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Research

Molecular Phylogenetics, Phylogenomics, and Phylogeography

Higher-Level Phylogeny and Reclassification of Lampyridae (Coleoptera: Elateroidea)

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Abstract

Fireflies (Lampyridae Rafinesque) are a diverse family of beetles which exhibit an array of morphologies including varying antennal and photic organ features. Due in part to their morphological diversity, the classification within the Lampyridae has long been in flux. Here we use an anchored hybrid enrichment approach to reconstruct the most extensive molecular phylogeny of Lampyridae to date (436 loci and 98 taxa) and use this phylogeny to evaluate the higher-level classification of the group. None of the currently recognized subfamilies were recovered as monophyletic with high support. We propose several classification changes supported by both phylogenetic and morphological evidence: 1) *Pollaclasis* Newman, Vestini McDermott (incl. *Vesta* Laporte, *Dodacles* Olivier, *Dryptelytra* Laporte, and *Ledocas* Olivier), *Photoctus* McDermott, and *Araucariocladus* Silveira & Mermudes are transferred to Lampyridae *incertae sedis*, 2) Psilocladinae Mcdermott, 1964 *status novum* is reestablished for the genus *Psilocladus* Blanchard, 3) Lamprohizini Kazantsev, 2010 is elevated to Lamprohizinae Kazantsev, 2010 *status novum* and *Phausis* LeConte is transferred to Lamprohizinae, 4) *Memoan* Silveira and Mermudes is transferred to Amydetinae Olivier, and 5) *Scissicauda* McDermott is transferred to Lampyrinae Rafinesque.

Key words: Firefly, phylogenomics, target capture, Amydetinae, Lamprohizinae

Fireflies (Lampyridae Rafinesque, 1815) are a cosmopolitan group of beetles with approximately 2,200 species (Branham 2010) and a varied and confounded history of classification (Olivier 1907, 1910a; Green 1959; McDermott 1966; Crowson 1972; Nakane 1991; Jeng 2008). Higher-level firefly classification schemes (e.g., Olivier 1907) have traditionally been framed in the context of morphological structures related to the production and detection of sexual signals (e.g., photic organs, eyes, and antennae). The morphological evolution of these features appears to have been driven by species-specific sexual communication, such as pheromones, glows, and flashes (Buck 1937, Lloyd 1971, Ohba 1983, Branham and Wenzel 2003, Stanger-Hall and Lloyd 2015, Stanger-Hall et al. 2018). Recent work suggests that bioluminescent sexual signals have evolved multiple times during firefly evolution and have been repeatedly lost, with a likely reversal to the use of pheromones for a sexual signal (Branham and Wenzel 2003, Stanger-Hall et al. 2007, Martin et al. 2017). Therefore, morphologies related to these signals (production/reception) may represent instances of convergent evolution and the continued dependence on these morphologies to support firefly classification and taxonomy (Branham and Wenzel 2003) needs to be reconsidered.

The first catalogue of Lampyridae was authored by Ernst Olivier in 1907 and updated in 1910. In this initial taxonomic effort, Olivier included 9 subfamilies (based almost entirely on antennal morphology) and approximately 1,000 species. Drawing on the earlier work of Green (1948, 1959), McDermott (1964) rearranged the taxa into seven subfamilies and added a tribal classification for the Lampyrinae. However, he noted that his classification, while logical, did not reflect phylogeny and was 'more or less arbitrary', as it relied heavily on characters such as antennae and photic organ

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morphology. This work leads to McDermott's (1966) supplement to the Olivier catalogue. Since McDermott, there have been two revised classification schemes for Lampyridae (Crowson 1972, Nakane 1991; see Table 1). The classification of the family by Crowson (1972) was incomplete as it did not include all lampyrid genera, and the work of Nakane (1991; published in Japanese) has largely been overlooked by current taxonomic workers. Recent phylogenetic efforts have provided deeper insight into the classification of fireflies by expanding morphological data sets (Branham and Wenzel 2001, 2003, Jeng 2008); molecular data sets (Stanger-Hall et al. 2007); or both (Martin et al. 2017). All of these studies highlighted the need to update the higher-level classification of this group within a phylogenetic framework. While focused on the evolution of specific traits, each of these studies recovered nonmonophyly of at least one subfamily. We are presenting here the first classification of Lampyridae that uses extensive taxon sampling and explicitly takes phylogenetic history into account.

Materials and Methods

Taxon Sampling

Our ingroup sample included 53 (of ~145) lampyrid genera and 88 species, representing seven of the eight subfamilies Sensu Nakane 1991 (Table 2). However, the Ototretadrilinae has since been synonymized under the Ototretinae (Janisova and Bocakova 2013). DNA-grade material for the Cheguevarinae was not available. The appropriate sister taxon to Lampyridae has been a topic of debate (Branham and Wenzel 2001, 2003, Stanger-Hall et al. 2007, Jeng 2008, Bocakova et al. 2007, Kundrata et al. 2014, Martin et al. 2017); therefore, 10 outgroup taxa from several closely related elateroid families were sampled: Omethidae, Eucnemidae, Cantharidae, Lycidae, Elateridae, Rhagophthalmidae, and Phengodidae (Table 2).

DNA Extraction

Specimens were collected in the field, preserved in 95% ethanol and stored at – 80°C for long-term storage. Each specimen was independently identified by at least two coauthors. Muscle tissue was removed from a single metacoxae, when possible, for each specimen. In some instances, the small size of the specimen necessitated more of the specimen to be used. DNA was then extracted using a Qiagen DNeasy extraction kit. DNA samples were sent to the Center for Anchored Phylogenomics at Florida State University, Tallahassee, FL for anchored hybrid enrichment sequencing. The specimens and remaining DNA samples were deposited as vouchers in the BYU Insect Genomics Collection in the Monte L. Bean Museum (BYU) of Natural History, Provo, UT, USA, the Lampyridae cryo-collection in the Stanger-Hall lab (UGA), Athens, GA, and the Coleção Entomológica Prof. José Alfredo Pinheiro Dutra, Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (DZRJ); see Table 2.

Table 1. Comparison of major classification schemes in Lampyridae

Olivier 1910	McDermott 1966	Crowson 1972	Nakane 1991
Amydetinae	Amydetinae	Amydetinae	Amydetinae
Luciolinae	Luciolinae	Luciolinae	Luciolinae
Photurinae	Photurinae	Photurinae	Photurinae
Lampyrinae	Lampyrinae	Lampyrinae	Lampyrinae
Dadophorinae			
Lamprocerinae			
Photininae			
Lucidotinae			
Megalophthalminae			
	Pterotinae	Pterotinae	Pterotinae
	Matheteinae		
	Rhagophthalminae		
		Ototretinae	Ototretinae
		Cyphonocerinae	Psilocladinae
		Ototretadrilinae	Ototretadrilinae

Probe Design

In collaboration with the Center for Anchored Phylogenomics (www.anchoredphylogeny.com), an AHE kit representing the diversity of Lampyridae was developed, targeting a subset of the low-copy AHE 941 loci (exons) that Haddad et al. (2018) developed for Coleoptera. To this end, genomic resources, assembled genomes, assembled transcriptomes, and unassembled low-coverage genomic reads (unpublished data, Kathrin Stanger-Hall (K.S.H.); see Supp Table 1 [online only] for details), for 14 species of Lampyridae were gathered. In order to collect the low coverage genomic reads, Illumina libraries were prepared following Lemmon et al. (2012) and each was sequenced at 5× coverage on an Illumina HiSeq 2500 with a 150bp paired-end protocol with an 8-bp indexing read. After demultiplexing with no mismatches tolerated, overlapping reads were merged following Rokyta et al. (2012).

Target regions appropriate for Lampyridae were identified by following the general methodologies described in Hamilton et al. (2016). The assembled genomes and transcriptomes were scanned using all of the 941 *Tribolium castaneum* reference sequences developed by Haddad et al. (2018). After reads were mapped and extended to the same references, the reads were extended up to 2,000 bp in each direction to produce longer sequences. The resulting sequences were then aligned in Mafft v. 7.407 (Katoh and Standley 2013) and visually inspected in Geneious. Well-aligned regions were selected for downstream analysis. Of the 941 beetle exons identified by Haddad et al. (2018), only 586 regions of >180 bp in which at least 16 of 19 taxa were present were identified. Seventy overlapping loci were removed. Repetitive regions were masked using analyses of kmer distributions (see Hamilton et al. 2016 for details).

