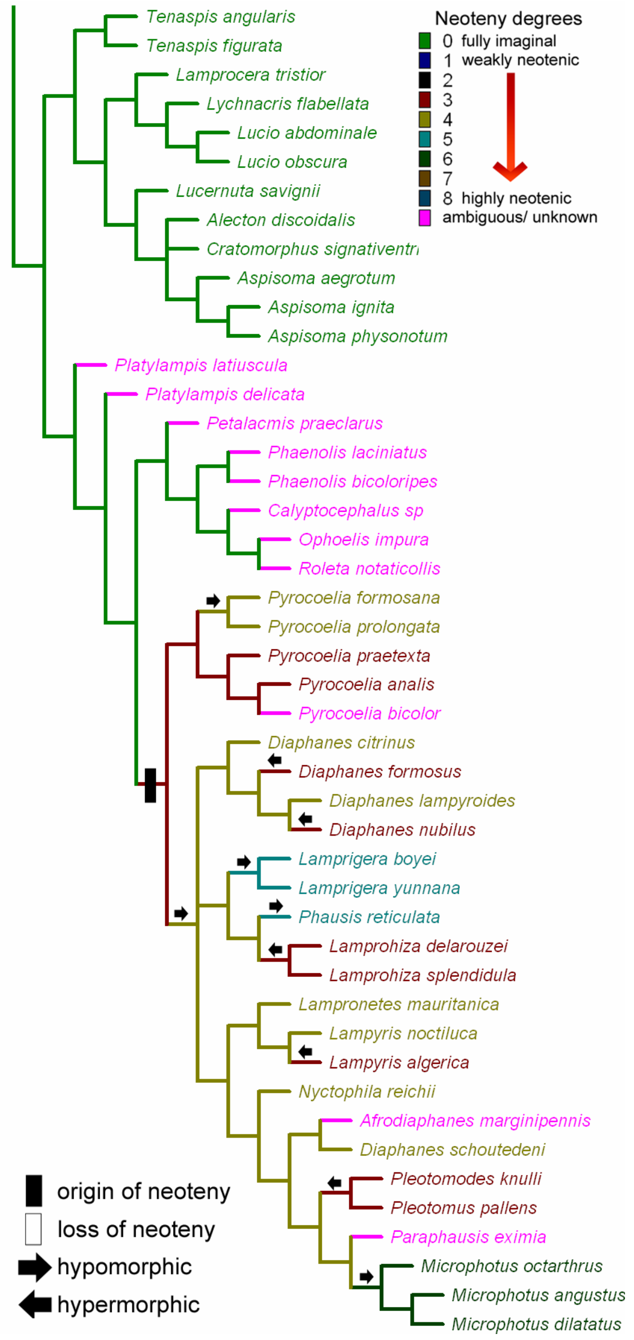
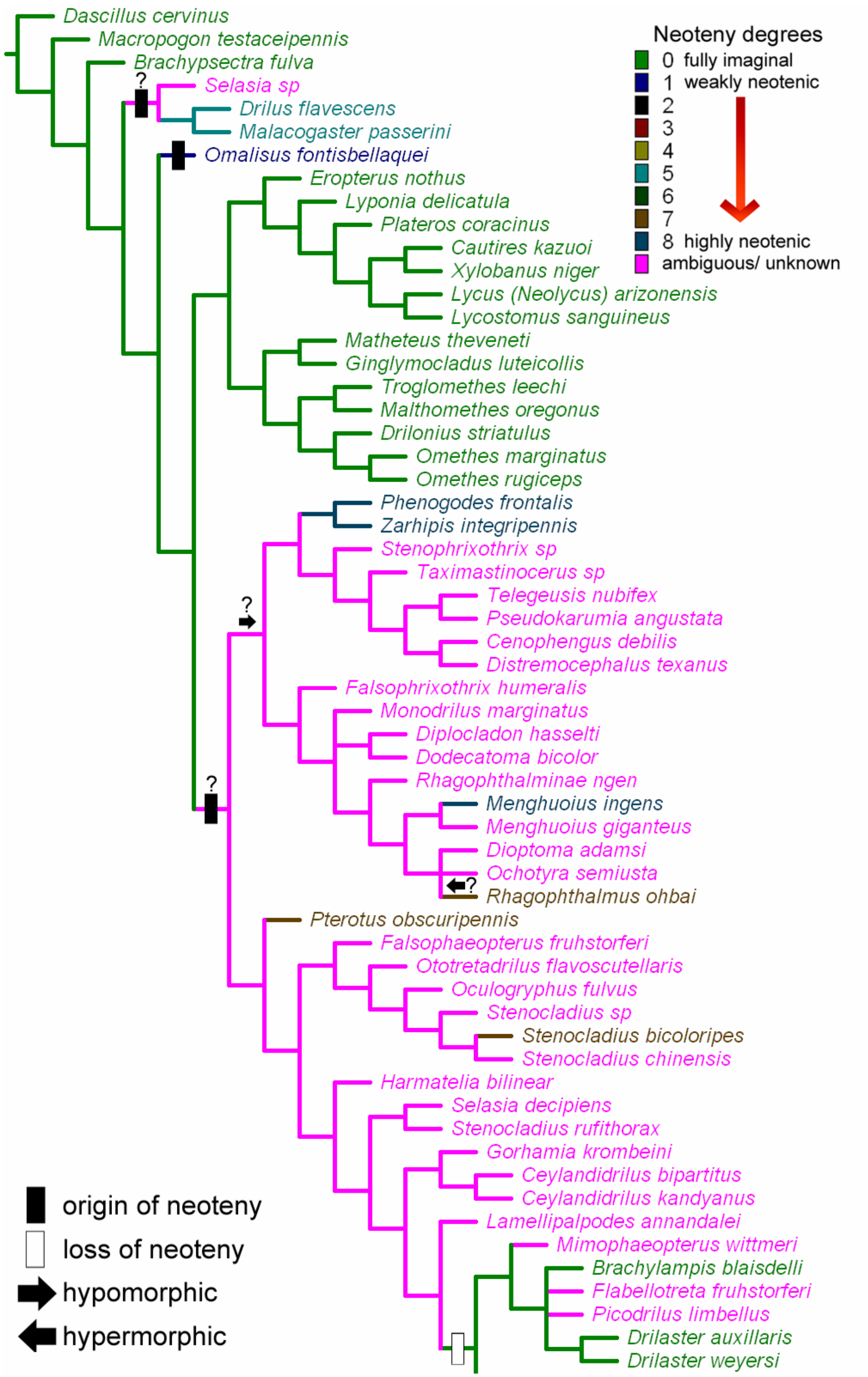


Fig. 14. Evolution of neoteny in elateroid/cantharoid families, with emphasis on Lampyridae. The consensus tree was resulted from 1008 most parsimonious trees obtained from a 220X411 data set with additive coding of the neotenic character. DELTRAN optimization was applied, showing transition of neoteny across the tree

Next four pages:

Fig. 15. Evolution of neoteny in elateroid/cantharoid families, with emphasis on Lampyridae. The consensus tree resulted from 1008 most parsimonious trees obtained from a 220X411 data set with non-additive coding of the neotenic character. Unambiguous optimization was applied, showing transition of neoteny across the tree.



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Macropogon testaceipennis
Brachypsectra fulva
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Drilus flavescens
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Eropterus nothus
Lyponia delicatula
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Zarhipis integripennis
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Pseudokarumia angustata
Cenophengus debilis
Distremocephalus texanus
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Falsophrixothrix humeralis
Monodrilus marginatus
Diplocladon hasselti
Dodecatoma bicolor
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Rhagophthalminae ngen
Menghuoius ingens
Menghuoius giganteus
Dioptoma adamsi
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Stenocladius bicoloripes
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Neoteny degrees
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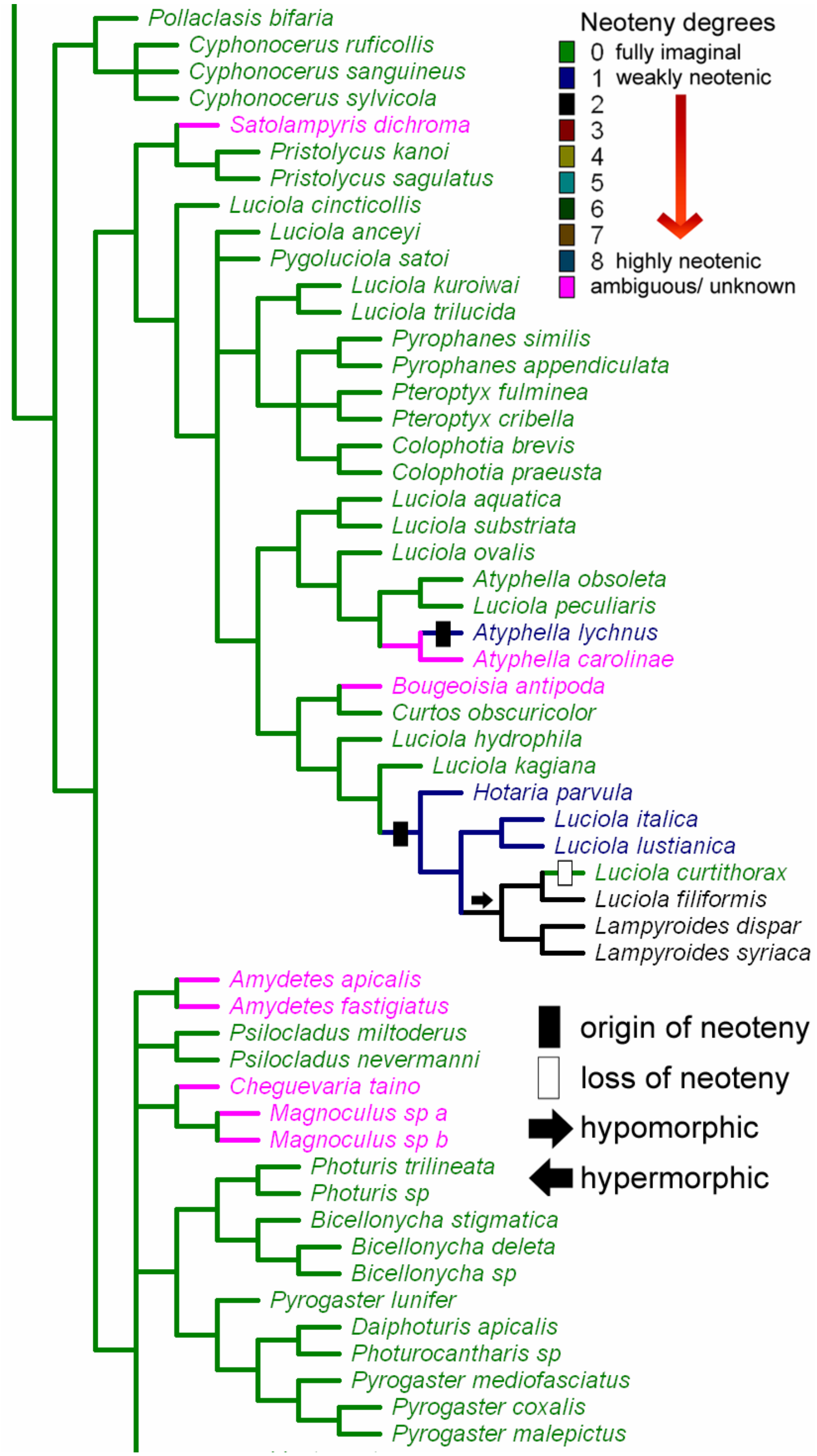
ambiguous/ unknown
origin of neoteny
loss of neoteny
hypomorphic
hypermorphic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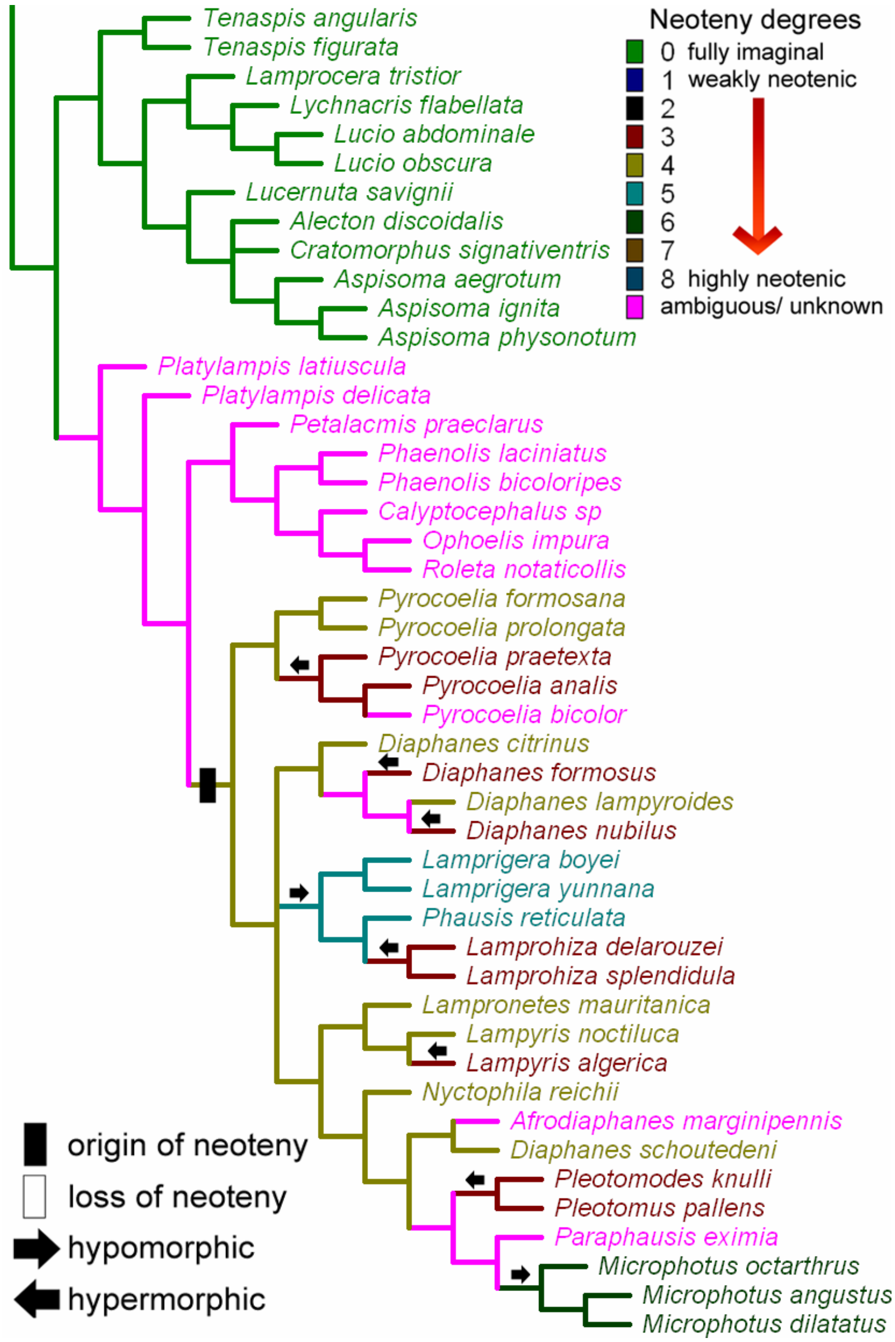

Fig. 15. Evolution of neoteny in elateroid/cantharoid families, with emphasis on Lampyridae. The consensus tree resulted from 1008 most parsimonious trees obtained from a 220X411 data set with non-additive coding of the neotenic character. Unambiguous optimization was applied, showing transition of neoteny across the

tree

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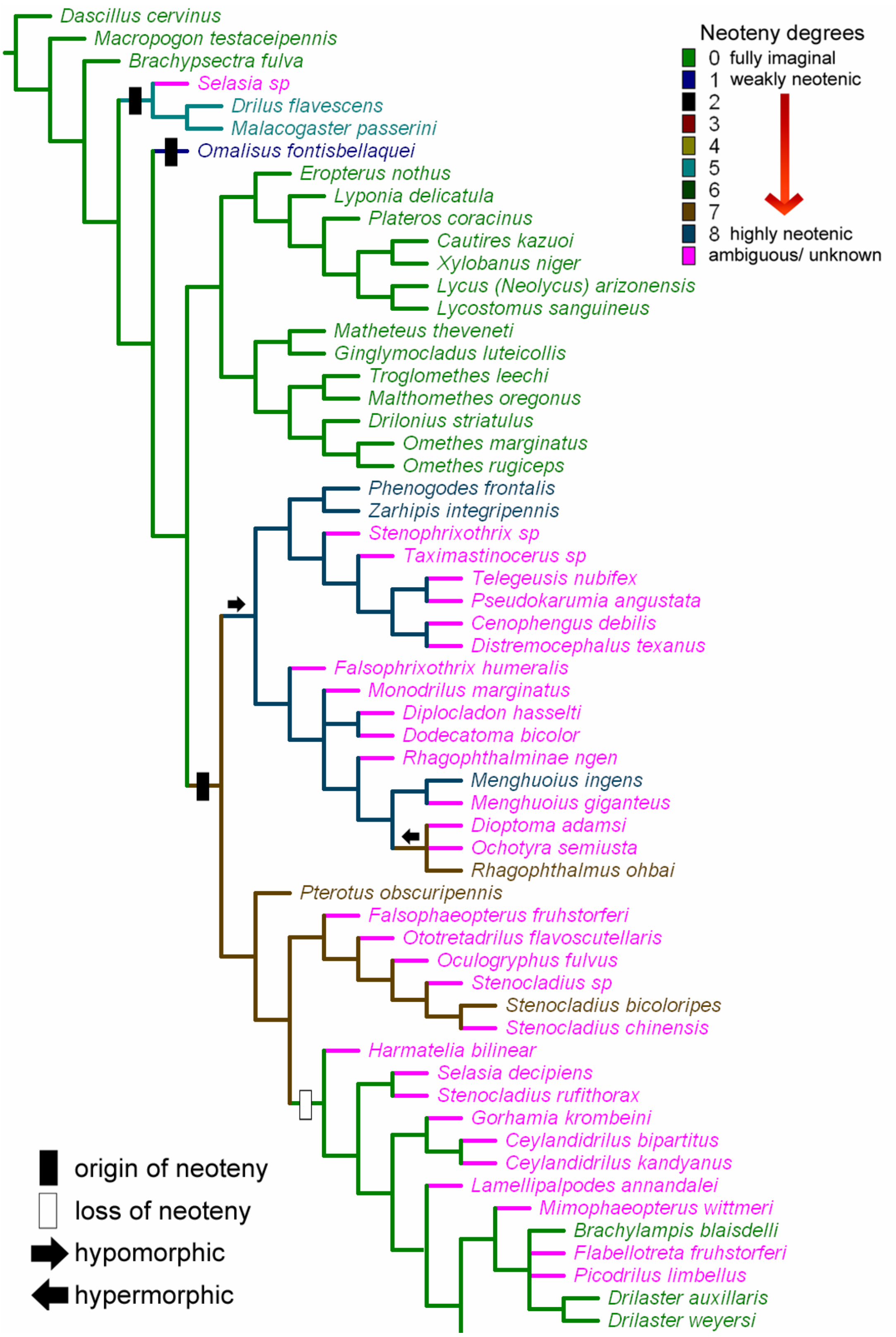

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Selasia sp
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Malacogaster passerini
Omalisus fontisbellaquei
Eropterus nothus
Lyponia delicatula
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Neoteny degrees
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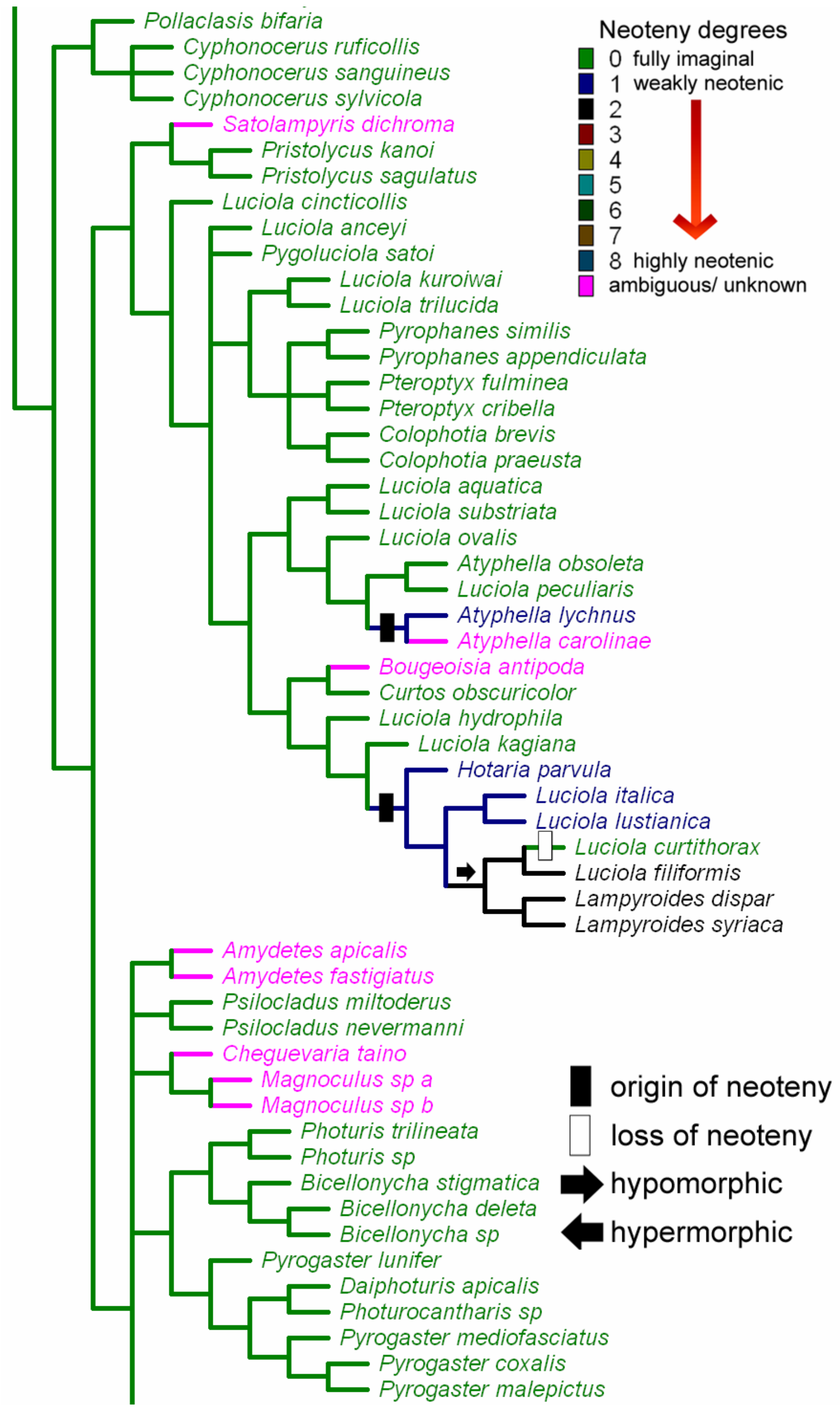
ambiguous/ unknown
origin of neoteny
loss of neoteny
hypomorphic
hypermorphic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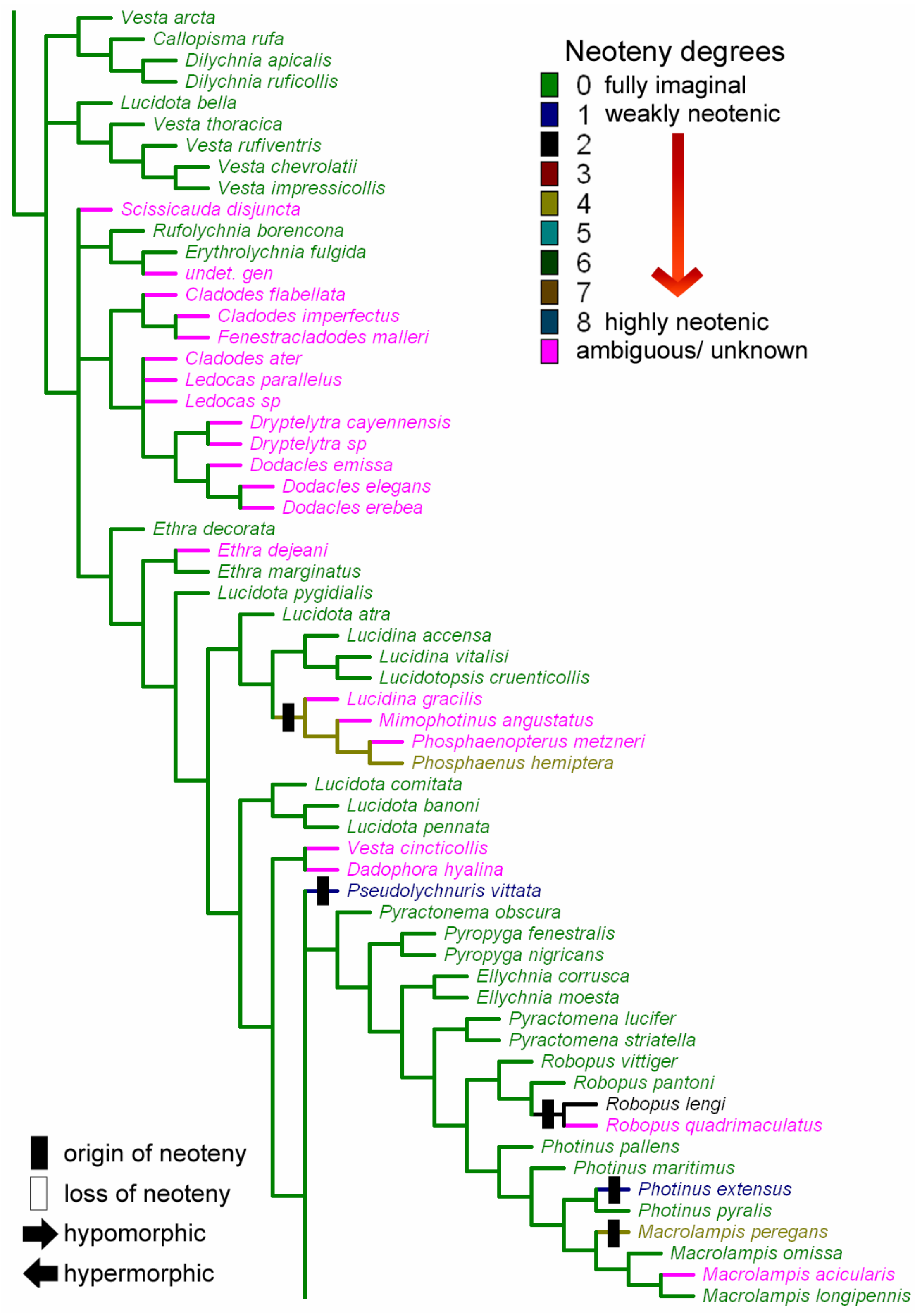
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Cladodes flabellata
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Dodacles emissa
Dodacles elegans
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Ethra dejeani
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Lucidota pygidialis
Lucidota atra
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Lucidotopsis cruenticollis
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Mimophotinus angustatus
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Lucidota banoni
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Pyractonema obscura
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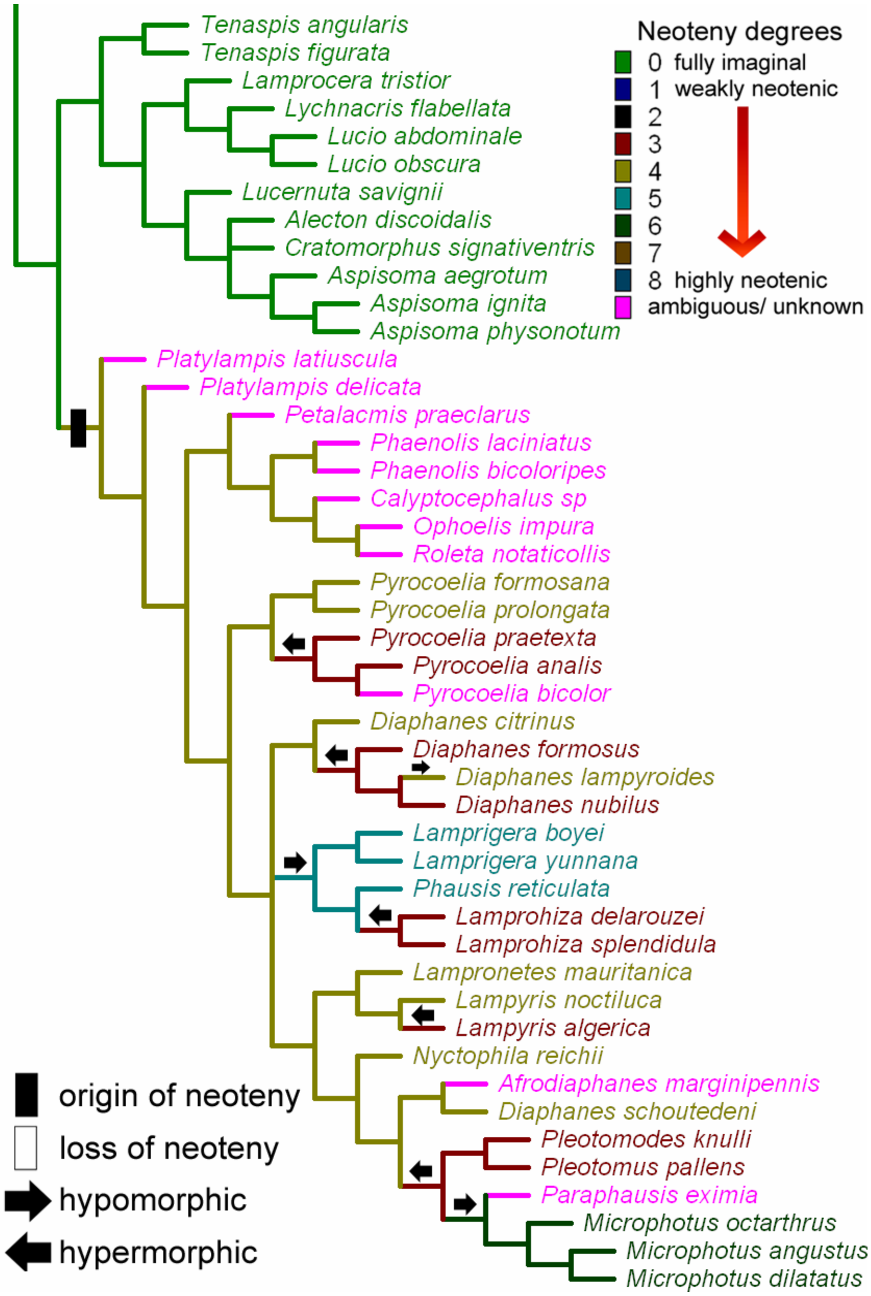

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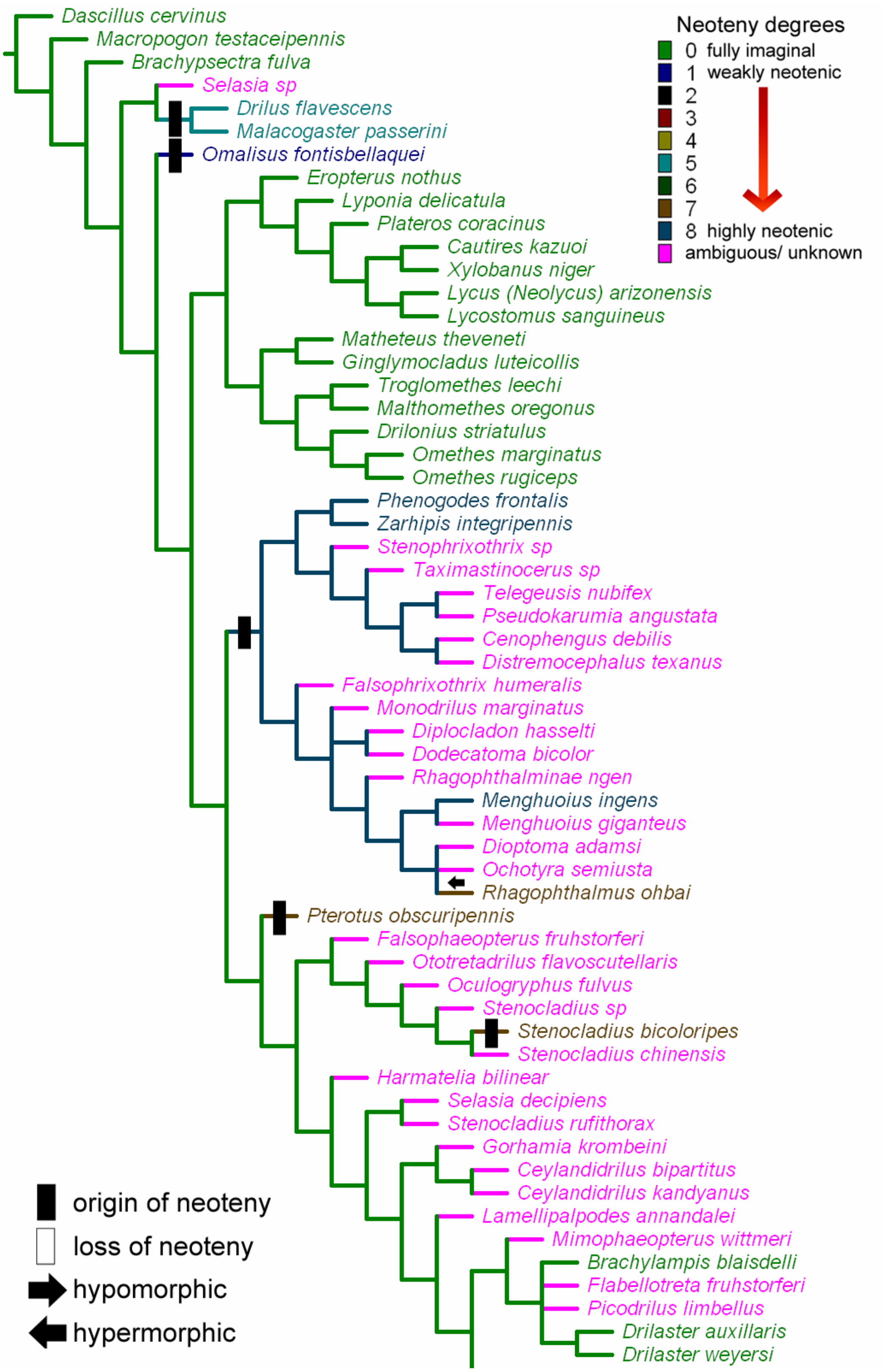
Fig. 17. Evolution of neoteny in elateroid/cantharoid families, with emphasis on Lampyridae. The consensus tree resulted from 1008 most parsimonious trees obtained from a 220X411 data set with non-additive coding of the neotenic character. DELTRAN optimization was applied, showing transition of neoteny across the tree.


