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Phylogeny of the Cladodes lineage, neotenic fireflies from the Neotropical Region (Coleoptera: Lampyridae)

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Abstract:	Phylogenetic relationships of Vestini with extensive sampling were inferred using 37 taxa scored for 66 morphological characters. Consistently with recent DNA analyses, Vesta was found sister to Photurinae rendering Vestini monotypic. Conversely, our parsimony and model based analyses robustly supported the monophyly of Cladodinae subfam.n. established for Neotropical species of the former Vestini. The cladodine lineage included Cladodes, Dodacles, Dryptelytra, Ledocas, plus newly proposed Andecladodes gen.n., and Brasilocladodes gen.n. While Ledocas was mostly paraphyletic, Cladodes was polyphyletic and therefore, Cladodes sensu stricto is introduced. Most trees further presented distinction of Nyctocrepis which is revalidated and included the subgenus Fenestratocladodes (transferred from Cladodes). Finally, a highly supported crown clade designated as the Dodacles lineage was regularly recovered splitting into two sister clades: (1) Dodacles, Brasilocladodes gen.n., and (2) Dryptelytra, C. proteus, C. solieri, Andecladodes gen.n. Four new species from the Andean region are described: Andecladodes cosangensis sp.n., A. ovalis sp.n., Dryptelytra pampahermosae sp.n., and Ledocas pikillactanus sp.n. To recover the monophyly of genera following new combinations are proposed: Brasilocladodes illigeri, B. carinatus, B. delalandei, Dodacles niger, and D. lateralis (transferred from Cladodes); Ledocas emissus, L. remixtus (from Dodacles); Cladodes proteus (from Ledocas); and Cladodes cincticollis, C. melanurus (from Vesta).

ADDITIONAL KEY WORDS: Amydetinae – Vestini – *Vesta* – Photurinae.

Introduction

Fireflies are a luminescent group of elateroid beetles with a widespread expression of neotenic features (Kundrata *et al.*, 2014) manifested mainly by wingless to larviform females (Cicero, 1988). Neoteny is assumed to be particularly common in genera traditionally placed in Amydetinae (McDermott, 1966; Crowson, 1972; Lawrence & Newton, 1995). McDermott split the subfamily Amydetinae into 3 subtribes: Amydetina, Vestina, and Psilocladina (the tribal rank mistakenly skipped). The latter was elevated to Psilocladinae (Jeng *et al.*, 1998) and the Amydetinae was restricted to members of Amydetini + Vestini (Bouchard *et al.*, 2011).

Phylogenetic analyses of morphological data revealed that Amydetinae sensu McDermott (1966) is polyphyletic (Branham & Wenzel, 2003). The tribe Vestini – bringing together the species of *Vesta* Laporte, 1833 and *Cladodes* lineage (Jeng, 2008, unpublished) – was particularly questionable, and morphological studies indicated that *Vesta* embraced unrelated Oriental and Neotropical lineages (McDermott, 1966; Jeng *et al.*, 2007). The first multigene phylogenetic analyses suffered from partial sampling including either *Vesta* (Bocakova *et al.*, 2007), or Photurinae (Stanger-Hall, 2007). Recently, the relationship of Vestini genera was substantially challenged by molecular evidence when *Vesta* was repeatedly revealed within the Photurinae clade (Martin *et al.*, 2017; 2019), being sister to *Bicellonycha* Motschulsky, 1853, or to *Pyrogaster* Motschulsky, 1853. Simultaneously, *Amydetes* and *Psilocladus* were shown to split off basally to Photurinae, while the genus *Cladodes* was recovered sister to the remaining Lampyrinae (Martin *et al.*, 2019). Therefore, the Amydetinae were restricted to three genera (*Amydetes* Illiger, 1807, *Magnoculus* McDermott, 1964, *Memoan* Silveira & Mermudes, 2013) and *Cladodes* Solier, 1849 was removed from Vestini to Lampyridae *incertae sedis* (Martin *et al.*, 2019). Presumably related *Dodacles* Olivier, 1885, *Ledocas* Olivier, 1885, and *Dryptelytra* Laporte, 1833, whose DNA was unavailable, were conservatively kept in Vestini and the tribe was also placed in Lampyridae *incertae sedis* (Martin *et al.*, 2019).