The final target regions were comprised of 516 target loci covering 578,322 bp. Probes were tiled at 2× coverage across each of the 19 lineages represented in the alignments. After removing redundant probes, 56,979 probes were submitted to Agilent Technologies for synthesis (SureSelect XP kit).

Library Preparation

From extracted DNA, libraries with standard Illiumina adapters were prepared following Lemmon et al. (2012) and Prum et al. (2015) using a Beckmann Coulter FXp liquid-handling robot. After adding 8 bp indexes, libraries were pooled in groups of ~16 and enriched using the Lampyridae-specific enrichment kit described above. Enriched library pools were then pooled and sequenced on three Illumina 2500 sequencing lanes with C-bot clustering and a paired-end 150 bp protocol (~100 Gb of raw data were collected).

Read Assembly and Orthology Assessment

Raw reads passing the CASAVA high-chastity filter were merged following Rokyta et al. (2012) and assembled using the quasi-de novo approach described by Hamilton et al. (2016), with probe region sequences from *Phausis reticulata*, *Pyractomena borealis*, *Photinus pyralis*, *Photinus scintillans*, *Phausis reticulata* and a soldier beetle (Cantharidae), serving as references. Assembly clusters derived from less than 42 reads were removed from downstream analyses in order to

Table 2. Taxa included in current study

Code	Family	Subfamily	Species	Coll.
CO1548	Cantharidae		Cantharidae sp. 1	BYU
KSH_12271	Cantharidae		Cantharidae sp. 2	UGA
CO1310	Elateridae		*Ampedus pomonae*	BYU
CO1077	Elateridae		*Pyrophorus* sp.	BYU
CO1309	Eucnemidae		*Microrhagus pygmaeus*	BYU
CO1545	Lycidae		*Calopteron reticulatum*	BYU
CO1286	Omethidae		*Telegeusis nubifer*	BYU
CO1544	Phengodidae		*Phengodes* sp.	BYU
CO1285	Phengodidae		*Zarhipis integripennis*	BYU
CO1304	Rhagophthalmidae		*Rhagophthalmus ohbai*	BYU
CO1212	Lampyridae	Amydetinae	*Amydetes fastigiata*	DZRJ
CO1211	Lampyridae	Amydetinae	*Cladodes illigeri*	DZRJ
CO1213	Lampyridae	Amydetinae	*Ethra axillaris*	DZRJ
CO1214	Lampyridae	Amydetinae	*Memoan ciceroi*	DZRJ
CO1216	Lampyridae	Amydetinae	*Psilocladus sigillatus*	DZRJ
CO1245	Lampyridae	Amydetinae	*Psilocladus* sp. 1	BYU
CO1218	Lampyridae	Amydetinae	*Psilocladus* sp. 2	BYU
CO1215	Lampyridae	Amydetinae	*Scissicauda disjuncta*	DZRJ
CO1305	Lampyridae	Amydetinae	*Vesta impressicollis*	BYU
CO1299	Lampyridae	Amydetinae	*Vesta saturnalis*	BYU
CO1219	Lampyridae	Amydetinae	*Vesta* sp.	BYU
CO1281	Lampyridae	Cyphonocerinae	*Pollaclasis bifaria*	BYU
CO1069	Lampyridae	Lampyrinae	*Aspisoma* sp.	BYU
CO1233	Lampyridae	Lampyrinae	*Aspisoma sticticum*	BYU
CO1234	Lampyridae	Lampyrinae	*Cratomorphus* sp.	BYU
CO1292	Lampyridae	Lampyrinae	*Diaphanes pectinealis*	BYU
CO1223	Lampyridae	Lampyrinae	*Diaphanes* sp. 1	BYU
CO1516	Lampyridae	Lampyrinae	*Diaphanes* sp. 2	BYU
CO1524	Lampyridae	Lampyrinae	*Diaphanes* sp. 3	BYU
CO1523	Lampyridae	Lampyrinae	*Diaphanes* sp. 4	BYU
KSH_6091	Lampyridae	Lampyrinae	*Ellychnia corrusca*	UGA
CO1197	Lampyridae	Lampyrinae	*Ellychnia* sp.	BYU
CO1067	Lampyridae	Lampyrinae	*Heterophotinus* sp.	BYU
CO1294	Lampyridae	Lampyrinae	*Lamprigera yunnana*	BYU
CO1060	Lampyridae	Lampyrinae	*Lamprocera* sp. 1	BYU
CO1459	Lampyridae	Lampyrinae	*Lamprocera* sp. 2	BYU
CO1457	Lampyridae	Lampyrinae	*Lamprocera* sp. 3	BYU
CO1231	Lampyridae	Lampyrinae	*Lamprocera* sp. 4	BYU
CO1287	Lampyridae	Lampyrinae	*Lamprohiza splendidula*	BYU
CO1071	Lampyridae	Lampyrinae	*Lampyris noctiluca*	BYU
CO1551	Lampyridae	Lampyrinae	*Lucidota atra*	BYU
CO1232	Lampyridae	Lampyrinae	*Lucio blattinum*	BYU
CO1226	Lampyridae	Lampyrinae	*Lychnacris* sp.	BYU
CO1092	Lampyridae	Lampyrinae	*Microphotus* sp.	BYU
CO1227	Lampyridae	Lampyrinae	*Petalacmis* sp.	BYU
CO1549	Lampyridae	Lampyrinae	*Phausis reticulata*	BYU
CO1289	Lampyridae	Lampyrinae	*Phosphaenopterus metzneri*	BYU
KSH_17651	Lampyridae	Lampyrinae	*Photinus ardens*	UGA
KSH_1028	Lampyridae	Lampyrinae	*Photinus australis*	UGA
KSH_9013	Lampyridae	Lampyrinae	*Photinus brimleyi*	UGA
KSH_9670	Lampyridae	Lampyrinae	*Photinus carolinus*	UGA
KSH_10061	Lampyridae	Lampyrinae	*Photinus floridanus*	UGA
KSH_14611	Lampyridae	Lampyrinae	*Photinus granulatus*	UGA
CO1074	Lampyridae	Lampyrinae	*Photinus macdermotti* 1	BYU
KSH_87151	Lampyridae	Lampyrinae	*Photinus macdermotti* 2	UGA
CO1547	Lampyridae	Lampyrinae	*Photinus pyralis*	BYU
CO1224	Lampyridae	Lampyrinae	*Photinus* sp. 1	BYU
CO1528	Lampyridae	Lampyrinae	*Photinus* sp. 2	BYU
CO1057	Lampyridae	Lampyrinae	*Photinus stellaris*	BYU
CO1230	Lampyridae	Lampyrinae	Photinini sp.	BYU
CO1307	Lampyridae	Lampyrinae	*Pleotomodes needhami*	BYU
KSH_4081	Lampyridae	Lampyrinae	*Pyractomena borealis*	UGA
CO1063	Lampyridae	Lampyrinae	*Pyractonema* sp. 1	BYU