Neoteny degrees
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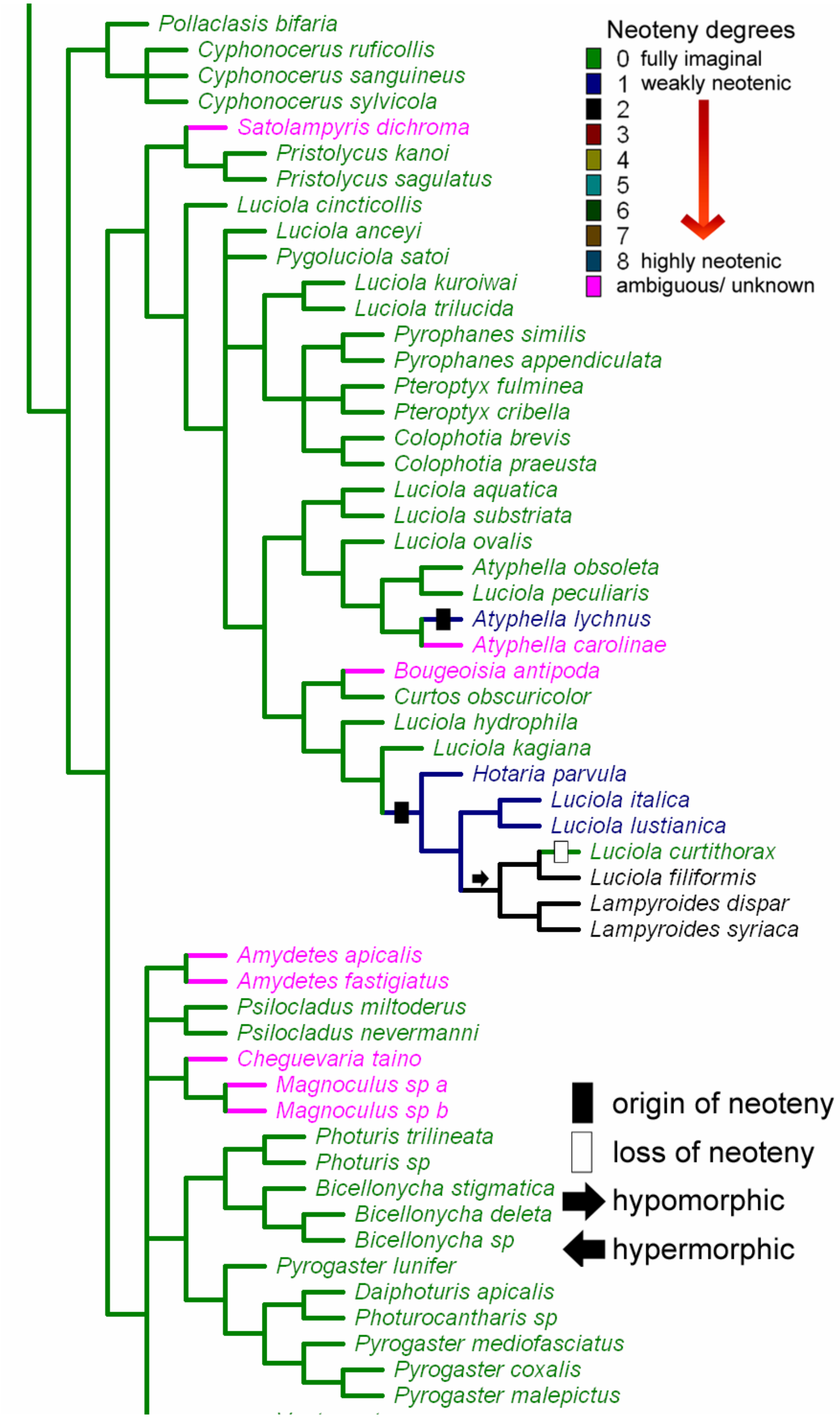
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hypomorphic
hypermorphic

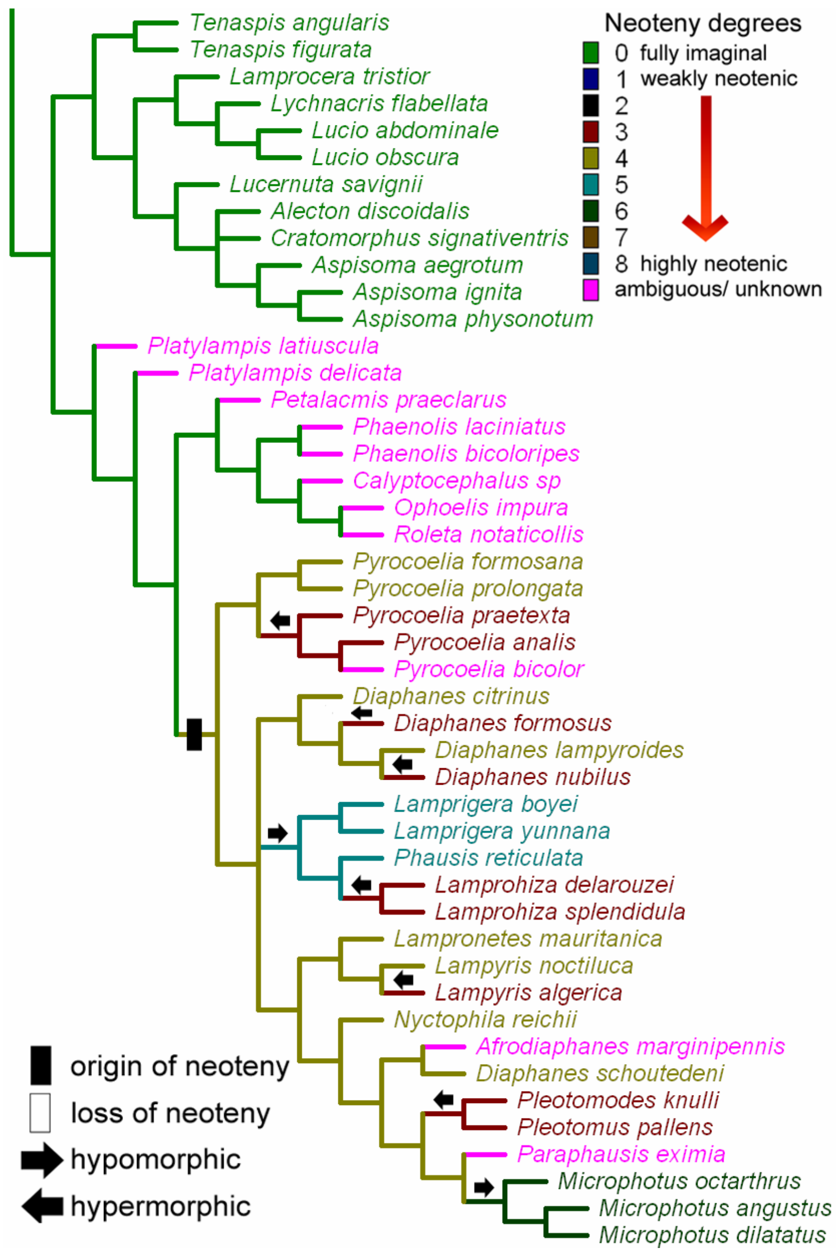
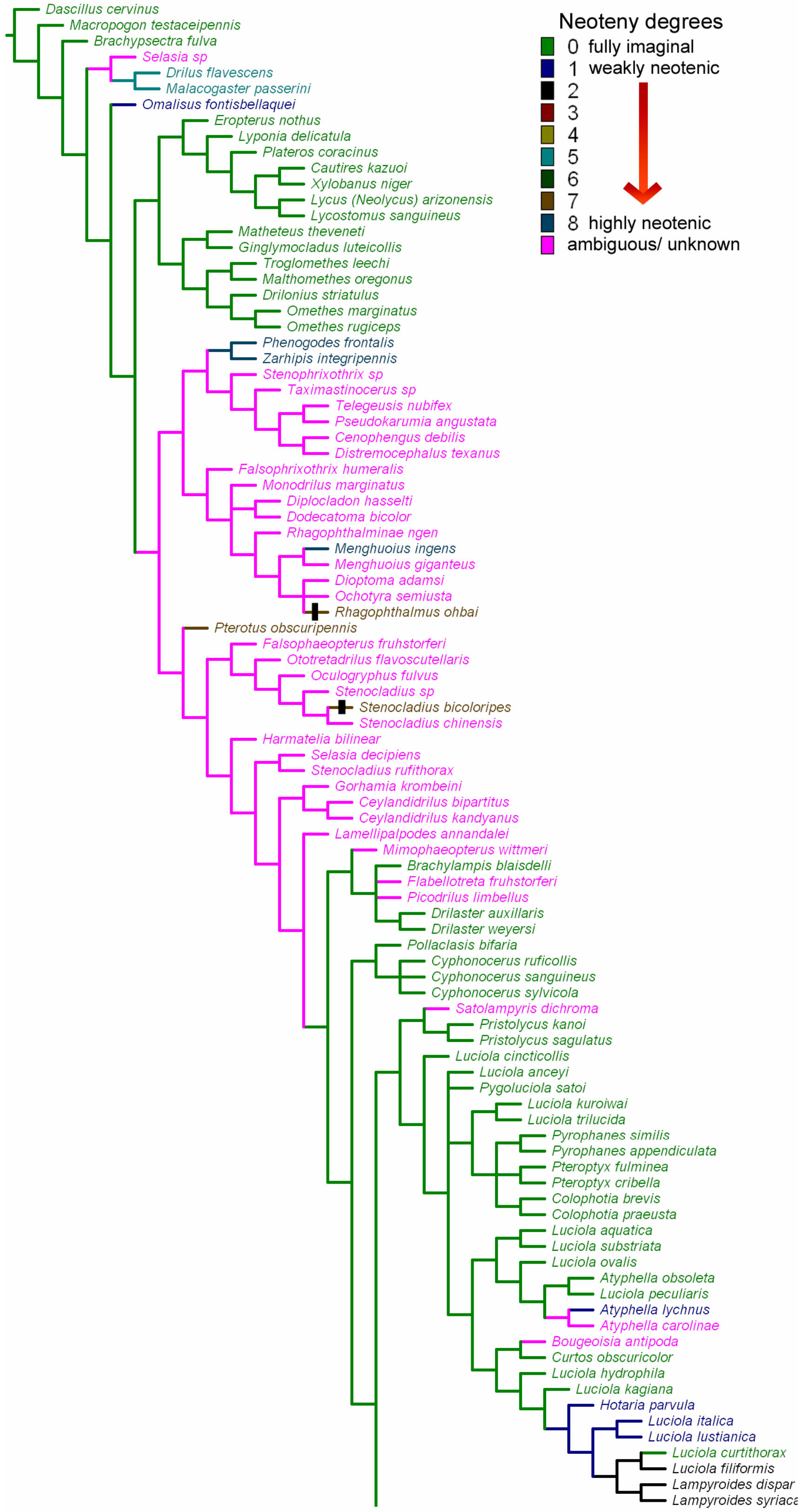


Fig. 17. Evolution of neoteny in elateroid/cantharoid families, with emphasis on Lampyridae. The consensus tree resulted from 1008 most parsimonious trees obtained from a 220X411 data set with non-additive coding of the neotenic character. DELTRAN optimization was applied, showing transition of neoteny across the tree.

Next two pages:

Fig. 18. Evolution of winter active groups in cantharoid beetles. Solid blocks indicate origins of winter occurrence and blank blocks for reversal.


Neoteny degrees
0 fully imaginal
1 weakly neotenic
2
3
4
5
6
7
8 highly neotenic
ambiguous/ unknown
Dascillus cervinus
Macropogon testaceipennis
Brachypsectra fulva
Selasia sp
Drilus flavescens
Malacogaster passerini
Omalisus fontisbellaquei
Eropterus nothus
Lyponia delicatula
Plateros coracinus
Cautires kazuoi
Xylobanus niger
Lycus (Neolycus) arizonensis
Lycostomus sanguineus
Matheteus theveneti
Ginglymocladus luteicollis
Troglomethes leechi
Malthomethes oregonus
Drilonius striatulus
Omethes marginatus
Omethes rugiceps
Phenogodes frontalis
Zarhipis integripennis
Stenophrixothrix sp
Taximastinocerus sp
Telegeusis nubifex
Pseudokarumia angustata
Cenophengus debilis
Distremocephalus texanus
Falsophrixothrix humeralis
Monodrilus marginatus
Diplocladon hasselti
Dodecatoma bicolor
Rhagophthalminae ngen
Menghuoius ingens
Menghuoius giganteus
Dioptoma adamsi
Ochotyra semiusta
Rhagophthalmus ohbai
Pterotus obscuripennis
Falsophaeopterus fruhstorferi
Ototretadrilus flavoscutellaris
Oculogryphus fulvus
Stenocladius sp
Stenocladius bicoloripes
Stenocladius chinensis
Harmatelia bilinear
Selasia decipiens
Stenocladius rufithorax
Gorhamia krombeini
Ceylandidrilus bipartitus
Ceylandidrilus kandyanus
Lamellipalpodes annandalei
Mimophaeopterus wittmeri
Brachylampis blaisdelli
Flabellotreta fruhstorferi
Picodrilus limbellus
Drilaster auxillaris
Drilaster weyersi
Pollaclasis bifaria
Cyphonocerus ruficollis
Cyphonocerus sanguineus
Cyphonocerus sylvicola
Satolampyris dichroma
Pristolycus kanoi
Pristolycus sagulatus
Luciola cincticollis
Luciola anceyi
Pygoluciola satoi
Luciola kuroiwai
Luciola trilucida
Pyrophanes similis
Pyrophanes appendiculata
Pteroptyx fulminea
Pteroptyx cribella
Colophotia brevis
Colophotia praeusta
Luciola aquatica
Luciola substriata
Luciola ovalis
Atyphella obsoleta
Luciola peculiaris
Atyphella lychnus
Atyphella carolinae
Bougeoisia antipoda
Curtos obscuricolor
Luciola hydrophila
Luciola kagiana
Hotaria parvula
Luciola italica
Luciola lustianica
Luciola curtithorax
Luciola filiformis
Lampyroides dispar
Lampyroides syriac

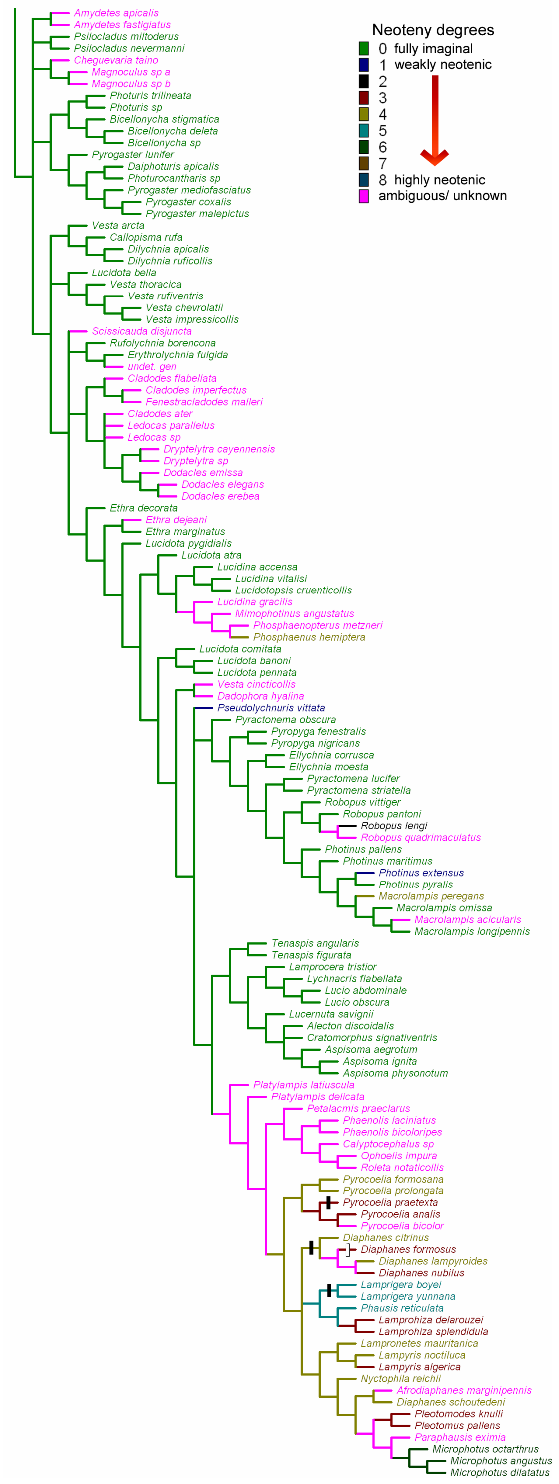


Fig. 18. Evolution of winter active groups in cantharoid beetles. Solid blocks indicate origins of winter occurrence and blank blocks for reversal.

Appendices

Appendix I. Documented genera of Rhagophthalminae and Lampyridae and their familial/ subfamilial placement in different classification[1]

	Family/subfamily placement			
Genus	**Crowson (1972)**	**McDermott (1966)**	**Olivier (1907)**	**Wittmer (1944)**
Bicladon Pic, 1921	Rhagophthalminae?[2]	—[2]	N/A[2]	Drilidae
Bicladodrilus Pic, 1921	Rhagophthalminae?	—	N/A	Drilidae
Cydistus Bourgeois, 1885	Phengodidae	—	—	Drilidae
Dioptoma Pascoe, 1860	Phengodidae	Rhagophthalminae	Rhagophthalmidae	Drilidae
Diplocladon Gorham, 1883	Phengodidae	—	—	Drilidae
Dodecatoma Westwood, 1843	Rhagophthalminae?	—	—	Drilidae
Falsophrixothrix Pic, 1937	Phengodidae	—	N/A	Drilidae
Haplocladon Gorham, 1883	Rhagophthalminae?	—	—	Drilidae
Menghuoius Kawashima, 2000	Rhagophthalminae?	N/A	N/A	N/A
Mimoochotyra Pic, 1930	Phengodidae	Rhagophthalminae	N/A	Drilidae
Monodrilus Pic, 1921	Rhagophthalminae?	—	N/A	Drilidae
Ochotyra Pascoe, 1862	Phengodidae	Rhagophthalminae	Rhagophthalmidae	Drilidae
Rhagophthalmus Motschulsky, 1845	Phengodidae	Rhagophthalminae	Rhagophthalmidae	N/A

(Continued on next page)

Genus	Crowson (1972)	McDermott (1966)	Olivier (1907)	Wittmer (1944)
Afrodiaphanes Geisthardt, 2006	Lampyrinae?	N/A	N/A	N/A
Alecton Laporte de Castelnau, 1833	Lampyrinae?	Lampyrinae	Lamprocerinae	—
Amydetes Illiger, 1807	Amydetinae?	Lampyrinae	Amydetinae	—
Aspisoma Laporte de Castelnau, 1833	Lampyrinae?	Lampyrinae	Photininae	—
Aspisomoides Zarazoga, 1995	Lampyrinae?	N/A	N/A	N/A
Atyphella Olliff, 1889	Luciolinae?	Luciolinae	Luciolinae (= *Luciola*)[3]	—
Baolacus Pic, 1915	[4]	—	N/A	Drilidae
Bicellonycha Motschulsky, 1853	Photurinae?	Photurinae	Photurinae (= *Photuris*)	—
Bourgeoisia Olivier, 1908	Luciolinae?	Luciolinae	N/A	—
Brachylampis VanDyke, 1939	Ototretinae	Ototretinae	N/A	—
Callopisma Motschulsky, 1853	Lampyrinae?	Lampyrinae	Lucidotinae (= *Lychnuris*)	—
Calotrachelum Pic, 1930		Lampyrinae	N/A	—
Calyptocephalus Gray, 1832	Lampyrinae?	Lampyrinae	Lamprocerinae	—
Cassidomorphus Motschulsky, 1853		Lampyrinae	Uncertain	—
Cephalophoturis Pic, 1927		Photurinae	N/A	—
Ceylanidrilus Pic, 1911	Ototretinae	—	N/A	Drilidae

(Continued on next page)

Genus	Crowson (1972)	McDermott (1966)	Olivier (1907)	Wittmer (1944)
Cheguvearia Kazantsev, 2006	Uncertain?[5]	N/A	N/A	—
Cladodes Solier, 1849	Ambiguous?[5]	Lampyrinae	Lamprocerinae	—
Colophotia Motschulsky, 1833	Luciolinae?	Luciolinae	Luciolinae	—
Cratomorphus Motschulsky, 1853	Lampyrinae?	Lampyrinae	Photininae	—
Curtos Motschulsky, 1845	Luciolinae?	Luciolinae	Luciolinae	—
Cyphonocerus Kiesenwetter, 1879	Cyphonocerinae	—	—	Drilidae
Dadophora Olivier, 1907	Lampyrinae?	Lampyrinae	Dadophorinae	—
Daiphoturis Pic, 1926	Photurinae?	Photurinae	N/A	—
Diaphanes Motschulsky, 1853	Lampyrinae?	Lampyrinae	Lampyrinae	—
Dilychnia Motschulsky, 1853	Lampyrinae?	Lampyrinae	Lucidotinae (= *Lucidota*)	—
Dodacles Olivier, 1885	Ambiguous?	Lampyrinae	Lamprocerinae	—
Drilaster Kiesenwetter, 1879	Ototretinae	Ototreninae	Luciolinae(= *Ototreta*)	Drilidae
Dryptelytra Laporte de Castelnau, 1833	Ambiguous?	Lampyrinae	Lamprocerinae	—
Ellychnia Blanchard, 1845	Lampyrinae?	Lampyrinae	Lucidotinae (= *Lucidota*)	—
Erythrolychnia Motschulsky, 1853	Lampyrinae?	Lampyrinae	Lucidotinae (= *Lychnuris*)	—

(Continued on next page)

Genus	Crowson (1972)	McDermott (1966)	Olivier (1907)	Wittmer (1944)
Ethra Laporte de Castelnau, 1833	Ambiguous?	Lampyrinae	Lamprocerinae	—
Eugeusis Westwood, 1853	Ototretinae?	—	—	Drilidae
Fabellototreta Pic, 1911	Ototretinae?	—	N/A	—
Falsophaeopterus Pic, 1911		—	N/A	Drilidae
Fenestratocladodes Pic, 1935		Lampyrinae	N/A	—
Gorhamia Pic, 1911		—	N/A	Drilidae
Harmatelia Walker, 1858	Ototretinae	Pterotinae	Megalophthalminae	Drilidae
Heterophotinus Olivier, 1894	Lampyrinae?	Lampyrinae		—
Hotaria Yuasa, 1937	Luciolinae?	Luciolinae	N/A	—
Hyperstoma Wittmer, 1979	Ototretinae?	—	N/A	—
Jamphotus Barber, 1941		Lampyrinae	N/A	—
Lamellipalpus Maulik, 1921	Ototretinae	—	N/A	Drilidae
Lampellipalpldes Maulik, 1921	Ototretinae?	—	N/A	Drilidae
Lamprigera Motschulsky, 1853	Lampyrinae?	Lampyrinae	Lampyrinae (= *Lamprophorus*)	—
Lamprocera Laporte de Castelnau, 1833	Lampyrinae?	Lampyrinae	Lamprocerinae	—
Lamprohiza Motschulsky, 1853	Lampyrinae	Lampyrinae	Lampyrinae (= *Phausis*)	—

(Continued on next page)

Genus	Crowson (1972)	McDermott (1966)	Olivier (1907)	Wittmer (1944)
Lampronetes Motschulsky, 1853	Lampyrinae?	Lampyrinae	Lampyrinae (=*Lampyris*)	—
Lampyris Geoffroy, 1762	Lampyrinae?	Lampyrinae	Lampyrinae	—
Lampyroidea Costa, 1875	Luciolinae?	Luciolinae	Luciolinae	—
Ledocas Olivierm 1885	Ambiguous?	Lampyrinae	Lamprocerinae	—
Lucernuta Laporte de Castelnau, 1833	Lampyrinae?	Lampyrinae	Lucidotinae	—
Lucidina Gorham, 1880	Lampyrinae?	Lampyrinae	Lucidotinae	—
Lucidota Laporte de Castelnau, 1833	Lampyrinae?	Lampyrinae	Lucidotinae	—
Lucidotopsis McDermott, 1960		Lampyrinae	N/A	—
Lucio Laporte de Castelnau, 1833	Lampyrinae?	Lampyrinae	Lamprocerinae	—
Luciola Laporte de Castelnau, 1833	Luciolinae	Luciolinae	Luciolinae	—
Lychnacris Motschulsky, 1853	Lampyrinae?	Lampyrinae	Lamprocerinae (= *Hyas*)	—
Lychnobius Geisthardt 1983	N/A	N/A	N/A	—
Macrolampis Motschulsky, 1853	Lampyrinae?	Lampyrinae	Photininae	—
Magnoculus McDermott, 1964	Amydetinae?	Lampyrinae	Megalophthalminae (= Megalophthalmus)	—
Microdiphot Barber, 1941		Lampyrinae	N/A	—

(Continued on next page)

Genus	Crowson (1972)	McDermott (1966)	Olivier (1907)	Wittmer (1944)
Microlampyris Pic, 1956		Lampyrinae	N/A	—
Micronaspis Green, 1948	Lampyrinae?	Lampyrinae	N/A	—
Microphotus LeConte, 1866	Lampyrinae?	Lampyrinae	Lampyrinae	—
Mimophaeopterus Pic, 1930	Ototretinae	—	N/A	Drilidae
Mimophotinus Pic, 1935		Lampyrinae	N/A	—
Nelsonphotus Cicero, 2006	Lampyrinae?	N/A	N/A	N/A
Nyctophila Olivier, 1884	Lampyrinae?	Lampyrinae	Lampyrinae	—
Oculogryphus Jeng, Engel & Yang, 2007	Ototretinae?	N/A	N/A	—
Oliviereus Pic, 1930		Lampyrinae	N/A	—
Ophoelis Olivier, 1911	Lampyrinae?	Lampyrinae	N/A	—
Ototretadrilus Pic, 1921	Ototretadrilinae	—	N/A	Drilidae
Ovalampis Fairmaire, 1898		Lampyrinae	Uncertain	—
Pachytarsus Motschulsky, 1861	Ototretinae?	—	—	Drilidae
Paraphausis Green, 1949	Lampyrinae?	Lampyrinae	N/A	N/A
Petalacmis Olivier, 1908	Lampyrinae?	Lampyrinae	N/A	—
Phaenolis Gorham, 1880	Lampyrinae?	Lampyrinae	Lamprocerinae	—
Phausis LeConte, 1852	Lampyrinae	Lampyrinae	Lampyrinae	—

(Continued on next page)

Genus	**Crowson (1972)**	**McDermott (1966)**	**Olivier (1907)**	**Wittmer (1944)**
Phosphaenopterus Schaufuss, 1870	Lampyrinae?	Lampyrinae	Lampyrinae	—
Phosphaenus Laporte de Castelnau, 1833	Lampyrinae?	Lampyrinae	Lampyrinae	—
Photinoides McDermott, 1963		Lampyrinae	N/A	—
Photinus Laporte de Castelnau, 1833	Lampyrinae?	Lampyrinae	Photininae	—
Photoctus McDermott, 1961		Lampyrinae	N/A	—
Photuris Dejean, 1833	Photurinae	Photurinae	Photurinae	—
Photurocantharis Pic, 1914	Photurinae		N/A	—
Photuroluciola Pic, 1937	Luciolinae?	Luciolinae	N/A	—
Picodrilus Wittmer, 1937	Ototretinae		N/A	Drilidae
Platylampis Motschulsky, 1853		Lampyrinae	Photininae (= *Photinus*)	—
Pleotomodes Green, 1948	Lampyrinae?	(Lampyrinae) = Lampyris	N/A	N/A
Pleotomus LeConte, 1861	Lampyrinae?	Lampyrinae	Lamprocerinae	—
Pollaclasis Newman, 1838	Cyphonocerinae	Lampyrinae	Lamprocerinae (= *Calyptocephalus*)	—
Presbyolampis Buck, 1947		Photurinae	N/A	N/A

(Continued on next page)

Genus	Crowson (1972)	McDermott (1966)	Olivier (1907)	Wittmer (1944)
Pristolycus Gorham, 1880	Lampyrinae?	Lampyrinae	—	—
Prolutacea Cicero, 2006	Lampyrinae?	N/A	N/A	N/A
Pseudolychnuris Motschulsky, 1853	Lampyrinae?	Lampyrinae	Lucidotinae (= *Lucidota*)	—
Psilocladus Blanchard, 1846	Ambiguous?	Lampyrinae	Lamprocerinae	—
Pteroptyx Olivier, 1902	Luciolinae?	Luciolinae	Luciolinae	—
Pterotus LeConte, 1859	Pterotinae	Pterotinae	—	—
Pygoluciola Wittmer, 1939	Luciolinae?	Luciolinae	N/A	—
Pyractonema Olivier, 1907	Lampyrinae?	Lampyrinae	Lucidotinae	—
Pyractomena Melsheimer, 1845	Lampyrinae?	Lampyrinae	Photininae (= *Lecontea*)	—
Pyrocoelia Gorham, 1880	Lampyrinae?	Lampyrinae	Lucidotinae (=*Lucernuta*)	—
Pyrogaster Motschulsky, 1853	Photurinae	Photurinae	Photurinaec(= *Photuris*)	—
Pyrophanes Olivier, 1885	Luciolinae?	Luciolinae	Luciolinae	—
Pyropyga LeConte, 1853	Lampyrinae?	Lampyrinae	Lucidotinae (= *Lucidota*)	—
Pyropygodes Zarogoza, 2000	Lampyrinae?	N/A	N/A	N/A
Robopus Motschulsky, 1853	Lampyrinae?	Lampyrinae	Photininae (= *Photinus*)	—
Roleta McDermott, 1962	Lampyrinae?	Lampyrinae	N/A	N/A

(Continued on next page)

Genus	**Crowson (1972)**	**McDermott (1966)**	**Olivier (1907)**	**Wittmer (1944)**
Rufolychnia Kazantsev, 2006	Lampyrinae?	N/A	N/A	N/A
Scissicauda McDermott, 1966		Lampyrinae	N/A	N/A
Stenocladius Deyrolle & Fairmaire, 1878	Ototreninae	—	—	Drilidae
Tenaspis LeConte, 1881	Lampyrinae?	Lampyrinae	Lucidotinae	—
Vesta Laporte de Castelnau, 1833	Ambiguous?	Amydetinae	Lamprocerinae	—

[1] : the list of valid genera was largely based on McDermott's (1966) catalogue, with adding of newly described, revived, or transferred genera since then. The first 13 genera were of Rhagophthalmidae/-inae, and the other 114 were of Lampyridae.

[2] : names without any marks mean the familial/subfamilial placement was explicitly specified by that classification; "?" means the genus was placed in that family/subfamily by subsequent authors; "N/A" refers that the genus was described after the classification published; "—" indicated the genus was in the other family when that specified classification was established.

[3] : the generic name in parenthesis was the valid name used by Olivier (1907) for that genus.

[4] : blank means the subfamilal placement of that genus was not mentioned by Crowson or any subsequent authors.

[5]: "Uncertain" indicated the identity of the genus was unclear or its subfamilial position was obscure; "Ambiguous?" means the familial/subfamilal placement by subsequent authors was inconsistent.

Appendix II. Taxon sampling of present study

Symbols and abbreviations

ⓣ: type species
ⓢ: species similar to type species
ⓓ: species dissimilar to type species
?: not compared with type species
♂♀: male/female, material availability
( )*: only female material, not included in matrix

AU/ET/NA/NT/OT/PA: Australian/ Ethiopian/ Nearctic/ Neotropical/ Oriental/ Palearctic zoogeographic realms

AMNH/ JENG/ MNHN/ NMB/ SNOW/ SBM: American Museum of Natural History, New York/ my personal collection/ Museum de la national Histoire naturelle, Paris/ Naturhistorisches Museum Basel/ Entomological division, Natural History Museum, Univ. Kansas/ Santa Barbara Museum of Natural History

Outgroup

Dascillidae

♂♀	ⓣ*Dascillus cervinus* L. (SNOW)	PA

Artematopodidae

♂♀	ⓢ*Macropogon testaceipennis* Motschulsky (SNOW)	NA

Brachypsectridae

♂	ⓣ*Brachypsectra fulva* LeConte (SNOW)	NA

Drilidae

♂♀	ⓣ*Drilus flavescens* G.A. Olivier (NMB)	PA
♂	ⓓ*Selasia decipiens* (Guérin) (NMB)	OT
♂	ⓢ*Selasia* sp. (NMB)	ET
♂	ⓣ*Malacogaster passerini* Bassi (NMB)	PA

Lycidae

Lycinae

♂♀	? *Lycus* (*Neolycus*) *arizonacus* (SNOW)	NA
♂♀	? *Lycus* (*Lycostomus*) *sanguineus* Gorham (JENG)	NA

	Platerodinae	
♂♀	? *Eropterus nothus* (Kiesenwetter) (JENG)	PA
♂♀	? *Lyponia delicatula* (Kiesenwetter) (JENG)	PA
♂♀	? *Plateros coracinus* (Kiesenwetter) (JENG)	PA
	Metriorrhynchinae	
♂♀	? *Cautires kazuoi* Sato and Ohbayashi (JENG)	PA
♂♀	? *Xylobanus niger* Ohbayashi (JENG)	PA
Omalisidae		
♂	ⓣ*Omalisus fontisbellaquei* Geoffroy (NMB)	OT
Omethidae		
	Driloniinae	
♂♀	ⓣ*Drilonius striatulus* Kiesenwetter (JENG)	PA
	Omethinae	
♂	ⓣ*Omethes marginatus* LeConte (SNOW)	NA
♂♀	ⓢ*Omethes rugiceps* (Lewis) (JENG)	PA
♂	ⓣ*Troglomethes leechi* Fender (SBM)	NA
♂	ⓣ*Malthomethes oregonus* Fender (SBM)	NA
	Matheteinae LeConte	
♂	ⓣ*Matheteus theveneti* LeConte (SBM)	NA
♂	ⓣ*Ginglymocladus luteicollis* Van Dyke (SBM)	NA
Phengodidae		
♂	ⓣ*Phenogodes frontalis* LeConte (JENG)	NA
♂	ⓢ*Zarhipis integripennis* (LeConte) (SNOW)	NA
♂	ⓣ*Cenophengus debilis* LeConte (SNOW)	NA
♂	ⓢ*Distremocephalus texanus* (LeConte) (SNOW)	NA
♂	? *Stenophrixothrix* sp. (SNOW)	NT
♂	? *Taximastinocerus* sp. (SNOW)	NT
Telegeusidae		
♂	ⓢ*Telegeusis nubifex* Martin (SNOW)	NA
♂	ⓣ*Pseudokarumia angustata* Pic (SNOW)	NT

Ingroup

Rhagophthalmidae (tentatively placed here)

Dioptoma Pascoe

♂ ⓣ*D. adamsi* Pascoe (MNHN)	OT
Diplocladon Gorham	
♂ ⓢ*D.* haselti Gorham. (NMB)	OT
Dodecatoma Westood	
♂ ⓣ*D. bicolor* Westwood (MNHN)	OT
Falsophrixothrix Pic	
♂ ⓣ*F. humeralis* Pic (JENG)	OT
Menghuoius Kawashima	
♂ ⓣ*M. ingens* (Fairmaire) (MNHN)	OT
♂ ⓢ*M. gigantus* (Fairmaire) (MNHN)	OT
Monodrilus Pic	
♂ ⓣ*M. marginatus* Pic (MNHN)	OT
Ochotyra Pascoe	
♂ ⓣ*O. semiusta* Pascoe (MNHN)	OT
Rhagophthalmus Motschulsky	
♂♀ ⓢ*R. ohbai* Wittmer (JENG)	OT
Undescribed genus and species (Rhagophthalminae n.gen in matrix)	
♂ sp. (JENG)	OT

Lampyridae

Afrodiaphanes Geisthardt	
♂ ⓣ*A. marginipennis* (Boheman) (NMB)	ET
Alecton Laporte de Castelnau	
♂♀ ⓣ*A. discoidalis* Laporte de Castelnau (NMB)	NA
Amydetes Hoffmannsegg	
♂ ⓢ*A. apicalis* (Germar) (NMB, MNHN)	NT
♂ ⓣ*A. fastigiatus* Hoffmannsegg (NMB)	NT
Aspisoma Laporte de Castelnau	
♂♀ ⓣ*A. ignita* (L.) (NMB)	NT
♂♀ ⓢ*A. physonotum* (Gorham) (NMB)	NT
♂♀ ⓢ*A. aerotum* (Gorham) (NMB)	NT
Atyphella Olliff	
♂ ⓣ*A. lychnus* Olliff (SNOW)	NT
♂♀ ⓓ*A. carolinae* Olivier (NMB)	OT