Among the 15 genera of the former Amydetinae (McDermott, 1966), only five (*Vesta, Ethra* Laporte, 1833, *Psilocladus* Blanchard, 1846, *Scissicauda* McDermott, 1964, and *Pollaclasis* Newman, 1838) have both sexes fully winged (McDermott, 1964; Jeng *et al.*, 2007; Jeng, 2008), a trait also shared with Photurinae. Nevertheless, the character was reconstructed as plesiomorphic (Jeng, 2008), and females of the lampyrid ancestor were inferred as winged, lacking neotenic features. Hence, morphological support for the phylogenetic placement of *Vesta* in Photurinae is missing. Conversely, known females of Vestini genera other than *Vesta* are neotenic – of these, females of *Cladodes* and

Ledocas were reported as larviform (Barber, 1923; McDermott, 1964; Cicero, 1988), while those of other genera remain unknown despite considerable efforts of recent studies on South American fireflies (Constantin, 2010; Silveira & Mermudes, 2014; Silveira *et al.*, 2015, 2020). Nevertheless, the absence of Vestini larviform females in museum collections and recent extensive Malaise (flight intercept) trap sampling indicate their flightlessness.

Here, we focus on Vestini to elucidate the evolutionary relationships of *Vesta* and *Cladodes* lineage to other neotenic, or fully winged fireflies. We present the first comprehensive phylogenetic analysis of Vestini.

Materials and Methods

Our morphological matrix (Table S1) was focused on tribe Vestini (McDermott, 1966). Ingroup taxa included species of all five genera (*Vesta*, *Cladodes*, *Dodacles*, *Ledocas*, *Dryptelytra*), in addition to both subgenera of *Cladodes* (*Cladodes* s.s., and *Fenestratocladodes* Pic, 1935) and taxa currently placed in synonymy (*Nyctocrepis* Motschulsky, 1853; *Rhipidophorus* Solier, 1849). To investigate the relationships of the Vestina, members of other lampyrid subfamilies (Amydetinae, Photurinae, Psilocladinae) were included, plus multiple outgroups representing Lampyrinae, Lamprohizinae, and Luciolinae. Our dataset was assembled in Mesquite 3.51 (Maddison & Maddison, 2018) and consisted of 37 terminal taxa scored for 66 male characters (44 binary characters, 22 multistates, Table S2). Most characters are newly defined to resolve the relationships within the *Cladodes* lineage. Several outgroup-relevant characters (e.g. 10, 14, 17) were adapted from Jeng (2008). Maximum parsimony analyses were performed using TNT software (Goloboff *et al.*, 2008) with all characters treated as unordered. Tree searches were conducted by the traditional approach applying branch swapping using tree bisection and reconnection (TBR) as well as subtree pruning and regrafting (SPR). An initial run with equal weights was followed by analyses under implied weighs (Goloboff, 1993) with concavity constants ranging from 1–25 to model the effect of homoplastic characters. The analyses were repeated from five different random seeds. Decay indices (Bremer, 1994), showing the number of extra steps required to break the clade, were calculated from the unweighted analysis for the clades present on the strict consensus tree using TNT. Branch support was assessed using standard bootstrapping and symmetric resampling with 1000 replicates. Finally, unambiguous character changes, as well as accelerated (ACCTRAN) and delayed (DELTRAN) transformations, were mapped on the strict consensus tree using WinClada (Nixon, 2002).

Alternatively, the dataset was analyzed using Bayesian (BA) and maximum likelihood (ML) approaches applying the MKV model (Lewis 2001). BA were run using MrBayes 3.2.7 (Ronquist et al.

2012) for 10 million generations. ML analyses were performed in IQ-TREE 2.1.2 (Minh et al. 2020) and the branch support was estimated by ultrafast bootstrapping with 1000 replicates.

Specimens and internal body structures were studied under an Olympus SZX12, or Leica M205 C stereoscopic microscopes. Dissection of genitalia and measurement procedures followed previous studies (Janisova K. & Bocakova M., 2013, Nascimento & Bocakova, 2017). Digital photographs were taken by a Canon EOS 1100D camera attached to the stereoscopic microscope, processed using QuickPHOTO CAMERA 3.0 software, stacked by Combine ZM 1.0.0, or processed and stacked by Leica Application Suite CV3 automatic photo editing software. Images were adjusted in Adobe Photoshop CS3.

Type specimens were examined particularly in Muséum National d'Histoire Naturelle, Paris, France (MNHN) and Natural History Museum, London, UK (NHML). Additional material was obtained from the following collections: Universidade Federal do Paraná, Museu de Entomologia Padre Jesus Santiago Moure, Curitiba, Brazil (DZUP – N. Ganho); Fundacão Instituto Oswaldo Cruz, Rio de Janeiro, Brazil, (FIOC – M. Félix); Montana State University, Bozeman, USA (MTEC – M. Ivie); Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP – S. Casari); Museo Nacional de Historia Natural, Santiago, Chile (MNNC – M. Elgueta); Universidade do Rio Janeiro, Museu Nacional, São Cristovão, Brazil (MNRJ – M. Monné); Museu Entomológico Fritz Plaumann, Seara, Brazil (MEFP – E. Zonta); University of Georgia Collection of Arthropods, Athens, USA (UCGA – R. Hoebeke); Palacky University Olomouc, Czech Republic (UPOL); Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (ZMB – B. Jaeger); Zoological Museum of Lomonosov University, Moscow, Russia (ZMLM – N. Nikitsky).