Table 2. Continued

Code	Family	Subfamily	Species	Coll.
COARG	Lampyridae	Lampyrinae	*Pyractonema* sp. 2	BYU
CO1293	Lampyridae	Lampyrinae	*Pyrocoelia pygidialis*	BYU
CO1552	Lampyridae	Lampyrinae	*Pyropyga decipiens*	BYU
CO1080	Lampyridae	Lampyrinae	*Pyropyga nigricans*	BYU
CO1306	Lampyridae	Lampyrinae	*Tenaspis angularis*	BYU
CO1291	Lampyridae	Luciolinae	*Abscondita cerata*	BYU
CO1297	Lampyridae	Luciolinae	*Asymmetricata circumdata*	BYU
CO1221	Lampyridae	Luciolinae	*Atyphella flammulans*	BYU
CO1520	Lampyridae	Luciolinae	*Australoluciola nigra*	BYU
CO1222	Lampyridae	Luciolinae	*Australoluciola* sp.	BYU
CO1298	Lampyridae	Luciolinae	*Curtos bilineatus*	BYU
CO1303	Lampyridae	Luciolinae	*Curtos obsuricolor*	BYU
CO1255	Lampyridae	Luciolinae	*Curtos* sp.	BYU
CO1295	Lampyridae	Luciolinae	*Emeia pseudosauteri*	BYU
CO1220	Lampyridae	Luciolinae	*Lloydiella uberia*	BYU
CO1518	Lampyridae	Luciolinae	*Luciola* sp. 1	BYU
CO1225	Lampyridae	Luciolinae	*Luciola* sp. 2	BYU
CO1505	Lampyridae	Luciolinae	Luciolinae nr. *Luciola* 1	BYU
CO1525	Lampyridae	Luciolinae	Luciolinae nr. *Luciola* 2	BYU
CO1510	Lampyridae	Luciolinae	Luciolinae nr. *Luciola* 3	BYU
CO1509	Lampyridae	Luciolinae	Luciolinae nr. *Luciola* 4	BYU
CO1534	Lampyridae	Luciolinae	Luciolinae sp.	BYU
CO1517	Lampyridae	Luciolinae	*Pteroptyx* sp.	BYU
CO1296	Lampyridae	Luciolinae	*Pygoluciola qinqyu*	BYU
CO1229	Lampyridae	Luciolinae	*Trisinuata* sp.	BYU
CO1308	Lampyridae	Ototretinae	*Drilaster* sp.	BYU
CO1302	Lampyridae	Ototretinae	*Stenocladius shirakii*	BYU
CO1290	Lampyridae	Photurinae	*Bicellonycha* sp. 1	BYU
CO1228	Lampyridae	Photurinae	*Bicellonycha* sp. 2	BYU
CO1546	Lampyridae	Photurinae	*Photuris congener*	BYU
CO1049	Lampyridae	Photurinae	*Photuris divisia*	BYU
KSH_406	Lampyridae	Photurinae	*Photuris frontalis*	UGA
KSH_8870	Lampyridae	Photurinae	*Photuris quadrifulgens*	UGA
CO1062	Lampyridae	Photurinae	*Pyrogaster* sp.	BYU
CO1550	Lampyridae	Pterotinae	*Pterotus obscuripennis*	BYU

mitigate the effects of any low-level contamination (clusters were typically comprised of 100–1,000 reads). Homologous consensus sequences were derived from the remaining clusters, with ambiguous base calls being made for each site with a base pattern that could not be explained by sequencing error, which was assumed to be no more than 1%. For each of the 516 target loci, orthologous sets of homologs were determined using a distance matrix (constructed by comparing kmer distributions) and a neighbor-joining approach for clustering (with at most one sequence per individual allowed in each ortholog cluster). After removing ortholog sets with less than 50% species representation (<51 of 98), 436 loci remained (Supp Table 2 [online only]).

Alignment

The sequences obtained for individual loci were aligned via Mafft v. 7.407 (Katoh and Standley 2013) using the default automatic alignment option. For maximum likelihood (ML) analyses, the alignments of the individual loci included flanking regions (head, tail, or both) of each locus and were concatenated before analysis and resulted in an alignment length of 1,833,533 base pairs. Breinholt et al. (2017) showed that trimming data from the probe or flanking region have little effect on the final topology; consequently, we elected not to trim these regions (Lemmon et al. 2012). However, it is possible that missing data may bias phylogenetic reconstruction (Lemmon et al. 2009; see also Wiens and Morrill 2011); therefore, we generated a second data set utilizing a portion of the pipeline of Breinholt et al. (2017) (alignment_DE_trim.py) to remove sites from the alignment with <75% density (i.e., completeness), and with entropy >1.5 (to account for sites estimated to be nearly random). This resulted in a trimmed alignment of 401,423 base pairs.

Phylogenetic Reconstruction

ML reconstruction was performed in IQ-Tree v 1.6.8 (Nguyen et al. 2015, Chernomor et al. 2016) with 1,000 ultrafast bootstrap iterations (UFBoot; Hoang et al. 2018). Model estimation for concatenated locus data sets was carried out using ModelFinder (Kalyaanamoorthy et al. 2017) implemented within IQ-Tree, using BIC criteria. GTR+F+R9 was selected as the best-fit model for the untrimmed data set and GTR+R9 was selected for the trimmed data set. To account for the potential effect of incomplete lineage sorting on our phylogenetic reconstruction, we also used a coalescent approach to estimate a species tree via ASTRAL-III (Zhang et al. 2018) for each dataset (trimmed and untrimmed). ML gene tree topologies for each locus were inferred via IQ-Tree (Sensu Breinholt et al. 2017) before estimating the ASTRAL topology for each data set. We used localized posterior probabilities (Sayyari and Mirarab 2016) to assess nodal support for the coalescent species trees as assessed in ASTRAL-III.

Nomenclature

This paper has been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:D43452DB-0140-4863-84A8-94BFA6FD39EE

Results

Phylogenetic Reconstruction

ML Reconstruction

Within the ML reconstruction of the untrimmed data set (Topology 1 (T1); Fig. 1), we find a strong support for a sister group relationship between the Elateridae, Rhagophthalmidae, and Phengodidae with the Lampyridae (Fig. 1). The Luciolinae + *Lamprigera* Motschulsky were recovered as the sister lineage to all other firefly subfamilies with strong support (UFboot 100%). Within the lineage of the remaining subfamilies, a clade comprised of (*Pterotus* LeConte + *Pollaclasis* Newman) + the monophyletic Ototretinae forms the sister group to the remaining fireflies. However, neither this clade, nor the Ototretinae clade are well supported (UFBoot: 72% for both nodes). The clade (*Lamprohiza* Motschulsky + *Phausis* LeConte) is recovered as sister to the clade ((*Psilocladus* Blanchard + (Amydetinae + Photurinae)) + Lampyrinae) with UFBoot support of 100% at each node.

The ML reconstruction of the trimmed data set (Topology 2 (T2); Supp Fig. 1 [online only]) was largely identical to T1, with the exception of the placement of the paraphyletic Ototretinae and *Pollaclasis* in T2. In T2, Ototretinae is rendered paraphyletic, as *Stenocladius* Fairmaire in Deyrolle and Fairmaire is recovered as the sister taxon to all other Lampyridae, while *Drilaster* Kiesenwetter is recovered as the sister taxon to a clade comprised of *Pterotus* + *Pollaclasis*, albeit with low support (UFBoot 77%). Compared with T1, there is also lower support along the backbone of T2 (Supp Fig. 1 [online only]).

Coalescent Reconstruction

The coalescent reconstruction of the untrimmed data set (Topology 3 (T3); Supp Fig. 2 [online only]) was largely congruent with the ML topology of the same data set, except for the placement of the Ototretinae (incl. *Pterotus*). In the coalescent analysis (T3), the Ototretinae are rendered polyphyletic by inclusion of *Pterotus*, and this clade is recovered as the sister group to all other fireflies, while in the ML analysis (T1) this position was held by Luciolinae + *Lamprigera* (Fig. 1; localized posterior probability (LPP): 0.95).

The coalescent reconstruction of the trimmed data set (Topology 4 (T4); Supp Fig. 3 [online only]) was identical in respect to subfamilial relationships in the untrimmed data set (T3), with only minor variation in species relationships within the major clades (i.e., placement of the lucioline clade comprised of *Abscondita cerata* and *Curtos* sp.; Supp Figs. 3 and 4 [online only]).

Consensus Among Analysis

In all analyses, Lampyridae was reconstructed as monophyletic with support values of UFboot: 100% or LPP: 1) With the exception of the Ototretinae (discussed separately below), our four different analyses yielded no topological differences that impact the monophyly of the subfamilies among Lampyridae. Therfore, we will use Topology 1 (Fig. 1) to discuss the phylogenetic relationships among the seven subfamilies sampled. Topology 1 (T1) is also the best supported (via ultrafast bootstrap analysis) and is based on the full, untrimmed data set.

In T1, the Luciolinae are reconstructed as paraphyletic with the inclusion of *Lamprigera*.