♂♀ ⓢ*A. obsoleta* Olivier (NMB)	AU
Bicellonycha Motschulsky	
♂♀ ⓣ*B. deleta* Motschulsky (NMB, MNHN)	NT
♂♀ ⓢ*B. stigmatica* (Olivier) (SNOW, NMB)	NT
♂♀ ⓓ*B.* sp. (JENG)	NT
Bourgeoisia Olivier	
♂ ⓣ*B. antipoda* (Bourgeois) (NMB)	OT
Brachylampis Van Dyke	
♂ ⓢ*B. blaisdelli* Van Dyke (SBM)	NA
Callopisma Motschulsky	
♂ ⓣ*C. rufa* (G.A. Olivier) (NMB)	NT
(*Calotrachelum* Pic)*	
♀ ⓣ*C. olivieri* Pic (MNHN)	NT
Calyptocephalus Gray	
♂ ⓢ*Calyptocephalus* sp. (SNOW)	NT
(*Cephalophoturis* Pic)*	
♀ ⓣ*C. excavaticeps* Pic (MNHN)	NT
Ceylanidrilus Pic, 1911	
♂♀ ⓣ*C. bipartitus* Pic (JENG)	OT
♂ ⓢ*C. kandyanus* (Bourgeois) (NMB)	OT
Cheguevaria Kazantsev	
♂ ⓣ*C. taino* Kazantsev (AMNH)	NT
Cladodes Solier	
♂ ⓣ*C. flabellata* Solier (NMB)	NT
♂♀ ⓓ*C. imperfectus* Olivier (NMB)	NT
♂ ⓓ*C. ater* (Solier) (MNHN)	NT
Colophotia Dejean,	
♂♀ ⓣ*C. praeusta* (Eschscholtz) (NMB)	OT
♂♀ ⓢ*C. brevis* Olivier (NMB)	OT
Cratomorphus Motschulsky	
♂ ⓢ*C. signativentris* Olivier (SNOW)	NT
Curtos Motschulsky	
♂♀ ⓢ*C. obscuricolor* Jeng & Lai (JENG)	OT
Cyphonocerus Kiesenwetter	

♂♀ ⓣ*C. ruficollis* Kiesenwetter (JENG)	PA
♂♀ ⓢ*C. sanguineus* Pic (JENG)	OT
♂ ⓢ*C. sylvanica* Jeng, Yang & Sato (JENG)	OT
Dadophora Olivier (monobasic)	
♂ ⓣ*D. hyalina* Olivier (NMB)	NT
Daiphoturis Pic	
♂♀ ⓢ*Daiphoturis apicalis* Pic (MNHN)	NT
Diaphanes Motschulsky	
♂♀ ⓓ*D. citrinus* Olivier (JENG)	OT
♂♀ ⓓ*D. formosus* Olivier (JENG)	OT
♂♀ ⓓ*D. lampyroides* (Olivier) (JENG)	OT
♂♀ ⓢ*D. nubilus* Jeng & Lai (JENG)	OT
♂♀ ⓓ*D. schoutedeni* Olivier (NMB)	ET
Dilychnia Motschulsky	
♂ ⓣ*D. guttula* (F.) (NMB)	NT
♂♀ ⓢ*D. apicalis* (NMB)	OT
Dodacles Olivier	
♂ ⓣ*D. elegans* Olivier (NMB, MNHN)	NT
♂ ⓓ*D. emissa* Olivier (NMB)	NT
♂ ⓢ*D. erebea* Olivier (NMB)	NT
Drilaster Kiesenwetter	
♂♀ ⓣ*D. auxillaris* Kiesenwetter (JENG)	PA
♂ ⓣ*D. weyersi* (Olivier) (type of *Ototreta*)(NMB)	OT
Dryptelytra Laporte de Castelnau	
♂ ⓣ*D. cayennensis* Laporte de Castelnau (MNHN)	NT
♂ ⓢ*D.* sp. (SNOW)	NT
Ellychnia Blanchard	
♂♀ ⓣ*E. corrusca* (L.) (NMB)	NA
♂♀ ⓓ*D. moesta* (Perty) (SNOW)	NA
Erythrolychnia Motschulsky	
♂♀ ⓢ*E. fulgida* (G.A. Olivier) (MNHN)	NA
Undescribed genus similar to *Erythrolychnia* (as undet. gen in matrix)	
♂ sp. (JENG)	NA
Ethra Laporte de Castelnau	

♂♀	ⓣ*E. marginatus* (Gray) (NMB)	NT
♂♀	ⓢ*E. decorata* (Olivier) (NMB)	NT
♂	ⓢ*E. dejeani* (Olivier) (NMB)	NT
Falsophaeopterus Pic (monobasic)		
♂	ⓣ*F. fruhstorferi* Pic (NMB)	OT
Fenestratocladodes Pic		
♂	ⓣ*F. malleri* Pic (NMB, MNHN)	NT
Flabellotreta Pic		
♂	ⓢ*F. fruhstorferi* Pic	OT
Gorhamia Pic		
♂♀	ⓢ*G. krombeini* Wittmer (NMB)	OT
Harmatelia Walker		
	ⓣ*H. bilinea* Walker(NMB)	OT
Hotaria Yuasa		
♂♀	ⓣ*H. parvula* (Kiesenwetter) (JENG)	PA
Lamellipalpodes Maulik		
♂	ⓣ*L. annandalei* Maulik (MNHN)	OT
Lamprigera Motschulsky		
♂	ⓣ*L. boyei* Motschulsky (JENG)	OT
♂♀	ⓢ*L. yunnana* (Fairmaire) (JENG)	OT
Lamprocera Laporte de Castelnau		
♂♀	ⓢ*L. tristior* Gorham (NMB)	NT
Lamprohiza Motschulsky		
♂♀	ⓣ*L. splendidula* (L.) (NMB)	PA
♂♀	ⓢ*L. delarouzei* (Jacquelin) (NMB)	PA
Lampronetes Motschulsky		
♂♀	ⓣ*L. mauritanica* (L.) (MNHN, NMB)	PA
Lampyris Geoffroy		
♂♀	ⓣ*L. noctiluca* (L.) (NMB)	PA
♂♀	ⓢ*L. algerica* Ancey (NMB)	PA
Lampyroidea Costa		
♂♀	ⓣ*L. syriaca* Costa (NMB)	PA
♂♀	ⓢ*L. dispar* (Fairmaire) (NMB)	PA
Ledocas Olivier		

♂ ⓣ*L. parallelus* Olivier (NMB)	NT
♂ ⓢ*L.* sp. (SNOW)	NT
Lucernuta Laporte de Castelnau	
♂♀ ⓢ*L. savignii* (Kirby) (NMB, NMB)	NT
Lucidina Gorham	
♂♀ ⓣ*L. accensa* Gorham (JENG)	PA
♂♀ ⓢ*L. vitalisi* Pic (JENG)	OT
♂ ⓓ*L. gracilis* Jeng (JENG)	OT
Lucidota Laporte de Castelnau	
♂♀ ⓣ*L. banoni* Laporte de Castelnau (NMB, MNHN)	NT
♂♀ ⓢ*L. bella* Gorham (MNHN)	NA
♂♀ ⓢ*L. pennata* Dejean (MNHN)	NA
♂♀ ⓢ*L. atra* (G.A. Olivier) (SNOW)	NA
♂♀ ⓓ*L. pygidialis* Oivier (NMB)	NA
Lucidotopsis McDermott	
♂♀ ⓣ*L. cruenticollis* (Fairmaire) (MNHN)	NT
Lucio Laporte de Castlnau	
♂ ⓣ*L. abdominale* Laporte de Castelnau(MNHN)	NT
♂♀ ⓢ*L. obscura* Olivier (NMB)	NT
Luciola Laporte de Castelnau	
♂♀ ⓣ*L. italica* (L.) (= *L. pedemontana* Motschulsky) (NMB)	PA
♂♀ ⓢ*L. curtithorax* Pic (JENG)	OT
♂♀ ⓢ*L. filiformis* Olivier (JENG)	OT
♂♀ ⓢ*L. kagiana* Matsumura (JENG)	OT
♂♀ ⓢ*L. lustitanica* Charpentier (NMB)	PA
♂♀ ⓓ*L. anceyi* Olivier (JENG)	OT
♂♀ ⓓ*L. cincticollis* Klug (NMB)	ET
♂♀ ⓓ*L. hydrophila* Jeng, Lai & Yang (JENG)	OT
♂♀ ⓓ*L. kuroiwai* Matsumura (JENG)	OT
♂♀ ⓓ*L.* (*Pyatyphella*) *peculiaris* (Olivier) (NMB)	AU
♂♀ ⓓ*L. substriata* Gorham (JENG)	OT, PA
♂♀ ⓓ*L. trilucida* Jeng & Lai (JENG)	OT
Lychnacris Motschulsky	
♂♀ ⓢ*L. flabellata* (F.) (NMB)	NT

Macrolampis Motschulsky		
♂♀	ⓣ*M. longipennis* Motschulsky(MNHN)	NT
♂	ⓢ*L. acicularis* (Olivier) (NMB)	NT
♂	ⓓ*M. omissa* (Olivier) (MNHN)	NA
♂	ⓓ*M. perelegans* (Gorham) (MNHN)	NA
Magnoculus McDermott (new name for *Megalophthalmus* Gray)		
♂	ⓢ*M.* sp.1 (NMB)	NT
♂	ⓢ*M.* sp.2 (SNOW)	NT
Microphotus LeConte		
♂	ⓣ*M. dilatatus* LeConte (SNOW, NMB)	NT
♂♀	ⓢ*M. angustus* LeConte (MNHN)	NA
♂	ⓢ*M. octarthrus* Fall (SNOW)	NA
Mimophaeopterus Pic		
♂	ⓢ*M. wittmeri* Pic (JENG)	OT
Mimophotinus Pic		
♂	ⓣ*M. angustatus* Pic (MNHN)	OT
Nyctophila Olivier		
♂♀	ⓢ*N. reichii* Jacquelin (NMB)	PA
Oculogryphus Jeng, Engel and Yang		
♂	ⓣ*C. fulvus* Jeng (JENG)	OT
(*Oliviereus* Pic)*		
♀	ⓣ*O. flavus* Pic (MNHN)	NT
Ophoelis Olivier		
♂	ⓣ*O. impura* Olivier (MNHN)	NT
Ototretadrilus Pic		
♂	? *O. flavoscutellaris* Wittmer (NMB, JENG)	OT
Paraphausis Green (monobasic)		
♂	ⓣ*P. eximia* Green (SNOW)	NA
Petalacmis Olivier		
♂	ⓣ*P. praeclarus* Olivier (NMB)	NT
Phaenolis Gorham		
♂	ⓣ*P. laciniatus* Gorham (NMB)	NT
♂	ⓢ*P. bicoloripes* Pic (NMB)	NT
Phausis LeConte		

♂ ⓣ*P. reticulata* (Say) (SNOW, MNHN)	NA
Phosphaenopterus Schaufuss	
♂ ⓣ*P. metzneri* Schaufuss (NMB)	PA
Phosphaenus Laporte de Castelnau	
♂♀ ⓣ*P. hemiptera* (Geoffroy) (NMB)	PA
Photinus Laporte de Castelnau	
♂ ⓣ*P. pallens* (F.) (NMB, MNHN)	NT
♂♀ ⓢ*P. maritimus* Olivier (MNHN)	NT
♂♀ ⓓ*P. extensus* Gorham (MNHN)	NA
♂♀ ⓓ*P. scintillans* (Say) (MNHN)	NA
♂♀ ⓢ*P. pyralis* (L.) (JENG)	NT
Photuris Dejean	
♂♀ ⓢ*P. trilineata* (Say) (SNOW, NMB)	NA
♂♀ ⓓ*P.* sp. (SNOW)	NT
Photurocantharis Pic	
♂♀ ? *Photurocantharis* sp. (MHHN)	NT
Picodrilus Wittmer	
♂ ? *P. limbellus* Wittmer (JENG)	OT
Platylampis Motschulsky	
♂ ⓣ*P. latiuscula* Motschulsky (MNHN)	NT
♂ ⓓ*P. delicata* Olivier (MNHN)	NT
Pleotomodes Green	
♂ ⓢ*P. knulli* Green (SNOW)	NA
Pleotomus LeConte	
♂♀ ⓣ*P. pallens* LeConte (SNOW, NMB)	NA
Pollaclasis Newman (monobasic)	
♂♀ ⓣ*P. bifaria* (Say) (= *P. ovatus* Newman)(SNOW)	NA
Pristolycus Gorham	
♂♀ ⓣ*P. sagulatus* Gorham (JENG)	PA
♂♀ ⓢ*P. kanoi* Nakane (JENG)	OT
Pseudolychnuris Motschulsky	
♂♀ ⓣ*P. vittata* Motschulsky (NMB)	NT
Psilocladus Blanchard	
♂ ⓣ*P. miltoderus* Blanchard (MNHN)	NT

♂♀ ⓢ*P. nevermanni* Pic (SNOW)	OT
Pteroptyx Olivier	
♂♀ ⓣ*Pteroptyx fulminea* Ballantyne (NMB)	AU
♂♀ ⓢ*P. cribellata* (Olivier) (NMB)	AU
Pterotus LeConte	
♂ ⓣ*P. obscuripennis* LeConte (JENG)	NA
Pygoluciola Wittmer	
♂♀ ⓢ*P. satoi* Ballantyne (JENG)	OT
Pyractenema Olivier (new name for *Pyractomena* Solier)	
♂♀ ⓓ*P. obscura* (Olivier) (JENG)	OT
Pyractomena Melsheimer	
♂♀ ⓣ*P. lucifera* Melsheimer (SNOW, NMB)	PA
♂♀ ⓢ*P. striatella* (Gorham) (NMB)	NA
Pyrocoelia Gorham	
♂ ⓣ*P. bicolor* (F.) (NMB)	OT
♂♀ ⓓ*P. analis* (F.) (JENG)	OT, PA
♂♀ ⓓ*P. praetexta* Olivier (JENG)	OT
♂♀ ⓓ*P. formosana* Olivier (JENG)	OT
♂♀ ⓓ*P. prolongata* Jeng, Lai & Yang (JENG)	OT
Pyrogaster Motschulsky	
♂♀ ⓢ*P. luniferi* (Eschscholtz) (SNOW)	NT
♂♀ ⓢ*P. mediofasciatus* Pic (NMB)	NT
♂♀ ⓢ*P. malepictus* Olivier (NMB)	NT
♂♀ ⓓ*P. coxalis* (Olivier) (NMB)	NT
Pyrophanes Olivier	
♂♀ ⓣ*P. similis* Olivier (NMB)	OT
♂♀ ⓢ*P. appendiculata* Olivier (NMB)	NT
Pyropyga Motschulsky	
♂♀ ⓣ*P. nigricans* (Say) (NMB)	NA
♂♀ ⓢ*P. fenestralis* (Melsheimer) (NMB)	NA
Rhagophthalmus Motschulsky	
♂♀ ⓢ*R. ohbai* Wittmer (JENG)	OT
Robopus Motschulsky	
♂♀ ⓢ*R. lengi* (Mutch.) (NMB)	NA

♂♀ ⓓ*R. pantoni* (Olivier) (MNHN)	NT
♂ ⓢ*R. quadrimaculatus* (Laporte de Castelnau) (MNHN)	NT
♂ ⓓ*R. vittiger* (Gyllenhal) (MNHN)	NT
Roleta McDermott	
♂ ⓣ*R. notaticollis* (Pic) (= *R. coracina* McDermott) (NMB)	NT
Rufolychniq Kazantsev	
♂♀ ⓣ*R. borencona* (Leng & Mutchler) (AMNH)	NT
Satolampyris Jeng, Engel and Yang (in preparation)	
♂ ⓣ*S. dichroma* Jeng (JENG)	OT
Scissicauda McDermott (new name for *Schistura* Olivier, monobasic)	
♂ ⓣ*S. disjuncta* (Olivier) (NMB)	NT
Stenocladius Deyrolle and Fairmaire	
♂ ⓓ*S. rufithorax* Wittmer (NMB)	OT
♂♀ ⓢ*S. bicoloripes* Pic (JENG)	OT
♂ ⓓ*S. chinensis* (Geisthardt) (JENG)	OT
♂ ⓢ*S.* sp. (Thailand) (JENG)	OT
Tenaspis LeConte	
♂ ⓣ*T. angularis* (Gorham) (NMB, MNHN)	PA
♂♀ ⓢ*L. figurata* Olivier (NMB)	NT
Vesta Laporte de Castelnau	
♂♀ ⓣ*V. chevrolati* Laporte de Castelnau (JENG)	OT
♂♀ ⓢ*V. impressicollis* Fairmaire (JENG)	OT
♂♀ ⓓ*V. rufiventris* (Motschulsky) (JENG)	OT
♂♀ ⓓ*V. thoracica* (G. A. Olivier) (SNOW)	NA
♂ ⓓ*V. cincticollis* (Blanchard) (NMB)	NT
♂ ⓓ*V. arcta* Olivier (NMB)	NT

Appendix III.

List of characters sampled (with values of consistency and retention indices for each character obtained from comprehensive phylogenetic analysis)

Antenna

001. Antennal length/head width: (CI = 0.06; RI = 0.74)

    0: 1.6-3.0X

    1: less than 1.5X

    2: greater than 3.1X

002. Shape of scape (looking from ventral aspect): (CI = 0.10; RI = 0.82)

    0: robust, slightly dilated apically

    1: elongate, slightly dilated apically

    2: robust, greatly dilated apically

003. Relative length of scape vs. pedicel: (CI = 1.00; RI = 1.00)

    0: longer than pedicel

    1: as long as pedicel

004. Pedicel: (CI = 0.04; RI = 0.67)

    0: about as long as broad

    1: shorter than broad

    2: clearly longer than broad (1.5X or more)

005. Number of antennomeres of flagellum: (CI = 0.57; RI = 0.85)

    0: 9

    1: fewer than 9 (7-8)

    2: 10

    3: more than 20

    4: 12

006. Relative length of flagellar article 1 (FA1) vs. pedicel: (CI = 0.34; RI = 0.65)

    0: clearly longer than pedicel if antennae 11-articled

    1: as long as pedicel if antennae 11-articled

2: shorter than pedicel if antennae 11-articled

3: clearly longer than pedicel if antennae 9~10-articled

4: shorter than pedicel if 9-articled

5: clearly longer than pedicel if antennae 12-articled

6: as long as pedicel if antennae 12-articled

7: clearly shorter than pedicel if antennae 12-articled

8: longer than pedicel if antennae have more than 20 articles

9: longer than pedicel if antennae 14-articled

007. Relative length of flagellar article 1 (FA1) vs. FA2: (CI = 0.18; RI = 0.51)

0: clearly longer if antennae 11-articled

1: as long as if antennae 11-articled

2: shorter if antennae 11-articled

3: clearly longer if antennae 9~10-articled

4: as long as if 9-articled

5: longer if antennae 12-articled

6: as long as if antennae 12-articled

7: clearly shorter if antennae 12-articled

8: as long as if antennae have more than 20 articles

9: as long as if antennae 14-articled

008. FA2 to pre-distal FA: (CI = 0.14; RI = 0.70)

0: serrate, subtriangular for each FA moderately thick

1: serrate**,** subtrapezoidal for each FA, broad, more or less compressed

2: intermediate of filiform/serrate, compressed, tapering toward distal article

3: intermediate of filiform/serrate, compressed, not tapering toward distal article

4: intermediate of filiform/serrate, compact, thick, somewhat cylindrical

5: filiform, FA elongate, cylindrical or slightly compressed

6: moniliform

7: unipectinate

8: bipectinate

009. FA2 to pre-distal FA if branched: (CI = 0.41; RI = 0.68)

0: unipectinate, with thick, rigid branches

1: unipectinate, with thin, soft, lobed branches
2: bipectinate, with slender, cylindrical branches
3: bipectinate, with long, thick rigid branches
4: bipectinate, with short, thick, rigid branches
5: bipectinate, with long, lobed, soft branches

010. Stem of FA2 to predistal FA if branched: (CI = 0.23; RI = 0.57)
0: clearly longer than width if unipectinate
1: much longer than width if unipectinate
2: about as long as wide or slightly shorter/longer if unipectinate
3: longer than width if bipectinate
4: much longer than width if bipectinate
5: about as long as wide or slightly shorter/longer if bipectinate

011. Stem of FA2 to predistal FA if branched: (CI = 0.33; RI = 0.72)
0: robust
1: compressed if unipectinate
2: cylindrical if unipectinate
3: compressed if bipectinate
4: cylindrical if bipectinate

012. FA2 to predistal FA if branched: (CI = 0.28; RI = 0.57)
0: all branches clearly arising from base if pectinate
1: branches broad at base (arising from middle of antennomere) if pectinate
2: all branches clearly arising from apex if pectinate
3: branches arising from middle in basal articles and gradually moving toward apex in distal articles if pectinate
4: all branches clearly arising from base if bipectinate
5: branches arising from middle of antennomere if bipectinate
6: all branches clearly arising from apex if bipectinate
7: branches arising from middle in basal articles and gradually moving toward apex in distal articles if bipectinate

013. Pubescence on branches of FA: (CI = 0.37; RI = 0.58)

0: covered with minute pubescence and decumbent short hairs

1: covered with minute pubescence and suberectus long hairs

2: covered with long, erectus hairs

3: covered mostly with short, decumbent hairs

014. Distribution of FA branches if exist: (CI = 0.53; RI = 0.72)

0: on FA1-8 if antenna unipectinate

1: on FA2-8 if antenna unipectinate

2: on FA1-8 if antenna bipectinate

3: on FA1-9 if antenna unipectinate

4: on FA1-9 if antenna bipectinate

5: on FA2-9 if antenna bipectinate

6: on FA1 to predistal if antenna with more than 20 articles

7: on FA1-10 if antenna 14-articled

8: on FA3-8 if antenna unipectinate

015. branch symmetry of FA2 to pre-distal FA if bipectinate: (CI = 1.00; RI = 1.00)

0: symmetric in length

1: asymmetric in length

016. Distal article of flagellum if 11 articled or less: (CI = 0.37; RI = 0.65)

0: cylindrical, stick like if antennae 11-articled

1: thick, somewhat compressed, broad and short if antennae 11-articled

2: thick, somewhat cylindrical, spindle like if antennae 11-articled

3: more or less compressed, broad and long if antennae 11articled

4: more or less compressed, slender and very long if antennae 11-articled

5: thick, somewhat cylindrical, uniformly broad if antennae 11-articled

6: dot like if antennae 11-articled

7: dot like if antennae 9-10 articled

017. Distal article of flagellum if 12 articled or more: (CI = 0.50; RI = 0.60)

0: spindle like if antennae 12-articled

1: rod like if antennae 12-articled

2: slender lobed if antennae with more than 20-articled

018. Small sensory appendages on flagellum: (CI = 0.71; RI = 0.88)

0: absent

1: present, on several FAs if antennae 12-articled

2: present, on several FAs if antennae 11-articled

3: present, on distal FA if antennae 10-articled

Compound Eyes

019. Eye size in frontal aspect (distance between eyes (DBE) vs. eye width): (CI = 0.06; RI = 0.63)

0: DBE 1.6-2.5X greater than eye width (eye moderately smaller than frontal width)

1: DBE 3X greater than eye width (eye much smaller than frontal width)

2: DBE smaller than 0.6-1.5 eye width (eye slightly greater than frontal width)

3: DBE smaller than 0.5 eye width (eye much greater than frontal width)

020. Distance between eyes in ventral aspect: (CI = 0.07; RI = 0.69)

0: about the same or slightly narrower than dorsal distance

1: moderately narrower than dorsal width

2: much narrower than dorsal width

021. Shape of eyes in lateral aspect: (CI = 0.08; RI = 0.59)

0: more or less higher than long

1: nearly as long as high

2: longer than high

022. Posterior margin of eyes in lateral aspect: (CI = 0.17; RI = 0.68)

0: nearly straight or slightly curved outward

1: round or nearly so

2: moderately emarginate

3: deeply emarginate

4: slightly sinuate

023. surrounding depression along posterior margin of eyes: (CI = 0.50; RI = 0.92)

0: absent or obscure

1: very clear

Head

024. Head visibility in dorsal aspect when fully retracted: (CI = 0.25; RI = 0.91)

0: partially exposed from pronotum (vertex and beyond; eyes partially visible)

1: largely exposed (occiput and beyond, eyes fully visible)

2: barely covered (eyes not visible from dorsal aspect)

3: fully covered by pronotum (pronotal frontal edge far surpassing head)

025. Head type: (CI = 0.20; RI = 0.83)

0: interstate between typically prognathous and hypognathous

1: typically prognathous (mouthparts nearly vertical to occipital foramen)

2: typically hypognathous (mouthparts nearly parallel to occipital foramen)

026. Greatest head width: (CI = 0.11; RI = 0.60)

0: about as wide as prothoracic reception collar

1: greater than prothoracic reception collar

027. Head contour in lateral aspect (antennal prominence not considered): (CI = 0.42; RI = 0.91)

0: asymmetrically pentagonal

1: elongate, with rostrum

2: somewhat flat above and round ventrally

3: depressed elliptical

4: lying ovate

5: less than a circle, 2/3 or 3/4 circle

6: round

7: roundly rhombus

8: lying trapezoidal

9: essentially pentagonal, with projection in upper frons

028. Eye length in relation to postgena: (CI = 0.07; RI = 0.63)

0: much greater than postgena (twice or more)

1: slightly greater than postgena (less than twice)

2: postgena entirely concealed by eyes or nearly so
3: about as long as postgena
4: smaller than postgena (greater than half)
5: much smaller than postgena (about half length or less)

029. Postgenal curvature behind eyes in dorsal aspect: (CI = 0.08; RI = 0.67)
0: very broadly rounded, dish-like, without clear corner
1: somewhat bowl-like, without clear corner
2: more or less parallel sided, with lateroposterior corner somewhat clear
3: convergent posteriorly, with lateroposterior corner somewhat clear
4: almost horizontal, or slightly backwards

030. Occiput: (CI = 0.50; RI = 0.50)
0: not narrow down or extended posteriorly
1: narrow-down and extended posteriorly as a neck

031. Upper margin of occipital foramen: (CI = 1.00; RI = 1.00)
0: not or slightly surpassing posterior wall of head
1: clearly surpassing any part of posterior wall of head

032. Ventral margin of occipital foramen in ventral aspect: (CI = 0.14; RI = 0.75)
0: moderately emarginate, reaching basal 1/4-1/3 length of head
1: deeply emarginate, reaching basal 2/5-1/2 length of head
2: slightly emarginate, reaching 1/5 head length or less
3: about at same level with dorsal posterior margin of head

033. Division of vertex convexity: (CI = 1.00; RI = 1.00)
0: not divided
1: divided by postcranial suture as two tubercles

034. Upper margin of frons between eyes: (CI = 0.05; RI = 0.58)
0: as high as eyes
1: slightly lower than eyes
2: much lower than eyes

035. Depression behind antennal prominence (on vertex): (CI = 0.05; RI = 0.67)

0: not depressed
1: weakly depressed
2: strongly depressed (as the deepest point of vertex)

036. Position of antennal sockets in relation to eyes (dorsal aspect): (CI = 0.50; RI = 0.50)

0: lying anteriad or slightly overlap with eyes
1: largely or totally overlap with eyes

037. Position of antennal sockets in relation to mandible (lateral aspect): (CI = 0.25; RI = 0.40)

0: more or less overlap with mandibles
1: behind mandibles

038. Position of antennal sockets in relation to mandibles (frontal aspect): (CI = 0.09; RI = 0.70)

0: a little distant from mandibular anterior articulation (slightly less or greater than 1X)
1: approximate to mandibular anterior articulation (about 0.5X or less)
2: moderately distant from mandibular anterior articulation (1.5X or more)
3: far from mandibular anterior articulation (more than 3X diameters)

039. Orientation of antennal socket: (CI = 0.40; RI = 0.82)

0: facing anterolaterally
1: almost facing laterally
2: almost facing anteriorly

040. Antennal sockets in dorsal aspect: (CI = 0.12; RI = 0.58)

0: not covered by epicranium in upper margin
1: partially covered by epicranium in upper margin

041. Upper margin of antennal fossa: (CI = 0.50; RI = 0.80)

0: normal
1: angled and partially covering antennal sockets above

042. Shape of antennal socket: (CI = 0.03; RI = 0.56)

0: about as high as width

1: wider than high

2: higher than width

043. Upper margin of antennal socket: (CI = 0.05; RI = 0.60)

0: round

1: elevated in upper corner

2: straight, horizontal

3: declined in upper corner

044. Position of antennifer: (CI = 0.08; RI = 0.67)

0: in lower inner corner of antennal socket

1: in lower corner

2: absent

045. Shape of antennifer: (CI = 0.04; RI = 0.42)

0: blunt or flat triangular

1: about right angle

2: prominently projected

046. Orientation of antennifer: (CI = 0.07; RI = 0.68)

0: pointing upperlaterally

1: pointing upward

2: pointing laterally

047. Definition of clypeus (frontoclypeal suture present or not): (CI = 1.00; RI = 1.00)

0: clear

1: blurred

048. Frontogenal ridge (from inner margin of antennal sockets to mandibular articulation): (CI = 0.06; RI = 0.71)

0: absent

1: present

049. Clypeus: (CI = 0.16; RI = 0.28)

0: normal

1: thickly strengthened

050. Lower margin of clypeus: (CI = 0.13; RI = 0.43)

0: broadly roundly emarginate

1: squarely emarginate

2: triangular emarginate

3: roundly emarginate

4: straight

5: triangularly projecting

051. Gena below antennal sockets: (CI = 0.09; RI = 0.74)

0: moderately and smoothly expanded ventrally toward mandibular articulations

1: abruptly expanded above mandibles, more or less vertical to frons

2: not or very slightly expanded

052. Mandibular articulations & pleurostoma: (CI = 0.16; RI = 0.80)

0: both anterior and posterior articulations clear; outer margin of pleurostoma deeply notched

1: both articulations clear; margin of pleurostoma shallowly notched, more or less oblique toward posteriorly

2: both articulations weak; margin of pleurostoma not notched or insignificantly

053. Margins of hypostoma in ventral aspect: (CI = 0.13; RI = 0.66)

0: roundly curved

1: bowl-shaped

2: shallowly emarginate (dish like)

3: narrowly V-shaped, nearly straight or weakly curved

4: somewhat parallel with each other, slightly curved

5: roundly curved, with posterior broader than anterior part

054. Posterior tentorial pits: (CI = 0.33; RI = 0.42)

0: a pair, separated

1: one large pit

2: two small pits in a large hole

055. Position of posterior tentorial pits: (CI = 0.21; RI = 0.50)

0: adjacent to mouthparts, behind cardos of maxillae

1: adjacent to mouthparts, behind submentum

2: a little distant from mouthparts, laterally

3: a little distant from mouthparts, centrally

4: far from mouthparts

056. Postgena in ventral aspect: (CI = 0.11; RI = 0.68)

0: largely horizontal

1: depressed anteriorly but more or less horizontal posteriorly

2: depressed throughout postgena

057. Gula: (CI = 0.16; RI = 0.44)

0: present

1: absent

058. Lower margin of occipital foramen in caudal view: (CI = 0.10; RI = 0.83)

0: as low as flat postgena

1: overall lower than postgena

2: deeper than gena

059. Gula shape: (CI = 0.10; RI = 0.60)

0: transversely trapezoidal

1: volcano-shaped

2: somewhat bowl-like, with anterior side broader than posterior

3: broad, curve inward laterally

4: I-shaped

5: suture only or nearly so

6: longitudinal stripe

7: very transversely quadrate or trapezoidal

8: trapezoidal as tall as wide

060. Posterior lip of postoccipital ridge (Cm, nec Duport 1960): (CI = 0.03; RI = 0.72)

0: weak

1: present, strongly elevated

061. Shape of occipital foramen: (CI = 0.13; RI = 0.68)

0: elongate quadrate

1: subquadrate, about as high as wide

2: highly transverse

3: higher than wide, with upper 1/2 subparallel sided

4: higher than wide, upper 1/2 more or less rounded or angled

5: higher than wide, with upper 1/2 tapering ventrally

6: higher than wide, upside-down subtriangular, gradually tapering ventrally

062. True occipital foramen/ head width: (CI = 0.05; RI = 0.54)

0: about 1/3 head width

1: less than 1/3

2: greater than 1/3

063. Postoccipital ridge: (CI = 0.09; RI = 0.37)

0: very narrow

1: present, in upper margin only, not surpassing occipital condyle

2: present, reaching occipital condyle

3: present, surpassing occipital condyle

064. True occipital foramen: (CI = 0.14; RI = 0.59)

0: large square in upper 2/3, short stem in basal 1/3

1: mushroom-like, with short stem in basal 1/3

2: upper and lower part about identical in length, subparallel sided in upper one

3: longitudinal square

4: somewhat triangular

5: longitudinal elliptical

6: upper and lower part about identical in length, roundly expanded in upper one

7: transversely elliptical, with a very short stem

Mouthparts

065. Labrum: (CI = 0.04; RI = 0.68)

0: more or less on same plane with frons

1: projecting forward, somewhat vertical to frons

066. Labrum (connection between labrum and clypeus): (CI = 0.05; RI = 0.68)

0: free clearly from clypeus, connected with a membrane

1: closely connected with clypeus, without clear membrane

2: solidly fused with clypeus

067. Labrum: (CI = 0.27; RI = 0.20)

0: one-pieced

1: with two separated pieces of sclerites

2: with two adjacent pieces of sclerites, bilobed

3: two adjacent pieces as triangular projections

068. Sclerotized area of labrum if one-piece: (CI = 0.50; RI = 0.62)

0: not very transverse

1: very transversely elliptical

2: very transversely triangular and notched apically

3: very transversely striped, with a small projection centrally in ventral margin

069. Sclerotized area of labrum if one-piece and not very transverse: (CI = 0.15; RI = 0.65)

0: small, subtriangular

1: transverse, emarginate apically

2: transverse, not emarginate

3: a curved band

4: moderately transversely subquadrate

5: moderately transverse, emarginate apically

6: moderately transverse, subpentagonal or with a pointed central apex

7: somewhat bowl-shaped, notched apically

8: elongate or as long as wide, upside down subtrapezoidal

9: inverted U-shaped

070. Labrum sclerotization: (CI = 0.05; RI = 0.58)

0: well sclerotized

1: partially sclerotized

071. Visibility of mandible: (CI = 0.25; RI = 0.76)

0: largely exposed from labrum

1: largely concealed by labrum

072. Shape of mandible: (CI = 0.31; RI = 0.75)

0: thick, triangular

1: smoothly curve in both inner and outer margins toward pointed apices

2: abruptly curved, basal 1/3 straight and then curved toward apex; inner margin not smoothly curve, slightly broadened in apical 1/3

3: like State 2, with apex turning downward

4: mostly straight, curve in apical 1/3

5: rod like, almost straight

6: hook like, with a backward apex

7: normally curved, with apical 1/2 abruptly diminished in width

8: with basal 2/3 straight, apical 1/3 abruptly diminished in width

9: elongate, weakly hooked apically

073. Hairs on mandibles: (CI = 0.33; RI = 0.88)

0: with hairs on base

1: with hairs on the whole mandible

2: bare

3: with hairs on 2/3 or 3/4 of mandibles

074. Inner brush of mandibles: (CI = 0.14; RI = 0.88)

0: simple, nothing

1: with brush in basal 1/2

2: with brush in basal 2/3

3: with brush in basal 1/3-1/4

075. Mandibular inner teeth: (CI = 0.50; RI = 0.83)

0: absent

1: present, at middle

2: present, at base

076. Mandibular sclerotization: (CI = 0.14; RI = 0.86)

0: fully and well sclerotized

1: partially sclerotized

2: weakly so

077. Mandible vs. maxilla: (CI = 1.00; RI = 1.00)

0: mandible not or slightly smaller than maxilla

1: mandible much smaller than maxilla

078. Orientation of maxillary stipes: (CI = 0.40; RI = 0.76)

0: more or less parallel

1: convergent anteriorly

079. Galea: (CI = 1.00; RI = 1.00)

0: well developed, as long as, slightly longer or shorter than stipe

1: stick-like

2: much shorter than stipe

080. Palpifer: (CI = 0.12; RI = 0.60)

0:moderately separated from stipe apically, as an individual segment

1: slightly separated from stipe apically, as an individual segment

2: clearly separated from stipe apically, as an individual segment

3: closely attached to stipe, elongate triangular

4: closely attached to stipe, broad triangular

081. Relative length of maxillary palpomere 4 to 1-3 combined: (CI = 0.10; RI = 0.69)

0: clearly shorter than 1-3 combined

1: about as long as or slightly shorter than 1-3 combined

2: much longer than 1-3 combined

082. Maxillary palpomere 4 lobed or not: (CI = 1.00; RI = 1.00)

0: not lobed

1: lobed, as a long stripe

2: lobed, as a broad piece

083. Maxillary palpomere 4 if not lobed: (CI = 0.22; RI = 0.77)

0: body cylindrical, more or less spindle like, with pointed or dull apex

1: body compressed, elongate, with dull apex

2: elongate, rod like

3: body thick, moderately long, with short and thin edge apically

4: body thick, moderately long, without clear thin edge but membranous ventral face