RESULTS

The phylogenetic reconstruction using unweighted parsimony resulted in 22 shortest trees (length, L=243 steps; consistency index, CI=39.5; retention index, RI=77) the strict consensus of which is presented here (Fig. 1A) with unambiguous synapomorphies mapped on branches. Alternative ACCTRAN and DELTRAN optimizations showed moderately different character state sets (Figs. S2A, S1B). Subsequent implied weighted (IW) analyses retrieved a single tree of two largely congruent topologies under different concavity constant values (Figs. S1A, S1B). Similar patterns were obtained by BA and ML analyses (Figs. 1B, S5).

Inferred trees recovered the monophyly of the cladodine lineage (*Cladodes*, *Ledocas*, *Nyctocrepis* (incl. *Fenestratocladodes*), *Dodacles*, *Dryptelytra* plus two new genera) with moderate to high support in MP analyses (Fig. 1A, BrS=7, SR=93, BS=87) and strong support in model-based approaches (Figs. 1B, S5, PP=1.0, ufBS=99). *Vesta* and the tribe Vestini sensu McDermott (1966) are demonstrated to be polyphyletic. The Oriental type species *Vesta chevrolatii* together with American *V. thoracica* are identified sister to Photurinae, while other species formerly placed in *Vesta*, are nested within the cladodine lineage. The Photurinae + *Vesta* clade is strongly supported in BA and ML trees (PP=0.92, ML=92), while the support is deficient in MP analyses (BrS=1, SR/BS=67/64). The clade is retrieved among early splits diverging from the backbone of Lampyridae before the distinction of the cladodine lineage (Figs. S1A, S1B, S3, S5).

Although deep level relationships are weakly supported, implied weighted and ML trees reveal that the cladodine lineage split off simultaneously with the distinction of Lampyrinae (Figs. S1A, S1B, S5). Our phylogenetic inference identifies *Ledocas* among basal lineages (Figs. S1A, S1B, S3) being recovered as a single clade with low support only in ML analysis (ufBS=78, Fig. S5) and on the majority-rule consensus tree from the initial unweighted MP analyses (Fig. S3). In other trees, *Ledocas* is rendered paraphyletic being split into 3 clades: 1. *L. remixtus* + *L. emissus*, 2. *L. xanthomus* + *L. pikillactanus* **sp.n.**, and 3. *L. parallelus* + *L. detectus* (Figs. 1A, 1B, S1A, S1B). The genus *Cladodes* sensu McDermott (1966) is retrieved as polyphyletic. Therefore, *Cladodes sensu stricto* restricted to *C. flabellatus*, *C. cincticollis*, and *C. melanurus* is here introduced (BrS=16, BS/SR=99/99, PP=1.0, ML=99) and *Nyctocrepis* (BrS=3, BS/SR=89/92, PP=0.93, ML=100) is revalidated. In addition, our analyses reveal a robust crown clade denoted as the *Dodacles* lineage (BrS=5, BS/SR=74/86, PP=1.0, ML=99, Figs. 1A, 1B) splitting mostly into two groupings.

DISCUSSION

PHOTURINAE + *VESTA* AND THE SPLIT OF VESTINI

Vesta was originally assumed to be related to *Cladodes*, *Dodacles*, and *Dryptelytra* within the subfamily Lamprocerinae (Olivier, 1907; 1910). McDermott (1964) transferred these genera to his newly erected Vestina within Lampyrinae and later placed the subtribe in the redefined Amydetinae (McDermott, 1966). Nevertheless, phylogenetic analyses performed in the last decades have never recovered such subfamily-level assignments. Morphological trees (Jeng, 2008, unpublished) rejected close relationships of *Vesta chevrolatii* and *Cladodes*, identifying their superficial similarities as putative homoplasies. Earlier molecular analyses included either Sumatran *Vesta* (Bocakova *et al.*, 2007) or Photurinae (Stanger-Hall *et al.*, 2007). Both taxa were included in the recent total evidence analysis as well as the anchored hybrid enrichment approach (Martin *et al.*; 2017, 2019), which revealed a close relationship between *Vesta* and Photurinae, with high support.

Previous assumptions on the relationships of *Vesta* and *Cladodes* were based on external similarities, particularly flabellate antennae and abdominal terga acutely lateroapically lobed. Nevertheless, when examined in detail, antennal branches of *Vesta* are compressed dorsoventrally, while lamellae of cladodines are flattened laterally resulting in fan-like antennal arrangements. Furthermore, *Vesta* significantly differs from *Cladodes* and allies in its relatively short and rounded laterotergite, a character that has been overlooked, while the laterotergite is well-developed and trapezoidal in cladodine taxa.