The Ototretinae were represented by two genera (*Drilaster* and *Stenocladius*) in our analyses, and these formed a monophyletic clade, albeit with low support (72%). T1 is the only topology to recover the Ototretinae as monophyletic and sister to a clade comprised of *Pterotus* and *Pollaclasis*. In both T2 and T4 (Supp Figs. 1 and 3 [online only]) *Stenocladius* was recovered as the sister lineage to all other fireflies with low support (UFboot: 77% & LPP: 0.75), while in T3 (Supp Fig. 2 [online only]) a clade consisting of *Stenocladius* + (*Drilaster* + *Pterotus*) is recovered as sister to the remaining fireflies (LPP: 0.95). Given this incongruence, the exact position of the Ototretinae among firefly subfamilies remains uncertain. However, in all phylogenetic reconstructions, *Pterotus* is either sister to, or a lineage within, the Ototretinae. The subfamily Amydetinae is recovered as polyphyletic and its taxa can be found closely associated with diverse subfamilies: *Psilocladus* is recovered as sister to the Amydetinae + Photurinae, *Pollaclasis* forms a clade with *Pterotus* (Pterotinae), *Vesta* Laporte is recovered within the photurine clade, and *Cladodes* Solier, *Ethra* Laporte, and *Scissicauda* McDermott are recovered within the Lampyrinae. The Photurinae are rendered paraphyletic by inclusion of the old-world *Vesta* (see Martin et al. 2017). Lampyrinae is recovered as polyphyletic: *Lamprigera* is recovered within the Luciolinae, and there is high support (UFboot: 100%) for a monophyletic *Lamprohiza* + *Phausis* clade outside the Lampyrinae (see above). In addition, several amydetine taxa (*Cladodes*, *Ethra*, *Scissicauda*) cluster within the remaining Lampyrinae.

As such, in T1, the only subfamily recovered as monophyletic, as currently classified, is the Ototretinae. However, across all other topologies, even the Ototretinae are also rendered nonmonophyletic.

Discussion

The higher-level classification of Lampyridae is in need of revision. Our molecular analyses confirm that a few morphological characters related to sexual communication, many likely convergent, cannot be central to diagnosing a natural classification of Lampyridae. The use of these characters in subfamilial classification needs to be reassessed in light of a more complete phylogenetic history of the group. Our phylogenetic analyses based on 436 loci and 98 taxa provide a robust framework for a revision of the classification of Lampyridae.

Luciolinae

The Luciolinae are a subfamily of fireflies that have received much attention over the years (for a taxonomic treatment, see Ballantyne et al. 2015) and seem to share stable morphological characters such as a reduced number of abdominal ventrites in the males (see discussion of *Lamprigera* below).

Our analyses largely agree with recent morphological analyses in terms of the major groupings of the Luciolinae (Ballantyne and Lambkin, 2013). Thanks in large part to the effort of Ballantyne and Lambkin (Ballantyne 1987a, Ballantyne and Lambkin 2009, 2013), there also exists a discussion of the aedeagal sheath, which has provided evidence in support of the current taxonomic framework for these taxa. Many of the morphological characters used in these analyses (Ballantyne and Lambkin 2009, 2013, Ballantyne et al. 2015, 2016) and the phylogenetic patterns they support, correlate well with the phylogenetic hypotheses generated from our molecular data. However, some minor differences between previous phylogenetic work and our overall topology do exist. For example, the *Atyphella* complex is not recovered as the the most highly derived lineage, as it is in Ballantyne and Lambkin (2013). Our molecular data set recovers this lineage as more basal compared with the other

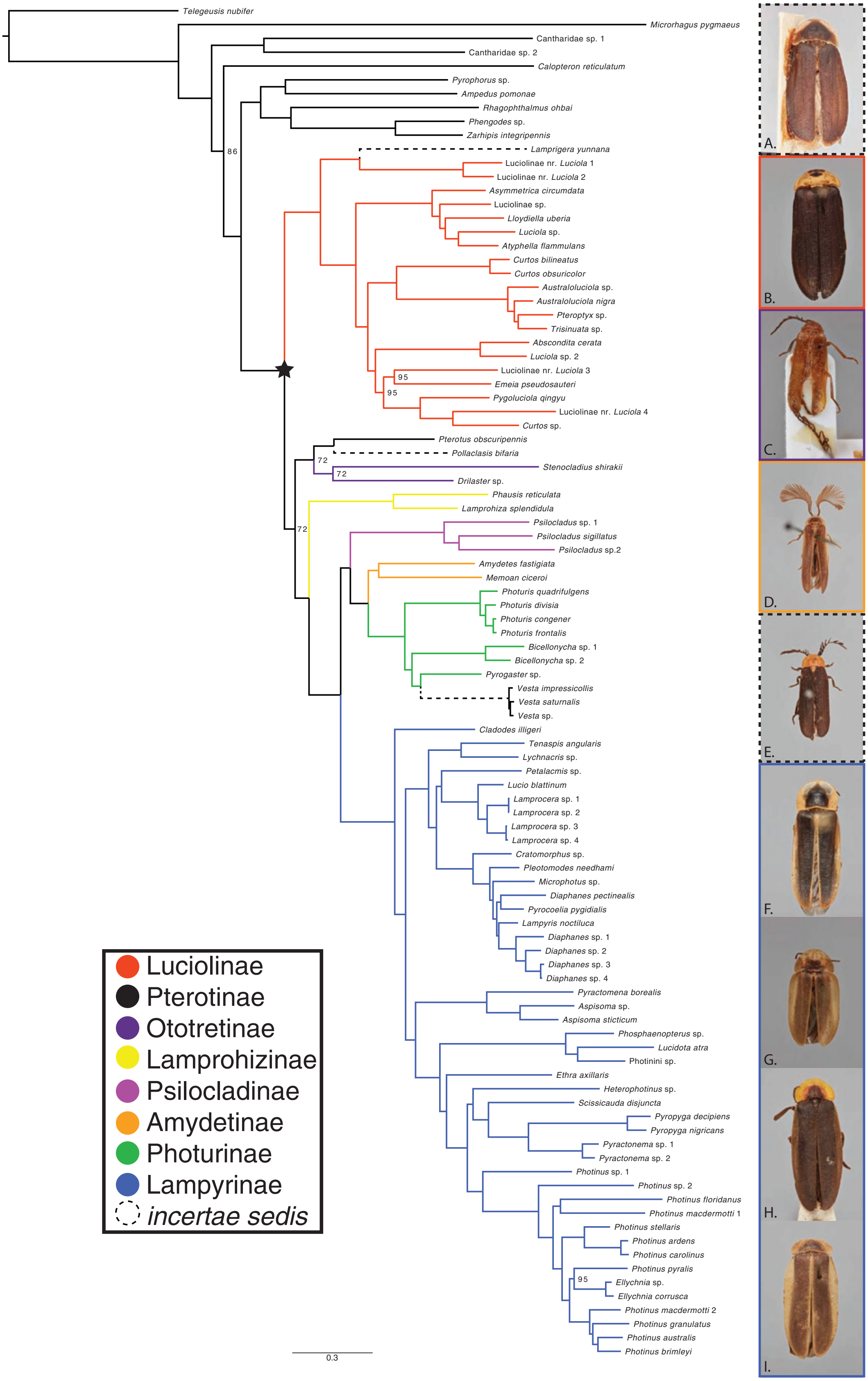

Fig. 1. ML reconstruction of full, untrimmed dataset aligned in MAFFT; log-likelihood = –26,321,164.240. The numbers at nodes indicate UFBoot support. Unlabeled nodes have UFBoot values of 100%, colors represent the newly proposed classification. Star at node depicts Lampyridae; A.-I. Dorsal habitus of genus representatives: A. *Lamprigera yunnana*; B. *Luciola cyathigera*; C. *Stenocladius davidi*; D. *Amydetes fastigiata*; E. *Vesta chevrolati*; F. *Diaphanes* sp.; G. *Aspisoma gentile*; H. *Ellychnia aurora*; I. *Photinus laticollis*;

Luciolinae. In addition, the lampyrine genus *Lamprigera* is recovered as a lineage within the lucioline clade.

Jeng et al. (2000) remarked that the systematic position of *Lamprigera* was uncertain and would hopefully be more accurately defined through future phylogenetic investigation. Previous analyses have recovered *Lamprigera* in various positions within the Lampyridae. In 2006, on the basis of the 16S mitochondrial marker, Li et al. performed a phylogenetic reconstruction of the Lampyridae. In this analysis, *Stenocladius* was recovered as the basal lineage, while *Lamprigera* was recovered in a surprising clade together with the amydetine genus *Vesta* sister to the remaining fireflies (Li et al. 2006), albeit with low support. In his thesis, Jeng (2008) recovered *Lamprigera* sister to the *Phausis* + *Lamprohiza* using >400 morphological characters. Wang et al. (2017) recovered *Lamprigera* as a member of the Lampyrinae on the basis of 13 mitochondrial genes. It should be noted, however, that the Wang et al. (2017) analysis suffered from a limited taxon sampling (six lucioline taxa and two additional lampyrine taxa from a single genus). Martin et al. (2017) recovered *Lamprigera* as sister to the monophyletic Luciolinae with high support and placed it as Lampyridae *incertae sedis*.