5: body thick, somewhat securiform, with long and thin edge apically

6: body thick, somewhat cylindrical, moderately long, with dull apex

7: body thick, short, with thin, compressed edge apically

8: body thick, with dilated apex

084. A large membranous area of maxillary palpomere 4 in inner side: (CI = 0.25; RI = 0.93)

0: absent

1: present

085. Submentum: (CI = 0.09; RI = 0.69)

0: clearly separated from anterior margin of gula by a suture

1: anterior margin of gula not separated from submentum (deemed as absent of submentum)

086. Shape of submentum: (CI = 0.17; RI = 0.40)

0: insignificant

1: present, very broadly triangular

2: very transverse, impressed apically

3: very transverse subquadrate

4: very transverse subtrapezoidal

5: as long as broad or elongate

087. Shape of submentum if elongate: (CI = 0.14; RI = 0.60)

0: tall trapezoidal

1: elongate and slender

2: elongate quadrate

3: elongate quadrate with dilated apex

4: quadrate apex with short stem

5: inverted trapezoidal, broad

6: quadrate, about as long as broad

088. Submentum in ventral view: (CI = 0.05; RI = 0.52)

0: more or less horizontal

1: moderately elevated

2: strongly elevated

089. Posterior margin of mentum: (CI = 0.03; RI = 0.60)

0: lying in about the same level with maxilla

1: lying considerably anteriad of maxilla (submentum is at basal 1/2 of maxillary stipes)

090. Shape of mentum: (CI = 0.50; RI = 0.75)

0: more or less elongate, not prominent

1: large, transversely trapezoidal

091. Labial palpigers fusion or not: (CI = 0.20; RI = 0.71)

0: fused as a piece, without a suture

1: fused with a suture or adjacent with each other

2: widely separated from each other

092. Terminal lobe of labium (lobe(s) beyond palps) (CI = 0.23; RI = 0.61)

0: reduced, a small triangle

1: very transverse

2: two transverse pieces

3: two broadly triangular pieces
4: two triangular pieces forming a triangular
5: two elongate sponge-like lobes

093. Labial palp: (CI = 0.23; RI = 0.50)
0: 3-articled
1: 2-articled

094. Labial palpomere 3 (for 3-articled palp only): (CI = 0.05; RI = 0.48)
0: normal size, shorter than 1+2
1: as long as 1+2 or longer
2: extraordinarily enlarged, much longer than 1+2

095. Labial palpomere 3 (for 3-articled palp only): (CI = 0.16; RI = 0.64)
0: wheat-seed-like, cylindrical, with somewhat pointed apex
1: elliptical or subquadrate, somewhat depressed, with membranous apex
2: tubule like, with an apical openning
3: very elongate elliptical, with ridged apex
4: securiform, depressed, with apex wider than base
5: somewhat securiform, slightly depressed, with apex about as wide as base
6: somehat securiform, depressed, more elongate than State 6
7: more or less triangular, depressed
8: lobe-like
9: somewhat similar with state 6, with two apical teeth

096. Labial palpomere 3 (for 3-articled palp only) if triangular: (CI = 0.18; RI = 0.72)
0: about right triangle
1: flat triangle
2: right angle with inner projections
3: somewhat crescent, with curved inner margin

097. Relative size of maxillary and labial palps: (CI = 0.50; RI = 0.66)
0: maxillary palp larger than labial one
1: about the same size

2: labial palp very reduced, much smaller than maxillary one

Prothorax

098. Pronotum/head ratio: (CI = 0.11; RI = 0.75)
0: slightly greater (1.2-1.6X)
1: as wide as (0.9-1.0X)
2: moderately wider (1.7-2.4X:1)
3: much wider (2.5-3.5X: 1)
4: extraordinary wider (greater than 3.5X:1)

099. Degrees of transverse of pronotum: (CI = 0.05; RI = 0.57)
0: very
1: moderately
2: nearly as wide as long
3: longer than wide

100. Pronotal collar immediately behind head: (CI = 0.33; RI = 0.33)
0: present
1: absent

101. Anterior part of anterolateral margin of pronotum: (CI = 0.09; RI = 0.67)
0: slightly arched (length of arch less than half length of pronotum)
1: straight
2: well arched (arch more than half length of pronotum)
3: wide triangular
4: rectangular triangular
5: somewhat straight at sides and triangularly projecting in middle

102. Reception collar for mesothorax vs. posterior margin of pronotum: (CI = 0.22; RI = 0.85)
0: collar with sides exposed, posterior margin continuous, not formed by any part of collar
1: collar totally exposed, posterior margin discontinuous, broken by collar
2: collar totally concealed by posterior margin of pronotum, posterior margin

continuous

103. Posterior margin of pronotum: (CI = 0.16; RI = 0.69)

0: trisinuate, with central notch smaller than side arch
1: bisinuate convex
2: deeply notch at sides, more or less straight in middle
3: broadly trisinuate, with each section about identical in length
4: trisinuate, with side greatly projecting posteriorly
5: trisinuate, convex
6: horizontal at side, convex in middle
7: broadly triangular, cnvex
8: broadly rounded, convex
9: broadly rounded, concave

104. Sublateral keels: (CI = 0.40; RI = 0.00)

0: present, incomplete
1: present, complete
2: absent

105. Anterolateral angle of pronotum: (CI = 0.11; RI = 0.76)

0: more or less clearly angled
1: dully projecting
2: greater than right angle, roundly cornered
3: without clear anterolateral angle

106. Posterolateral angle of pronotum: (CI = 0.15; RI = 0.70)

0: acute and clearly projecting outward
1: right angle or slightly greater, with lateral side straight
2: clearly greater than right angle, with lateral side straight
3: somewhat foot-like
4: dull at point and projecting lateroposteriorly
5: more or less acute, projecting posteriorly
6: more or less right angle, with lateral side tapering toward posteriorly, angle facing posteriorly

7: slightly less than right angle, with lateral side straight

8: slightly less than right angle, with lateral side divergent toward posteriorly; angle broadly rounded

9: more or less right angle, with lateral side divergent and posterior side oblique

107. Width of lateral expansion of pronotum: (CI = 0.09; RI = 0.67)

0: no clear expansion

1: very narrow (limited to lateral margins)

2: narrow (1/6 width of half central disc or less)

3: moderate (about quarter width of central disc)

4: broad (about one third to half width of central disc)

5: very broad (as wide as central disc)

108. Anterior margin of pronotum: (CI = 0.06; RI = 0.67)

0: flat, not reflex

1: weakly reflexed

2: strongly reflexed

109. Lateral margin of pronotum: (CI = 0.12; RI = 0.65)

0: sloping down from central disc toward lateral margin

1: with lateral expansion descent

2: with lateral expansion flat or slightly elevated

3: with lateral expansion strongly reflexed

110. Posterior margin of pronotum: (CI = 0.28; RI = 0.54)

0: not elevated

1: weakly elevated in middle

2: strongly elevated in middle

111. Separation of pronotal main disc from posterior margin of pronotum: (CI = 0.18; RI = 0.81)

0: nothing

1: by a flat area

2: by a row of punctures

3: by a groove

112. Posterolateral angles of pronotum: (CI = 0.12; RI = 0.76)
    - **0:** thick, triangular, with posterior margin connecting angle and cavity rim
    - **1:** thick, triangular, with separate posterior margin and cavity rim
    - **2:** thick, triangular, with posterior margin connecting angle but not cavity rim
    - **3:** thin, with posterior margin, angle and cavity rim joint together
    - **4:** rounded, no clear angle

113. Posterolateral angles: (CI = 0.11; RI = 0.67)
    - **0:** strongly roof-like
    - **1:** slightly roof-like
    - **2:** not roof-like

114. Deep impressions in inner side of posterolateral angles: (CI = 0.13; RI = 0.82)
    - **0:** absent
    - **1:** shallow
    - **2:** deep

115. Face of posterolateral angle, lateral view: (CI = 0.08; RI = 0.68)
    - **0:** oblique outward
    - **1:** vertical
    - **2:** oblique forward
    - **3:** thin

116. Lateral margin of pronotum (from joint of pleurite to posterolateral angles): (CI = 0.33; RI = 0.84)
    - **0:** arising from anterior toward posterior margins
    - **1:** obscure in anterior and arising posteriorly
    - **2:** convex
    - **3:** concave
    - **4:** convex, lateral margin well elevated
    - **5:** weakly convex
    - **6:** strongly sinuate

7: very weakly concave

8: down sloped, linear

117. Central disc groove or subdivided cells: (CI = 1.00; RI = 1.00)

0: absent

1: with central groove

2: with subdivided cells

118. Subdivision of pronotal central disc: (CI = 0.15; RI = 0.76)

0: not divided or divided into cells

1: divided into two discs

2: with two well-defined bold tubules

119. Pronotal convexity in subapical area: (CI = 0.16; RI = 0.83)

0: undifferentiated from central disc (pronotum hump as a whole)

1: shorter than central disc, convergent anteriorly

2: shorter than central disc, divergent anteriorly

3: about as long and wide as central disc

4: longer or wider than central disc, usually bulb-lamp like

120. Pronotal windows: (CI = 0.25; RI = 0.60)

0: absent

1: present, subapically, convex independently, not on disc

2: present, on convexity of disc

3: present, on lateral sides of apical disc

121. Surface of sublateral area of pronotum: (CI = 0.12; RI = 0.64)

0: moderately punctate

1: finely and sparsely punctate

2: finely and densely punctate

3: densely punctate

4: coarsely punctate

5: very coarsely punctate

6: two large impressions

122. Punctuation on subapical area of pronotum: (CI = 0.10; RI = 0.65)

0: moderately punctate

1: finely and sparsely punctate

2: finely and densely punctate

3: densely punctate

4: coarsely punctate

5: very coarsely punctate

123. Surface on central disc of pronotum: (CI = 0.14; RI = 0.70)

0: moderately punctuated

1: finely and densely punctuated

2: finely and sparsely punctate

3: densely punctate

4: coarsely punctuated

5: very coarsely punctuated

6: finely granulate

7: smooth

124. Pubescence of pronotal margins: (CI = 0.12; RI = 0.85)

0: short

1: long

2: minute, looking bold

125. Backfold of pronotum in prothoracic cavity: (CI = 0.05; RI = 0.78)

0: as a narrow band, about identical in width

1: with a broad projection in posterior margin

126. Inner collar of head cavity: (CI = 0.05; RI = 0.35)

0: thin

1: thick

127. Hypomeron height/length ratio (lateral explanation not accounted): (CI = 0.48; RI = 0.60)

0: tall, slightly elongate (greater than 1/2)

1: moderately elongate (about 1/2)

2: short (less than 1/2)

3: very short (less than 1/5)

4: slender

128. Anterior margin of hypomeron: (CI = 0.10; RI = 0.64)

0: slightly oblique

1: moderately oblique

2: very oblique

3: curve outward

4: curve, somewhat V-shaped

5: curve, inward

129. Connection of hypomeron with pronotum in anterior margin: (CI = 0.20; RI = 0.95)

0: reaching pronotal margin, forming a Y-face

1: not reaching pronotal margins

130. Greatest height of hypomeron: (CI = 0.07; RI = 0.55)

0: closer to posterior margin than to anterior

1: about in the middle

2: closer to anterior margin than to posterior

3: about equal in height

131. Anterior margin of hypomeron: (CI = 0.07; RI = 0.56)

0: with margin facing forward

1: with anterior outer plane somewhat deflexed inward

2: with anterior inner plane somewhat reflexed outward

132. Anterior margin of hypomeron: (CI = 0.08; RI = 0.73)

0: not reflexed outward

1: slightly reflexed outward, short

2: slightly reflexed outward, long

3: widely reflexed outward, long

133. Connection between hypomeron and prosternum: (CI = 0.07; RI = 0.59)
0: near anterior margin of pleurite
1: in anterior third length of pleurite
2: in middle of pleurite
3: in front rather in anterior

134. Ventral margin of hypomeron behind prosternum: (CI = 0.08; RI = 0.64)
0: about in right angle, with angle ventrally
1: slightly bent, arising posteriorly
2: greater than right angle, roundly arising posteriorly
3: nearly linear

135. Posterior margin of hypomeron: (CI = 0.19; RI = 0.74)
0: with a definable angle about in right angle; posterior margin bent
1: without definable angle; posterior margin oblique, bent in upper corner
2: without definable angle; posterior margin more or less broadly rounded
3: with a clearly projecting and sharp angle; posterior margin curved
4: without definable angle; posterior margin oblique, diminishing toward posteriorly
5: with definable angle slightly greater than right angle, with corner rounded;
6: with definable angle less than right angle but not clearly projecting
7: without definable angle; posterior margin oblique toward posterolateral angle
8: with a definable angle much greater than right angle; posterior margin vertical
9: with a definable angle less than right angle; posterior margin obliquely backward

136. Reception cavity for mesothorax vs. posterior margin of hypomeron: (CI = 0.10; RI = 0.90)
0: not part of hypomeron margin, exposed independently
1: merged as part of hypomeron margin

137. Pubescence of hypomeron: (CI = 0.33; RI = 0.90)
0: much denser in margins than in main disc
1: about equally dense in margins and main disc

138. Connection between pronotum and hind margin of hypomeron: (CI = 0.07; RI = 0.71)

0: without modifications

1: with a complete, triangular wall

2: triangular wall not reaching posterior ventral margin of hypomeron

139. Mesothoracic spiracles: (CI = 1.00; RI = 1.00)

0: moderately projecting outwards, not surpassing ventral margin of hypomeron

1: greatly projecting outwards, surpassing ventral margin of hypomeron

140. Hypomeron: (CI = 0.04; RI = 0.79)

0: reaching lower margin of head

1: not as tall as head

141. Ventral margin of hypomeron: (CI = 0.06; RI = 0.87)

0: thinly or moderately strengthened

1: thickly rimmed

142. Keel of hind angle in ventral side: (CI = 0.50; RI = 0.94)

0: present

1: absent

143. Procoxal bridge: (CI = 0.09; RI = 0.65)

0: connecting to outer wall of hypomeron

1: connecting to inner wall of hypomeron

2: connecting to projecting point of inner wall of hypomeron

3: with expansion attached to inner wall of hypomeron

144. Procoxal bridge: (CI = 0.03; RI = 0.40)

0: about equal in width

1: narrowed centrally and dilated apically

2: tapering toward apex

145. Procoxal bridge: (CI = 0.09; RI = 0.64)

0: essentially flat

1: weakly twisted

2: strongly twisted, with inner margin reflexed outward

146. Prosternum, frontal aspect: (CI = 0.22; RI = 0.72)

0: broadly rounded or somewhat triangular in ventral margin

1: flat in ventral margin

147. Prosternal central elevation, frontal aspect: (CI = 0.25; RI = 0.78)

0: absent

1: present

148. Procoxal bridge: (CI = 0.37; RI = 0.66)

0: Much broader than femoral width

1: slightly broader than femoral width

2: as broad as femoral width

3: as broad as or slender than tibial width

149. Lateral margin of procoxal bridge: (CI = 0.04; RI = 0.56)

0: divergent anteriorly

1: divergent posteriorly

2: subparallel sided

150. Procoxal bridge: (CI = 0.25; RI = 0.25)

0: reflexed in posterior margin

1: not reflexed

151. A transverse impression in central disc of prosternum: (CI = 1.00; RI = 1.00)

0: absent

1: present

152. Prosternal process: (CI = 0.24; RI = 0.70)

0: long and narrow, reaching mesosternum

1: moderate in length and width, not reaching mesosternum

2: broadly triangular, apex not surpassing procoxal cavities

3: insignificant or absent

4: short, broadly trapezoidal

5: very narrow, ridged

6: narrow, finger like

Mesothorax

153. Anterior margin of mesoscutum: (CI = 0.11; RI = 0.68)

0: very wide V-shaped (greater than right angle)

1: narrow V-shaped then wide V

2: wide V-shaped (about in right angle)

3: U-shaped (Phengodidae)

4: narrow V then horizontal

5: flat with a small notch

154. Mesoscullar notch: (CI = 0.40; RI = 0.78)

0: not elevated or nearly so

1: slightly elevated apically

2: elevated as a plateau

3: greatly elevated, vertically or recurrently basally

155. Anterior margin of mesoscutellum: (CI = 0.14; RI = 0.50)

0: very weakly arched, nearly straight

1: well arched, somewhat angled anteriorly

2: horizontal at sides and triangular centrally

3: convergent anteriorly then horizontal centrally

4: narrowly and sharply angled

5: not recognizable (scutum fused with scutellum)

156. Mesoscutum: (CI = 0.25; RI = 0.76)

0: ridged at side and expanded outward anteriorly

1: subparallel laterally

2: thickly strengthened laterally

3: divergent toward apex laterally

157. Mesoscutal depression at base: (CI = 0.15; RI = 0.59)

0: rounded anteriorly, well defined at lateral edges
1: oblique anteriorly, well defined at lateral edges
2: oblique or horizontal anteriorly, poorly defined at lateral edges
3: absent, fundamentally flat

158. Anterior margin of mesoscutellum and mesoscutellum: (CI = 0.09; RI = 0.59)

0: distant from each other, central longitudinal sulcus not reaching mesoscutellum
1: slightly distant from each other, connected with a clear central sulcus
2: close to each other, connected with a blur sulcus
3: contact with each other
4: somewhat overlap with each other
5: not recognizable (mesoscutum fused with mesoscutellum)

159. Mesoscutellum: (CI = 0.14; RI = 0.34)

0: fundamentally horizontal
1: elevate apically
2: elevated both basally and apically, lowered centrally

160. Mesoscutellum: (CI = 0.12; RI = 0.58)

0: subparallel sided
1: convergent toward apex, broad
2: convergent toward ape, narrow
3: curve basally then subparallel sided
4: divergent toward apex

161. Apex of mesoscutellum: (CI = 0.07; RI = 0.44)

0: broadly rounded
1: subtriangular
2: more or less truncated
3: weakly notched
4: deeply notched

162. Elytra length: (CI = 0.22; RI = 0.74)

0: about as long as abdomen or longer

1: about half length of abdomen or shorter

2: longer than half abdomen but far from apex

163. Elytra shape: (CI = 0.09; RI = 0.36)

0: paralleled-sided or slightly oval, as wide as pronotal width or slightly broader

1: distinctly expanded in basal half, much broader than pronotum

2: distinctively expanded in the middle, much broader than pronotum

3: distinctively expanded in apical half, much broader than pronotum

4: broad, subparallel sided, much broader than pronotum

5: slightly expanded in basal half, slightly broader than pronotum

6: slightly expanded posteriorly, slightly broader than pronotum

7: slightly expanded in middle, slightly broader than pronotum

164. Small triangular sclerite in inner basal margin of elytra: (CI = 0.03; RI = 0.73)

0: invisible

1: exposed

165. Anterior margin of elytra: (CI = 0.07; RI = 0.63)

0: humerus not prominent, moderately oblique from humerus toward scutellum

1: humerus prominent, sinuate toward scutellum

2: humerus prominent, quite oblique toward scutellum

3: humerus prominent and somewhat clearly angled

166. Elytral costae 2 and 3rd: (CI = 0.07; RI = 0.48)

0: hard to recognize

1: recognizable but quite weak

2: clear but not superimposed

3: well developed as strong costae

167. Elytral surface: (CI = 0.50; RI = 0.85)

0: more or less punctate, either finely or coarsely, but without reticulate rows

1: with reticulate rows

168. Elytral lateral margin at humeral area: (CI = 0.07; RI = 0.72)

0: humerus not concealed by lateral margin, clearly visible from ventral view

1: humerus rightly concealed by elytral lateral explanation from ventral view

2: humerus totally concealed by elytral lateral explanation, invisible ventrally

3: lateral explanation of elytra with anterior margin leveled with humerus

169. Apex of elytra: (CI = 0.18; RI = 0.45)

0: quarterly rounded

1: more or less independently rounded

2: somewhat acute

3: with ventral back-folds

170. Locking device in sutural margin: (CI = 0.50; RI = 0.66)

0: present

1: absent

171. Width of “epipleuron” in middle of elytron: (CI = 0.17; RI = 0.77)

0: none or very narrow

1: narrower than 1/4 elytral width

2: moderate, about 1/4 elytral width

3: wide, about 1/3 elytral width

4: very wide, 1/2 elytral width or broader

172. Elytral suture: (CI = 0.23; RI = 0.56)

0: well match each other from apex of scutellum to elytral apex

1: slightly dehiscent subapically

2: sinuate, dehiscent between apical half to subapex then convergent

3: dehiscent from half to apex of elytra

4: dehiscent from apex of scutellum to elytral apex

5: widely separated from each other, not contact at all

173. Extension piece outside costa 7: (CI = 0.09; RI = 0.75)

0: absent (costa 7 as marginal costa)

1: present, subtriangular

2: present, subtrapezoidal

3: present, very narrow

174. Elytral costa 7: (CI = 0.11; RI = 0.80)

0: Fuse with costa 6 at very base

1: fuse with costa 6 at apical 1/5 or beyond

2: adjacent to each other as a strengthened marginal costa

3: separated, more or less parallel to apical 1/3

175. Basal costae connecting elytral costae: (CI = 0.25; RI = 0.76)

0: well developed

1: poorly developed or not recognizable

176. Elytral costa 4: (CI = 0.04; RI =0.56)

0: faint basally but stronger in disc, recognizable

1: carinate, clearly seen

2: very weak and not recognizable

177. Elytral costa 5: (CI = 0.22; RI = 0.63)

0: faint basally but stronger in disc, recognizable

1: carinate, clearly seen

2: very weak and not recognizable

178. Elytral costa 6: (CI = 0.03; RI = 0.59)

0: lower in base then arising toward apex

1: about horizontal from base to apex

179. Outer margin of elytra at very base: (CI = 0.20; RI = 0.76)

0: not reflexed

1: reflexed

180. Elytral costa 6: (CI = 0.04; RI = 0.74)

0: clearly originate from very base of elytra (humeral area)

1: obscure at very base of elytra

181. Height of elytra in relation to metathorax in lateral view: (CI = 0.11; RI = 0.81)
    0: about as high as exposed metathorax
    1: shorter than exposed metathorax (elytra quite flat)
    2: greater than exposed metathorax or totally conceal it laterally

182. Elytral humerus: (CI = 0.11; RI = 0.77)
    0: more or less vertical
    1: roundly folded
    2: somewhat sharply folded
    3: weakly folded, decline toward lateral margin

183. Elytral pubescence: (CI = 0.16; RI = 0.44)
    0: not velvet
    1: velvet

184. Elytral hairs: (CI = 0.10; RI = 0.61)
    0: short
    1: long
    2: minute

185. Inner margin of elytra: (CI = 0.19; RI = 0.52)
    0: largely straight
    1: incurve
    2: sinuate
    3: oblique
    4: round
    5: very mildly out-curving

186. Cavity in base of elytra: (CI = 0.50; RI = 0.95)
    0: present, broad
    1: present, restricted to alary sclerites
    2: absent

187. Relative width of mesepisternum and mesepimeron: (CI = 0.08; RI = 0.68)
0: about the same width
1: mesepimeron wider
2: mesepisternum wider

188. Mesepimeron: (CI = 0.28; RI = 0.63)
0: subtriangular, with posterior margin broadly rounded
1: broad triangular, with posterior margin notched
2: elongate triangular, with posterior margin notched
3: crescent
4: elongate triangular, with outer angle low
5: broad triangular, with outer angle low
6: reduced, narrowly subquadrate

189. Mesepimeron: (CI = 0.11; RI = 0.70)
0: largely flat
1: deeply impressed or bent

190. Mesepisternum: (CI = 0.50; RI = 0.66)
0: flat, not ridged
1: ridged through the sclerite (anterior part for reception of procoxal)

191. Mesepisternum: (CI = 0.18; RI = 0.81)
0: broadened apically
1: about same width from base to apex (*Amydetes*)
2: broaden apically and with an arm

192. Apex of mesepisternum: (CI = 0.12; RI = 0.59)
0: straight
1: flat, slightly bent
2: bent in narrower angle
3: bent about in right angle

193. Width of mesoventrite bridge in relation to mesepisternum: (CI = 0.15; RI = 0.45)

0: 3/4 width of the latter or more

1: 1/2-2/3 width of the latter

2: less than 1/2 width of the latter

194. Mesepisternal suture with mesoventrite: (CI = 0.05; RI = 0.82)

0: clear

1: very weak, obscure or absent

195. Orientation of mesepisternum: (CI = 0.12; RI = 0.63)

0: convergent toward apex

1: more or less parallel, slightly convergent toward apex

196. Reception cavity for precoxae in mesoventrite: (CI = 0.50; RI = 0.75)

0: present (with ridge)

1: absent (without ridge)

197. Side arms of mesoventrite: (CI = 0.14; RI = 0.75)

0: V-shaped, with arms about same width

1: V-shaped, with arms diminishing in width toward central area

2. similar to state 1, but with posterior margin horizontal

3: V-shaped, with arms widened in width toward central area

4: V-shaped, with arms sinuate, narrowest in middle

5: Curved

6: very short or absent

7: somewhat inverted triangular, broadest in middle

198. Central area of mesoventrite: (CI = 0.06; RI = 0.78)

0: well sclerotized

1: weakly sclerotized

199. Apex of mesoventrite: (CI = 0.10; RI = 0.60)

0: somewhat truncated

1: with a keel

2: with a process

3: broad V-shaped, about in right angle

4: broadly rounded, with or without a small apical projection

200. Mesoventrite: (CI = 1.00; RI = 1.00)

0: thin or moderately thick

1: very thick

201. Apex of Mesoventrite: (CI = 0.33; RI = 0.50)

0: notched

1: not notched

202. Mesoventrite anterior margin: (CI = 0.06; RI = 0.57)

0: flat, straight

1: V-shaped

2: __/-shaped, somewhat dish like

3: shallowly roundly emarginate

Metathorax

203. Metanotal groove: (CI = 0.10; RI = 0.54)

0: reaching posterior margin of metascutellum or nearly so

1: somewhat distant from posterior margin of metascutellum (within apical 1/3)

2: distant from posterior margin of metascutellum (within basal 1/2)

3: far from posterior margin of metascutellum (within basal 1/4)

204. Metanotal groove: (CI = 0.04; RI = 0.71)

0: open posteriorly (scutoprescutal ridge meet posteriorly)

1: close posteriorly or nearly so (scutoprescutal ridge not meet posteriorly)

205. Metanotal scutellar ridge: (CI = 0.18; RI = 0.70)

0: present as a strong ridge

1: absent, only a longitudinal suture

2: absent, flat and nothing

206. Metascutum: (CI = 0.18; RI = 0.62)

0: transverse

1: about as long as wide

2: elongate

207. Metascutellum: (CI = 0.03; RI = 0.60)

0: flat or right triangular

2: narrow and tall triangular

208. Metepimeron: (CI = 0.33; RI = 0.00)

0: somewhat stripe-like, base slightly greater than apex

1: more or less triangular, base much greater than apex

209. Subdivision of metepisternum: (CI = 0.25; RI = 0.85)

0: present, top-bottom subdivision

1: present, head-tail subdivision

2: absent

210. Sutural area between metepisternum and metepimeron: (CI = 0.14; RI = 0.88)

0: flat

1: depressed

211. Metaventrite between mesocoxae: (CI = 0.17; RI = 0.64)

0: a process on the same level with mesocoxae

1: broadly and mildly elevated but not ridged

2: narrowly elevated and ridged, leveled with metaventrite

3: narrowly elevated and ridged, lower than metaventrite

4: flat and broad

212. Mesocoxal cavity in metaventrite: (CI = 0.33; RI = 0.66)

0: well defined

1: blurrily defined

213. Centroapical notch of metaventrite: (CI = 0.06; RI = 0.65)

0: projections about on same level with metaventrite, forming part of notch contour

1: projections located deeply, subparallel apically; not part of notch contour

2: projections located deeply, convergent apically; not part of notch contour

3: projections invisible

214. Subcentroapical notch of metaventrite above metacoxae: (CI = 0.16; RI = 0.66)

0: absent or very weakly notched

1: present, clearly notched

215. Metaventrite central longitudinal suture: (CI = 0.08; RI = 0.65)

0: clear and almost complete, beyond 1/2 metaventrite

1: clear, about 1/2 ventrite length

2: very short or absent, in basal 1/4 at most

216. Metaventrite: (CI = 0.05; RI = 0.48)

0: not elongate

1: elongate

217. Metaventral transverse sulcus: (CI = 1.00; RI = 1.00)

0: present

1: absent

Legs

218. Visibility of prothoracic trochantin: (CI = 0.50; RI = 0.33)

0: largely exposed from hypomeron, at least apical projections visible

1: totally exposed, separated from prothoracic hypomeron

2: almost totally concealed by hypomeron, barely visible

219. Shape of prothoracic trochantin (exposed part): (CI = 0.57; RI = 0.86)

0: asymmetrically bifurcated, with a long and moderately thick upper projection, and a short and broad lower projection

1: similar to state 0, but with a fairly slender and curved upper projection and smaller lower projection

2: similar to state 1, but with lower projection pointed toward ventrally

3: elongate triangular, knife like, main body gradually tapering toward apex

4: main body broad, about right triangular; projection short and angle like

220. Prothoracic trochantin: (CI = 0.04; RI = 0.75)

0: glabrous
1: setiferous

221. Prothoracic coxal shape: (CI = 0.28; RI = 0.81)

0: upper margin strongly curve
1: upper margin smoothly or weakly curve; conical part short, transverse
2: upper margin smoothly or weakly curve; conical part elongate

222. Prothoracic coxa shape if upper margin strongly curved: (CI = 0.50; RI = 0.66)

0: quite broad, somewhat egg-shaped
1: elongate

223. Lower margin of prothoracic coxa: (CI = 0.25; RI = 0.83)

0: moderately projecting in both inner and outer sides
1: projecting much more in inner side than in outer side

224. Coxal reception groove for femur of prothoracic leg: (CI = 0.25; RI = 0.76)

0: more or less symmetrical, frontal wall about as prominent as back wall
1: asymmetric, with frontal wall much more prominent than back wall

225. Coxal reception groove for femur of prothoracic leg: (CI = 0.50; RI = 0.83)

0: glabrous
1: setiferous

226. Thick setae on ventral area of protrochanters: (CI = 0.50; RI = 0.66)

0: absent
1: present

227. Broadest point of prothoracic trochanter: (CI = 0.05; RI = 0.77)

0: subapically, trochanter more or less quadrilateral
1: apically, trochanter subtriangular

228. Apex of trochanter vs. base of femur of prothoracic leg: (CI = 0.20; RI = 0.42)

0: about the same width

1: apex of trochanter broader than femoral base

229. Femoral attachment to trochanter in prothoracic leg: (CI = 0.40; RI = 0.70)

0: at apex, joint weakly oblique

1: at apex**,** joint fairly oblique

2: more or less at upper corner, with inner margin of femur subparallel to outer margin of trochanter

230. Prothoracic femur width: (CI = 0.09; RI = 0.56)

0: more or less evenly dilated, broadest in the middle

1: broader in basal 1/2 than in apical 1/2, broadest in basal 2/5 or 1/3

231. Thickness of prothoracic tibiae: (CI = 0.08; RI = 0.82)

0: cylindrical

1: more or less depressed

2: heavily depressed

232. Curvature prothoracic tibiae: (CI = 0.07; RI = 0.56)

0: not curve

1: curve in outer margin but straight or almost so in inner margin

2: both side curved inward

3: curve in both outer and inner margin, in opposite direction (somewhat dilated)

4: both side curved outward

233. Tibial spurs: (CI = 0.06; RI = 0.74)

0: absent

1: 2 small spurs

2: 2 large spurs

234. Inner apical margin of prothoracic tibia: (CI = 0.20; RI = 0.00)

0: not produced

1: clearly produced

235. Relative lengths of prothoracic tarsi vs. tibia: (CI = 0.16; RI = 0.37)

0: about the same length

1: tibia longer

236. Tarsal pulvilli: (CI = 0.33; RI = 0.73)

0: absent

1: on tarsomere 4 only

2: on tarsomeres 3-4

3: right beneath tarsomeres 1-4

4: on tarsomeres 1-4, apically

5: on tarsomeres 2-4, apically

237. Relative lengths of tarsomeres 1-4 of prothoracic leg (longest tarsomere): (CI = 0.07; RI = 0.57)

0: 1 > 4

1: 1 = 4

2: 1 < 4

238. Relative lengths of tarsomeres 1-4 of prothoracic leg (shortest tarsomere): (CI = 0.07; RI = 0.72)

0: 3 > 4

1: 3 = 4

2: 3 < 4

239. Tarsomere 1 of prothoracic leg: (CI = 0.25; RI = 0.00)

0: no ventral comb

1: with a tuft of comb beneath

240. Tarsomere 2 of prothoracic leg: (CI = 0.04; RI = 0.67)

0: elongate (longer than height)

1: abbreviated (as long as height)

241. Tarsomere 3 of prothoracic leg: (CI = 0.20; RI = 0.91)

0: elongate (longer than height)

1: abbreviated (as long as height)

242. Tarsomere 4 of prothoracic leg: (CI = 0.04; RI = 0.51)

0: elongate

1: abbreviate (as long as height)

243. Tarsomere 4 of prothoracic leg: (CI = 0.33; RI = 0.90)

0: not lobed

1: lobed beneath

244. Tarsomere 4 of prothoracic leg: (CI = 0.13; RI = 0.79)

0: lateral sides not folded up

1: lateral sides folded up, widely open above (U-shaped)

2: lateral sides folded up, narrowly open above (narrowly V-shaped)

245. Tarsomere 5 of prothoracic leg: (CI = 0.10; RI = 0.81)

0: barely overlapping with tarsomere 4 (T5 greatly surpassing T4)

1: moderately overlapping with tarsomere 4 (ca. 1/2 T5 surpassing T4)

2: greatly overlapping with tarsomere 4 (1/3 or less T5 surpassing T4)

246. Claws of prothoracic and mesothoracic legs: (CI = 0.22; RI = 0.50)

0: not toothed basally

1: toothed in one claw basally

247. Claws of prothoracic and mesothoracic legs: (CI = 1.00; RI = 1.00)

0: not toothed apically

1: bifid in both claws apically

2: bifid in one claw apically

3: bifid in both claws apically

3: dull in one side, sharp in the other

248. Mesothoracic trochantin: (CI = 0.07; RI = 0.78)

0: glabrous

1: setiferous

249. Small angle in inner corner of mesotrochanters: (CI = 1.00; RI = 1.00)

0: absent

1: present

250. Coxal reception groove for femur of mesothoracic leg: (CI = 0.33; RI = 0.75)

0: more or less symmetrical, frontal wall slightly weaker than back wall

1: asymmetric, with front wall much less prominent than back wall

251. Broadest point of mesothoracic tibiae: (CI = 0.05; RI = 0.66)

0: without clear broadest point, about identical in width except thinner base

1: near apex

2: dilated from middle to apex

252. A row of dents in inner mesotibiae: (CI = 1.00; RI = 1.00)

0: absent

1: present

253. Relative lengths of tarsomeres 1-4 of mesothoracic leg (longest tarsomere): (CI = 0.08; RI = 0.71)

0: 1 > 4

1: 1 = 4

2: 1 < 4

254. Relative lengths of tarsomeres 1-4 of mesothoracic leg (shortest tarsomere): (CI = 0.08; RI = 0.74)

0: 3 > 4

1: 3 = 4

2: 3 < 4

255. Tarsomere 1 of mesothoracic leg (shortest tarsomere): (CI = 0.50; RI = 0.00)

0: not combed beneath

1: combed beneath

256. Conical part of metacoxae: (CI = 0.09; RI = 0.64)

0: short, very transverse

1: slightly broader than long

2: longer than broad

257. Front side of metathoracic coxae: (CI = 0.28; RI = 0.64)

0: obliquely diminishing in width from conical part toward ourter apex

1: sinuately diminishing in width from conical part toward lateral apex

2: abruptly narrowed down from conical part, about identical in width toward outer apex