McDermott (1964, 1966) pointed out that Southeast Asian and South American species of *Vesta* may represent two different genera and listed Oriental and Neotropical species separately. The distinction between these lineages was supported by recent morphological analyses (Jeng, 2008, unpublished). Our study, which included the type species *Vesta chevrolatii* from Java confirms that *Vesta* is more closely related to Photurinae (Figs. 1A, 1B) than to *Cladodes*.

Amongst other characters, special consideration should be given to the male genitalia of *Vesta* species, particularly to the presence of a thin rod-like projection attached to each paramere laterally. This character is absent in cladodine taxa, but it might be taken as possible evidence of common ancestry between *Vesta* and some Photurinae. Resemblances between slender aedeagal appendages of *Vesta* and *Photuris* were first recorded by Green (1959). However, these rod-like processes arise from the paramere midlength in *Vesta* (Figs. 9N1–N2), while are attached to the phallobase in *Photuris*. Moreover, these are absent in the photurine *Pyrogaster* and *Bicellonycha*. Thus, the different attachment points of the rods in *Vesta* and *Photuris* rather indicate parallel evolution than shared ancestry. Nevertheless, the formation of such appendages could be a result of homologous mating behavior, but such comparisons remain elusive due to the lack of field observations of *Vesta* species.

An aedeagus with slender fragile attachments was until recently reported in Lampyridae only in *Photuris* (Green 1959, p. 93; McDermott, 1962; Souto *et al.*, 2018). A recent study (Silveira *et al.* 2016) revealed the presence of similar digitiform processes attached ventrobasally to each paramere also in *Scissicauda.* Nevertheless, the shape of phallus and the strongly twisted phallobase reflect the highly derived position of *Scissicauda* among the Lampyrinae, as confirmed by the most recent phylogenomic study (Martin *et al*., 2019). In addition, the tips of the parameres in some Lampyrini are similarly membranous, elongated, and slender (e.g. *Lampyris* Geoffroy, 1762; see Kazantsev, 2010). Therefore, the meaning of these similarities should be considered under close scrutiny in taxonomic assessments.

Close relationships of *Vesta* and Photurinae is supported by three unambiguous synapomorphies: (terminal maxillary palpomere fusiform, with a membranous inner edge opening (character 15, state 1); terminal labial palpomere boomerang-shaped or at least subtriangular (character 18, state 3); and abdomen with laterotergite sclerotized and its outer margins rounded (character 40, state 2). The blatant morphological differences observed between *Vesta* and the other Photurinae could be the outcome of divergence related to the predatory habits seen in the latter (Souto et al, 2018).

CLADODINE LINEAGE

After the placement of *Vesta* in Photurinae, the remaining genera of Vestini became unclassified in Lampyridae and the concept of Amydetinae sensu McDermott (1966) was challenged. Therefore, *Cladodes* and related genera proposed here as cladodine lineage, are investigated. The monophyly of the group (see below) is supported by 7 unambiguous synapomorphies (Fig. 1A), particularly: the eye inner margin rounded in frontal view, prosternum at least as long as pedicel, pygidium with acute lateroapical corners, the basally constricted and sinuose phallus bearing short basal struts curved outwards.

PARAPHYLETIC *LEDOCAS*

Most of our trees recovered *Ledocas* as paraphyletic and shared characters were recognized as symplesiomorphies. The genus was only corroborated in ML analyses with deficient support. Here we apply a conservative approach and keep *Ledocas* as a single genus until the group is thoroughly examined. Amongst other cladodines it is distinctive by parallel-sided pronotum and elytra and the shape of male genitalia, particularly straight parameres about as long as the phallus. Interestingly enough, all species of *Ledocas* as here defined, dwell in relatively dry areas of the South American Dry Diagonal, namely the Caatinga (Northeastern Brazil) and the Argentinian Semi-desert (e.g. La Rioja region).

CLADODES S.S., *NYCTOCREPIS*

Cladodes traditionally served as a “collective genus” and was recovered polyphyletic with respect to *Ledocas*, *Dodacles*, and *Dryptelytra*. To resolve this conundrum, here we introduce the concept of *Cladodes s.s.* from Chile and Peru and withdraw *Nyctocrepis* from synonymy. All genera are tightened up and two new genera are proposed. The herein defined *Cladodes s. s.* includes the type species *C. flabellatus* and two species hitherto placed in *Vesta*: *C. cincticollis* and *C. melanurus*. To accommodate *Nyctocrepis demoulini* and related Brazilian species, *Nyctocrepis* is here revalidated and its generic status reestablished. Although originally erected within *Cladodes*, the monotypic subgenus *Fenestratocladodes* Pic, 1922 appears within, or sister to *Nyctocrepis demoulini* + *N. stellata* clade and consequently is here placed in *Nyctocrepis*. Phylogenetic relationships of many unstudied *Cladodes* remain unsolved. The two other species analyzed, *Cladodes ater* and *C. gloriosus* were alternatively recovered sister to *Dodacles* lineage and are temporarily kept in *Cladodes* although their relationships to the *C. flabellatus* clade were rejected.