Here we recover *Lamprigera* as a member of the Luciolinae for the first time with both strong support and congruence between all of our analyses. However, this placement is based on a single *Lamprigera* species and major morphological differences between Lamprigera and the luciolines, e.g., the number of abdominal ventrites, need to be addressed. A major, long-standing morphological synapomorphy for Luciolinae has been males with six abdominal ventrites, whereas all other Lampyridae have seven or eight abdominal ventrites. Males of *Lamprigera* exhibit the 'typical' abdominal morphology of Lampyridae with seven ventrites.

In certain elateroid lineages, ventrite number is known to vary greatly, even within recently derived tribes/subfamilies (Kundrata and Bocak 2019). In contrast, ventrite number has not been shown to vary in Luciolinae. To rigorously test the classification of *Lamprigera* relative to the Luciolinae, an expanded taxon sampling including deeper species coverage within the Lamrigera, combined with an in-depth morphological investigation, including the plasticity of ventrite number across these taxa will be needed. Until these analyses can be done, we elect to keep *Lamprigera* as Lampyridae *incertae sedis* (Martin et al., 2017).

Pterotinae, Cyphonocerinae, and Psilocladinae (McDermott, 1964) stat. nov.

Jeng et al. 1998, 2006, summarizing the work of McDermott (1966), Crowson (1972), and Nakane (1991), were the first to formally delineate the Psilocladinae (previously known as Cyphonocerinae), by identifying the constituents of the group (*Cyphonocerus* Kiesenwetter, *Psilocladus*, and *Pollaclasis*) and laying out nine morphological features uniting the group. Jeng et al. (1998) also recognized Cyphonocerinae as a subjective synonym of Psilocladinae based on priority. In 2016, Silveira et al. treated *Scissicauda* as a member of the amydetine subtribe Psilocladina sensu McDermott 1964, distinguishing *Scissicauda* from the other members of the group (*Ethra*, *Photoctus* McDermott, *Psilocladus*, and *Pollaclasis*). In 2017, another genus (*Araucariocladus* Silveira & Mermudes) was added to the Psilocladina sensu McDermott. As a consequence of recognizing Psilocladina sensu McDermott instead of Psilocladinae sensu Jeng/Nakane, *Cyphonocerus* was left as the sole member of the Cyphonocerinae.

Our phylogenetic analyses supports in part the classification presented by Crowson (1972) and Nakane (1991) and supports the classification of *Psilocladus* as a separate lineage from the Amydetinae. Without *Cyphonocerus* in our taxon sample, the placement of *Psilocladus* within the Cyphonocerinae cannot truly be tested; however, given that *Psilocladus* did not form a monophyletic lineage with Pollaclasis, we formally recognize the subfamily Psilocladinae, distinguished by the antennae with 11 articles, articles 2–11 with two weak, ciliate branches, with the only constituent genus being *Psilocladus*.

Following McDermott (1966) and Silveira et al. (2016), *Pollaclasis* is classified as a member of the Amydetinae. However, both our ML and coalescent analyses challenge this classification. The ML analysis places *Pollaclasis* as a sister taxon to the North American *Pterotus*, the sole member of the Pterotinae (Fig. 1). In contrast, the coalescent analysis places *Pollaclasis* as sister to a *Phausis* + *Lamprohiza* clade (Supp Fig. 2). Hypothesized to be a close relative of *Cyphonocerus*, *Pollaclasis* has previously been classified in the Psilocladinae based on the morphology of antennae, mandibles, and abdominal segmentation (see Jeng et al. 1998). The present analyses do not support the monophyly of *Pollaclasis* and *Psilocladus*. On the basis of this evidence, as well as the absence of *Cyphonocerus* in our taxon sample, we transfer *Pollaclasis* to Lampyridae *incertae sedis*. Future efforts need to be made to ascertain whether *Pollaclasis* is indeed a member of the Cyphonocerinae, or as the ML analyses suggest, more closely related to *Pterotus*.

Ototretinae

Our analyses indicate that there may be a close relation between the Ototretinae and the Pterotinae. Recently, the Ototretinae were revised, and their taxonomic placement was addressed (Janisova and Bocakova 2013). In that study, the monotypic Ototretadrilinae were synonomized under the Ototretinae, and the ototretine lineage was transferred from Elateriformia *incertae sedis* to Lampyridae. In addition, the genus *Stenocladius* was transferred from Elateriformia *incertae sedis* to Ototretinae. Our analyses corroborate these transfers; however, as our taxon sample included only 2 of the 18 genera from the Ototretinae, *Stenocladius* and *Drilaster*, a wider generic sampling is needed to address the phylogenetic history of this lineage.

Two other genera, *Anadrilus* Kirsch, 1875 and *Pachytarsus* Motschulsky, 1861, were both excluded from the Ototretinae by Janisova and Bocakova (2013) on the basis of lack of type material to examine. As we were also unable to sample these genera, they remain Lampyridae *incertae* sedis. Of note, when he described *Pachytarsus*, Motschulsky (1861) was apparently unaware of the true bug genus by the same name, having been described the year before: *Pachytarsus* Fieber, 1860 (for current usage, see Ballal et al. 2018). Due to the name *Pachytarsus* being preoccupied, we propose the replacement name *Crassitarsus* Martin.

Crassitarsus Martin

New Replacement Name

Pachytarsus **Motschulsky, 1861**

Included species: *Crassitarsus basalis* (Motschulsky, 1861) **NEW COMBINATION,** *Crassitarsus* bicolor (Pic, 1929) **NEW COMBINATION,** *Crassitarsus* bryanti (Wittmer, 1940) **NEW COMBINATION,** *Crassitarsus* lateralis (Motschulsky, 1861) **NEW COMBINATION,** *Crassitarsus* longicornis (Pic, 1921) **NEW COMBINATION,** *Crassitarsus* minutus (Pic, 1933) **NEW COMBINATION,** *Crassitarsus* obscurus (Pic, 1927) **NEW COMBINATION,** *Crassitarsus* testaceus (Motschulsky, 1861) **NEW COMBINATION.**

Etymology: *Crassus,* a synonym for *pachy*, both meaning thick, seems an apt replacement to conserve the original thoughts of Motschulsky.

Lamprohizinae Kazantsev, 2010 stat. nov.

There is strong support for a *Lamprohiza* + *Phausis* clade in all our topologies. This is supported by a high degree of morphological similarity between these two genera (Fig. 2). *Phausis* was erected for *Lampyris reticulata* Say by LeConte (1852) and *Lamprohiza* was erected in 1853 by Motschulsky for *Lampyris splendidula* Linnaeus. *Lamprohiza* was later synonymized with *Phausis* by Lacordaire in 1857. In contrast, Mulsant, 1862 treated *Lamprohiza* as an independent genus, but in 1881 LeConte wrote '[*Phausis*] is not sufficiently distinct from the European *Lamprohiza*, and in fact the European species seems to have been naturalized in Maryland and Illinois' and included *L. splendidula* within *Phausis*. This classification was accepted until 1964 when McDermott separated *Lamprohiza* from *Phausis* by the 'minute appendage on the 11th antennal article' of the latter. However, Fender (1966) treated the two genera as one in his treatment on the '*Phausis*' of North America, while Miksic (1969) followed McDermott in treating them as separate genera. From a phylogenetic perspective, Stanger-Hall et al. (2007) found *Phausis* as sister to Photurinae + Lampyrinae, similar to our results. In 2008, Jeng found support for these genera as members of Lampyrinae, however, he noted that they differed from the traditional Lampyrinae in the 'unmodified mandibles *sensu* Green (1949), dorsal abdominal spiracles, and a symmetrical aedeagal sheath.' Our analyses, based on the type species of each genus, strongly support the rank of subfamily and we herein elevate Lamprohizini Kazantsev, 2010 to Lamprohizinae Kazantsev, 2010 **stat. nov.**