258. Meron: (CI = 0.09; RI = 0.73)

0: largely exposed from frontal face of coxa

1: moderately visible frontal face of coxa

2: barely exposed from frontal face of coxa

3: invisible, totally blocked by frontal face of coxa

259. Conical part of metacoxae: (CI = 0.07; RI = 0.78)

0: not surpassing meron

1: passing meron

260. Articulations of metathoracic coxae: (CI = 0.08; RI = 0.78)

0: projecting in both inner and outer

1: projecting more in inner side than in outer side

2: not projecting in inner and outer sides

261. Merathoracic trochanter: (CI = 0.33; RI = 0.33)

0: elongate

1: as long as broad

262. Femoral attachment to trochanter in metathoracic leg: (CI = 0.16; RI = 0.81)

0: on upper lateral corner of trochanter

1: at apex, joint weakly oblique

2: at apex, joint fairly oblique
3: on upper margin of trochanter, joint nearly horizontal

263. Metathoracic femur width: (CI = 0.25; RI = 0.50)
0: moderately dilated
1: greatly dilated in apical 1/2

264. Reception groove for tibia in prothoracic leg (not the membranous area but a groove on femoral ventral side): (CI = 0.09; RI = 0.58)
0: restricted to apical 1/2 of femur
1: more than 1/2 femur
2: restricted to very apex
3: absent

265. Curvature metathoracic tibiae: (CI = 0.09; RI = 0.66)
0: not curve
1: curve at outer margin but straight or almost so in inner margin
2: both side curved inward
3: curved in both outer and inner margin, opposite direction (dilated)
4: both side curved outward

266. Relative length of tibia vs. femur of metathoracic leg: (CI = 0.07; RI = 0.68)
0: tibia longer
1: about the same
2: femur longer

267. Relative lengths of metathoracic tarsi vs. tibia: (CI = 0.33; RI = 0.33)
0: about the same length
1: tibia longer

268. Relative lengths of tarsomeres 1-4 of prothoracic leg (longest tarsomere): (CI = 0.08; RI = 0.62)
0: 1 > 4
1: 1 = 4

269. Relative lengths of tarsomeres 1-4 of prothoracic leg (shortest tarsomere): (CI = 0.08; RI = 0.76)

0: 3 > 4

1: 3 = 4

2: 3 < 4

270. Tarsomere 1 of metathoracic leg: (CI = 0.04; RI = 0.41)

0: elongate (longer than height less than 3X)

1: quite elongate (3X longer than high)

2: very elongate (5X longer than high)

271. Tarsomere 2 of metathoracic leg: (CI = 0.07; RI = 0.64)

0: elongate (longer than high)

1: abbreviated (as long as high)

272. Tarsomere 3 of metathoracic leg: (CI = 0.10; RI = 0.86)

0: elongate (longer than high)

1: abbreviated (as long as high)

273. Tarsomere 4 of metathoracic leg: (CI = 0.05; RI = 0.67)

0: elongate

1: abbreviated

274. Tarsomere 5 of hind leg: (CI = 0.09; RI = 0.80)

0: barely overlapping with tarsomere 4 (T5 greatly surpassing T4)

1: moderately overlapping with tarsomere 4 (ca. 1/2 T5 surpassing T4)

2: greatly overlapping with tarsomere 4 (1/3 or less T5 surpassing T4)

275. Hind claws: (CI = 1.00; RI = 1.00)

0: simple

1: both claws bifid apically

2: bifid apically in one claw

Abdomen

276. Abdominal ventrite connection: (CI = 1.00; RI = 1.00)
 - **0:** partially connation, rigidly articulated in the first few ventrites
 - **1:** all freely articulated

277. Lateral outline of ventrites: (CI = 0.50; RI = 0.66)
 - **0:** margins exactly or nearly continuous
 - **1:** continuously sinuate
 - **2:** discontinuous, hind margin of preceding ventrite greater than basal margin of next ventrite

278. Segment 1: (CI = 0.22; RI = 0.92)
 - **0:** entirely invisible ventrally
 - **1:** barely visible laterally as a small pleurite next to metacoxae

279. Sternite 2 (S2) visibility: (CI = 0.06; RI = 0.64)
 - **0:** entirely invisible, blocked by metacoxae
 - **1:** largely exposed (hind margin surpassing metacoxae)
 - **2:** partially exposed (hind margin reaching or slightly distant from apex of metacoxae)
 - **3:** barely exposed (hind margin distant from apex of metacoxae, shorter than 1/2 of conical part of metacoxae)

280. S2 hind margin: (CI = 0.02; RI = 0.50)
 - **0:** round
 - **1:** straight or nearly so

281. Hind angle of S2: (CI = 0.22; RI = 0.30)
 - **0:** clear, not projecting
 - **1:** clear and slightly projecting
 - **2:** poorly defined, more or less rounded in lateral margin

282. S3 visibility: (CI = 0.14; RI = 0.42)
 - **0:** totally or largely exposed from metacoxae (hind margin surpassing metacoxae)
 - **1:** partially concealed by metacoxae which reach S3 hind margin or nearly so)

2: largely concealed by metacoxae which surpass S3 hind margin

283. Anterior margin of S3: (CI = 0.50; RI = 0.66)

0: with metacoxal process

1: no metacoxal process

284. Lateral margins of S5: (CI = 0.04; RI = 0.60)

0: convergent toward apex

1: subparallel sided

2: divergent toward apex

285. Hind angle of S5: (CI = 0.25; RI = 0.50)

0: clear, not lobed

1: clear and more or less prominent, slightly lobed

2: poorly defined, more or less rounded in lateral margin

286. Lateral margins of S6: (CI = 0.05; RI = 0.69)

0: convergent toward apex

1: subparallel sided

2: divergent toward apex

287. Hind angle of S6: (CI = 0.33; RI = 0.50)

0: clear, not projecting

1: clear and slightly projecting

2: poorly defined, more or less rounded in lateral margin

288. S7 overall length vs. width: (CI = 0.33; RI = 0.63)

0: transverse

1: about as long as wide

2: elongate

289. S7 vs. S6: (CI = 0.14; RI = 0.70)

0: longer than S6

1: not longer than S6

290. Lateral margins of S7 in basal half: (CI = 0.07; RI = 0.72)

0: convergent toward apex

1: subparallel sided

2: divergent toward apex

291. Hind margin of S7: (CI = 0.50; RI = 0.97)

0: with central apex as most distal point

1: with central apex not surpassing subapical margin

292. Central ape of S7 if as distal: (CI = 0.41; RI = 0.65)

0: rounded apically

1: rounded apically, with a small central flat projection

2: somewhat trapezoidal, with wide flat apex

3: subtrapezoidal at base and subtriangular at apex

4: trisinuate

5: elongate triangular

293. Median apex of S7 if with middle projection: (CI = 1.00; RI = 1.00)

0: not bifurcate

1: bifurcate

294. Hind margin of S7: (CI = 1.00; RI = 1.00)

1: without claspers

2: with a pair of setose claspers (*Pteroptyx, Colophotia*)

295. Hind angles of S7: (CI = 0.27; RI = 0.79)

0: no clear hind angle (continuously rounded apically)

1: clear, not projecting

2: clear, short, projecting posteriorly

3: clear, elongate and narrow, sharply projected posteriorly

296. Upper lateral sides of S7: (CI = 1.00; RI = 1.00)

0: normal, not strengthened

1: strengthened, thick and hard

297. Curvature of S7: (CI = 0.25; RI = 0.45)

0: largely horizontal

1: smoothly up-curving

2: abruptly up-curving

298. Contact of S7-T8: (CI = 0.25; RI = 0.50)

0: closely contact

1: with clear gap between them

299. S8 visibility in ventral aspect: (CI = 0.66; RI = 0.97)

0: back folded into body, partially sclerotized

1: back folded into body, membrane

2: exposed, sclerotized

300. S8 vs. S7: (CI = 0.20; RI = 0.50)

0: no longer than S7

1: longer than S7

2: much shorter than S7, S8 barely exposed

301. S8 (overall length vs. width): (CI = 0.25; RI = 0.53)

0: transverse

1: about as long as wide

2: elongate

302. Lateral margins of S8 in basal half: (CI = 0.15; RI = 0.67)

0: convergent toward apex

1: subparallel sided

2: divergent toward apex

303. S8 apex: (CI = 0.06; RI = 0.74)

0: without apical modification

1: with central notch, large or small

2: with apical projection, large or small

304. S8 apex if notched in central apex: (CI = 0.08; RI = 0.47)

0: shallowly notched, somewhat like bisinuate

1: deeply emarginate

305. Apical projection of S8: (CI = 0.25; RI = 0.57)

0: weak and broad

1: about right angular

2: slender triangular

3: finger-like

4: slender and bifurcate apically

5: broad and long, bifurcate apically, with apex bent down and thickened

6: broad and long, bifurcate, projecting outward but not bent down

306. Hind angles of S8: (CI = 0.08; RI = 0.61)

0: not clear, poorly defined

1: clearly defined, not projecting

2: clearly defined, more or less lobed

3: clearly defined, projecting and pointed apically

307. S9 visibility: (CI = 0.13; RI = 0.73)

0: not exposed

1: exposed part much longer than S8

2: exposed part as long as or shorter than S8

3: barely visible, largely concealed by S8

308. Photogenic organs on S5: (CI = 1.00; RI = 1.00)

0: absent

1: present

309. Photogenic organs on S6: (CI = 0.27; RI = 0.76)

0: absent

1: fully occupying S7

2: a transverse stripe

3: a large, transversely elliptical central spot

4: a small, round spot adjacent to apical margin of S7

5: three central spots

6: two lateral squares

310. Photogenic organs on S7: (CI = 0.11; RI = 0.78)

0: absent

1: present if S7 being distal segment

2: present if S7 not distal segment

311. Photogenic organs on distal S7: (CI = 0.54; RI = 0.37)

0: fully occupying S7 or nearly so (e.g. not in apical small projection and lateral sides)

1: fully occupying S7 except central ridge divided lantern into two pieces

2: a large triangular or V-shaped piece occupying central area

3: an elliptical or round piece occupying central area

4: occupying basal 1/2-2/3

5: two lateral pieces

6: occupying basal 1/2, inverted U-shaped

312. Photogenic organs on regular S7: (CI = 0.62; RI = 0.82)

0: fully occupying S7

1: a transverse stripe

2: one large spot in central disc

3: one small spot in central disc

4: one small spot adjacent to apex

5: two lateral spots

313. Photogenic organs on S8: (CI = 0.09; RI = 0.71)

0: absent

1: present, two small lateral spots

2: present, two large lateral spots

314. Pubescence of ventrites: (CI = 0.18; RI = 0.71)

0: suberectus, dense and short
1: suberectus, sparse and long
2: decumbent, short
3: decumbent, minute, somewhat velvet

315. Visibility of T5 ventrally: (CI = 0.09; RI = 0.69)
0: invisible ventrally
1: exposed little, only hind angle barely visible
2: clearly exposed

316. Visibility of T6 ventrally: (CI = 0.07; RI = 0.73)
0: invisible ventrally
1: exposed little, only hind angle barely visible
2: clearly exposed

317. Visibility of T7 ventrally: (CI = 0.08; RI = 0.79)
0: invisible ventrally
1: exposed little, only hind angle barely visible
2: clearly exposed

318. T8 vs. distal sternites: (CI = 0.21; RI = 0.87)
0: about reaching apex of S7
1: about reaching apex of S8
2: slightly surpassing apex of S8
3: far surpassing S8, reaching apex of S9 or beyond

319. Hind angle of T5: (CI = 0.06; RI = 0.83)
0: not projecting (not surpassing hind central margin)
1: projecting lateroposteriorly or posteriorly (beyond hind central margin)

320. Hind margin of T5 if with projecting hind angles: (CI = 0.18; RI = 0.57)
0: broadly roundly emarginate
1: broadly and shallowly emarginate, with apex nearly straight
2: emarginate in a flat triangular shape

3: deeply emarginate, with central apex nearly straight

4: with central margin sinuate

321. Hind angle of T6: (CI = 0.12; RI = 0.92)

0: not projecting (not surpassing hind central margin)

1: projecting lateroposteriorly or posteriorly (beyond hind central margin)

322. Hind margin of T6 if with projecting hind angles: (CI = 0.16; RI = 0.65)

0: broadly roundly emarginate

1: broadly and shallowly emarginate, with apex nearly straight

2: emarginate in a flat triangular shape

3: deeply emarginate, with central apex nearly straight

4: with central margin sinuate

323. Hind angle of T7: (CI = 0.14; RI = 0.93)

0: not projecting (not surpassing hind central margin)

1: projecting lateroposteriorly or posteriorly (beyond hind central margin)

324. Hind margin of T7 if with projecting hind angles: (CI = 0.16; RI = 0.64)

0: broadly roundly emarginate

1: broadly and shallowly emarginate, with apex nearly straight

2: emarginate in a flat triangular shape

3: deeply emarginate, with central apex nearly straight

4: with central margin sinuate

325. Cuticle of T7: (CI = 0.18; RI = 0.65)

0: opaque, no clear transparent part

1: partially transparent (in contrast with rest opaque area)

2: totally transparent

326. T7 vs. T6: (CI = 0.33; RI = 0.86)

0: not longer than T6

1: longer than T6

327. T8: (CI = 0.05; RI = 0.57)

0: transverse

1: about as long as wide

2: elongate

328. Shape of T8: (CI = 0.16; RI = 0.68)

0: subpentagonal

1: subquadrate or subtrapezoidal

2: round apically

3: bisinuate apically

4: trisinuate or with central projection very reduced

5: triangular

6: expanded posteriorly, with hind apex notched centrally

7: asymmetric

8: with two sharp and remarkable projections in central apex

329. Basal angles of T8: (CI = 0.10; RI = 0.75)

0: about right angled

1: sharp angled

2: as short arms

3: as long arms

330. Apex of T8: (CI = 0.33; RI = 0.00)

0: flat or gradually decline toward ventrite

1: clearly bent down to meet ventrite

331. Central vertical flips of T8 in ventral aspect: (CI = 0.28; RI = 0.37)

0: absent

1: present, more or less tubular-like

2: as thickened ridges

332. Location of abdominal spiracles (additive): (CI = 0.25; RI = 0.90)

0: in pleurite membrane, not embedded by parasternites

2: embedded by parasternites

3: on ventral edge or on ventral side slightly distant from edge

333. T9: (CI = 0.08; RI = 0.54)
0: clearly not reaching apex of S9
1: reaching apex of S9 or nearly so

334. T9: (CI = 0.20; RI = 0.94)
0: symmetric bilaterally
1: asymmetric

335. Abdominal 10th segment: (CI = 0.33; RI = 0.86)
0: not tube-like
1: tube-like

336. Segment 10: (CI = 0.06; RI = 0.54)
0: reaching apex of S9 or nearly so
1: surpassing apex of S9
2: far from apex of S9
3: whole segment beyond S9

337. Segment 10: (CI = 0.25; RI = 0.92)
0: freely articulated with T9
1: connation with T9, either fused or separated

338. T10: (CI = 1.00; RI = 1.00)
0: flat
1: bent down at margins

339. S9 symmetry: (CI = 0.33; RI = 0.97)
0: symmetrical bilaterally
1: asymmetrical, either weakly or strongly

340. S9 shape if symmetric: (CI = 0.29; RI = 0.65)
0: short and broad, shield like

1: short and broad, inverted ovate

2: body either elongate or broad, with a sharp pointed apex

3: elongate, elliptic

4: elongate, subquadrate

5: elongate, arrowhead-shaped

6: elongate, inverted ovate

7: elongate, inverted teardrop shape

341. S9 shape if asymmetric: (CI = 0.33; RI = 0.92)

0: apical half (distal side) not broader than basal half (body side)

1: apical half generally broader than basal half

342. S9 curvature if asymmetric and apical 1/2 not broader than basal half: (CI = 0.40; RI = 0.70)

0: slightly skewed

1: clearly skewed in apical 1/2

2: not clearly skewed laterally but clearly asymmetric apically

343. S9 shape if asymmetric and narrower in basal half: (CI = 0.26; RI = 0.57)

0: moderately skewed, moderately broad, with long stem

1: moderately skewed, elongate, with narrower body and longer stem

2: moderately skewed, elongate, with very slender stem

3: highly skewed, elongate and narrow, as a curve strip

4: moderately skewed, moderately broad, curve in different direction with above

5: slightly skewed, very broad, without differentiation of stem/ body

6: slightly skewed, elongate, broad in body and slightly asymmetric in stem

7: slightly skewed, broad in body and stem

8: highly skewed, elongate and narrow, with long stem

344. S9 apex emarginate or not: (CI = 0.03; RI = 0.59)

0: no

1: yes

345. S9 sclerotization: (CI = 0.14; RI = 0.79)

0: uniformly

1: not uniformly, weaker in basal half except strengthened margins

346. S9 articulation with T10: (CI = 0.28; RI = 0.82)

0: largely membranous or weak sclerotized

1: as well sclerotized points, both sides at about same level

2: as well sclerotized points, both sides at different levels

347. T9 position: (CI = 0.50; RI = 0.75)

0: about in middle of S9

1: in near-body half of S9

348. Paraprocts (nec. Ballantyne) of T9 present or not: (CI = 1.00; RI = 1.00)

0: absent

1: present

349. T9 sclerotization: (CI = 0.25; RI = 0.57)

0: as a piece

1: as a pair of sclerites, clearly divided

350. T9 apical margin: (CI = 0.09; RI = 0.57)

0: deeply and somewhat squarely emarginate

1: deeply emarginate in a V shaped

2: moderately emarginate in a flat V shape

3: moderately emarginate, somewhat bisinuately

4: shallowly and broadly emarginate like a dish

5: nearly straight or very weakly, broadly emarginate

6: blurred

351. T10 vs. T9 in length: (CI = 0.04; RI = 0.60)

0: T9 longer

1: about the same

2: T10 longer

Male genitalia

352. Male genitalia in aedeagal sheath: (CI = 0.18; RI = 0.87)

  0: not rotating

  1: slightly rotating, about 30 degrees

  2: rotating 90 degrees, with lateral sides facing dorsal-ventral sides of sheath

353. General shape of male genitalia: (CI = 0.07; RI = 0.50)

  0: short, longer than wide by 2 times or less

  1: elongate, moderately broad

  2: elongate and narrow

  3: extraordinary slender

354. Male genitalia coloration: (CI = 0.20; RI = 0.42)

  0: more or less uniformly testaceous except membranous area

  1: darkened in tips of median lobe and parameres.

Basal piece

355. Length of basal piece vs. parameres (in lateral view): (CI = 0.06; RI = 0.61)

  0: shorter than parameres (about 2/3 paramere length)

  1: much shorter than parameres (less than 1/2)

  2: about as long as parameres

  3: longer than parameres

356. Greatest width of basal piece vs. that of parameres: (CI = 0.50; RI = 0.40)

  0: about as broad as parameres

  1: clearly broader than parameres

  2: clearly narrower than parameres

357. Overlapping with parameres: (CI = 0.25; RI = 0.45)

  0: shortly

  1: greatly

  2: totally

358. Basal piece vs. axis of male genitalia in lateral aspect: (CI = 0.10; RI = 0.45)

0: more or less horizontal

1: bent, in an clear angle with parameres

359. Shape of basal piece (overall length vs. broadest width): (CI = 0.03; RI = 0.59)

0: transverse

1: about as long as broad or slightly longer

2: elongate

360. Distal margin of basal piece in ventral aspect: (CI = 0.09; RI = 0.65)

0: broadly roundly emarginate

1: moderately emarginate, somewhat V-shaped

2: deeply emarginate, somewhat U-shaped

3: nearly truncated

4: bisinuate

5: broadly roundly projecting

361. Basal piece: (CI = 0.33; RI = 0.33)

0: one piece

1: two asymmetrical pieces

2: two reduced lateral stripes

362. Symmetry of basal piece if one-pieced: (CI = 0.10; RI = 0.80)

0: exactly symmetrical in lateral and body-side margins

1: different in lateral length but symmetric in body-side margin

2: not symmetrical apically

363. Shape of basal piece if symmetrical in body-side margin: (CI = 0.16; RI = 0.75)

0: as a broad piece

1: as a semi-ring

2: nearly a full ring

364. Body-side margin of basal piece if symmetric: (CI = 0.18; RI = 0.53)

0: very broadly rounded

1: emarginate

2: tapering
3: somewhat truncated and with two side angles
4: broadly rounded
5: flat V-shaped
6: with a round projection

365. Shape of basal piece if asymmetrical in body-side margin: (CI = 0.30; RI = 0.75)
0: bowl like, with big opening ventrally
1: lateral sides abruptly narrowed toward slightly asymmetric apex
2: apex broad, slightly asymmetric and twisted
3: roundly V-shaped, asymmetric and weakly twisted
4: apex broad, moderately twisted, asymmetric but in different direction from state 2
5: somewhat roundly V-shaped, asymmetric and moderately twisted
6: apex broad and twisted, asymmetric
7: apex more or less rounded, moderately twisted
8: more or less y-shaped, strongly twisted

366. A pair of appendages arising from basal piece: (CI = 1.00; RI = 1.00)
0: absent
1: present, as slender arms
2: present, as lobe like pieces

Parameres

367. Parameres: (CI = 0.66; RI = 0.66)
0: present, normal
1: present, very weakly sclerotized
2: absent or highly reduced

368. Paramere symmetry in terms of length (from dorsal aspect): (CI = 0.13; RI = 0.27)
0: identical in length
1: different in length, with right arm longer
2: different in length, with left arm longer

369. Parameres in dorsal aspect: (CI = 0.15; RI = 0.57)

0: not fused in any part
1: fused at least basally
2: largely fused with each other forming a tegum

370. Paramere separation if not forming tegum (in dorsal aspect): (CI = 0.15; RI = 0.54)
0: widely separated apically and slightly convergent toward base
1: widely separated apically and strongly convergent toward base
2: convergent basally and apically, widely separated in middle
3: sinuate in inner margin, at least broadened in front of fusion
4: narrowly separated largely until front of fusion
5: narrowly separated largely, except central section
6: narrowly separated mostly, more or less parallel or sinuate (very narrow)
7: curved in inner margin and broadened in front of fusion (somewhat ovate)
8: widely separated apically and then convergent to a very narrow separation

371. Length of parameres in dorsal vs. ventral aspect: (CI = 0.10; RI = 0.55)
0: about identical
1: dorsum longer
2: venter longer

372. Area of parameres in dorsal vs. ventral aspects: (CI = 0.10; RI = 0.21)
0: about the same
1: dorsum greater than venter
2: venter greater than dorsum

373. Apex of parameres: (CI = 0.16; RI = 0.54)
0: not bifurcate
1: bifurcate

374. Apical setae of parameres: (CI = 0.09; RI = 0.62)
0: absent
1: present

375. Apex of parameres in outer margin: (CI = 0.14; RI = 0.00)

0: not hooked outward

1: hooked outward

376. Apex of parameres in inner margin: (CI = 0.14; RI = 0.53)

0: not hooked inward

1: hooked inward

377. Apical ventral hook of parameres (in lateral view): (CI = 0.07; RI = 0.45)

0: absent

1: present

378. Membranous area parameres in inner margin: (CI = 0.50; RI = 0.50)

0: absent

1: present as a cell enclosed by well sclerotized surroundings

379. Apex of parameres in dorsal view: (CI = 0.16; RI = 0.44)

0: not very slender in relation to the rest part

1: very slender in relation to the rest part, arising from uniformly sclerotized base

2: very slender in relation to the rest part, arising from more or less weakly sclerotized base

380. A pair of weakly sclerotized, bud-like projections on apex of parameres: (CI = 0.25; RI = 0.00)

0: absent

1: present

381. A pair of slender appendage arising from dorsal subapex of parameres: (CI = 0.66; RI = 0.83)

0: absent

1: present, slender, tentacle-like

2: present, moderately broad, sword-like

382. Setae in inner margin of subapex of parameres: (CI = 0.44; RI = 0.90)

0: absent

1: present, with 3 or more setae

2: present, with 1-2 setae

383. Outer margin of parameres: (CI = 1.00; RI = 1.00)

0: more or less continuous

1: disrupted in apical 2/5 where margin extraordinarily narrowed down

384. Dorsal inner margin in apical 1/4-2/5: (CI = 0.21; RI = 0.59)

0: not deflected

1: narrowly deflected but not hooked

2: moderately deflected and forming a hook

3: broadly deflected as axe like projections

4: broadly deflected but not hooked

385. Deflection in dorsal inner margin within basal 2/5-1/5: (CI = 0.33; RI = 0.84)

0: absent

1: present, not hooked

2: present, as an angle

386. Depression near inner suture in basal 1/3: (CI = 1.00; RI = 1.00)

0: absent

1: preset

387. A transverse suture across parameres in basal 1/3-1/5: (CI = 0.50; RI = 0.85)

0: absent

1: present

388. Dorsal base: (CI = 0.11; RI = 0.66)

0: weakly elevated if any

1: well elevated, subvertical

389. Dorsal base: (CI = 1.00; RI = 1.00)

0: not forming a ridge like extension

1: forming a ridge like extension

390. Basal margin of parameres in dorsal aspect: (CI = 0.11; RI = 0.42)

0: symmetrical

1: asymmetrical

391. Visibility of parameres in dorsal aspect: (CI = 0.50; RI = 0.80)

0: largely exposed from median lobe

1: concealed by median lobe in apex

392. Modifications on ventral apical margin of parameres: (CI = 0.50; RI = 0.33)

0: absent

1: with a pair of short angles

2: with a pair of long and sharp projections

393. Ventral inner margin of parameres: (CI = 0.50; RI = 0.85)

0: more or less smoothly outlined, not sharply curved in middle

1: with a pair of short angles

2: sharply curved in middle, forming large hook like projections

3: narrowly projecting toward body-side

394. Lateral contour of parameres: (CI = 0.04; RI = 0.55)

0: dorsum and venter about evenly tapering toward apex

1: dorsum declined more than venter arising (venter more or less flat)

2: venter arising more than dorsum (dorsum more or less flat)

Median lobe

395. Length of median piece vs. parameres: (CI = 0.06; RI = 0.51)

0: about as long as parameres, slightly shorter or beyond

1: shorter than parameres

2: much shorter than parameres

3: surpassing parameres

4: far beyond parameres (1.5 paramere length or more)

396. Greatest width of median lobe vs. of parameres: (CI = 0.05; RI = 0.65)

0: about as broad as paramere

1: narrower than paramere

2: broader than paramere

397. Median lobe: (CI = 0.50; RI = 0.85)

0: not abruptly narrowed in apical 1/4

1: broad mostly and abruptly narrowed in apical 1/4

398. Dorsal expansion of median lobe in apical 1/3: (CI = 0.25; RI = 0.40)

0: absent

1: present

399. Median lobe: (CI = 0.11; RI = 0.20)

0: not twisted, symmetrical bilaterally

1: twisted, asymmetrical bilaterally

400. Median lobe in dorsal aspect: (CI = 0.06; RI = 0.58)

0: more or less flat or slightly convex

1: cylindrical

2: ridged on a flat piece

401. Median lobe in lateral aspect: (CI = 0.08; RI = 0.78)

0: down-curving toward venter in apex

1: more or less horizontal, flat

2: up-curving toward dorsum in apex

402. Sclerotization of median lobe: (CI = 0.30; RI = 0.58)

0: entirely sclerotized

1: partially sclerotized

2: strongly sclerotized laterally

3: weakly sclerotized

403. Apex of median lobe in dorsal aspect: (CI = 0.09; RI = 0.16)

0: not knob like

1: knob like

404. Apex of median lobe laterally: (CI = 0.25; RI = 0.57)
    - **0:** not hooked
    - **1:** as a pair of heavily sclerotized hooks at apicolateral corner

405. Subapex of median lobe in dorsal aspect: (CI = 0.33; RI = 0.50)
    - **0:** not hooked subapically
    - **1:** backward hooked in subapex

406. Genital whip arising from ventral subapex of median lobe: (CI = 0.50; RI = 0.80)
    - **0:** absent
    - **1:** present

407. A pair of sword-like appendages arising from base of median lobe laterally: (CI = 1.00; RI = 1.00)
    - **0:** absent
    - **1:** present

408. A pair of stout appendages arising from base of median lobe ventrally: (CI = 0.33; RI = 0.55)
    - **0:** absent
    - **1:** present, as strengthened margin or like arms
    - **2:** present, well developed, block-like

409. Sclerotized central strut in ventral aspect: (CI = 0.40; RI = 0.00)
    - **0:** absent
    - **1:** present, as a thick piece with apical hook
    - **2:** present, as a flat piece

410. Median lobe vs. basal piece: (CI = 0.28; RI = 0.50)
    - **0:** far from reaching basal margin of basal piece
    - **1:** reaching basal margin of basal piece or nearly so in a form of basolateral apophyses
    - **2:** reaching basal margin of basal piece or nearly so in a form of median lobe itself

3: surpassing basal margin of basal piece in a form of basolateral apophyses
4: surpassing basal margin of basal piece in a form of median lobe itself

For Chapter VI, female neoteny

411. Neoteny states (accumulative): (CI = 0.33; RI = 0.55 for non-additive coding; CI = 0.15; RI = 0.72 for additive coding)
0: normal adult morphology, similar with their males
1: hind wing reduced, minor or major physogastrous, elytra shortened
2: complexion biphysiological
3: integument unsclerotized and unpigmented
4: elytra lost
5: first abdominal segment fully exposed
6: complimentary sternite complete
7: high reduction in number of tarsomeres
8: pygodium and/or tarsunguli present

Appendix IV. Full data set of male morphology with 220 species and 410 characters

	0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000001
Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Dascillus_cervinus	00020005-------0-01000100004100000100101011121000411004010-001330000200100100103006003-10125011-0001
Macropogon_testaceipennis	20000115-------0-01000100103100000001201011010100410004010-111210100200100100100001003-10205011-0010
Brachypsectra_fulva	00000007020108-1-02000100000000000100001000012111011002100001000010000000000000000000003-10001010-0000
Drilus_flavescens	00000017000301-2-01000000005100100000111000012111000000010-110210100100100100000003001-10001010-0000
Selasia_decipiens	20010117121130-4-010000000011000000001010110001000001001000010200100100100000004006015221014010-0001
Selasia_sp	00000007121300-4-00000000000000101000101000012111010000210-110210100100100100000003003-21001010-0001
Malacogaster_passerini	00010017020101-2-010000000051001000001110010121100002001001110210100100200100002003011-21021010-0020
Lycus_(Neolycus)_arizonensis	20010001-------3-010000220131001012003000101201000224040017040260100500430011003005014-00010015-0311
Lycostomus_sanguineus	20010001-------3-010000220131001012003000101201000224040017040260100500430011003003014-00010015-0311
Cautires_kazuoi	20010017101130-4-00000020001100100200000001000100000000010-050261100200600000104003013-00010006-0021
Plateros_coracinus	20000011-------3-00000020003100100200000011010100000000010-040160100200600000104005011-00010006-0011
Lyponia_delicatula	20000017101330-4-000000200031001002001000010101000000001100050160100200600000104003011-00010016-0011
Eropterus_nothus	20020025-------2-000000200031001002001000010001000001000100040061100200100000104003011-00000016-0011
Xylobanus_niger	20010011-------3-00000020003100100200000001000110000000110-040260100200600000104003014-01010015-0031
Omalisus_fontisbellaquei	20020125-------2-020000000031000002000000011211100100001010010071100200100000001006005210104000-0011
Omethes_marginatus	20020015-------2-010000000052000000000000011211010002000001011210101-00200100101001003-10124013-0001
Omethes_rugiceps	20020015-------2-010000000052000000000000011211010002000001011210101-00200100101001003-10124013-0001
Troglomethes_leechi	20000025-------2-01000000191?0??000000100111211000000000003?????012---010?100103001003-10124016-0111

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Malthomethes_oregonus	20000125-------2-010000101032001001000000111211013000021001122270000500100100003001004-10124013-0111
Drilonius_striatulus	20000000-------2-010000000031001000001000111011000000000010-040130100900620100101001003-20124013-0001
Matheteus_theveneti	20000127111111-3-0100002010100??001000000111211014000???????????010020010?1001010010????0124013-0201
Ginglymocladus_luteicollis	20000127112231-2-010000200031000001000000111211010000000003120270100200100100101001002-00124013-0001
Phenogodes_frontalis	000127782444250-1000000111200103002110011111211004102230005120070102-00200000001002013-00022002-0101
Zarhipis_integripennis	000126782444250-100010011120010300011001111121100410223000512007112--00200000001002013-00023002-0101
Cenophengus_debilis	000027783344350-000000011134301300100101101121100010100000402007001--002000000040080052110031---2131
Distremocephalus_texanus	000027783344350-000010011133301300000101101121100010100000502107002--00200000004008005211003000-2121
Stenophrixothrix_sp	200127782444250-1021000111233013000000001112121100020321000512027001--102000000040080051110031---2111
Taximastinocerus_sp	000027783344350-0010100111331013000000011011211000102110005021270102-00300000001008002-000031---2101
Telegeusis_nubifex	00000116-------2-010100111343013001001100111211004101010006021370003-0020020000121-002-00004028-1121
Pseudokarumia_angustata	00000016-------2-010100111352113001001100111211004102010006021330003-0030020000121-001-000041---2131
Pterotus_obscuripennis	20000017111130-4-0200000000110000010010100112110000000210110122601002001000000004006003-00014011-0001
Brachylampis_blaisdelli	20000013-------5-0000000000310000010010000002110000000021000110201001-00100000003006004-10014011-0201
Ceylandidrilus_bipartitus	01000013-------2-0100000000340000010010001110110000000021000011301001-00100000004006003-00014010-0011
Ceylandidrilus_kandyanus	01000023-------2-010000000041000001001000001011000102001004011301001-10200000004006000-00014010-0011
Drilaster_auxillaris	21020023-------2-00000000001100000100100000002010000000021000011201000200100000000300500521101401710201
Drilaster_weyersi	21020023-------2-00000000001100000100100000002110000000021000011201000200100000000300600561001401710201

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Lamellipalpodes_annandalei	01000013-------2-00000000001100000100100000001100000000100003120100020010000000422-013-20014028-1001
Flabellotreta_fruhstorferi	20010017101130-2-020000000011000001001000210201000000021000011201000200100000003105005211014011-0201
Falsophaeopterus_fruhstorferi	20020013-------2-01000000003200000000100010101100000100200203000001--10600000004006015210014010-0211
Gorhamia_krombeini	21000021-------2-010000000031000001001000001011000000021000031331000210100000004006004-10014000-0001
Harmatelia_bilinea	21000027112231-2-010000000011000001001000011211000000021000011331000110100000004005015211014011-0001
Mimophaeopterus_wittmeri	21000011-------2-000000000011000001001000000211000000021000?????1000200100000003006005211014011-0201
Oculogryphus_fulvus	00020015-------2-032230001020000010001000201211000003??2024?????000011010?0000040000????1014000-0111
Picodrilus_limbellus	20000013-------2-000000000011000001001000000211000000021000?????123--00100000003006005610014011-0201
Stenocladius_rufithorax	21000017101230-4-000000000031000001001000010101000001001000031361000210100000004006005610014001-0001
Stenocladius_bicoloripes	00000017102030-4-022140000020000001001000011201000003002024030020000210600000004000015120014000-0011
Stenocladius_chinensis	00000017102030-4-022140000020000011001000011201000003002024030020000210600000004000015120014000-0011
Stenocladius_sp	00000017102030-4-022140000020000001001000011201000003002024030020000210600000003000015120015000-0011
Ototretadrilus_flavoscutellaris	00000027101131-2-00010000001100000000101000121100000102100703100001--10600000003000010-20014010-0001
Dioptoma_adamsi	10002660--------01322300114200020000021002010010001030020261412?00002001000000?2000015120005010-0101
Diplocladon_hasselti	000125583547140-102112001040000200000100000120100010101202401020001--10100000013000010-20004010-0001
Dodecatoma_bicolor	00012557122313--002214001040000200000100001120100000101202411020001--10100000014000010-20004010-0001
Falsophrixothrix_humeralis	100125683544140-102004001040000000000000001120100000100202701127001--10100000013000015221004010-0101
Menghuoius_ingens	11022660--------0121230010400002020012010001201005112212025010000102-10200000012001010-01014008-0001