THE *DODACLES* LINEAGE

Members of the *Dodacles* lineage can be easily differentiated from other cladodine genera by complex rearrangements of male antennae with the increasing length of antennomeres III–X, while the length of antennal lamellae is decreasing towards the apex (Figs. 3E–3I). The *Dodacles* lineage was composed of two clades, the first one (incl. *Dodacles* and a new Brazilian genus) represented by robust taxa exhibiting strong almost right-angled mandibles, while the other clade included the enigmatic *Dryptelytra* with greatly dehiscent elytra and slender arcuate mandibles similar to those of small Andean species established below as another new genus (Figs. 1A, 1B). *Dodacles* lineage is supported by a single unambiguous synapomorphy, (i) length of antennal lamellae decreasing towards the apex, and 13 putative homoplasies, particularly (ii) terminal antennomere at least 5× longer than penultimate one, and (iii) metepisternum twice longer than wide. The other synapomorphies as the mandibular insertion more posterior than antennal sockets, the posterior pronotal corners rounded, median glabrous carina in the anterior third of pronotum, and the phallus with a dorsolateral keel are also characteristic of the *Dodacles* lineage, although these derived states were sometimes recorded in other genera. Members of the *Dodacles* lineage, with the exception of the Andean new genus, share several genitalic characters as phallus shorter than parameres, parameral apices bisinuate, and parameres dorsoventrally compressed.

The redefined genera *Dodacles* and *Dryptelytra*, as well as the two new genera were corroborated with high support. Species *Cladodes proteus* and *C. solieri* were usually retrieved sister to the Andean clade, although the support values were low and male genitalia characters suggest relationships to *Cladodes ater*.

TAXONOMY

Cladodinae Bocakova, Campello-Gonçalves & Silveira subfam.n.

Type genus: *Cladodes* Solier, 1849 (hereby designated).

Diagnosis. Antennae uniflabellate, fan-like, lamellae laterally compressed, long, 2.3–8× longer than antennomere length, terminal antennomere 2–5× longer than the subapical. Inner margin of eyes in frontal view rounded, frons depressed. Mandibles well-developed, overlapping, arcuate or almost right-angled. Terminal maxillary palpomere flattened. Pronotum expanded anteriorly and laterally, prosternum long, at least as long as antennal pedicel. Hind leg tarsomere 1 longer than 2. Laterotergite robust, trapezoidal. Abdominal spiracles dorsal, enclosed by back-folded sterna. Terga with posterior corners projected. Pygidium large, bisinuate to trilobed posteriorly, posterolateral corners mostly acute. Sternum VIII half as long as pygidium, bisinuate posteriorly, median projection often mucronate. Terga IX–X coalescent forming syntergite with lateral margins convergent posteriorly. Sterna II–IX visible in males, II-VIII in females. Aedeagal parameral apices bent inwards, convergent, phallobase symmetrical, phallic basal struts reaching basal third of phallobase or less, thin rod-like appendages absent, phallus basally constricted, apically convergent. Females larviform.

Included genera. *Cladodes* Solier, *Ledocas* Olivier, *Nyctocrepis* Motschulsky, *Andecladodes* **gen.n.,** *Dryptelytra* Laporte, *Brasilocladodes* **gen.n.**, *Dodacles* Olivier.

Distribution. Central and South America.

Natural history and Biogeography. Diurnal, particularly abundant in moist broadleaf rainforests and cloud forests (Silveira *et al.*, 2015). Males are slow, poor flyers, usually secret strong scents when disturbed. Widely distributed in the Amazon basin, Atlantic Rainforest, and South American Dry Diagonal (Chaco, Cerrado, and Caatinga).

Cladodes Solier, 1849

(Figs. 2A–C, 3A, 4A, 5A, 10A)

Cladodes Solier, 1849: 444. Type species. *Cladodes flabellatus* Solier, 1849: 445 (by monotypy).

Diagnosis. Eyes as wide as 1/4–1/5 head width in frontal view, interocular distance 2–3× longer than eye width in frontal view, mandibles almost semicircular. Antennal sockets separated by 3/4, 1/3, or 1/4 clypeus width in frontal view. Branch of antennomere III at least 3/4 as long as IV. Pronotum semicircular or almost triangular, translucent spots absent. Abdominal terga with corners strongly projected, sternum VIII bisinuate, median projection acute, 3–3.5× longer than corners. Pygidium 1.5×

wider than long, with central portion and lateral corners of the same length or with central region rudimentary to absent. Phallus ⅓ longer to ⅓ shorter than parameres. Parameres with lateral margins almost parallel-sided, sometimes slightly emarginate medially, strongly convergent posteriorly, with posterior margin acute or rounded.