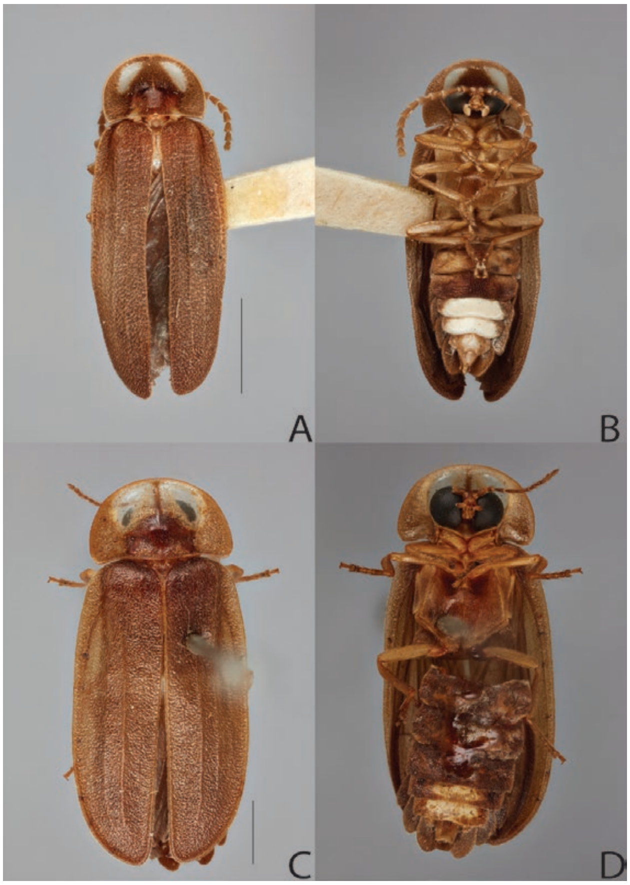

Fig. 2. Lamprohizinae habitus images; A: *Phausis reticulata* dorsal; B: *Phausis reticulata* ventral; C: *Lamprohiza delarouzei* dorsal; D: *Lamprohiza delarouzei* ventral.

Diagnosis

The Lamprohizinae are distinguished from all other subfamilies with the following combination of characters, based on adult males: mandibles unmodified (i.e., not reduced in size); antennae filiform, 11-segmented, with or without terminal sensorium, if without then posterior margin of ventrite 7 with weak to strong medial projection, projection emarginate at midline; tarsal claws simple, not bifid; abdomen with seven–eight ventrites; abdominal spiracles dorsal; aedeagal sheath symmetrical.

Key to the genera of Lamprohizinae

Terminal antennomere with small, beadlike sensorium; abdominal ventrite 7 unmodified; ventrite 8 apparent ....*Phausis*
Terminal antennomere without small, beadlike sensorium; abdominal ventrite 7 with weak to strong medial projection; ventrite 8 not apparent ....*Lamprohiza*

Amydetinae

McDermott (1964) recognized the Amydetini as a tribe within the Lampyrinae based on the mandibles being 'normal, arcuate, regularly narrowing to tips', antennae bearing rami or branches, and lack of secondary elytral pubescence of the males. To further classify the rather heterogenous group of genera included in the Amydetini, McDermott (1964) recognized three subtribes based on variation in antennal morphology: Amydetina ('Antennae with more than 14 articles, uniramose'), Vestina ('Antennae with 11 articles, Antennae uniramose, rami remiform, relatively broad, folding like a fan'), and Psilocladina ('Antennae with 11 articles, Antennae bi-or uniramose, rami either long and diffuse, or if short and straight, not fan-folding'). In his 1966 update to the classification, McDermott elevated the Amydetini to the subfamily level. Nakane (1991) reduced the Amydetinae to *Amydetes* Hoffmannsegg in Illiger and *Magnoculus* McDermott; however, Silveira and Mermudes (2013) described the new genus *Memoan* Silveira and Mermudes and, based on it having features of both the Amydetinae and the Lampyrinae, placed it in Lampyridae *incertae sedis*.

Owing to the phylogenetic position of *Memoan* as sister to *Amydetes*, and the morphological features shared by *Memoan* with other taxa within the Amydetinae (as identified by Silveira and Mermudes, 2013), including a 'continuous glow, pleuralventral suture, ventral approximate eyes, deep punctures on pronotum and scutellum, and absence of tibial spurs', we formally transfer *Memoan* to the Amydetinae, thus the Amydetinae now include *Amydetes*, *Magnoculus*, and *Memoan*.

Cheguevariinae

Kazantsev (2006) described two enigmatic species in the genus *Cheguevaria* Kazantsev, 2006, one from Puerto Rico, and one from Dominican Republic. In the description, he remarks on the similarity of *Cheguevaria* to the Phengodidae; however, he does note the differences, and allies *Cheguevaria* with the Lampyridae based on the structure of the genital capsule. While he suspected that the genus represented a unique lampyrid subfamily, given the peculiar morphology of the genus, as well as the lack of phylogenetic stability at the time, Kazantsev placed the Cheguevariini as Lampyridae *incertae sedis* (Kazantsev, 2006). Recent phylogenetic analyses have corroborated the placement of *Cheguevaria* within the Lampyridae and, confirming the suspicion of Kazantsev, elevated the tribe to subfamilial status (Ferreira, et al. 2019). We were unable to sample the Cheguevariinae for the present analyses.

Photurinae and Lampyrinae

All photurine genera in our analyses (we were unable to sample *Presbyolampis* Buck, 1947) were recovered in a monophyletic lineage with the old-world *Vesta*. Known only from the New World, the Photurinae are typically characterized by bifurcate claws in males, and eyes expanding beyond the hypomeron. Nakane (1991) transferred the members of the Vestina (*Vesta*, *Cladodes*, *Ledocas* Olivier, *Dodacles* Olivier, and *Dryptelytra* Laporte) to the Lampyrinae, and moved *Psilocladus* to the Cyphonocerinae (see above) and *Ethra* to the Lampyrinae; he did not mention *Scissicauda* or *Photoctus*. Our analyses agree with Nakane (1991) in the placement of *Cladodes* and *Ethra*; however, the old-world *Vesta* sampled for our analyses formed a monophyletic lineage within the Photurinae, a new-world clade. *Vesta* is a speciose genus with representatives in both the Old and New World. McDermott (1964) recognized that *Vesta* might not be a natural group. In his 1966 catalogue he continued to treat the new-world taxa as potentially independent from the old-world taxa. As we were unable to sample the new-world *Vesta*, or the other members of the Vestini, our analyses are inconclusive with regard to the subfamilial placement of the *Vesta*. Therefore, we transfer *Vesta* and the other members of the Vestini (*Dodacles*, *Dryptelytra*, and *Ledocas*) to Lampyridae *incertae sedis* pending further morphological and phylogenetic analyses.

The Lampyrinae are a diverse assemblage of genera lacking any stable morphological characters (McDermott 1964; Jeng 2008). It is in part due to this that we believe so many 'lampyrine' genera are/have been mis-classified. Based on our present phylogenetic analyses, we transfer the genus *Scissicauda* from Amydetinae into Lampyrinae. Since neither *Photoctus* nor *Araucariocladus* were included in the present analyses we transfer these to Lampyridae *incertae sedis,* pending further phylogenetic analyses.

Conclusions

With 88 lampyrid taxa in 53 genera for seven of the eight previously recognized subfamilies, these analyses represent the largest molecular phylogeny of the group, thereby providing a unique opportunity to robustly test the monophyly of each subfamily. The results of our four phylogenetic reconstructions were largely congruent, with the only major difference concerning the placement of the Ototretinae, which were under-sampled in this study. The inclusion of additional ototretine taxa will likely aid the resolution of their placement. Aside from the monotypic Pterotinae, among the subfamilies in the current analyses, only the Ototretinae (as currently defined) were reconstructed as monophyletic (T1). As a result, we propose several changes to the higher-level classification of Lampyridae, with an updated higher-level classification scheme for the family. *Pollaclasis*, *Vesta* (as well as the other constituents of the Vestini: *Dodacles*, *Dryptelytra*, and, *Ledocas*), *Photoctus*, and *Araucariocladus* are transferred to Lampyridae *incertae sedis*. Psilocladinae is re-established for *Psilocladus*. Amydetinae is limited to *Amydetes*, *Magnoculus*, and *Memoan* with *Scissicauda* being transferred to the Lampyrinae. Lamprohizini is elevated to the rank of subfamily, *Phausis* is transferred to Lamprohizinae. This comprehensive classification of firefly lineages will provide the phylogenetic scaffold in support of future studies into the evolution of the fascinating morphology and behavior of fireflies.