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Menghuoius_giganteus	11022660--------0121230010400002020012010000221005112212025010000102-10200000012001010-01014008-0001
Monodrilus_marginatus	00002670--------002102001041100100000000000020100000100202401000001--10100000013000013-11014010-0001
Ochotyra_semiusta	10002660--------0122230011420002020000100000001000001002025011260000210100000012000010-00014010-0101
Rhagophthalmus_ohbai	10022650--------013223001142000202000010020010100010302202501120001--101000000120000????0004010-0101
Rhagophthalminae_ngen	10022660--------0121230010400002000001010000101000101012025010200000110100000014000015120004010-0001
Cyphonocerus_ruficollis	2000001843443202-020000200031000001001000111211000004002000010001000100103000004005015620015005-0201
Cyphonocerus_sanguineus	2000001843443202-020000200031000001001000111211000004002000010001000100103000004005015620015005-0201
Cyphonocerus_sylvicola	2000001843443202-020000200031000001001000111211000004002000010001000100103000004003015620015005-0201
Pollaclasis_bifaria	2000001843443202-020000200011000011001000010211000004002000010001000100103000003005005620014006-0201
Atyphella_lychnus	11020116-------1-032020200620000022000000200101002104002024131260100500103000000004115121015000-0001
Atyphella_carolinae	01020016-------2-03210000062000002200000020020100210400202413124010020010300000000411512101400720001
Atyphella_obsoleta	01020015-------2-03110020062000002000000023020100210500202013124010050010300000300411512101401720001
Bougeoisia_antipoda	01020016-------1-0321200006200000200000002001010020040010261302601004001030000000001????1014000-0001
Colophotia_brevis	01020015-------2-02110000070000002000100001021100000400202314126010050010300000310411512001401710001
Colophotia_praeusta	01020015-------2-02100000070000002000100001021100000400202314126010010010300000310411512101401710001
Curtos_obscuricolor	01020016-------2-03212000062000002000100022000100000400202104134010020010300000300411512101401710101
Hotaria_parvula	01020015-------2-03214000062000001000000021010100000400202114126010050010300000300411512101401720001
Lampyroidea_dispar	11020015-------2-03214000060000001000000021010100000400202104124010050010300000300411512101401720001

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Lampyroidea_syriaca	11020015-------2-022140000600000010000000210101000004002021?????010050010200000300411512101401720111
Luciola_anceyi	21020015-------2-02100000070000001000000010000100001400202112126010010010300000300411522101400720001
Luciola_aquatica	01020015-------2-03104000060000000000000020010100000400202313126010050010300000300411521101500720001
Luciola_cincticollis	01020015-------2-02100000072000000000100000010100100400202004024010020010300000300410521101400720021
Luciola_curtithorax	01020015-------2-03210010162000001000000021010100200400202112124010010010300000300411531101401720101
Luciola_filiformis	01020015-------2-03215000062000002000000021000100000400202412134010010010300000300411512101400720101
Luciola_hydrophila	01020015-------2-03114000060000001000000021010100100400202013124010050010300000300411512101401720001
Luciola_italica	01020015-------2-03204000060000002000000021010100000300202114124010051010300000300411512101401720001
Luciola_kagiana	01020015-------2-03104000062000002000000021000100300400202114126010050010300000300411512101401720001
Luciola_kuroiwai	01020015-------2-03100000070000002000100010000100000400202312126010010010300000300411512101401710101
Luciola_lustianica	01020015-------2-03204000060000002000000021010100000300202114124010051010300000300411512101401720001
Luciola_ovalis	01020015-------2-03204020062000002000000021000100100400202103124110050010300000310411532101401720001
Luciola_peculiaris	01020015-------2-03200020062000001000000023020100010400202013124010040010300000000411531101401720201
Luciola_substriata	01020015-------2-03104000060000001000000011010100200400202313126010050010300000300411521101500720001
Luciola_trilucida	01020015-------2-03110000070000002000100010000100000400202314126010010010300000300411532101401710101
Pteroptyx_fulminea	01020015-------2-03100000070000002000100023020100000400202114126010020010300000310411512101401710101
Pteroptyx_cribella	01020015-------2-03100000070000002000100000020100000400202114126010020010300000310411512101401710101
Pygoluciola_satoi	01020015-------2-02000000070000001000000000010100100400202011127010040000300000300411522101400720001

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Pyrophanes_similis	01020215-------2-021000000700000020001000101101000004002020141260100200103000003104115121014006-0001
Pyrophanes_appendiculata	01020215-------2-021000000700000010001000111101000004002025141260100200103000003104115121014006-0001
Bicellonycha_deleta	01020025-------2-02011100170000002000220020010100-00100200403126120060020300000300411512101401730021
Bicellonycha_stigmatica	01020025-------2-02011100170000002000220020010100-00100200403126120060020300000300411512101401730021
Bicellonycha_sp	01020025-------2-02011100170000002000220020010100-00100200403126120060020300000300411512101401730021
Daiphoturis_apicalis	21020023-------2-02001100070000001000220022020100-00100200403126120060023300000300411532101401730021
Photuris_trilineata	01020125-------2-03011100070000001000220000020100-00100200403126120060020300000300411512101400730011
Photuris_sp	01020125-------2-03011100070000001000220023020100000100200603126110060020300000300411532101400730021
Photurocantharis_sp	21020023-------2-02001100070000000000220022020100-00100200403126120060023300000300411532101401730021
Pyrogaster_coxalis	21020025-------2-03000100070000001000220022020100-00100200403126120060023300000300411512101401730011
Pyrogaster_lunifer	21020125-------2-02011100071100000000220000020100-00100200401121120060023300000300411532101401730001
Pyrogaster_malepictus	21020025-------2-03000100070000001000220022020100-00100200403126120060023300000300411512101401730011
Pyrogaster_mediofasciatus	21020025-------2-02011100070000001000220022020100-00100200403126120060023300000300411531101401730021
Amydetes_apicalis	21023887121336--2021000210800000011200100023010110100102100102207100010010000000000015111014010-0001
Amydetes_fastigiatus	21023887121336--2021000210800000011200100023010100100102100102027100010010000000000015111014010-0001
Cladodes_flabellata	22010027121230-4-000000300841000000100000230201101014002010041250100500101000003005015121014004-0321
Cladodes_imperfectus	22010027101330-4-02000030083100000010000023010110000400200004125000010010100000310501532101401710301
Cladodes_ater	02010127121330-4-00000030083100200100000023000110-004002010041261200700101000003005015211014016-0321

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Dodacles_elegans	02010117121330-4-0200003008120020010000000302111 0-001002001051261200100103000003005015121014007002 01
Dodacles_emissa	02010127121330-4-02110030080000201100000010111110-001002021051251200700103000003005015121014006-0211
Dodacles_erebea	02010117121330-4-02000030081200200100000020011110-001002001051261200700103000003005015121014007002 01
Dryptelytra_cayennensis	02010117121330-4-02000030081100200100000023010110-214002000050261200700101000003003015321014000-0301
Dryptelytra_sp	02010117121330-4-02000030081100200100000023010110-214002000040261200700101000003003015321014005-0301
Ethra_decorata	21010017101030-4-00000030081000000200100013121100120400200715126100010010100000300501531101400700211
Ethra_dejeani	21010017101230-4-01000030083100000100100010121100100400200715126100010010100000300501532101 4005-0221
Ethra_marginatus	21010017101230-4-01000030083100000100100021121100100400200715126000010010100000300501532101401700221
Fenestracladodes_malleri	22010027101330-4-02000030083100000100000023010110000400200004125000010010100000310501532101401710301
Ledocas_parallelus	22010127101330-4-02000030083100200100200023020110-001002021051241200700103000003005015121014017103 11
Ledocas_sp	22010117121330-4-02000030083200200100200013000110-001002001051241200700103000003003015121014000-0311
Magnoculus_sp_a	01010017121330-4-0100002102520030000000000000000100-002110005011210200010200000004003000-11015000-0011
Magnoculus_sp_b	01010017121330-4-000000200031002001001000000011000004111005010240100700103000004003000-11015000-0011
Psilocladus_miltoderus	2101001823442202-0200002008110010010000000001011010040020070502602005001010000030050151210 14000-0201
Psilocladus_nevermanni	2101001823442202-0200002008110010010000002001011010040020000502602005001010000030050151210 14000-0201
Scissicauda_disjuncta	21000017111020-4-02000030080000000100100023010100120400200705126100010010100000300501531001 4014-0221
Vesta_chevrolatii	21010027101130-3-00000030081100000100100012020110-004002002131260200210103000003104115211014004-0211
Vesta_impressicollis	21010027101130-3-00000030081100000100100012020110-004002002131260200510103000003104115211014004-0211

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Vesta_rufiventris	21000020-------3-00000030081100000100100022020110-004002000130260200510103000004104115211014004-0211
Vesta_arcta	21000027101130-3-020000300811000001001000100201000004002000130260100200103000003004115221014004-0201
Vesta_cincticollis	20010011-------3-00000030081100000100100012121100100400200705124110020010100000310501532101400730221
Vesta_thoracica	21000027101130-3-00000030081100001100100010020110-00400200313126020050010300000300411522101400700201
Afrodiaphanes_marginipennis	11001334-------7-03212031052400202200100020000100-214002025?????120080151201000400501??20014010-0021
Alecton_discoidalis	00010017020300-1-02000030081300100100000020020100120400202714126110040073201000300501532101401730221
Aspisoma_aegrotum	01000013-------5-02114031050000000000100020020100121400202714126010040073201000310501532101401730301
Aspisoma_ignita	01000013-------5-02114031050000000000100020000100121400202714126010040073201000310501532101401730301
Aspisoma_physonotum	01000013-------5-02114031050000000000100020000100121400202714126010040073201000310501532101401730301
Callopisma_rufa	21000021-------2-020000300813000001000000120101001004002000130260100110101000003104115221014004-0201
Calyptocephalus_sp	2201012853363204-02003030083100200000000023020110-214002013041160200310832010003003015521015000-0301
Cratomorphus_signativentris	01020012-------5-03203031052400202100000020020110220400202404124100070073201000310501532101501730221
Dadophora_hyalina	00010021-------5-030000300833000001001000130201000004002023151261000100101000003005015321014005-0211
Diaphanes_citrinus	11020002-------1-03202031052400202200000020020110-214002024041341200801512010003005015121015010-0221
Diaphanes_formosus	11020013-------2-031030310524002021000000200201103214002023140241100801512010003005015121015010-0211
Diaphanes_lampyroides	01010011-------3-03203031052400202200000021020110-214002021140241200801512010003005015121015010-0211
Diaphanes_nubilus	01020013-------2-03202031052400202200000000010110-214002024140221200801512010003005015121015010-0021
Diaphanes_schoutedeni	11020004-------2-03212031052400202200100020010110-214002025?????1200801512010004005015121014010-0021

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Dilychnia_ruficollis	21000021-------2-02005030062000001200000022010100-004002020131260200500101000003104115321014004-0201
Ellychnia_corrusca	01000013-------2-0100003008430010000010001302110010040020071412601001001010000031050155210140 14-0311
Ellychnia_moesta	01000013-------2-010000300843001001001000130211001004002007141260100100101000003105015521014014-0311
Erythrolychnia_fulgida	01020013-------2-0310003006200000210000002202011030140020201412401005008320100031050153210140171 0211
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Lamprigera_boyei	11120210-------6-232020310504002020001000232--100-2130020260610412008009030002200030151210100 00-0201
Lamprigera_yunnana	11120200-------6-232020310504002020001000202--100-213002026061041200800903000220003015121010000-0201
Lamprocera_tristior	2101012855363204-020000300800000001001000230201000214002007051260000410832010003105015311015017 10301
Lamprohiza_delarouzei	11020113-------2-0320303105200020220000000002011032140020211402411008006010000030030151200140 16-0201
Lamprohiza_splendidula	11020113-------2-032030310520002022000000000201103214002021140241000100601000003003015120014016-0201
Lampronetes_mauritanica	11000012-------2-022030310520002011001000010101 00-21300202104014120080051201000000501512101401 6-0021
Lampyris_noctiluca	11020012-------2-02203031052000202100100020020100-213002021140261200800512010004005015121014016-0211
Lampyris_algerica	11020012-------2-022030310520002021000000200101103213002026?????1000800512010003005015121014016-0011
Lucernuta_savignii	21020010-------3-02003030051300001100000000020100220500202014123110070083200000310501532101401710301
Lucidina_accensa	20010011-------3-00000030083100000100100013121100000400200714026000010010100000310501542101401710211
Lucidina_vitalisi	20010011-------3-00000030083100000100100013121100000400200714026000010010100000310501542101401710211
Lucidina_gracilis	20010011-------5-000000300831000001001000131211001004002007140260100500101000003005015221014015-0221

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Lucidota_atra	20010011-------3-000000300831000001001000131211000004002007140260000200101000003105015321014014-0211
Lucidota_banoni	20010011-------3-00000030081100000100100000121100000400200705124100020010100000310501522101401720211
Lucidota_bella	20010021-------3-00000030081100000100100012020100-00400200013121120050010100000300411522101401700211
Lucidota_comitata	20000011-------3-000000300811000001001000130211001004002007141260000100101000003105015221014014-0211
Lucidota_pennata	20010017101130-3-000000300811000001001000101211000004002007041260000100101000003105015221014014-0211
Lucidota_pygidialis	20010017101130-3-000000300831000001001000110201001004002007141240000200101000003105015321014014-0221
Lucidotopsis_cruenticollis	20010011-------3-00000030083100000100100013121100000400200714026000010010100000310501542101401710211
Lucio_abdominale	0201011855353214-02000030081300000100100023020100121400200704126000041073201000310501531101501730401
Lucio_obscura	0201011855353214-02000030081300000100100023020100021400200704126000051073201000310501531101501730401
Lychnacris_flabellata	21010117121130-4-02000030080300000100100023020100321500200704126000031083201000310501561101501720401
Macrolampis_acicularis	21020013-------2-022110300624000011001000100201000003002027051260000500101000003003015121014014-0231
Macrolampis_longipennis	21020013-------2-021110300624000011001000130211000004002027051260000500101000003005015121014014-0231
Macrolampis_omissa	01020013-------2-021110300624000010001000220211000004002027051240000500101000003005015321014004-0221
Macrolampis_perelegans	21020013-------2-020110300624000001001000101201000004002020041240000500101000003105015321014014-0231
Microphotus_angustus	10001334-------7-33203031052400202200100000020110-213002026140241200801512010004007015120014100-0021
Microphotus_dilatatus	10001334-------7-33203031052400202200100000000110-213002026140241200801512010004007015120014100-0021
Microphotus_octarthrus	10001334-------7-33203031052400202200100020020110-213002026140241200801512010004007015120014100-0021
Mimophotinus_angustatus	20010013-------5-0100003008310000010010001312110000040020071220700002002030000003103015321014010-0221

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	0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000001
Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Nyctophila_reichii	01020023-------2-032030310524002021001000200201100213002026041241100800512010003005015120014001-0011
Ophoelis_impura	2201011855363204-02000030083100200000000023010110-214002013040260200310831010004003010-1-0-------301
Paraphausis_eximia	02010014-------6-00000030084100000200100010020100-010002022142041200811411010004007015111004????2021
Petalacmis_praeclarus	02001404---------02103030060000001200100000021110-014002001140041100800411010003007015120010000-0311
Phaenolis_laciniatus	2201011853363204-02003030081300200100000023010110-214002010040260200310831010003003014-20015000-0201
Phaenolis_bicoloripes	2201011853363204-02003030081300200100000023020110-214002010040260200310831010003003014-20015000-0301
Phausis_reticulata	00000012-------2-021030310524002022000000000020110-214002024122070200800601000004107015120014006-0311
Phosphaenopterus_metzneri	20010013-------5-010000300852001002001000131211000004002007122060100100101000003007015321014014-0221
Phosphaenus_hemiptera	20010013-------5-010000300852001002001000131211000004002007122060100100101000003007015221014014-0221
Photinus_maritimus	01020013-------2-02111030062400000100100000121100000400202205126010040010100000310501532101401710211
Photinus_extensus	01000013-------2-0211103006240000010010001312110002040020270????0100500101000003105010321014014-0211
Photinus_pallens	01020015-------2-02011030062400000000100020120100000400202205124010040010100000310501532101401710211
Photinus_pyralis	01000013-------2-021110300624000001001000031211000204002027051260100200101000003105015321014014-0211
Platylampis_latiuscula	21020013-------2-000000300811002001000000230101001014002007151160100500831000003005015221014014-0301
Platylampis_delicata	21020013-------2-12010030080000000100000023020100301500202014126010050083101000300501512101401730311
Pleotomodes_knulli	10010004-------6-032030310524002022001000230201103213002026141241100801811010004007015120014010-0021
Pleotomus_pallens	120149984537370--02203031052400202200100023020110-214002023141241200300811010004007015120014016-0021
Pristolycus_kanoi	20000021-------3-02000020083100000100000021011100100400200713124010040010300000300301502001501720301

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Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Pristolycus_sagulatus	20000011-------3-02000020083100000100000001011100100400200713124010040010300000300501502101501720301
Pseudolychnuris_vittata	21000013-------2-010000300831000001001000030211001004002007131260100100101000000105015321010014-0311
Pyractomena_lucifer	01000013-------2-02110030062000000100100000021100000400202704106010050083101000310501511101401720211
Pyractomena_striatella	01000013-------2-02110030062000000100100000021100000400202704106010050083101000310501511101401720211
Pyractonema_obscura	21000011-------2-000000300831000001001000100111001004001007130260100500101000003105015521014014-0211
Pyrocoelia_analis	00000010-------3-02100030080000002100000020020110-215002023141241200800512010004005015121014005-0311
Pyrocoelia_bicolor	00000011-------3-02100030080000002200000020020110-215002020140241200800512010003005015121014015-0311
Pyrocoelia_formosana	20000011-------3-02000030083100000100000000021110-215002000140240200800512010003005015121014010-0311
Pyrocoelia_praetexta	00000011-------3-02100030080000002200000023020110-21500202014124120080051201000300501512101401710311
Pyrocoelia_prolongata	20000011-------3-02000030083100002100000000020110-215002000140240200800512010003005015121014004-0331
Pyropyga_fenestralis	21000013-------2-010000300831001001001000100211001004002007141240100200101000003105015521014014-0211
Pyropyga_nigricans	21000013-------2-010000300831001001001000200211001004002007141260100100101000003105015521014014-0211
Robopus_lengi	01020013-------2-03203031052000002100100021121100020400202315124010050110100000300501532101400720021
Robopus_pantoni	01020013-------2-03203031052000001100100020021100-00400202005104120040110100000300501532001400720021
Robopus_quadrimaculatus	01020013-------2-03203031052000002100100020121100020400202315124010050110100000300501532101400720011
Robopus_vittiger	21000021-------2-020000300500001000000000001201000004002022051241000400101000003105015511014014-0221
Roleta_notaticollis	2201011855363204-0000003008310020010000000130101101004002013?????0000310831010003005014-11014000-0221
Rufolychnia_borencona	21000011-------2-0200003008130000010010001202110000004002007??1??010010010200000310501542101401710211

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Species	**Character number**
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Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Satolampyris_dichroma	20000021-------3-020000200831000001000000000101100004102007?????01004001030000003005015021014019-0301
Tenaspis_angularis	21020021-------3-000000300831000001000000230101001215002007141260100200831010003005014-1101400730401
Tenaspis_figurata	21000021-------5-00100030081000001100000003020100221400200014126000051083101000310501512101401730401
Cheguevaria_taino	00010021-------??0100001113520030001110000001211000101011005051240000110300000000400300522001?000-0001

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	1111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111112
Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Dascillus_cervinus	1232060003002025000022121121001000011001000000021005500001015000010000003100200001000020010000007020
Macropogon_testaceipennis	0272010003002021000044410000000000111000001000021102200011115001010000003200000101010020010110007020
Brachypsectra_fulva	0000000000000000000000000000300000000020000000000000000000100061010100101200000101000000010000007020
Drilus_flavescens	02120110231323200000402100200000001110000101001021111101002110001110011022102200101015024000010010020
Selasia_decipiens	0220030104321223000033301020011001111000010000032102102313110000110021043102200111013022000110010130
Selasia_sp	01200000013022200000012100000000022000000000001022115102001121001000011122202200101015011100100007020
Malacogaster_passerini	02120010033322210000012100200000001110000000001020111101002112001010011022102200101015024000110017030
Lycus_(Neolycus)_arizonensis	523214403432221410100012103211220170111100100030100504121131030031011010010110022121224102320016001
Lycostomus_sanguineus	523214403432221410100012103001220170111100000030100504121133070031011010010100002121201102320016031
Cautires_kazuoi	5232042034322224201044121123012213701111002000022102004131134070031011010011100001121223000210013030
Plateros_coracinus	2262042034322224101044121020012211701111000100020102004131133000031011010010100001021223000210013030
Lyponia_delicatula	0262012034322224101044121010002102701101000100020102004133133000031011010011100011121223000210013030
Eropterus_nothus	0262042034322224001044101110012103701101002100020102004131133000031011010011100001001223100210013030
Xylobanus_niger	0242042034322224201044120024012211701111002010022102004123134000031011010011100002121223000210013030
Omalisus_fontisbellaquei	0101001120002012000055200110022101110200100000010001104001121000010000103211200001000011110000007020
Omethes_marginatus	1282020023132130000044000023010031110001003000030102200122030000000011023102200101000223000010114140
Omethes_rugiceps	1282020023132130000044000023010031110001003000030102200122030000000011023102200101000223000010114140
Troglomethes_leechi	128202102314203000000020?02501110211−001000000003110?20112103300000000?102310220010100022300002011????

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Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Malthomethes_oregonus	127292000304203000000060100002000111-001000200030104400021133000000011023102200101000223000310114120
Drilonius_striatulus	027202000324203000000020000001100211-000000200031104203123033000031011023101000101000223000000114140
Matheteus_theveneti	0282294123232033011044101000120132110201003200030102200123233060020201323301110023100?0300001011????
Ginglymocladus_luteicollis	028222212324203300104400000001010111-001000200031102202021033000000011023102200001000223000010110020
Phenogodes_frontalis	0112242024312030000040111033011131510201003021031004325315132150210021050102200111002223001110010140
Zarhipis_integripennis	0162212023312010000040111033010131510201003021031004325315130260010011022102200111000221000001011140
Cenophengus_debilis	027202000504202000000000004102100141-001001001121101110310143160000011042102200111005222001111111140
Distremocephalus_texanus	2162210005032030000022100020011001510001001011121102110310140161000011040102200111005222001211010140
Stenophrixothrix_sp	0162010005032030000011210033011031410001003011131101105335133201300021050102200111013223001211111140
Taximastinocerus_sp	0162210023032030000011210031021001410001000001131104105305143161300011050102200111013222001211011140
Telegeusis_nubifex	127202002504203000006121004402010141-001001001121103100131043100000011050102200111003226000321114120
Pseudokarumia_angustata	127202002504203000006121004402011141-001001001121103100121042100000011050102200111003226000321114120
Pterotus_obscuripennis	0262011123232130000044101013012132111000001011130102101324232001120011022100000111000222100110010120
Brachylampis_blaisdelli	1222030003320223000011101010011002111100110110030102201331110071110011122200210101000202101210110120
Ceylandidrilus_bipartitus	0262030003320223000033301120021001111001011010031102102333130000110011023100200111005224100210010120
Ceylandidrilus_kandyanus	0262030003321123000033301010001002111001011110031102112313130000110011023102200111000224100210011120
Drilaster_auxillaris	0222030103320223000011101110011002111000010010031102201331130071110011122200210101000201101210010120
Drilaster_weyersi	1222030103320223000011101110011002111000010110031102201331111070110011122200210101000202101210010120

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Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Lamellipalpodes_annandalei	1262030003320223000011101010011002111000010010030102101333111050110011123100200111000201101210010120
Flabellotreta_fruhstorferi	1222030004320223000011101110011002111000010010031102201331110070110111122200210101000201101210010120
Falsophaeopterus_fruhstorferi	0262030023321223000033311110011002111000010110030102101333133001110011023100200011000222100210013130
Gorhamia_krombeini	0262230003320223000033301010011002111001010110031102101333130000110011023100200111000222100210010130
Harmatelia_bilinea	0260230123321226000034301010020001111001010110031102102333132000110011023100200111000202100210010120
Mimophaeopterus_wittmeri	0222030023320223000033311110010002111000010010031102201331110000110011122200210101000201101210010120
Oculogryphus_fulvus	0222050103322023000033301000010102111001012200030102101333110061100011023102200011000222100210013130
Picodrilus_limbellus	0222030103320223000011101110011002111001010010031102201331110000110111122200210101000201101220010120
Stenocladius_rufithorax	0262030003321123000033301020001001111000010010031102102313132050110011023100200101000222100210010120
Stenocladius_bicoloripes	0262030123321223000033311000010002111000112000030102101333132001110011023100210011000222101210013120
Stenocladius_chinensis	0262030103321223000033311000012102111000112200030102101333132001110011023100200011000222101210013120
Stenocladius_sp	0262030103321223000033301000010002111000112200030102101333132001110011023100200011000222101210013120
Ototretadrilus_flavoscutellaris	0222050103320223000033301010030001111000010100030102102334112251110021043100200011003201000210013130
Dioptoma_adamsi	01222600033320350000443111110030003510201000000030103115015110250220111033100200010005105101010010040
Diplocladon_hasselti	0122050003311025000000011023011001510201002111132104115335110200010111022100200011010101101200010140
Dodecatoma_bicolor	0122050003311025000000011023011001510201002111132104111331110251020021042100200011005102101210010130
Falsophrixothrix_humeralis	0122010003311025000044011023012101510201002111020104115315132250010011043102200111015122001210010140
Menghuoius_ingens	5122063023332030000002111011012112510201002221130104111311120260110111021100200111015105101200012140

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Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Menghuoius_giganteus	5122063023332030000002111011012112510201002221130104111311121260010111021100200111015105101200012140
Monodrilus_marginatus	0122040003311025000000011123011011510201002101130104115335112251020111022100200111010122101210010140
Ochotyra_semiusta	3162010003311025000000011023012101510201002111130104115315113251020111053100200111002102001210110140
Rhagophthalmus_ohbai	0162050003311025000011011013012102510201002111132102115315110261220111022100200111000101101210110130
Rhagophthalminae_ngen	0122040003312025000000011023011111510201002111131104115315132201010111021100200011010101101220010130
Cyphonocerus_ruficollis	0222232123201223010055401113011012611200001110031102201331111061010111122200200001000201101210010120
Cyphonocerus_sanguineus	0222232123200223010055401113011012611200001110031102201331110061130111122200200001100201101210010120
Cyphonocerus_sylvicola	0222233123200223010055401010010002611200001110032102201331110001110111122200200001100201101210010120
Pollaclasis_bifaria	0022232123200223010055401013001022611200001110032102201313110061000211122202210001010201101210010120
Atyphella_lychnus	0122264113202223010044401005012312201201001212030104001331110061030211122211011000000101101211014120
Atyphella_carolinae	0122263114201233010033301005012312611201001010030104001331110061130211122210001000000101101211014120
Atyphella_obsoleta	0122263124201233010055501011012312201201001012030104001331110001010211122210001000000101101211014120
Bougeoisia_antipoda	0162011015202125000033311005012312611201001210030103201331110001110111122202200100005101101211010130
Colophotia_brevis	0122012123202225010044301011012312111201001010030106201331110001010211121202210000000101101201114120
Colophotia_praeusta	0122012123202225010044301010012312111201001010030106101331110001010211121202210000000101101201114120
Curtos_obscuricolor	0122262113202220010033301005012312611201001210030104201331132001100111122201200000000101101211011120
Hotaria_parvula	0122061113202225010044301105012312611201001010030104201331110001010111121200200100000101101211014120
Lampyroidea_dispar	0122062113202225010044301100012312611201001010030104101333110001010011121200200101000101101211014120

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Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Lampyroidea_syriaca	0162011113202225010044301001012312611201001010030104101333110001010011121200200101000101101211014120
Luciola_anceyi	0122062113202223010044101000011312611200001010030106101333111061010211121200200100000101101211014120
Luciola_aquatica	5122062003201225010044401115012312611201001010030102201331110001110211121202200000000101101211014120
Luciola_cincticollis	0122062023202225000044301121011311611200001010030102201331112001100111122202210101000101101211014120
Luciola_curtithorax	5122061123202225010044301101012312611201001010030104201331112001000111121202200101000101101211014120
Luciola_filiformis	5122061013202225010044301101012312611201001110030104201333110001000111121202200100000101101211014120
Luciola_hydrophila	5122061003202225010044301005011312611201001010030104201331110001010111121202200100000101101211014120
Luciola_italica	0122061113202225010044301105012312611201001010030104201333110001010111121200200101000101101211014120
Luciola_kagiana	5122061113202225010044301105012312611201001010030104101333110001110111121202200100000101101211014120
Luciola_kuroiwai	5162012123202225010033301110012312111201001110030106101331110001000211121202210000000101101211014120
Luciola_lustianica	0122061113202225010044301105012312611201001010030104201331110001110111121200200101000101101211014120
Luciola_ovalis	0122263113200235010044301005011312201201001010030104001331110061120211121200210000000101101211014120
Luciola_peculiaris	0122263124201233010055501005012312201201001012030104001331110001010211122210001000000101101211014120
Luciola_substriata	5122062003201225010044401115011312611201001010030102201331110001110211121202200000000101101211014120
Luciola_trilucida	5162012123202225010033301110012312111201001010030106201331110001100111122202210000000101101211014120
Pteroptyx_fulminea	5162012123202225010044301015012312111201001010030106201331110001010231121202210000000101101201114120
Pteroptyx_cribella	0162212123202225010044301110012312111201001010030106201331110001010231121202210000000101101201114120
Pygoluciola_satoi	5122153013102225000033301023012311611201001112030106201331110001010101121200200000005101101211014120

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Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Pyrophanes_similis	5162212123202225010044301010012312111201001010030106201331110001010201121202210000000101101201114120
Pyrophanes_appendiculata	0162212123202225010044311010012312111201001010030106201331110001010201121202210000000101101201114120
Bicellonycha_deleta	2242353023301217002000020020122101511201102110031105201031111001000111121302200110000201100310012110
Bicellonycha_stigmatica	0242353023301217002000120020122101511201102010031105001031111021000111121302200110000201100310012110
Bicellonycha_sp	0242343023301217002000020120122101511201102010031105201031111021000111121302200110000201100310012110
Daiphoturis_apicalis	2242302023301217002000010021122101511201102010031106001031110001010111121200200110110201100210012120
Photuris_trilineata	2232364023301217002000420021122101511201102010031106201031111061000111121302200110000224100310012110
Photuris_sp	2232343023301217002000210021122101511201102210031106001031111061000011121202200111010201100310012120
Photurocantharis_sp	2242303023301214002000010021122101511201102010031106201031110001000111121200200110110201100210012120
Pyrogaster_coxalis	2242343023331237002000210021122101511201102210031106001131111061010011121200200111010221100310012120
Pyrogaster_lunifer	2242303033331237002000110021122101511201102010031106201131110061010211121300200110000201100310012110
Pyrogaster_malepictus	2242343023331237002000210021122101511201102210031106001131111061010011121200200111010221100310012120
Pyrogaster_mediofasciatus	2242353023331234002000110021122101511201102210031106001131111061010011121200200111010221100310012120
Amydetes_apicalis	2232243123202225010055000000022202801000101210030102102322230001110111122200200101000201101110010140
Amydetes_fastigiatus	2232243123202225010055000000022202801000101210030102102322233001110111122200200101000201101110010130
Cladodes_flabellata	4222352123202225000055621021112201801200101110030102101011232000010121122300210010005211101210011130
Cladodes_imperfectus	3232364123232237001055621021112101701101100100030102101331112020110211222300200010000201100210011130
Cladodes_ater	4232343123302227001044121021112101901201101112030102202331110060010211121300200000000211101210011030

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	1111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111112
Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Dodacles_elegans	2232253123302217001044121023112211701100001200031102101333210250010121142300200011025211101210010030
Dodacles_emissa	2232253123332227001044121013112211901200001200030102111333210000010121142300200011005211101210010030
Dodacles_erebea	2232253123302217001044121023112211701100001200031102101333210250010121142300200011025211101210010030
Dryptelytra_cayennensis	3232364223202217001044621021122131801200102200031102201133112250110221242300200010002211101210010030
Dryptelytra_sp	3232364223202217001044621021122101701100102200031102001131112250110221242300200010002211101210010030
Ethra_decorata	2232373123202127001004121021112101801200101200031102101333110020010211221300210000000201101210011120
Ethra_dejeani	4232372123202127001044121021112101801200101200031102101333212000000111123202200010000201101210011130
Ethra_marginatus	4232373123202127001044121021112101801200101200031102101333210000100111121202200010000201101210011130
Fenestracladodes_malleri	3232364123232237001155621021112101701101100101030102101331132020110211222300200000000201100210011130
Ledocas_parallelus	2232353123202117001055121021112101701101101000030102201331110000020111122300200110000211101210011130
Ledocas_sp	2232354223302117001044621021112101701101000010020102201333122000110211121300200000000211100210010130
Magnoculus_sp_a	2242253223202117021055521011122111801201001020030102201333110061130011123211200101000201101210011130
Magnoculus_sp_b	2242253223202117021055521025112101801201001000030102201333110001130011123211200101000201101210011130
Psilocladus_miltoderus	2242252123202127011044121011012102801200001000031102201331110001120111122200200110000201100210010030
Psilocladus_nevermanni	2242252123202127011044121010012102801200001000031102201333112001120111122200200110000201100210010030
Scissicauda_disjuncta	4292373123202117001044120025122101111001001100031102101331110020000211221302210010005201100210011120
Vesta_chevrolatii	3232242123232237011044120011112102901200101010031106203331112000120111121200000010000201101210014130
Vesta_impressicollis	3232242123232237011044120011112102901200101010031106203331112000120111121200000010000201101210014130

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Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Vesta_rufiventris	3232252123232223701104412101111211280120010101003110620333111207011021112120000001000020110121001130
Vesta_arcta	2242253123232223701104412101111220180120010221003110220133313200111021112120020011000021110131001120
Vesta_cincticollis	4232352123232223700103312101112210190120010121003010220333221000001021112130021001000020110121001020
Vesta_thoracica	2232253123202227011044220011122112801200101010030106103331112060120111121200000010000201101210012130
Afrodiaphanes_marginipennis	2292213123202127004265620012102323801201102210030102101333210001110111122302200010000201101110010030
Alecton_discoidalis	4232363123232137003055620011122102901200102010030102201333110040000211121302210010000211101311011020
Aspisoma_aegrotum	3252393113232138003033121020121001301000000010030102101331111010010311421300211023020211101311011020
Aspisoma_ignita	3252393113232138003033121020121001901000000010030102101333111010010311421300211023020211101311011020
Aspisoma_physonotum	3252393113232138003033121020121001301000000010030102101333111010010311421300211023020211101311011020
Callopisma_rufa	2242254123232227001044121011112201801200102210031102201331132071110211121200200100000211101310011120
Calyptocephalus_sp	3132284233202124001045620021122301801100101110030102201331113000010211121300210010000201101210010130
Cratomorphus_signativentris	2232374223232137004244620031112323301201102210030102101331111040010311321300201023020211101311011020
Dadophora_hyalina	3292374123232237001033120010122101801200101110030102101331110000010211121200200011020211101311014020
Diaphanes_citrinus	2232274123232137004245620021122311901201101210030102201334133070120211221300200010000201101110010120
Diaphanes_formosus	2292274223232137004245620011112322301201101210030102201331130060110211221300200010000201101110010120
Diaphanes_lampyroides	2232273123232137004245620011122322801201101210030102201334121061120211221300210010000201101110010120
Diaphanes_nubilus	2292274123232137004245620011122322801201101210030102201333133001110211221300200010000201101110010120
Diaphanes_schoutedeni	2292264223202127004245620032102323901201101210032102101334121001110211121302210000000201101110010120