Species included. *Cladodes flabellatus* Solier, 1849, *C. cincticollis* (Blanchard, 1846) **comb.n.**, *C. melanurus* (Laporte, 1833) **comb.n.**, *C. ater* (Solier, 1849), *C. gloriosus* (Olivier, 1885), *C. proteus* Olivier, 1894 **comb.n.**, *C. solieri* Kirsch, 1865.

Distribution. Bolivia, Brazil, Colombia, Chile, Peru.

Comments. Cladodes proteus Olivier, 1894 was transferred to *Ledocas* by McDermott (1966) and is here placed in *Cladodes* again. *Cladodes cincticollis* (Blanchard, 1846) **comb.n.** and *C. melanurus* (Laporte, 1833) **comb.n.** are transferred from the genus *Vesta*. Resolving the relationships of *Cladodes ater*, *C. gloriosus*, *C. proteus*, and *C. solieri* would require more extensive sampling. Although male genitalia of the four species show several similarities, the absence of antennal rearrangement in *C. gloriosus* and *C. ater* resulted in a nested tree pattern. Therefore, the taxonomic placement of the group is difficult and the species are provisionally kept in *Cladodes*.

Cladodes *sensu stricto*

(Figs. 2A–B, 3A, 4A, 5A, 10A)

Diagnosis. Frontoclypeal suture membranous, pronotum triangular, prothorax with the suture between hypomeron and prosternum fused to obliterate, metepisternum 2× longer than wide, pygidium with median apical projection at least 1.5× wider than lateral projection.

Species included. Cladodes flabellatus Solier, 1849, *Cladodes cincticollis* (Blanchard, 1846) **comb.n.**, *Cladodes melanurus* (Laporte, 1833) **comb.n.**

***Ledocas* Olivier, 1885**

(Figs. 2D, 3B–C, 4B–C, 5B–C, 6A, 7A–B, 8A–D, 9A–B, 10B1–C2)

Ledocas Olivier, 1885: 136. Type species. *Ledocas parallelus* Olivier, 1885 (by monotypy).

Diagnosis. Pronotum and elytra subparallel-sided. Eyes small to medium-sized, mandibles semicircular, never right-angled, antennae uniflabellate, fan-like, branches of median antennomeres about 4× longer than the antennomere body, flabella of antennomere III markedly shorter than the following branches, translucent spots on pronotum absent. Abdomen strongly laterally lobed, sternum VIII bisinuate, mucronate, pygidium usually as long as wide, widest medially, with median extension about half as long as the lateral corners, lateral margins rounded. Male genitalia small, parameres as long as phallus, parameral apices simply straight.

Species included. *Ledocas parallelus* Olivier, 1885, *Ledocas detectus* Olivier, 1908, *Ledocas xanthomus* Olivier, 1894, *Ledocas emissus* (Olivier, 1908) **comb.n.,** *Ledocas remixtus* (Olivier, 1911) **comb.n.,** *Ledocas pikillactanus* **sp.n.**

Distribution. Argentina, Brazil, Peru, Venezuela, Paraguay.

***Ledocas pikillactanus* sp.n.**

(Figs. 2J, 3C, 4C, 5C, 6A, 7A–B, 8C–D, 9B, 10C1–C2)

Holotype, male, “PERU: Cuzco prov., Pikillacta, 3200 m, 24. 1. 2011, K. Dolezel leg.” (UPOL). *Paratypes*, PERU: the same data (1 male, UPOL); Cuzco prov., Pikillacta, X.1994, P. Gerhard col. (4 males, MZSP).

Diagnosis. Whole body black, only humeral spots brightly orange. Anterior margin of pronotum semicircular, with lateral margins almost parallel-sided (whereas they are arcuately produced laterally in *L. xanthomus* Olivier, 1894), posterior corners right-angled. Elytra parallel-sided, orange humeral spots small (while as long as 1/5 of elytral length and as wide as 1/3 of humeral width in *L. xanthomus*), phallus as long as parameres.

Description. Body black, orange humeral spots small, as long as 1/10 of elytral length and as wide as 1/5 of humeral width, paired luminous spots on sternum VIII and pygidium pale. Head with small eyes, interocular distance over 2× longer than eye diameter. Antennae short (Fig. 27), reaching humeral region, branches of antennomeres III–X robust, spathuliform, branches of antennomeres IV–X about 4× longer than antennomere body, lamella of antennomere III a quarter shorter. Mandibles strong, arcuate (Fig. 34). Labrum fused to clypeus, deeply bilobed, with each lobe bearing a group of robust setae, projected anteriorly. Maxillary palps slender, terminal palpomere 3× longer than penultimate one, labial palps with terminal palpomere ovate (Fig. 34), both maxillary and labial palps setose.