List of Genera

Subfamily Luciolinae Lacordaire, 1857

Abscondita Ballantyne, Lambkin, & Fu *in* Ballantyne et al., 2013
 Luciola terminalis Olivier, 1883: 330
Aquatica Fu, Ballantyne, and Lambkin, 2010
 Aquatica wuhana Fu, Ballantyne, and Lambkin, 2010: 8
Aquilonia Ballantyne *in* Ballantyne and Lambkin, 2009
 Luciola costata Lea, 1921: 66
Asymmetricata Ballantyne *in* Ballantyne and Lambkin, 2009
 Luciola circumdata Motschulsky, 1854b: 50
Atyphella Olliff, 1890
 Atyphella lychnus Olliff, 1890: 647
Australoluciola Ballantyne *in* Ballantyne and Lambkin, 2013
 Lampyris australis Fabricius, 1775: 201
Colophotia Motschulsky, 1853
 Lampyris praeusta Eschscholtz, 1822: 57
Convexa Ballantyne *in* Ballantyne and Lambkin, 2009
 Luciola wolfi Olivier, 1910b: 343
Curtos Motschulsky, 1845
 Curtos mongolicus Motschulsky, 1845: 36
Emarginata Ballantyne *in* Ballantyne et al., 2019
 Luciola trilucida Jeng and Lai *in* Jeng et al., 2003: 248
Emeia Fu, Ballantyne and Lambkin, 2012
 Curtos pseudosauteri Geisthardt, 2004: 1
Inflata Boontop *in* Ballantyne et al., 2015
 Luciola indica Motschulsky, 1854b: 53
Kuantana Ballantyne *in* Ballantyne et al., 2019
 Kuantana menayah Ballantyne *in* Ballantyne et al., 2019: 82
Lampyroidea Costa 1875
 Lampyroidea syriaca Costa 1875: CLXIX
Lloydiella Ballantyne *in* Ballantyne and Lambkin, 2009
 Luciola majuscula Lea, 1915: 495
Luciola Laporte, 1833
 Luciola pedemontana Motschulsky, 1853: 53
Magnalata Ballantyne *in* Ballantyne and Lambkin, 2009
 Luciola limbata Blanchard, 1853: 73
Medeopteryx Ballantyne *in* Ballantyne and Lambkin, 2013
 Pteroptyx effulgens Ballantyne, 1987b: 141
Missimia Ballantyne *in* Ballantyne and Lambkin, 2009
 Missimia flavida Ballantyne *in* Ballantyne and Lambkin, 2009
Pacifica Ballantyne *in* Ballantyne and Lambkin, 2013
 Atyphella salomonis Olivier, 1911c: 172
Photuroluciola Pic, 1931
 Photuroluciola deplanata Pic, 1931: 12
Pteroptyx Olivier, 1902
 Luciola testacea Motschulsky, 1854b: 48
Pygatyphella Ballantyne, 1968
 Atyphella obsoleta Olivier, 1911c: 174
Pygoluciola Wittmer, 1939
 Pygoluciola stylifer Wittmer, 1939: 22
Pyrophanes Olivier, 1885
 Pyrophanes similis Olivier, 1885: 370
Sclerotia Ballantyne *in* Ballantyne et al., 2016
 Luciola aquatilis Thancharoen *in* Thancharoen et al., 2007: 56
Serratia Ballantyne *in* Ballantyne et al. 2019
 Serratia sibuyania Ballantyne *in* Ballantyne et al., 2019: 147
Triangulara Pimpasalee *in* Ballantyne et al., 2016

Triangulara frontoflava Pimpasalee *in* Ballantyne et al., 2016: 242
Trisinuata Ballantyne *in* Ballantyne and Lambkin, 2013
Trisinuata caudabifurca Ballantyne *in* Ballantyne and Lambkin, 2013: 117

Tribe Pristolycini Kazantsev, 2010

Pristolycus Gorham, 1883
Pristolycus sagulatus Gorham, 1883: 407

Subfamily Pterotinae LeConte, 1861

Pterotus LeConte, 1859
Pterotus obscuripennis LeConte, 1859: 86

Subfamily Ototretinae McDermott, 1964

Baolacus Pic, 1915
Baolacus lajoyei Pic, 1915: 21
Brachylampis Van Dyke, 1939
Brachylampis sanguinicollis Van Dyke, 1939: 16
Brachypterodrilus Pic, 1918
Brachypterodrilus pallidipes Pic, 1918: 1
Ceylanidrilus Pic, 1911
Ceylanidrilus bipartitus Pic, 1911a: 187
Drilaster Kiesenwetter, 1879
Drilaster axillaris Kiesenwetter, 1879: 311
Emasia Bocakova and Janisova, 2010
Emasia dentata Bocakova and Janisova, 2010: 61
Eugeusis Westwood, 1853
Eugeusis palpator Westwood, 1853: 239
Falsophaeopterus Pic, 1911
Falsophaeopterus fruhstorferi Pic, 1911a: 187
Flabellopalpodes Bocakova and Bocak, 2016
Flabellopalpodes flavus Bocakova and Bocak, 2016: 372
Flabellototreta Pic, 1911
Flabellototreta fruhstorferi Pic, 1911b: 156
Gorhamia Pic, 1911
Gorhamia compressicornis Pic, 1911a: 187
Harmatelia Walker, 1858
Harmatelia bilinea Walker, 1858: 281
Hydaspoides Bocakova and Janisova, 2013
Hydaspoides kanarensis Janisova and Bocakova, 2013: 7
Hyperstoma Wittmer, 1979
Hyperstoma marginata Wittmer, 1979: 86
Lamellipalpodes Maulik, 1921
Lamellipalpodes annandalei Maulik, 1921: 584
Lamellipalpus Maulik, 1921
Eugeusis nigripennis Pascoe, 1887: 10
Ototretadrilus Pic, 1921
Ototretadrilus atritarsis Pic, 1921: 13
Picodrilus Wittmer, 1938
Ototreta drescheri Pic, 1937: 138
Stenocladius Fairmaire *in* Deyrolle and Fairmaire, 1878
Stenocladius davidis Fairmaire *in* Deyrolle and Fairmaire, 1878: 113

Subfamily Lamprohizinae Kazantsev, 2010

Phausis LeConte, 1852
Lampyris reticulata Say, 1825: 163
Lamprohiza Motschulsky, 1853
Lampyris splendidula Linnaeus, 1767: 644

Subfamily Cyphonocerinae Crowson, 1972

*Cyphonceru*s Kiesenwetter, 1879
Cyphonocerus ruficollis Kiesenwetter, 1879: 312

Subfamily Psilocladinae McDermott, 1964

Psilocladus Blanchard, 1846
Psilocladus miltoderus Blanchard, 1846: 122

Subfamily Amydetinae Olivier *in* Wytsman, 1907

Tribe Amydetini Olivier *in* Wytsman, 1907

Amydetes Hoffmannsegg *in* Illiger, 1807
Homalisus apicalis Germar, 1824: 67
Magnoculus McDermott, 1964
Meglophthalmus bennetti Gray, 1832: 371
Memoan Silveira and Mermudes, 2013
Memoan ciceroi Silveira and Mermudes, 2013: 84

Subfamily Cheguevariinae Kazantsev, 2006

Tribe Cheguevariini Kazantsev, 2006

Cheguevaria Kazantsev, 2006
Cheguevaria taino Kazantsev, 2006: 370

Subfamily Photurinae Lacordaire, 1857

Bicellonycha Motschulsky, 1853
Bicellonycha deleta Motschulsky, 1854b: 58
Photuris Dejean, 1833
Lampyris versicolor Fabricius, 1798: 123
Presbyolampis Buck, 1947
Presbyolampis immigrans Buck, 1947: 75
Pyrogaster Motschulsky, 1853
Pyrogaster grylloides Motschulsky, 1853: 53

Subfamily Lampyrinae Rafinesque, 1815

Tribe Cratomorphini Green, 1948

Aspisoma Laporte, 1833
Lampyris ignita Linnaeus, 1767: 645
Aspisomoides Zaragoza-Caballero, 1995
Aspidosma bilineatum Gorham, 1880b: 86
Cassidomorphus Motschulsky, 1853
Cassidomorphus silphoides Motschulsky, 1853: 36
Cratomorphus Motschulsky, 1853
Photinus fabricii Laporte, 1840: 268
Micronaspis Green, 1948
Micronaspis floridana Green, 1948: 63
Paracratomorphus Zaragoza-Caballero, 2013
Paracratomorphus reyesi Zaragoza-Caballero, 2013: 145
Pyractomena Melsheimer, 1846
Pyractomena lucifera Melsheimer, 1846: 304