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	1111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111112
Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Dilychnia_apicalis	3242254123232227013044121011112301801200102210031102201331132071110211121200200100000211101210011120
Dilychnia_ruficollis	3242254123232227013044121011112301801200102210031102201331132071110211121200200100000211101210011120
Ellychnia_corrusca	2232273123232137001044121021121201901200101010030102103333110060100211221302210010000201101310010120
Ellychnia_moesta	2232273123232137001044121021122201901200101010030102103333110060100211221302210010000201101310010120
Erythrolychnia_fulgida	3232274123232137004044120021112211801200102210031102201331113050100211122302210110000201101211014120
undet._gen	4242353123202127001044121021112301801200102010031102201331113060100211122302210110000201101211014120
Lamprigera_boyei	0262284213232138001054500005122102111201101110030102201333121061110211121202210003000201101210010130
Lamprigera_yunnana	0262284213232138001054500005122112111201101110030103201333121061110211121202210003000201101210010130
Lamprocera_tristior	3252394123232137003033121021122101301200001010031102101333110010010311321300211023020211101210011120
Lamprohiza_delarouzei	2232214123232237004255220011122302801201101010030102201333121061110211122300210010000201101210010120
Lamprohiza_splendidula	2232214123232237004255220011122302801201101010030102201333121061110211122300210010000201101210010120
Lampronetes_mauritanica	2232273123332237004244220032122211901201102010031102201333110050110221132200200010005201101211011020
Lampyris_noctiluca	2232273123202127004244620011122302801201001010030102201333112000120111122202200010000201101211011030
Lampyris_algerica	2232274223202127004244620022112322901201101010030102201333212000020211122300200010000201101211010030
Lucernuta_savignii	3252294223232137003133620021122101901201102210030102101331111010010311321300201023020211101311011020
Lucidina_accensa	4232373124202127001033621021112101701100101110030102101323113070010211122200210010000201101211014020
Lucidina_vitalisi	4232373124202127001033621021112101701100101110030102101323133070110211122200210010000201101211014020
Lucidina_gracilis	4262371123202127001033621011122101801100101010030106201323132000000011112200200111001201101211014020

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	1111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111112
Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Lucidota_atra	4232373124202227001033621021112201701200101110031102101333110071110211122200210010000201101211014020
Lucidota_banoni	3232373223202127003033120021112201901000101110031102101332110070010211121202210010000201101211014020
Lucidota_bella	3242273123202127001034220021122101801000102110031102101331112060120111121200200010000201101210014130
Lucidota_comitata	2232273123202127001033120011122101801000102210031102103333112060110211221302210013005201101211014020
Lucidota_pennata	3232373123202127001033120021122201801000102010031102103333112070010211121302210011000201101211014020
Lucidota_pygidialis	4232373123202127001044121021112101801200101200031102103333210000100211121202200010000201101211014020
Lucidotopsis_cruenticollis	4232373124202127001033621021112101701100101110030102101323133070110211122200210010000201101211014020
Lucio_abdominale	3252395123232137003033621022112111301200001010030102101331110010010311421302211023020211101210011120
Lucio_obscura	3252395123232137003033621022112111301200001010030102101331110010010311421302211023020211101210011120
Lychnacris_flabellata	3252395123232137003033621022112111901200001110030102001331110010010311421302211023020211101210011120
Macrolampis_acicularis	4232362123202227001044120010122102801201102010030102103333132001110111121202210010000201101211014020
Macrolampis_longipennis	4232362123202227003233120015122102801201101010030102101333110000010111121200210010000201101211014020
Macrolampis_omissa	2232263123232137001033120020122101801201101010031102101331110050110211221300210010000201101211014020
Macrolampis_perelegans	4292362123202127003044120021122101801201101110031102103333110000110211121202200010000201101211014020
Microphotus_angustus	2232274123232137004055620032112322701101101010030102201332120200110121142200200010005201101211010130
Microphotus_dilatatus	2292263123232137004055620032112322701101101010030102201332113200110121142200200010005201101211010130
Microphotus_octarthrus	2292263123232137004055620032112322701101101010030102201332130200110121142200200010005201101211010130
Mimophotinus_angustatus	4262311123202127001034621021112101701101101010030102201323132001000111112202200010001201101211010120

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	1111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111112
Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Nyctophila_reichii	2232213123202127004245620022112322801201101210030102203331210000010111122200200010000201101211011130
Ophoelis_impura	3252284233232134001045620021122201701100101110030102001331112040010211221300210013000201101210011120
Paraphausis_eximia	2232373123232137001055620021112211701101101010030102103333113200110121132202200010005201101211010130
Petalacmis_praeclarus	2252285233232134003044620021112211701100101010030102201333111041110211221300210010000221101211011120
Phaenolis_laciniatus	3252284223202127001045620021112201701100101010031102201334113061010211221300210010000201101211011120
Phaenolis_bicoloripes	3252284223202127001045620021112201701100101010031102201334121061010211221300210010000201101211011120
Phausis_reticulata	22322141232322237004255220011122311801201101000030102201333123001110211122300210010000201101210010130
Phosphaenopterus_metzneri	4292372123202127001034620021112101701101101100031106401332121000000111112202210010001201101210011120
Phosphaenus_hemiptera	4292372123202127001034620021132103701101101100031106401333002160000211142202200013004201101210011120
Photinus_maritimus	3292262123202127004044120021122101801001101010030102103333110000010111121202210010000201101211014030
Photinus_extensus	3292262123202127003033120021122101801001101010030102101333130000010211121202210010000201101211014020
Photinus_pallens	3292263123202127004033120021122101801001101010030102103333110000010111121202200010000201101211014020
Photinus_pyralis	3292262123202127003033120021122101801001101010030102101333130000010211121202210010000201101211014020
Platylampis_latiuscula	3252294123232137001033121021122101701100101010031102101333111020010311321302211013000201101211011130
Platylampis_delicata	2252384123232137004133220022122311901200101010030102103333111061000311321302211013000201101210011120
Pleotomodes_knulli	2232254123232037004255620032112321801201102010031102203333110060010111132300200010005201101210010020
Pleotomus_pallens	2292253123232137004145620021112313801201101010030102203333110040020111142300200010005201101211011020
Pristolycus_kanoi	5222043023231235013044401023012221801200001110031102001231113071130011123201200001000101101210014020

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	1111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111111112
Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Pristolycus_sagulatus	5222043023231235023044401023012221801200001110031102201231111071130011123201210001000101101210014020
Pseudolychnuris_vittata	2232263123232137001033121020112101801200100110031102201333110000010211121302201010000211101210011020
Pyractomena_lucifer	4292372123232137003322720021112101901000101010030102101333112000010211121202200010020201101210013030
Pyractomena_striatella	4292372123232137003322720021112101901000101000030102101333110000010211121302200010020201101210010030
Pyractonema_obscura	3232273123202127011033621021112111901200101010031102101333112060010211122200200010020201101211011020
Pyrocoelia_analis	3232384123232137003144620021122311801200101010031102201331132041102112203002000100202111011111010120
Pyrocoelia_bicolor	3232384223232137003044620021122311801200101010031102201331132060120211220300200010020201101111010120
Pyrocoelia_formosana	2292284123232137003144621011122111801200101210031102403331110040120211221302200010020211101111010130
Pyrocoelia_praetexta	3232284123232137004144620021122311801200101010031102201331112060120211220300200010020211101111011120
Pyrocoelia_prolongata	4292384223232137003144620021112111901200101010031102403331112070110211221302200010020201101111010130
Pyropyga_fenestralis	2292273123202127001044121021122101801200101010030102101323112000010111121200210010000201101211011030
Pyropyga_nigricans	2292273123202127001044121021122101801200101010030102201323110000010111121202210011000211101211011030
Robopus_lengi	2292363123232137004044320001122302801201001010030102101333112000110211121300210111000201101211011030
Robopus_pantoni	2292363123232137004044320001122302801201001210030102101333112000110211221302210010000201101211014030
Robopus_quadrimaculatus	2292263123232137004044320001122302801201001010030102101333112000110211121300210111000201101211011030
Robopus_vittiger	2292363123232137001044120021112101801201001010031102101333112050010211121202210010000201101211014020
Roleta_notaticollis	3232283233202124001045620032112211701100101010030102101333212200010021141200200011002211101210010030
Rufolychnia_borencona	4232373123202127001044121021122101801200101110030102103334110000100211122302210110000201101211011120

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Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Satolampyris_dichroma	0222264023232237010044401021010011201200001010032102201231110001110211123200010001000101101210014020
Tenaspis_angularis	3232395123232137003033121032111011701100100110031102403331111010010311321302211023000211101211011020
Tenaspis_figurata	3252395123232137003033121021122201801200101110030102403331110010010311321302211023000201101211011020
Cheguevaria_taino	0232253123202217001011221011122111801201001200030102201333113051010011043001210000003201101210010130

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	2222222222222222222222222222222222222222222222222222222222222222222222222222222222222222222222222223
Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Dascillus_cervinus	0100200101000000003100011010101420131100001110010110110112100002401110000100000--000000000000000000-
Macropogon_testaceipennis	01002000010000000031001010101100201511100011100100001110030000010010010001000030000100001000-000000-
Brachypsectra_fulva	000000000000001012??2-0000001000000000000000000000000000301000100000000000000000--00000000000-000000-
Drilus_flavescens	111010112031012010002-010000100100121100000000010120010112010000100010000001102030122220121--010--20
Selasia_decipiens	110010110011002010102-010000101100111100111100000120010010000210101011011001213000110000101--010--20
Selasia_sp	1300211120200120100100010000100000121000000000010100000102010000001000000001200--1100000101--010--20
Malacogaster_passerini	131011012011002110002-010000100100121100000000000120010111010000101010000001102000122200121--010--20
Lycus_(Neolycus)_arizonensis	130100012041000010211-101011002210131100001110010020110000010102211010000101212110121110111--020--20
Lycostomus_sanguineus	131100012041100010211-101011002210131100001110010020110001010102211010000101212110121210111--020--20
Cautires_kazuoi	132001112041300110201-101011002110131100001110000020110002010102111010000101211100120100101--010--20
Plateros_coracinus	132001112041300110201-101010002110131100001110000010110002010100111010000101212000110000101--010--20
Lyponia_delicatula	132001112041300110211-100011002210131100001110000020110002010002211010000101211100120100101--010--20
Eropterus_nothus	131001112041100110211-100010002110131100001110000020110002010002111010000101202100110000101--010--20
Xylobanus_niger	132001112041300110211-101011002110131100001110000020110002010000111010000101201100120000101--010--20
Omalisus_fontisbellaquei	0210101000200111100000010011000000011000001110000010000011201000001001001001213000110100101--010--20
Omethes_marginatus	1300111111111101103100110000100010120100111110010100010120010002001011000101000--1110000101--010--20
Omethes_rugiceps	1300111111111101103100110000100010120100101110010100010120010002001011000101000--1110000101--010--20
Troglomethes_leechi	?301111111?11101103100110000100010120100011110010100010120100002001002001101203000110000101--010--20

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Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Malthomethes_oregonus	1211111111311101113100110000100010120100011100010100010120110000001001001001200––1110000101––010––20
Drilonius_striatulus	1310211111111101113100110000100010120100101110010100010122010002001011000101200––1110000101––010––20
Matheteus_theveneti	???????111?12110103100110000100010120100001110010100010120110002001012000101003000110000101––010––20
Ginglymocladus_luteicollis	0210111111312101103100110000100010130100001110010100010020010002001011000101200––1110000101––010––20
Phenogodes_frontalis	1320201121110020100100010000101200120000010000010120000020000000101002000001201100110100111––010––20
Zarhipis_integripennis	1110201121310010100100010010101200120000010000010120000020000000101002000001201100120100111––010––20
Cenophengus_debilis	1110121111111101100101010010101300120000010000010120000120000000100001001001201100110100111––010––20
Distremocephalus_texanus	1110121111111101100101010010101300120010010000010120001120000002100000001001201000110100111––010––20
Stenophrixothrix_sp	1220111121111020101101010000201300100000000000010120000220100002101002000001201100110100111––010––20
Taximastinocerus_sp	1210121111111111101101010000101300000110010000010120000120000002101001001001201100120100111––010––20
Telegeusis_nubifex	1230221110311101114100010000201020100100010000010110000220100000101001001001202000110100111––010––20
Pseudokarumia_angustata	1230221110311101114100010000201120100100010000010110000220100000101001001001202000110100111––010––20
Pterotus_obscuripennis	131011111021011010102–010010101120010000001100000110000011000000001002001001202100110000101––010––20
Brachylampis_blaisdelli	110010010031012010102–010010101310110100111100000120010020000201101011011001203000110000101––010––20
Ceylandidrilus_bipartitus	110000010031012010102–010010101100111201111110000120010022000011101010111101203001110000101––010––20
Ceylandidrilus_kandyanus	110000110031012010102–010010101100110101111110000120020020000011101011011101203000110000101––010––20
Drilaster_auxillaris	110000010130112010102–010010101110111100111110000100010021000001001011011101203000110000101––010––20
Drilaster_weyersi	110000010130112010102–010010101110110200111110000100010020000201001011011101203000110000101––010––20

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Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Lamellipalpodes_annandalei	110000010011012010102–010000101310110100111110000120010020000000101010011101203000110000101––010––20
Flabellotreta_fruhstorferi	110000010101112010102–010010101110111200101110000100020020000201001021010101203000110000101––010––20
Falsophaeopterus_fruhstorferi	111000110011112110112–010000101310110100011100010120010020000000101012001001202100100000101––010––20
Gorhamia_krombeini	110000110031112010102–010000101100110100111110000120010020000001101011011101203000110000101––010––20
Harmatelia_bilinea	110000110011011010102–010000101100110100001110000120010020000000001012001101202100100000101––010––20
Mimophaeopterus_wittmeri	110000010131012010102–010010101110110100111110000100010020000001001012011101203000110000101––010––20
Oculogryphus_fulvus	111000112031212010112–010001101100010100011100000120000020100000101002001001202000110000101––010––20
Picodrilus_limbellus	110000010131112010102–010010101310110100101110010100010121000001001011011101203000110000101––010––20
Stenocladius_rufithorax	110000110031002010102–010000101300110101111110000120010022000011101010111101203000110000101––010––20
Stenocladius_bicoloripes	111000112011112110112–010000101100010100011100010120000020100000001002001001202100100000101––010––20
Stenocladius_chinensis	111000112011112110112–010000101100010100011100010120000020100000001002001001202100100000101––010––20
Stenocladius_sp	111000112011112110112–010000101100010100011100010120000020100000001002001001202100100000101––010––20
Ototretadrilus_flavoscutellaris	111000110011012010112–010000201310110100001110010100010020000000001002001101203000110000101––010––20
Dioptoma_adamsi	110020112021011010112–010001101310140100000000010120010022000001311001000001202100100000101––000001–
Diplocladon_hasselti	130020112021011010112–010000100010141100000000010120110120020001311010000001201100120100111––010––20
Dodecatoma_bicolor	111020112021011010112–010000100020140000010000010100000122000001011001001001201100120100111––010––20
Falsophrixothrix_humeralis	131020112021010010102–010000101320111100010000010120000120000000311001000001203100120200121––010––20
Menghuoius_ingens	1310201120210110101000110000100020140100000000010100010120100001011011000001201100110000101––010––20

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Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Menghuoius_giganteus	1310201120210110101000110000100020140100000000010100010120100001011011000001201100110000101--010--20
Monodrilus_marginatus	131020112021011010102-0100001003101411000000000101200001200000003110010010012021001100001 01--010--20
Ochotyra_semiusta	131020112021011110112-01000010001014010000000001010001002002000001100000000120110011000010 1--010--20
Rhagophthalmus_ohbai	131020112021011010112-01000010002014110000000001010000012010000001100100100120210011000010 1--010--20
Rhagophthalminae_ngen	111020112021011110102-01000010031014110000000001010000012000000131100100100120210011000010 1--010--20
Cyphonocerus_ruficollis	130000110031211110102-01000010000011010011111000010001012000000000101101110121110011000010 1--010--20
Cyphonocerus_sanguineus	130000110031211010102-01000010000011010011111000010001012000000000101101110121110011000010 1--010--20
Cyphonocerus_sylvicola	130000110031211110102-01000010000011010011111000010001012102000000101101110121110011000010 1--010--20
Pollaclasis_bifaria	130000110031211010102-01000010000011010011111000010001012102000000101101110120310011000010 1--010--20
Atyphella_lychnus	120000110131011010102-0100001001101112011011100001000201221000000010210101012020001000001002000000 1-
Atyphella_carolinae	130100010131011010102-0100101001001112001011100001000201221000000010210101012030001000001002000000 1-
Atyphella_obsoleta	120000110131011010102-0100001100101112001011100001000201221000000010210101012030001000020005000101 1-
Bougeoisia_antipoda	110000010131011010102-0100101000001101001111100001000101221002000010110111012020001000001001-00000 1-
Colophotia_brevis	120100110131311010102-0100001000001112001011100001000201221002000010220101012020001001010104103020 1-
Colophotia_praeusta	120100110131311010102-0100001000001112001011100001000201221002000010220101012020001001010104103020 1-
Curtos_obscuricolor	120000110131311010102-0100001000001112001011100001000201221000000010210101012021001000001002000000 1-
Hotaria_parvula	110000110131311010102-0100001000001112001011100001000201221000000010110111012021001000001003000000 1-
Lampyroidea_dispar	110000010131311010102-0100001000001101001111100001000101221000000010120111012021001100001003000010 1-

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Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Lampyroidea_syriaca	110000010131311010102–01000010000011010011111000010001012210000000101201110120210011000010030000101–
Luciola_anceyi	120000010131311010102–01000010000011120010111000010002012210020000102201010120200010000100000–000001–
Luciola_aquatica	120000010131311010102–010000100000111200101110000100020122101000001022010101202000100000000020000011–
Luciola_cincticollis	120000010131311010102–010010110000110100111110000100010122100200001011000101203001100000000030000211–
Luciola_curtithorax	120000110131311010102–0100001000001101001111100001000101221002000010110001012030011100001000–000001–
Luciola_filiformis	120000110131311010102–0100001000001101001011100001000101221002000010120111012030001100001001–000001–
Luciola_hydrophila	130000110131011010102–010010100000111200101110000100020122101000001021010101203100100000100200000001–
Luciola_italica	110000110131311010102–010000100000111200101110000100020122100000000101101110120300011000010030000001–
Luciola_kagiana	110000110131311010102–010010100100111200111110000100020122100000000101100010120310011000010030000001–
Luciola_kuroiwai	130000110131311010102–010000100000111200101110000100020122100200001021010101203001110001000400100001–
Luciola_lustianica	110000110131311010102–010000100000111200101110000100020122100000000101101110120310011000010030000001–
Luciola_ovalis	130000110131211010102–010010100110111200101110000100020122100000000102101010120200011010000030010111–
Luciola_peculiaris	120000110131011010102–010000111110111200101110000100020122100200001021010101203001100002000500011111–
Luciola_substriata	120000010131311010102–010000100000011200101110000100020122100000000102101010120210010000000020000111–
Luciola_trilucida	130000110131311010102–010000100000111200101110000100020122100200001021010101203100110001000200100–1–
Pteroptyx_fulminea	120000110131311010102–01000010000011120010111000010002012210020000102201010120310110010101041020201–
Pteroptyx_cribella	130000110131311010102–01000010000011120010111000010002012210020000102201010120310110010101041020201–
Pygoluciola_satoi	120000110131111010102–010010100000111200101110000100020122100000000102201010120310011010200050000211–

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Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Pyrophanes_similis	130000110131311010102-0100001001001112011011100001000202221112103110220101012031021202000104113 0101-
Pyrophanes_appendiculata	130000110131311010102-0100001001001112011011100001000202221112103110220101012031021202000104113 0101-
Bicellonycha_deleta	110000110031011010102-010000101000111200101120110100120222010002001021000211213001110100101--010--20
Bicellonycha_stigmatica	110000110031011010102-010000101200112200101120110120120222010002201021000211213001110100101--010--20
Bicellonycha_sp	110000110031211010102-010000101000111200101120110100120222010002001021000211212101110000101--010--20
Daiphoturis_apicalis	130000110031011010112-010100111000112200101120011100120222110002201021000201213101110000101--010--20
Photuris_trilineata	110000110031211010112-010000101100112200101120210100120222110302201022000221212001110100101--010--20
Photuris_sp	110000110031211010112-010000101000111200101210210100020222110002201022000121212001110100101--010--20
Photurocantharis_sp	130000110031011010112-010100111000112200101220011120120222110202001021000201212000110000101--010--20
Pyrogaster_coxalis	130000110031211010102-010000101100111200101220311121120222110201101012000201213001110000101--010--21
Pyrogaster_lunifer	110000110031011010112-010100111200112200101220011120220222110202201021000201212000110000101--010--20
Pyrogaster_malepictus	130000110031211010102-010000101100111200101220311121120222110201101012000201213001110000101--010--21
Pyrogaster_mediofasciatus	130000110031011010112-010100111100112200101220011120120222110002201022000201212100110000101--010--20
Amydetes_apicalis	131002111031111110102-110010101100110100001110000120010022110200101012000101212100110000111--010--20
Amydetes_fastigiatus	111002111031111110102-110010101100110100001110000120010022110200101012000101212100110000111--010--20
Cladodes_flabellata	110100010031111010112-010010101100110100111110010120010021110200101011011101212000120100111--010--20
Cladodes_imperfectus	110100010031011010112-010010101010110100101110010100010121110200001012011101212100120100111--010--20
Cladodes_ater	111100010031211010112-010010101100111201101120010110120121110200111021010201211100120200121--010--20

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Character number	000000000111111111122222222223333333333444444444455555555556666666666777777777788888888889999999990
Species	123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Dodacles_elegans	131100010031111010112-010010101310111201101120010120120121110200101021010201212100120100111--010--20
Dodacles_emissa	130100110031111110112-010010101310110100101110010120010121110200001001000101211100120100111--010--20
Dodacles_erebea	131100010031111010112-010010101310111200101110010120120121110200101001010101211100120100111--010--20
Dryptelytra_cayennensis	130100110011211010112-010010101110111200101110010100020121110200001021010101211100120100111--010--20
Dryptelytra_sp	130100110031211010112-010010101110111200101110010100020121110200001022010101211000120100111--010--20
Ethra_decorata	110100110031110010112-010010101110111201101220010120120121110200111021010201212100100100101--010--20
Ethra_dejeani	110100110031111010112-010010101110111201101222010120120121110200111120110201211100120200111--010--20
Ethra_marginatus	110100110031111010112-010010101110111201101221010120120121110200111021010201212000120200111--010--20
Fenestracladodes_malleri	110100010031011010112-010010101010110100101110010100010121110200001012011101212100120100111--010--20
Ledocas_parallelus	111000110031111010112-010010101300111200101110010100020122110200001012010101211100120200111--010--20
Ledocas_sp	111100110031211010112-010010101100111200101110010100020121110200001022010101211100120200111--010--20
Magnoculus_sp_a	110100110031111010112-010000101300111200101110010120020121100200111011010101202000110100101--010--20
Magnoculus_sp_b	110100110031111010112-010000101300110100101110010120020121100200111011011101202000010000101--010--20
Psilocladus_miltoderus	110100110031110010112-010010101100110100101110010120020121100200001011010101211100110100101--010--20
Psilocladus_nevermanni	110100110031110010112-010010101100110100101110010120020121100200001012010201211100110100101--010--20
Scissicauda_disjuncta	110100110031111010102-010010101110111200101120010100020221100200001022010201212000110100101--010--20
Vesta_chevrolatii	120000110031111010102-010010101110111200001110010100020121110200011021010101211110121210111--020--20
Vesta_impressicollis	120000110031111010102-010010101110111200101110010100020121110200011021010101211110121210111--020--20

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Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Vesta_rufiventris	110000110031111010102–010010101110111200101110010100020121110200011021010101211010121210121––020––20
Vesta_arcta	110100010031111010102–010010101010111200101120010100010121110200011011010201212000110100101––010––20
Vesta_cincticollis	110000010031111010112–010010102110112211101220010110120122110200111121110201212100120100101––010––20
Vesta_thoracica	120000010031111010102–010010101110112201101110010120120121110200011020010101212000121210111––020––20
Afrodiaphanes_marginipennis	110001110031211010112–010010102100111201101110010120120121110200111020010101211000110100111––010––20
Alecton_discoidalis	110000010031111010102–010010111110111201101210010120020122100200111020110101211100100000101––010––20
Aspisoma_aegrotum	110000010031111010102–010010112110122201101221010120120122110200101121110201211100110000101––010––20
Aspisoma_ignita	110000010031111010102–010010112110122201101221010120120122110200101121110201211100110000101––010––20
Aspisoma_physonotum	110000010031111010102–010010112110122201101221010120120122110200101121110201211100110000101––010––20
Callopisma_rufa	110100010031211010102–010010102310111201101120010110120121110200011021010201212000110000101––010––20
Calyptocephalus_sp	111000110011110010112–010010101000110100101120010100020122110200001021010201211110121210121––010––21
Cratomorphus_signativentris	110000010031011010112–010010112110122201101221010120120122110200101121110201211100120100101––010––20
Dadophora_hyalina	110100010031111010112–010010112111121201101221010110120122110100101120110201211100110100101––010––20
Diaphanes_citrinus	110000010031111010112–010010102101111200101110010120020121110200111021010101211000110100111––010––20
Diaphanes_formosus	110000110031111010112–010010101300111200101110010120020121110200301021010101211100110100111––010––20
Diaphanes_lampyroides	110000110031111010112–010010101100111200101110010120120121110200101021010101211100110100111––010––20
Diaphanes_nubilus	110000110031111010112–010010101000110100111110010100010121110200001011000101211100110100111––010––20
Diaphanes_schoutedeni	110001110031211010112–010010101101111201101110010120120121110200101021010101211000110100111––010––20

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Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Dilychnia_apicalis	110100010031211010102–0100101021101112001011200101001201211102000110210102012120001100000101––010––20
Dilychnia_ruficollis	110100010031211010102–0100101010101112001011200101001201211102000110210102012120001100000101––010––20
Ellychnia_corrusca	110000110031111010112–010010102310112201101220010120120122100200111121110201212000110100101––010––22
Ellychnia_moesta	111100110031111010112–010010102310112201101220010120120122100200111121110201212000110100101––010––22
Erythrolychnia_fulgida	110100010021211010112–010010101110111201101120010110120122100200011021010201212000110100101––010––21
undet._gen	110100110021211010112–010010101110111201101120010110120122100200011021010201212000110100101––010––21
Lamprigera_boyei	111000010031212010102–010010102120111201101110000120020122110200111022010101211100100000101––010––20
Lamprigera_yunnana	111000010031212010102–010010102120111200001110000120020122110200111022010101211100100000101––010––20
Lamprocera_tristior	110100010031011010112–010010102110111201101221010120120122110200101021010201211100110100111––010––20
Lamprohiza_delarouzei	130100010031111010112–010010101110110101111110010120010121100000011011011101202000110100101––010––20
Lamprohiza_splendidula	130100010031111010112–010010101110110101111110010120010121100000011011011101202000110100111––010––20
Lampronetes_mauritanica	110100010021011010111–010010102111010101101110010120120022100210121120110101212110121200121––020––20
Lampyris_noctiluca	110000010021111010112–010010102110111100101210010120020121100201111021010101212100120200121––010––20
Lampyris_algerica	110000010021011010112–010010102110111100101210010120020121100200111021010101212100120200121––010––20
Lucernuta_savignii	110100010031012010112–010010112110111201101220010120020122110200111021010201211100110100111––010––20
Lucidina_accensa	131000110031111010112–010010101100111201101121010120120122110200001121110201212100120100121––010––20
Lucidina_vitalisi	131000110031111010112–010010101100111201101121010120120122110200001121110201212100120100121––010––20
Lucidina_gracilis	130001110031110110112–010010101000111201101120010100120122110200001121110201212100120200121––010––20

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Character number	0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990
Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Lucidota_atra	131000110031111010112–010010102100111201101121010120120122110200111121110201212100120200121––010––20
Lucidota_banoni	110100110031011010112–010000102310112201101220010120120122110200111021110201212000110100101––010––20
Lucidota_bella	110000010031111010112–010010101110111200101110010120020121110200101021010101212010121120111––020––20
Lucidota_comitata	130100110031111010112–010010102300111201101210010120020122110200111021110101212100110100101––010––20
Lucidota_pennata	110100110031111010112–010010102310111200101220010120120122110200111121110201212000110100101––010––20
Lucidota_pygidialis	130100110031111010112–010010102110111201101221010120120121110200111021110201212000110100101––010––20
Lucidotopsis_cruenticollis	131000110031111010112–010010101100111201101121010120120122110200001121110201212100120100121––010––20
Lucio_abdominale	110100010031011010112–010010112110112201101220010120120122110200101021110201211100120200111––010––20
Lucio_obscura	110100010031011010112–010010112110112201101220010120120122110200101021110201211100120200111––010––20
Lychnacris_flabellata	110100010031011010112–01001011211011120010122001012012012210020000102101020121111012020010–––0–0––20
Macrolampis_acicularis	111100110031111110112–010010102300111201101210010120120121110200101021010101211100110100111––010––20
Macrolampis_longipennis	110100110031111010112–010010101110121200101120010120020221110200101021010201211100110100111––010––20
Macrolampis_omissa	110100110031111010112–010010102110112201101220010120120121110200101021110201211100120200111––010––22
Macrolampis_perelegans	110100110031111010112–010010102310112201101220010120120121110201101021110201211100110100111––010––22
Microphotus_angustus	110100110031111010112–010010102100110100111110010110010121000200101011011101211100120200111––010––20
Microphotus_dilatatus	110100110031111010112–010010102100110100111110010110010121000200101011011101211110121220111––010––20
Microphotus_octarthrus	111000110031111010112–010010102100110100111110010120010121110200101011011101211100120200111––010––20
Mimophotinus_angustatus	112000110031112110112–010010102100111201101112010120120121110200111121110101212100120200121––010––20

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Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Nyctophila_reichii	110000110031011010112−010010102101111201111110010120020121110200121020010101211100100100111−−010−−20
Ophoelis_impura	130100110031110010112−010010101000110100101120010100020122110200001021010201211110121200121−−010−−20
Paraphausis_eximia	110100110031111010112−010010102300110100111110010120010121110200101011011101211100120200111−−010−−20
Petalacmis_praeclarus	112000110031011010112−010010102100110100101110010120020122100200101022010101211100120000101−−010−−20
Phaenolis_laciniatus	110100110031011010112−010010101000110100101110010100020122110200001021010101211100120200121−−010−−21
Phaenolis_bicoloripes	110100110031011010112−010010101000110100101110010100020122110200001021010101211100120200121−−010−−21
Phausis_reticulata	120100010011111010112−010010101110110101111110010100010121000000011011011101202000110100111−−010−−20
Phosphaenopterus_metzneri	121000110031212010102−010010102200111201101212000120120122110201211120110101221000120100111−−010−−20
Phosphaenus_hemiptera	121000110031212010102−010010102200111201111212000120120022010201211120110101211000120100111−−010−−20
Photinus_maritimus	110100110031111010112−010010101310111201101220010120120122110200011021010201212100100100111−−010−−20
Photinus_extensus	110100110031111010112−010010102310111201101220010120120122100200311121110201212100110100111−−010−−22
Photinus_pallens	110100110031111010112−010010102310112201101220010120120122110200111121010201211000110100111−−010−−20
Photinus_pyralis	110100110031111010112−010010102310111201101220010120120122100200311121110201212000110100111−−010−−22
Platylampis_latiuscula	110100110031011010112−010010112310111200101120010100020222110200001022010201212100110100101−−010−−20
Platylampis_delicata	130100110031012010112−010010101110111200101120010120020122110200001021010201212000111100101−−020−−22
Pleotomodes_knulli	130100110031011010112−010010112110111101101110010120020121110200111021010101211100100000101−−010−−20
Pleotomus_pallens	130100110031010010112−010010112110111101101110010120020121110200111021010101211100100100111−−010−−20
Pristolycus_kanoi	120000010111311010112−0100001001101112001011100101000201221002000110210101012021001001011002−000−−1−

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Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Pristolycus_sagulatus	120000010111311010112-0100001001101112001011100101000201221002000110210001012021001001010002-000--1-
Pseudolychnuris_vittata	110000010031111010112-0100101023101112011012200101201201221002001111211102012121001101000001--010--22
Pyractomena_lucifer	130100110031111010112-0100101023101122011012200101201201221002001111211102012120001101001001--010--20
Pyractomena_striatella	130100110031111010112-0100101023101122011012200101201201221002001111210102012120001101001001--010--20
Pyractonema_obscura	110100110031111010112-0100101123101112011012200101201201221102001011211102012120001101001001--010--20
Pyrocoelia_analis	131100010031011010112-0000101021001112001011100101200201211102001110210101012111001001001001--010--20
Pyrocoelia_bicolor	131100010031010010112-0000101021001112001011100101200201211102001110211101012111001001001001--010--20
Pyrocoelia_formosana	131100010031011010112-0000101021001112001011100101200201211102000110210101012111001001001001--010--20
Pyrocoelia_praetexta	131100010031011010112-0000101021001112001011100101201201211102000110210101012111001202001001--010--20
Pyrocoelia_prolongata	110100010031011010112-0000101021001112001011100101200201211102000110210101012111001201001001--010--20
Pyropyga_fenestralis	110100110031110010112-0100101023101112011011200101201201221102001011211102012111001101001001--010--20
Pyropyga_nigricans	110100110031110010112-0100101023101112011011200101201201221102001011211102012110001101001001--010--20
Robopus_lengi	110100110021111010112-0100101021001112001011200101200201221002001010210102012121001101001001--010--20
Robopus_pantoni	110100110021111010112-0100101011001112001011200101201201221102001010220102012121001101001001--010--20
Robopus_quadrimaculatus	110100110021111010112-0100101021001112001011200101200201221002001010210102012121001100001001--010--20
Robopus_vittiger	110100110021111010112-0100101021101112011012200101201202221102001011211102012121001101001001--010--20
Roleta_notaticollis	112000110011110010112-0100101023001112011011200101201201221102001010210102012111001202001001--010--21
Rufolychnia_borencona	110000110021111010112-01001010110011??0????12?010110120122100200011021010201212000110100101--010--21

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Species	1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Satolampyris_dichroma	120100110131311010112−0100001000101101001111100101000101221002000010110001012021001001010002−000−−1−
Tenaspis_angularis	130100110031111010112−010010112310111200101120010120020121110200301021010201211100120200111−−010−−21
Tenaspis_figurata	130100110031111010112−010010112310111201101120010120120121110200101021010201212100110100101−−010−−20
Cheguevaria_taino	112001110031310010112−0100001011001112001011100101100101201102001110110110012 0?000110000101−−010—20

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Species	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Dascillus_cervinus	------0000--0200000-000-0001000000000000---000000000000000000010-000002001001000000000000000020000001000000010
Macropogon_testaceipennis	------0000---200000-0-0-0001000000000003---010000110200000150002-000101200000000000000000000000100000000000001
Brachypsectra_fulva	--10--0000---000000-0-0-0000000000000003---010000100100000100001-000000101100000000000000000000100011000000000
Drilus_flavescens	0010-11000--0100010-0-0-0000000000000001---000100510103000110012-000022101010000000000000000023100012010100000
Selasia_decipiens	000--12000--0000010-0-0-0001000100020002---010000220002000040014-000022000010000000000000000013100012000000000
Selasia_sp	000--12000--0100010-0-0-0000000000000001---000100510003000120012-000012101000000000000000000020100012000100000
Malacogaster_passerini	0010-11000--0100010-0-0-0001000000000004---000100520003000120012-000022101010000000000000000023100012000100000
Lycus_(Neolycus)_arizonensis	0111-21000--0300010-0-0-0000000100010105---0000022030---00002--002-------------------------------0001100000000
Lycostomus_sanguineus	0111-31000--0300010-0-0-0000000100010105---0000022030---00002--002-------------------------------0000101000000
Cautires_kazuoi	0011-31000--0300010-0-0-0000000100010105---000000210201000000021-010100200000000000000000000004200001000000004
Plateros_coracinus	0011-31000--0000010-0-0-0000000100010105---0000022030---00002--0000------------------------------0011100000000
Lyponia_delicatula	0010-11000--0300010-0-0-0000000100010105---000000210201000000021-010100200000000000000000000004200001000000004
Eropterus_nothus	0010-11000--0000010-0-0-0000000100010105---000000320200200110000-000130100000000000000000000003100011000000000
Xylobanus_niger	0011-31000--0000010-0-0-0001000100010105---0000042020---01002--002-------------------------------0010100000000
Omalisus_fontisbellaquei	000--12000--0000020-0-0-0001000000000001---000000000100000110003-000101000100000000000000000001000011000000000
Omethes_marginatus	000--12000--0000010-0-0-0001000000000002---000000120000010050000-000021201000000000000000000022000001000000001
Omethes_rugiceps	000--12000--0000010-0-0-0001000000000002---000000120000013050000-000021201000000000000000000022000001000000001
Troglomethes_leechi	000--12000--0000010-0-0-0001?00000020002---000000??0?0???????????000????0?000000000???????00?02???00?00000????