Pronotum with anterior margin regularly semicircular, anterior corners absent, lateral margins almost parallel-sided, sometimes slightly convergent backward (Figs. 3, 5). Discal area elevated, finely punctured, glabrous, anterior and lateral edges of pronotum strongly punctured. Scutellum with lateral margins moderately convergent backward, apex obtusely triangular. Elytra about 3× longer than humeral width, widest in elytral quarter. Each elytron with 4 weak longitudinal costae, costa 4 diminishing in distal third, obsolete, marginal costa absent, sutural margins dehiscent in distal 2/5. Abdominal terga laterodistally lobed (Figs. 4, 73). Sternum VIII with conical median point and small, well-marked, paired luminous spots (Fig. 41). Apical margin of pygidium trilobite, median extension rounded, short, half as long as slender lateral lobes, their utmost portion rounded (Fig. 40), syntergite asymmetrical (Fig. 42). Male genitalia symmetrical, distal half of phallus almost parallel-sided (Figs. 86–87) with apex uncleft. Parameres indistinctly shorter than phallus, their dorsobasal fused projection short, about half as long as phallobase. Female unknown. Body length: 13–15 mm, humeral width: 3.5–4 mm.

Etymology. Derived from Pikillacta, in the eastern valley of Cuzco, Peru.

Distribution. Peru.

Nyctocrepis Motschulsky, 1853

(Figs. 2E–F, 3D, 4D, 5D, 7E, 8S–T, 9J, 10D1–D2)

Nyctocrepis Motschulsky, 1853: 33. Type species. *Nyctocrepis demoulini* Motschulsky, 1854:10 (original designation).

Diagnosis. Antennal branches shorter than in other cladodine genera, median lamellae only 2.3–3.5× longer than antennomere itself. Labium with apical palpomere of the right triangle shape. Anterior margin of pronotum rounded (triangularly produced forwards in *Cladodes* s. str.), submarginal punctures on anterolateral corners of pronotum fused, forming vitreous spots, deeper than lateral punctures, phallus as long as parameres.

Species included. *Nyctocrepis demoulini* Motschulsky, 1854, **comb.n.,** *N. stellata* (Gorham, 1880), **comb.n.**, *N.* (*Fenestratocladodes*) *malleri* (Pic, 1935), **comb.n.**

Distribution. Brazil.

Comments. Considering the absence of triangular pronotum in *Fenestratocladodes* (the synapomorphy of *Cladodes* s. str.) and phallus as long as parameres, the subgenus *Fenestratocladodes* is here placed in *Nyctocrepis*.

Dodacles lineage

Diagnosis. The lineage is characteristic by (i) rearranged male antennae having antennomeres III–X increasing in length, while the length of lamellae is decreasing towards the apex (lamella of antennomere III is the longest). Among other synapomorphies belong (ii) terminal antennomere at least 5× longer than penultimate one, (iii) mandibular insertion in lateral view more posterior than antennal socket, and (iv) metepisternum 2.4–3× longer than wide.

Comments. Regardless of the high support and several identified synapomorphies, the *Dodacles* lineage is not established here formally as a tribe. The remaining cladodine clades are gradually splitting off rendering such a group paraphyletic, the basal tree pattern was unstable with low support.

Dodacles Olivier, 1885

(Figs. 2G3I–K, 4I–K, 5G, 7F–G, 8M–R, 9G–I, 10G1–H2, 10K1-K3)

Dodacles Olivier, 1885: 136. Type species *Dodacles elegans* Olivier, 1885: 141 (subsequent designation by McDermott, 1964).

Diagnosis. Head with medium-sized eyes, pronotum covering the head and basal ¼ of antennae (Figs. 18–23), mandibles right-angled, antennae flabellate, lamellae slender, not spathuliform, length of lamellae decreasing towards the apex. Pronotum and elytra covered only with minute dense secondary pubescence. Abdomen strongly lobed, pygidium almost as long as wide, sternum VIII bisinuate to trilobate, with the median triangular point about as long as third of the sternal length, the apex of phallus simple, parameral apices moderately curved.

Species included. *Dodacles elegans* (Olivier, 1885), *D. niger* (Pic, 1931), **comb.n.**, *D. lateralis* (Pic, 1931), **comb.n.**, *D. erebeus* Olivier, 1896.

Distribution. Brazil, Ecuador, Paraguay, Peru, Nicaragua, Panama.

Brasilocladodes **gen.n.**

(Figs. 2H–I, 3G, 4G, 8U–X, 9K–L, 10I1–J3)

Type species. *Lampyris illigeri* Kirby, 1818.