Tribe Lamprocerini Olivier, 1907

Alecton Laporte, 1833
Alecton discoidalis Laporte, 1833: 135

Lamprocera Laporte, 1833
Homalisus grandis Sturm, 1826: 58
Lucernuta Laporte,1833
Lampyris savignii Kirby, 1818: 388
Lucio Laporte, 1833
Lucio abdominalis Laporte, 1833: 136
Lychnacris Motschulsky, 1853
Lychnacris triguttula Motschulsky, 1853: 33
Tenaspis LeConte, 1881
Hyas angularis Gorham, 1880: 7

Tribe Lampyrini Rafinesque, 1815

Afrodiaphanes Geisthardt, 2007
Lampyris marginipennis Boheman, 1851: 439
Diaphanes Motschulsky, 1853
Diaphanes luniger Motschulsky, 1853: 45
Lampyris Geoffroy, 1762
Lampyris noctiluca Linnaeus, 1767: 643
Lychnobius Geisthardt, 1983
Lampyris conspicua Gyllenhal *in* Schönherr, 1817: 20
Microlampyris Pic, 1956
Microlampyris basilewski Pic, 1956: 193
Microphotus LeConte, 1866
Microphotus dilatatus LeConte, 1866: 90
Nelsonphotus Cicero, 2006
Nelsonphotus aridus Cicero, 2006: 201
Nyctophila Olivier, 1884
Lamprotomus caucasica Motschulsky, 1854a: 19
Ovalampis Fairmaire, 1898
Ovalampis crispaticollis Fairmaire, 1898: 404
Paraphausis Green, 1949
Paraphausis eximia Green, 1949: 4
Pelania Mulsant, 1860
Lampyris mauritanica Linnaeus, 1767: 645
Petalacmis Olivier, 1908
Petalacmis praeclarus Olivier, 1908: 187
Prolutacea Cicero, 2006
Lampyris pulsator Cicero, 1984: 322
Pyrocoelia Gorham, 1880
Lampyris bicolor Fabricius, 1801: 100

Tribe Photinini LeConte, 1881

Ankonophallus Zaragoza-Caballero and Navarrete-Heredia, 2014
Ankonophallus zuninoi Zaragoza-Caballero and Navarrete-Heredia, 2014: 126
Aorphallus Zaragoza-Caballero and Gutierrez-Carranza, 2018
Aorphallus cibriani Zaragoza-Caballero and Gutierrez-Carranza, 2018: 160
Callopisma Motschulsky, 1853
Lampyris rufa G.A. Olivier, 1790: 28
Calotrechelum Pic, 1930
Calotrachelum olivieri Pic, 1930: 88
Dadophora Olivier *in* Wytsman, 1907
Dadophora hyalina Olivier *in* Wytsman, 1907: 27
Dilychnia Motschulsky, 1853
Dilychnia basalis Motschulsky, 1853: 30
Ellychnia Blanchard, 1845
Lampyris corrusca Linnaeus, 1767: 644
Erythrolychnia Motschulsky, 1853
Erythrolychnia dimidiatipennis Motschulsky, 1853: 29
Heterophotinus Olivier, 1894
Photinus limbipennis du Val, 1857: 86
Jamphotus Barber, 1941
Jamphotus tuberculatus Barber, 1941: 11
Lucidina Gorham, 1883
Lucidina accensa Gorham, 1883: 408
Lucidota Laporte, 1833
Lucidota banoni Laporte, 1833: 137
Lucidotopsis McDermott, 1960
Lucidota cruenticollis Fairmaire, 1889: 38
Luciuranus Silveira, Khattar, and Mermudes *in* Silveira et al., 2016
Luciuranus josephi Silveira, Khattar, and Mermudes *in* Silveira et al., 2016 377
Macrolampis Motschulsky, 1853
Macrolampis longipennis Motschulsky, 1853: 37
Microdiphot Barber, 1941
Microdiphot cavernarum Barber, 1941: 13
Mimophotinus Pic, 1935
Mimophotinus angustatus Pic, 1935: 9
Oliviereus Pic, 1930
Oliviereus flavus Pic, 1930: 88
Phosphaenopterus Schaufuss, 1870
Phosphaenopterus metzneri Schaufuss, 1870: 61
Phosphaenus Laporte, 1833
Lampyris hemiptera Geoffroy *in* Fourcroy, 1785: 58
Photinoides McDermott, 1963
Photinoides penai McDermott, 1963: 87
Photinus Laporte, 1833
Lampyris pallens Fabricius, 1798: 124
Platylampis Motschulsky, 1853
Platylampis latiuscula Motschulsky, 1853: 44
Pseudolychnuris Motschulsky, 1853
Pseudolychnuris vittata Motschulsky, 1853: 32
Pyractonema Solier *in* Gay, 1849
Pyractonema compressicornis Solier *in* Gay, 1849: 446
Pyropyga Motschulsky, 1852
Lampyris nigricans Say, 1823: 179
Pyropygodes Zaragoza-Caballero, 2000
Pyropygodes huautlae Zaragoza-Caballero, 2000: 20
Robopus Motschulsky, 1853
Robopus roseicollis Motschulsky, 1853: 42
Rufolychnia Kazantsev, 2006
Callopisma borencona Leng and Mutchler, 1922: 440
Uanauna Campello-Gonçalves, Souto, Mermudes, and Silviera, 2019
Uanauna angaporan Campello-Gonçalves, Souto, Mermudes, and Silviera, 2019: 67
Ybytyramoan Silveira and Mermudes, 2014
Ybytyramoan praeclarum Silveira and Mermudes, 2014: 328

Tribe Pleotomini Summers, 1875

Calyptocephalus Gray *in* Griffith and Pidgeon, 1832
Calyptocephalus fasciatus Gray *in* Griffith and Pidgeon, 1832: 371
Ophoelis Olivier, 1911
Ophoelis impura Olivier, 1911: 48
Phaenolis Gorham, 1880
Phaenolis laciniatus Gorham, 1880: 10
Pleotomodes Green, 1948
Pleotomodes needhami Green, 1948: 65
Pleotomus LeConte, 1861

Pleotomus pallens LeConte, 1866: 88
Roleta McDermott, 1962
Roleta coracina McDermott, 1962: 69

Lampyrinae *incertae sedis*

Cladodes Solier *in* Gay, 1849
Cladodes flabellatus Solier *in* Gay, 1849: 445
Ethra Laporte, 1833
Cladophorus marginatus Gray *in* Griffith and Pidgeon, 1832: 371
Scissicauda McDermott, 1964
Lucidota disjuncta Olivier, 1896: 1

Lampyridae *incertae sedis*

Anadrilus Kirsch, 1875
Anadrilus indus Kirsch, 1875: 37
Araucariocladus Silveira and Mermudes, 2017
Araucariocladus hiems Silveira and Mermudes, 2017: 209
Crassitarsus Martin, nom. nov.
Pachytarsus basalis Motschulsky, 1861: 135
Lamprigera Motschulsky, 1853
Lamprigera boyei Motschulsky, 1853: 48
Oculogryphus Jeng, Engel, and Yang, 2007
Oculogryphus fulvus Jeng *in* Jeng, Engel, and Yang, 2007: 7
Photoctus McDermott, 1961
Photoctus boliviae McDermott, 1961: 174
Pollaclasis Newman, 1838
Pollaclasis ovatus Newman, 1838: 385

Subtribe Vestini McDermott, 1964

Dodacles Olivier, 1885
Dodacles elegans Olivier, 1885: 141
Dryptelytra Laporte, 1833
Dryptelytra cayennenis Laporte, 1833: 139
Ledocas Olivier, 1885
Ledocas parallelus Olivier, 1885: 140
Vesta Laporte, 1833
Vesta chevrolati Laporte, 1833:133

Supplementary Data

Supplementary data are available at *Insect Systematics and Diversity* online.

Data Availability Statement

Data from this study are available from the Dryad Digital Repository: doi:10.5061/dryad.737c8t8.

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