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Character number	00000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999901111111111
Species	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Malthomethes_oregonus	000--12000--0000010-0-0-0001000010000002---000000400101010030005-000001001000010000000000002000000001000000003
Drilonius_striatulus	000--12000--0000010-0-0-0001100000011002---0000006-000001005000-000021101000000000000000000220000010000000001
Matheteus_theveneti	000--12000--0000010-0-0-0001?000000200?????0???????0?0????????????000????010000000?????????00????????????0??????
Ginglymocladus_luteicollis	000--12000--0000010-0-0-0001000000020002---0000003100000200050001-0000212010000000000000000000002000001000000003
Phenogodes_frontalis	1010-12000--0000020-0-0-0013000000100003---110000200200000250003-000100110000000000000000000013100002010010002
Zarhipis_integripennis	0011-12000--0000020-0-0-0001000000100003---110000320200000250003-000100110000000000000000000013100002010010002
Cenophengus_debilis	0011-12000--0000030-0-0-0013000000000004---110000310101000100002-000180100000000000000000000010100001000010002
Distremocephalus_texanus	0010-12000--0000010-0-0-0011000000100003---010000500201000--2----000180100000010000000000000010100002000010002
Stenophrixothrix_sp	0010-11000--0100020-0-0-0001000000100004---010000500201000100000-000180100000000000000000000013000002010010000
Taximastinocerus_sp	0010-11000--0100020-0-0-0001000000100003---010000500101000--2----002180100000000000000000000010100002000010002
Telegeusis_nubifex	000--12000--0000010-0-0-0001000010130002---000100500202010230001-000101101000000000000000000010100012000000000
Pseudokarumia_angustata	000--12000--0000010-0-0-0000000010130002---000100500202010230001-000101101000000000000000000010100012000000000
Pterotus_obscuripennis	0011-31000--0000020-0-0-0001000000000006---010000120100000000000-000001010000000000000000000023100002010000000
Brachylampis_blaisdelli	000--12000--0000120-0-0-0000000100001006---010000220003000120010-000010101010000000000000000023000002000000000
Ceylandidrilus_bipartitus	0011-32000--0000030-0-0-0001000100011001---010000000002000040004-000122100010000000000010000000000002000000001
Ceylandidrilus_kandyanus	0011-32000--0000130-0-0-0001000100011006---010000110003010140012-000122101010000000000010000013000022000000000
Drilaster_auxillaris	000--12000--0000120-0-0-0001000100001001---010000220002000120010-000090101010000000000000000023000022000000000
Drilaster_weyersi	000--12000--1000130-0-0-0001000100001001---010000220002000120010-000020101000000000000000000010000002000000000

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Species	Character number
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	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Lamellipalpodes_annandalei	0011-32000--0000030-0-0-0001000100001004---0100004200020000200014-0001211010100000000000000000001010002200000000
Flabellotreta_fruhstorferi	0010-12000--0000120-0-0-0000000100021001---0100000200100000000010-000021100001000000000010000002100022000000000
Falsophaeopterus_fruhstorferi	000--12000--0000020-0-0-0000000000001004---0100003101000000220014-000001100100000000000000000002010000100000000
Gorhamia_krombeini	000--12000--0000130-0-0-0001000100001001---0100001100030001200010-000121101010000000000001000001310002200000000
Harmatelia_bilinea	000--12000--1000020-0-0-0000000000001001---0100002000030001200015-000121101010000000000001000002300002200000000
Mimophaeopterus_wittmeri	000--11000--0000130-0-0-0000000100021006---0100002200000001200014-000111101010000000000001000001300000200000000
Oculogryphus_fulvus	000--12000--0000020-0-0-0000000000001001---0100002200030001200012-000102100000000000000000000002300000200000000
Picodrilus_limbellus	000--12000--0000120-0-0-00000001000010?????0??
Stenocladius_rufithorax	000--12000--0000020-0-0-0001000100001002---0100002200020000400004-000022000010000000000000000001310001200000000
Stenocladius_bicoloripes	000--12000--1000020-0-0-0000000000001004---0100002201030001000005-000101100000000010000000000023000002000000000
Stenocladius_chinensis	000--12000--1000020-0-0-0000000000001004---0100002201030001000005-000101100000000010000000000023000002000000000
Stenocladius_sp	000--12000--1000020-0-0-0000000000001004---0100002201030001000005-000101100000000010000000000023000002000000000
Ototretadrilus_flavoscutellaris	000--12000--0000020-0-0-0000000000001001---0100002201000001200004-200000100000000000000010000020000002000100000
Dioptoma_adamsi	-----22000---100000-0-0-0000000000001004---1110001002010002000001-000101000000000000002000000000310001100000000
Diplocladon_hasselti	000--12000--0100020-0-0-0001000010130006---1000005000002000000003-000131100000000000002000000000310001200000000
Dodecatoma_bicolor	000--12000--0100020-0-0-0001000010130006---0000005000002001000003-000171100000000000002000000000310001100000000
Falsophrixothrix_humeralis	020--21000--0100020-0-0-0001000010130003---0100005000000200000005-001000100010000000000000000000300000200000000
Menghuoius_ingens	000--12000--0100020-0-0-0001000010130006---0000005000000000000003-000131000000000000002000000000000000100000000

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Species	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Menghuoius_giganteus	000--12000--0100020-0-0-0001000010130006---000000500000000000003-000131200000000000020000000000000001000000000
Monodrilus_marginatus	000--12000--0100020-0-0-0001000010130007---000000500100000000003-000171100000000000020000000004100002000000000
Ochotyra_semiusta	000--12000--0100020-0-0-0001000010130006---000000500000000030003-000131000000000000020000000003000001000000000
Rhagophthalmus_ohbai	000--12000--0100020-0-0-0001000010130006---000000500000010220004-000111100010000000020000000000000001000000000
Rhagophthalminae_ngen	000--12000--0100020-0-0-0001000010130007---000000500000200030003-000100200000000000020000000013000001000000000
Cyphonocerus_ruficollis	0010-12000--0000030-0-0-0000000100001006---010000520201000000013-000162111000000000000000000220100012000000000
Cyphonocerus_sanguineus	0010-12000--0000030-0-0-0001000100001006---010000520201000000013-000162111000000000000000000220100012000000000
Cyphonocerus_sylvicola	0010-12000--0000030-0-0-0001000100001006---010000520201000000013-000162111000000000000000000220100012000000000
Pollaclasis_bifaria	0010-12000--0000030-0-0-0000000100001006---010000520201000000013-000162111000000000000000000220100012000000000
Atyphella_lychnus	------00110--000000-0-0-201000010100101-01-011000310101000020012-000101100000000010000000000010000011000000000
Atyphella_carolinae	------00110--000000-0-0-001210010100101-01-011000510201000020014-000161100000000010000000000010100011010000020
Atyphella_obsoleta	------00114--000000-0-0-212530211103101-01-011000520201000111----000161100100000010000000100013000011000000000
Bougeoisia_antipoda	------00110--000000-0-0-00020011100310??????11000510001001021----000161100000000010000000000021100012000000000
Colophotia_brevis	------00111--000000-0-0-012630110100101-00-011000410201000110004-0002-0100000000000--0000010023200001000000000
Colophotia_praeusta	------00111--000000-0-0-012630110100101-00-011000410201000110004-0002-0100000000000--0000010023200001000000000
Curtos_obscuricolor	------00113--000000-0-0-000010011103101-00-012000520100000111----001101100001000010000000000010100012000000001
Hotaria_parvula	------00110--000000-0-0-200020010100101-00-011000100200000120014-000161110000000010000010000320010012000000001
Lampyroidea_dispar	------00110--000000-0-0-100020010100101-00-012000320002000121----000161100000000010000010000323010012000000001

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Species	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Lampyroidea_syriaca	------00114--000000-0-0-100020010100101-01-012000320002000121----000161100000000010000010000320100012000000001
Luciola_anceyi	------00110--000000-0-0-010230011103101-1-61100006-0000000110114-0002-0101001000010--00001000200000002000000020
Luciola_aquatica	------00112--000000-0-0-212230011103101-01-112000510002000120014-001161100001000010200000000020000012000000001
Luciola_cincticollis	------00213--000000-0-0-010031010100101-1-60110006-00020012202--70002-2100000000010--00000000200000002000000020
Luciola_curtithorax	------00110--000000-0-0-200030010100101-00-011000100200000220014-000161110000000010000010000320010002000000000
Luciola_filiformis	------00110--000000-0-0-201120010100101-00-111000100100000120014-000101100000000010000010000320010002000000000
Luciola_hydrophila	------00114--000000-0-0-000210011103101-01-0110006-0201000020114-001162100000000010000010100013110012000000000
Luciola_italica	------00110--000000-0-0-100020010100101-00-011000100200000120014-001161110000000010000010000320010012000000001
Luciola_kagiana	------00110--000000-0-0-200010010100101-00-1110006-0200000120014-000161110000000010000010000320010012000000001
Luciola_kuroiwai	------01110--000000-0-0-211110010100101-00-0110004202020001202--30002-0100001000020--0000010024200001000000000
Luciola_lustianica	------00110--000000-0-0-200020010102101-00-011000100200000120014-001161110000000010000010000320010012000000001
Luciola_ovalis	------00110--000000-0-0-212731011100101-02-1110005001010000002--2001101100000000010000010100020000002000000000
Luciola_peculiaris	------00116--000000-0-0-212530210100101-01-011000520201000110114-000101100000000010000000100013000001000000000
Luciola_substriata	------00112--000000-0-0-212230011103101-01-012000520002000120014-001161100001000010200000000020000012000000001
Luciola_trilucida	------01110--000000-0-0-211110010100101-00-011000420201000120014-0012-0100000000020--0000010023200001000000000
Pteroptyx_fulminea	------00110--000000-0-0-211630010100101-00-0110004202010001202--3000160100001000020000000000020200001001000000
Pteroptyx_cribella	------00110--000000-0-0-211630010100101-00-0110004202010001202--3000160100001000020000000000020200001001000000
Pygoluciola_satoi	------00113--000000-0-0-012531011103101-1061110002002000002-1----0011411000000000000020000100012000002000000020

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Species	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Pyrophanes_similis	------00115--000000-0-0-211630110100101-00-1110104202010001202--30002-0100001000020--0000010023200101000000000
Pyrophanes_appendiculata	------00115--000000-0-0-211630110100101-00-0110104202010001202--30002-0100001000020--0000010023200101000000000
Bicellonycha_deleta	102-202012-00200030-0-0-002500010002101-1-10100006-02010001002--2000161100000000000000000000000000001000000000
Bicellonycha_stigmatica	102-202012-00200030-0-0-202500010000101-1-10100006-02010000002--2000161100000000000000000000000000001000000000
Bicellonycha_sp	102-202012-00200030-0-0-202500010002101-1-10100006-02010001002--2000161100000000000000000000000000001000000000
Daiphoturis_apicalis	002-002012-00200030-0-0-0014000100001007---0100003002000002102--1000101100000000000011100000220000001000000000
Photuris_trilineata	102-102012-00200030-0-0-202500010002101-1-20100006-02010001002--1100151100000010000000000000223100001000000000
Photuris_sp	102-102012-00200030-0-0-202000010000101-1-20100006-02010001002--1100151100000010000000000000223100001000000000
Photurocantharis_sp	002-312012-00200030-0-0-0010000100021007---0100003002000002102--1000101100000000000011100000220000001000000000
Pyrogaster_coxalis	202-302042-40200030-0-0-0024000100021007---0100003002000002102--1000101100000000000011100000220000001000000000
Pyrogaster_lunifer	102-402012-00200030-0-0-0024000100001007---0100003002000001102--1000101100000000000011100000220000001000000000
Pyrogaster_malepictus	202-302042-40200030-0-0-0024000100021007---0100003002000002102--1000101100000000000011100000220000001000000000
Pyrogaster_mediofasciatus	102-212012-00200030-0-0-0010000100021007---0100003001000002102--1000101100000000000011100000223000001000000000
Amydetes_apicalis	000--22022-10012230-0-0-000400010100101-1-51100003002010000002--2000171100000000000000000000003000002000000001
Amydetes_fastigiatus	000--22022-1001223111111000400010100101-1-10100005001010010002--2000171100000000000000000000003000001000000000
Cladodes_flabellata	022-322000--101223131313001410010102101-1-0010000500201000000000-000131100000000000020000000003000001000000000
Cladodes_imperfectus	022-222000--102223131313001400010100101-1-1010000310201000000000-000131100000000000020000000001000001000000000
Cladodes_ater	022-122000--102223131313000410010100101-1-1110000500201000000000-000131100000010000020000000001000001000000000

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Species	Character number
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	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Dodacles_elegans	022-222000--102223131313000410010100101-1-10100005102010001002--2000131100000010000020000000011000001000000000
Dodacles_emissa	022-122000--102223131313000410010100101-1-10100003002010001002--2002131100000000000010000000010000001000000000
Dodacles_erebea	022-222000--102223131313000410010100101-1-10100005102010001002--2000131100000010000020000000011000001000000000
Dryptelytra_cayennensis	022-122000--102223131313001410010100101-1-01100003102010001002--2002131100000010000020000000011000001000000000
Dryptelytra_sp	022-122000--102223131313000410010100101-1-01100003102010001002--2002131100000010000020000000011000001000000000
Ethra_decorata	002-012032-30000130-1010001000010102101-1-00100006-12000002202--2000101100000000000000000000021000021000000000
Ethra_dejeani	000-012000--100113111111001410010100101-1-10100000012010012202--5000101100000000000000000000004200001000000000
Ethra_marginatus	000--12000--101123111111001410010102101-1-10100000012010012202--5000101100000000000000000000004200001000000000
Fenestracladodes_malleri	022-222000--102223131313001400010100101-1-1010000310201000000000-000131100000000000020000000010000001000000000
Ledocas_parallelus	022-322000--102223131313001410010102101-1-1110000310201000110000-002131100000000000010000000000000001000000000
Ledocas_sp	022-222000--102223131313001410010100101-1-1110000310201000000001-000131100000010000020000000011000001000000000
Magnoculus_sp_a	012-222000--000113111111000410010100101-1-0010000201100000220014-000171100000000000100010000023000002000000000
Magnoculus_sp_b	012-101000--000223131313000010010100101-1-0010000201100000220014-000131100000000000100010000023000002000000000
Psilocladus_miltoderus	0010-12030--000013101010000010010102101-1-40100005002010001002--2000141100000000000000000000010000002000000000
Psilocladus_nevermanni	0010-12000--000013101010000010010102101-1-40100005002010001002--2000141100000000000000000000010000002000000000
Scissicauda_disjuncta	0210-00000--100123131313001810110100101-1-10100005102000002002--2000181000000000000000000000011000001000000000
Vesta_chevrolatii	022-312000--102223131313000400010102101-1-41100006-02010001102--2000141100001000100000000000013200001000000000
Vesta_impressicollis	022-322000--101113131313000400010102101-1-41100006-02010001202--2000141100001000100000000000013200001000000000

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Character number	00000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999901111111111
Species	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Vesta_rufiventris	022-312000--102223131313000400010102101-1-41100006-02010001102--2000101100001001100000000000013200001000000000
Vesta_arcta	012-222000--1001230-1111000400010102101-1-41100001-02010001102--2000101100001000100000000000013200001000000000
Vesta_cincticollis	0011-10032-30000130-1111001210011101101-1-81100005012001012102--5002161100000000000000000000021000002000000000
Vesta_thoracica	012-212000--1000130-1111000400010102101-1-41100006-02010001102--2000101100001000100000000000013200001000000000
Afrodiaphanes_marginipennis	0010-10000--102223101010000410030100101-1-11100004211000001102--6000161100000000000100000000010100010000000000
Alecton_discoidalis	0010-10000--120223101010000010010100101-1-00100000112000012102--8000101000000000000100000000012100022000000000
Aspisoma_aegrotum	0010-22012-0120123101010000000010100101-1-00100000112000002102--6002101100000000000200000000021000022000000000
Aspisoma_ignita	0010-22012-0120123101010000000010100101-1-00100000112000002102--6002101100000000000200000000021000022000000000
Aspisoma_physonotum	0010-22012-0120123101010000000010100101-1-00100000112000002102--6002101100000000000200000000021000022000000000
Callopisma_rufa	002-422000--101223101010000400010102101-1-41100006-12010001002--2000141100001000200000000000013200001000000000
Calyptocephalus_sp	212-500000--021223141414001400030100101-1-01100002212000012202--6000171100000000000000010000024000012000000000
Cratomorphus_signativentris	0010-10052-5030222101010000000010100101-1-10100001012000002002--6000101100000000000200000000000000022000000000
Dadophora_hyalina	002-222000--031113111111000010010102101-1-01100003012000002102--6000101100000000000000000000021000002000000000
Diaphanes_citrinus	0010-00022-1031223101113000410030100101-1-11100005112000001102--8000111100000000000200000000014000002010000000
Diaphanes_formosus	0010-00022-1031223131313000410030101101-1-11100005012000002102--8000161100000000000000000000010100012000000000
Diaphanes_lampyroides	0010-00022-1032223131313001410030100101-1-11100005112000002102--8000161100000000000200000000013101102010000000
Diaphanes_nubilus	0010-00022-1032223141414001410030100101-1-11100005112000011102--8000101100000000000300000000000100112000000000
Diaphanes_schoutedeni	0010-10000--122222101010000410030100101-1-11100005112000012102--8000161100000000000200000000010101012000000000

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Character number	00000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999901111111111
Species	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Dilychnia_apicalis	002-322032-30001230-1010000400010102101-1-41100006-02000001002--2000141100001000200000000000013200001000000000
Dilychnia_ruficollis	002-322032-30001230-1010000400010102101-1-41100006-02000001002--2000141100001000200000000000013200001000000000
Ellychnia_corrusca	0011-22000--0000130-1010001110010102101-1-0010001110212000200004-000101100000100000000000000011000101100000100
Ellychnia_moesta	0011-22000--0001130-1010001410010102101-1-1010001110213000200002-000101100000100000000000000010000001200000100
Erythrolychnia_fulgida	0010-00030--0001220-0-0-000410010102101-1-0010000??01000011102--6000181100001000000200000000011000021001000000
undet._gen	002-200000--100122111111000410010102101-1-00100000201000011102--8000101100000000000200000000001000002001000000
Lamprigera_boyei	002-013000--102223131313000300000102101-1-51000005122000002202--6000171101000000000000000000003100011010000000
Lamprigera_yunnana	002-013000--102223131313000300000102101-1-51000005122000002202--6000171101000000000000000000003100011010000000
Lamprocera_tristior	0011-22030--020223121212000400020102101-1-30100003012000012202--6000101100000020000200000000023100112000000000
Lamprohiza_delarouzei	002-412022-10012231313130003000100001004---110000300100000120011-000101100000000000000000000013100012000000000
Lamprohiza_splendidula	002-412022-10012231313130003000100001004---110000300100000120011-000101100000000000000000000013100012000000000
Lampronetes_mauritanica	0010-10000--101113131313000000030102101-1-11100005112000002102--5000101100000000000300000000010101002000000000
Lampyris_noctiluca	0010-10000--101223111111000010020100101-1-11100005111000002102--6000101100000000000300000000010101002000000000
Lampyris_algerica	0010-10000--101223111111000010020100101-1-11100005111000002102--6000101100000000000300000000010101002010000000
Lucernuta_savignii	0011-12022-1002223121212000410030100101-1-11100003112000011002--6000101100000000000100000000010100012010000000
Lucidina_accensa	022-322000--101123131313001410010100101-1-11100006-12010012502--4000161100000000000000001100011200101300001000
Lucidina_vitalisi	022-322000--101123131313001410010100101-1-11100006-12010012502--4000161100000000000000001100010200001300001000
Lucidina_gracilis	022-322000--101123111111001410010100101-1-10100006-12010012502--4000151100000000000000001100010200001300001000

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Character number	00000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999901111111111
Species	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Lucidota_atra	022-322000--101123111111001410010100101-1-11100006-12010012502--4000161100000000000000001100011200001300001000
Lucidota_banoni	002-022000--1011130-1010000410010102101-1-01100002001000002102--6000121100000000000000000000110200001100000100
Lucidota_bella	012-322000--101113111111000410010102101-1-41100006-12010002002--5000141100001010000000000000013200001000000000
Lucidota_comitata	0010-22000--101113101010000410010102101-1-00100005012000012102--6000161100100000000000000000000100002000000000
Lucidota_pennata	002-022000--101113101010000410010102101-1-01100002001000002102--6000121100000000000000000000110200001100000100
Lucidota_pygidialis	002-012000--101123111114001410010102101-1-01100001112000012202--5000161100000000000000000000004200001000000000
Lucidotopsis_cruenticollis	022-322000--101123131313001410010100101-1-11100006-12010012502--4000161100000000000000001100010200001300001000
Lucio_abdominale	002-022000--120123121212002310020100101-1-30100003012000002102--6000101100000020000200000000023100012000000000
Lucio_obscura	002-022000--120123121212002310020100101-1-30100003012000002102--6000101100000020000200000000023100012000000000
Lychnacris_flabellata	0011-20000--021113131313002410020100101-1-31100003012000012102--5000181100000020000000000000002100002200000000
Macrolampis_acicularis	0010-12000--0000030-0-0-001000010102101-1-00100003011000001002--6000101100000001000000000000023000002000000000
Macrolampis_longipennis	0010-12012-00000030-0-0-001010010100101-1-0010000101212000200002-0001010000000000000000000000010000001000000200
Macrolampis_omissa	0010-12012-01000030-0-0-000010010100101-1-0010000101200000100002-0001011000000000000000000000010000001000000200
Macrolampis_perelegans	0010-12012-00000030-0-0-000010010100101-1-0010000301113000100004-0001211000000100000000000000010000121100000200
Microphotus_angustus	002-312000--1002230-1010200410020100101-1-11100005111001010002--8000101100000000000300000000010100012000000000
Microphotus_dilatatus	002-312000--1002230-1010200410020100101-1-11100005111001010002--8000101100000000000300000000010100012000000000
Microphotus_octarthrus	002-312000--1001230-1010201410020100101-1-11100005111001010002--8000101100000000000300000000010100012000000000
Mimophotinus_angustatus	022-322000--101123111111001410010100101-1-10100006-12000002502--4000161100000000000000001000010200001300001000

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Character number	00000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999901111111111
Species	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Nyctophila_reichii	002-212000--1022231313132004100301001 01-1-1110000511200000210 2--5000101100000000000300000000010101002000000000
Ophoelis_impura	022-520000--101223131313001410030101101-1-0110000521200001 2202--7000171100001000000000010000240000120000000000
Paraphausis_eximia	002-212000--0001230-0-110014000201001 01-1-0010000511200000 1002--6000101100000001000100000000131000120000000000
Petalacmis_praeclarus	0010-22032-200122314141400141003010 0101-1-7010000??0100001 1002--6000111100000001000000000000000000002000000000
Phaenolis_laciniatus	112-502000--002223141414000400031103101-1-0010000221200001 2202--6000171100000000000000001000002400001200000000
Phaenolis_bicoloripes	112-502000--0022231414140004100311 03101-1-0010000221200001 2202--6000171100000000000000001000002400001200000000
Phausis_reticulata	002-412022-10012231313130003100100001004---110000300100000120010-0001011000000000000000000000101000120000000000
Phosphaenopterus_metzneri	002-022000--1012231313130014100101001 01-1-1010000511201000 2102--5000161100000000001000001000011100001000001000
Phosphaenus_hemiptera	002-022000--1012231111110014100101001 01-1-1010000511201000 2102--5000161100000000001000001000011100001000001000
Photinus_maritimus	0010-12012-00000130-0-0-001210010102101-1-10100013002130002 00004-0001211000000000000000000000110000011000000200
Photinus_extensus	0010-12012-00000130-0-0-000410010102101-1-11100013012130002 00002-0001211000000000000000000000110000011000000100
Photinus_pallens	0010-12012-00000130-0-0-001210010102101-1-11100003012020002 00006-0001011000000000000000000000110000021000000000
Photinus_pyralis	0010-12012-00000130-0-0-000210010102101-1-11100013012130002 00002-0001211000000000000000000000110000011000000100
Platylampis_latiuscula	0110-02000--10122313141400141001010 2101-1-10100005012020102 40000-0001310000000100000000000020002000011000000000
Platylampis_delicata	0011-320?2-2101113131414000410020102101-1-0010000501202000 1202--6000101100000020000000000000210000220000000000
Pleotomodes_knulli	0010-10000--101223101010000010030100101-1-11100005112020002 202--6000101100000000000100000000010100012000000000
Pleotomus_pallens	0010-10000--1022231313130004100301001 01-1-1110000401200000 2102--6000101100000000000100000000010100012000000000
Pristolycus_kanoi	-----00000---000000-0-0-001120010102101-01-1110005202010001 002--2000140100000000010000000100003000002000000000

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Character number	00000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999901111111111
Species	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Pristolycus_sagulatus	-----00000---000000-0-0-000120010102101-01-1110005102010002002--2000140100000000010000000100003000001000000000
Pseudolychnuris_vittata	0011-12000--001223101111000400010102101-1-0110000401202001202--6000161100100000000000000000000100002000100000
Pyractomena_lucifer	0010-12012-01000030-0-0-000410010102101-1-10100005002030002002--8000101000000000000000000000000001201000000
Pyractomena_striatella	0010-12012-01000030-0-0-000410010102101-1-10100005002030002002--8000101000000000000000000000000001201000000
Pyractonema_obscura	002-022000--001113111111001410010102101-1-00100015112000001002--5000101000100000000000000002021000001201000000
Pyrocoelia_analis	0010-00022-1002223131313000410030100101-1-11100005112000001102--80001011000000000000100000000010100002000000000
Pyrocoelia_bicolor	0010-00022-1002223131313000410030100101-1-11100005112000001102--8000101100000010000100000000010100002000000000
Pyrocoelia_formosana	0010-00000--102223131313000410030100101-1-11100005112000001102--80001011000000000000100000000010100002000000000
Pyrocoelia_praetexta	0010-00022-1002223131313000410030100101-1-11100005112000001102--80001011000000000000100000000010100002000000000
Pyrocoelia_prolongata	0010-00000--102223131313000410030100101-1-11100005112000001102--80001011000000000000100000000010100002000000000
Pyropyga_fenestralis	0011-22000--000013111111001410010102101-1-0110001501202010250004-000161100000000000200100001020100011000000000
Pyropyga_nigricans	0011-22000--000013111111001410010102101-1-1110001501202010250004-000161100000000000200100001020100011000000000
Robopus_lengi	0010-22000--2001231111111000010010100101-1-10100003002000011102--6000101100000000000200000000001100001000000000
Robopus_pantoni	000--12000--200123101111000010010102101-1-00100003002020001002--600016110000000000000000000011100002000000000
Robopus_quadrimaculatus	000--12000--200003111111000010010100101-1-10100003002000011102--6000101100000000000200000000001100001000000000
Robopus_vittiger	0011-32000--2000030-0-0-001210010100101-1-1010000300202000200004-000121000000000000000000000011000001100000100
Roleta_notaticollis	112-510000--102223131313001410031103101-1-5110000221102001220014-000171100000000000000010100024100112000000000
Rufolychnia_borencona	0010-12000--2000130-1414001200210102101-1-31100005002030002202--5000101100001000000400000000020000002001000000

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Character number	00000000011111111112222222222333333333344444444445555555555666666666677777777778888888888999999999901111111111
Species	12345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901234567890
Satolampyris_dichroma	-----000616--000000-0-0-001020010102101-01-0100001202010000002--2001101100000000010000000100000000002000000000
Tenaspis_angularis	102-630000--001223111112001310020102101-1-10100005012030002102--2000181100000020000000000000020000001000000000
Tenaspis_figurata	0010-22000--001123111112000400120100101-1-10100001012020011102--6000101100000020000200000000003100021000000000
Cheguevaria_taino	012-232000--0000130-0-0-002510010000101-1-00100006-0200000210002-000101100000000000000010000023100002000000000

(End)

Appendix V. Neotenic states of females in our material

Dascillidae	
Dascillus_cervinus	0
Artematopodidae	
Macropogon_testaceipennis	0
Brachypsectridae	
Brachypsectra_fulva	0
Drilidae	
Drilus_flavescens	5
Selasia_decipiens	?
Selasia_sp	?
Malacogaster_passerini	(5)
Lycidae	
Lycus_(Neolycus)_arizonensis	0
Lycostomus_sanguineus	0
Cautires_kazuoi	0
Plateros_coracinus	0
Lyponia_delicatula	0
Eropterus_nothus	0
Xylobanus_niger	0
Omalisidae	
Omalisus_fontisbellaquei	1
Omethes_marginatus	0
Omethes_rugiceps	0
Troglomethes_leechi	0
Malthomethes_oregonus	0
Drilonius_striatulus	0
Matheteus_theveneti	0
Ginglymocladus_luteicollis	0
Phengodidae	
Phenogodes_frontalis	(8)
Zarhipis_integripennis	(8)
Cenophengus_debilis	?
Distremocephalus_texanus	?
Stenophrixothrix_sp	?
Taximastinocerus_sp	?
Telegeusidae	
Telegeusis_nubifex	?
Pseudokarumia_angustata	?
Rhagophthalmidae	
Dioptoma_adamsi	?
Diplocladon_hasselti	?
Dodecatoma_bicolor	?
Falsophrixothrix_humeralis	?
Menghuoius_ingens	?
Menghuoius_giganteus	?
Monodrilus_marginatus	?
Ochotyra_semiusta	?
Rhagophthalmus_ohbai	7
Rhagophthalminae_n.gen.	?
Lampyridae	
Pterotinae	
Pterotus_obscuripennis	(7)
Ototretinae & Ototretadrilinae	
Brachylampis_blaisdelli	0
Ceylandidrilus_bipartitus	?
Ceylandidrilus_kandyanus	?
Drilaster_auxillaris	0
Drilaster_weyersi	0
Lamellipalpodes_annandalei	?
Flabellotreta_fruhstorferi	?
Falsophaeopterus_fruhstorferi	?
Gorhamia_krombeini	?
Harmatelia_bilinea	?
Mimophaeopterus_wittmeri	?
Oculogryphus_fulvus	?
Picodrilus_limbellus	?
Stenocladius_rufithorax	?
Stenocladius_bicoloripes	7
Stenocladius_chinensis	?
Stenocladius_sp	?
Ototretadrilus_flavoscutellaris	?
Cyphonocerinae	
Cyphonocerus_ruficollis	0
Cyphonocerus_sanguineus	0
Cyphonocerus_sylvicola	0
Pollaclasis_bifaria	0
Luciolinae	
Pristolycus_kanoi	0
Pristolycus_sagulatus	0
Satolampyris_dichroma	?
Atyphella_lychnus	(1)
Atyphella_carolinae	?
Atyphella_obsoleta	0
Bougeoisia_antipoda	?
Colophotia_brevis	0
Colophotia_praeusta	0
Curtos_obscuricolor	0
Hotaria_parvula	1
Lampyroidea_dispar	2
Lampyroidea_syriaca	2
Luciola_anceyi	0
Luciola_aquatica	0
Luciola_cincticollis	0
Luciola_curtithorax	0
Luciola_filiformis	2
Luciola_hydrophila	0
Luciola_italica	1
Luciola_kagiana	0
Luciola_kuroiwai	0

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Luciola_lustianica	1
Luciola_ovalis	0
Luciola_peculiaris	0
Luciola_substriata	0
Luciola_trilucida	0
Pteroptyx_fulminea	0
Pteroptyx_cribella	0
Pygoluciola_satoi	0
Pyrophanes_similis	0
Pyrophanes_appendiculata	0
Photurinae	
Bicellonycha_deleta	0
Bicellonycha_stigmatica	0
*Bicellonycha*_sp	0
Daiphoturis_apicalis	0
Photuris_trilineata	0
*Photuris*_sp	0
*Photurocantharis*_sp	0
Pyrogaster_coxalis	0
Pyrogaster_lunifer	0
Pyrogaster_malepictus	0
Pyrogaster_mediofasciatus	0
Amydetinae	
Amydetes_apicalis	?
Amydetes_fastigiatus	?
Cheguevarinae	
Cheguevaria_taino	?
Magnoculus_sp_a	?
Magnoculus_sp_b	?
Psilocladinae	
Psilocladus_miltoderus	0
Psilocladus_nevermanni	0
Lampyrinae	
Cladodes_flabellata	?
Cladodes_imperfectus	?
Cladodes_ater	?
Dodacles_elegans	?
Dodacles_emissa	?
Dodacles_erebea	?
Dryptelytra_cayennensis	?
Dryptelytra_sp	?
Ethra_decorata	0
Ethra_dejeani	?
Ethra_marginatus	0
Fenestracladodes_malleri	?
Ledocas_parallelus	?
Ledocas_sp	?
Scissicauda_disjuncta	?
Vesta_chevrolatii	0
Vesta_impressicollis	0
Vesta_rufiventris	0
Vesta_arcta	0
Vesta_cincticollis	?
Vesta_thoracica	0
Afrodiaphanes_marginipennis	?
Alecton_discoidalis	0
Aspisoma_aegrotum	0
Aspisoma_ignita	0
Aspisoma_physonotum	0
Callopisma_rufa	0
Calyptocephalus_sp	?
Cratomorphus_signativentris	0
Dadophora_hyalina	?
Diaphanes_citrinus	4
Diaphanes_formosus	3
Diaphanes_lampyroides	4
Diaphanes_nubilus	3
Diaphanes_schoutedeni	4
Dilychnia_apicalis	0
Dilychnia_ruficollis	0
Ellychnia_corrusca	0
Ellychnia_moesta	0
Erythrolychnia_fulgida	0
undet._gen	?
Lamprigera_boyei	5
Lamprigera_yunnana	5
Lamprocera_tristior	0
Lamprohiza_delarouzei	3
Lamprohiza_splendidula	3
Lampronetes_mauritanica	4
Lampyris_noctiluca	4
Lampyris_algerica	3
Lucernuta_savignii	0
Lucidina_accensa	0
Lucidina_vitalisi	0
Lucidina_gracilis	?
Lucidota_atra	0
Lucidota_banoni	0
Lucidota_bella	0
Lucidota_comitata	0
Lucidota_pennata	0
Lucidota_pygidialis	0
Lucidotopsis_cruenticollis	0
Lucio_abdominale	0
Lucio_obscura	0
Lychnacris_flabellata	0
Macrolampis_acicularis	?
Macrolampis_longipennis	0
Macrolampis_omissa	0

(Continues on next page)

Macrolampis_perelegans	4	*Phausis_reticulata*	(5)	*Pseudolychnuris_vittata*	1	*Robopus_lengi*	2
Microphotus_angustus	6	*Phosphaenopterus_metzneri*	?	*Pyractomena_lucifer*	0	*Robopus_pantoni*	0
Microphotus_dilatatus	?	*Phosphaenus_hemiptera*	(4)	*Pyractomena_striatella*	0	*Robopus_quadrimaculatus*	?
Microphotus_octarthrus	?	*Photinus_maritimus*	0	*Pyractonema_obscura*	0	*Robopus_vittiger*	0
Mimophotinus_angustatus	?	*Photinus_extensus*	1	*Pyrocoelia_analis*	3	*Roleta_notaticollis*	?
Nyctophila_reichii	4	*Photinus_pallens*	0	*Pyrocoelia_bicolor*	?	*Rufolychnia_borencona*	0
Ophoelis_impura	?	*Photinus_pyralis*	0	*Pyrocoelia_formosana*	4	*Tenaspis_angularis*	0
Paraphausis_eximia	?	*Platylampis_latiuscula*	?	*Pyrocoelia_praetexta*	3	*Tenaspis_figurata*	0
Petalacmis_praeclarus	?	*Platylampis_delicata*	?	*Pyrocoelia_prolongata*	4		
Phaenolis_laciniatus	?	*Pleotomodes_knulli*	(3)	*Pyropyga_fenestralis*	0		
Phaenolis_bicoloripes	?	*Pleotomus_pallens*	(3)	*Pyropyga_nigricans*	0		

Notes: neotenic level was assigned to each species according to the modified classification of Cicero (1988). Number in parenthesis refers to a literature-based assignment. The mark “?” indicated no female specimen or related information