Diagnosis. Head with medium-sized eyes, anterior edge of pronotum covering head including basal antennomeres, mandibles stout, (i) almost right-angled, antennae uniflabellate, lamellae slender, not spathuliform, branch of antennomere III the longest of all, abdomen strongly lobed, pygidium transverse, bisinuate, sternum VIII bisinuate with short median triangular point, phallus apically cleft, parameral apices strongly curved in ventral view. Amongst other characters belong: (ii) submarginal punctures on anterolateral pronotal corners fused, forming vitreous spots, (iii) deeper than lateral punctures, (iv) ventral margin of hypomeron strongly sinuose, (v) elytral costae II and III subparallel with suture, (vi) posterior corners of abdominal sterna V–VII rounded, (vii) lateroapical corners of pygidium broadly rounded, and (viii) pygidium with medioapical projection wider than the lateral ones.

Etymology. The prefix is derived from Brazil, the country of origin of included species. The root word "*cladodes*" refers to relationships to other Cladodinae. Gender masculine.

Distribution. Brazil.

Species included. *Brasilocladodes illigeri* (Kirby, 1818), **comb.n.**, *Brasilocladodes delalandei* (Olivier, 1885), **comb.n.**, *Brasilocladodes carinatus* (Olivier, 1899), **comb.n.**

Dryptelytra Laporte, 1833

(Figs. 3H, 3L, 4H, 4L, 5H–I, 7H, 8I–L, 9E–F, 10L1–M3)

Dryptelytra Laporte, 1833: 128. Type species *Dryptelytra cayennensis* Laporte, 1833:129 (by monotypy).

Diagnosis. Elytra considerably dehiscent on inner margin, each elytron narrowed in the basal quarter, consequently, elytra separated by elytral width in distal half. Head with eyes about as long as interocular distance, pronotum extended over the head and base of antennae forward, mandibles slender, simply arcuate (not right-angled). Antennae flabellate, apical margin of antennomere I rounded, slightly hornlike, lamellae very slender (not spathuliform), their length decreasing apically, the extent of inner sulcus on the internal margin of apical maxillary palpomere 1/2 or less. Pronotum and elytra with long (primary) pubescence. Abdomen strongly lobed, abdominal sternum VII widened posteriorly, pygidium considerably widened distally, widest in the distal quarter, mesiodistal point of sternum VIII broad and short, apex of phallus cleft, parameral apices curved, acute.

Distribution. French Guiana, Bolivia, Brazil, Colombia, Ecuador, Venezuela, Paraguay, Peru, Panama.

Dryptelytra pampahermosae, **sp.n.**

(Figs. 3L, 4L, 5I, 7H, 8K–L, 9F, 10M1–M3)

Holotype, male, “PERU, 20 km NW San Ramon, Pampa Hermosa, 1250m, 11°07.11’S 75°22.04’W, 22 Nov 2012, KJMB lgt.” (UPOL).

Diagnosis. Body largely yellow, posterior half of elytral margins black (Fig. 24), tarsi and adjacent third to half of tibiae black, parameres of constant width medially, half of their basal width, parameral apices acuminate, not tubuliform. Species close to *D. brevivittis* Pic, 1911 from which it can be differentiated by upper portions of tibiae black.

Description. Largely yellow, only head, mouthparts, dorsal margins of antennae, apical portion of antennae ventrally, whole tarsi and adjacent 1/3 of tibiae, and lateral longitudinal stripes on elytra black, antennal tubercles testaceous. Head with eyes mediocre (Fig. 25), interocular distance 1.1× longer than eye diameter. Antennae short, reaching humeral region, bicolored, apical 2/3 of antennal lamellae black dorsally, extent of yellow coloration larger ventrally (Fig. 32) occupying basal 2/3.

Antennomere III with lamella largely black, other lamellae gradually bicolored with internal portion of lamellae yellow and tenuous margins black. Frontoclypeus and labrum with longitudinal blackish stripe medially. Pronotum with anterior margin semicircularly produced forwards (Fig. 24). Elytra bicolored, with basal 2/5, longitudinal sutural stripe and apex yellow, with black longitudinal stripe in 3/5–1/7 on outer margins of elytra (Fig. 24). Sternum VIII with broadly attached, short, median point, lateroapical margins of sternum VIII almost straight, semicircular emarginations near median point absent (Fig. 71). Pygidium with lateral projections almost right-angled (Fig. 70). Apex of sternum VIII spoon-like, as long as ¼ of its length, basal tenuous projections 3× longer (Fig. 72). Male genitalia with long parameres, phallus 1/3 shorter (Figs. 115–117). Parameres broad basally, tapered to half width in basal ¼–1/3, parameral width constant in median portion, parameral apices acuminate. Body length: 11 mm, humeral width: 3.5 mm. Female unknown.

Etymology. Named in reference to the type locality.

Distribution. Peru.

Andecladodes **gen.n.**

(Figs. 3E–F, 4E–F, 5E–F, 6B–C, 7C–D, 8E–H, 9C–D, 10E1–F2)

Type species. *Andecladodes cosangensis* **sp.n.**

Diagnosis. Antennomere I stout with a small horn as long as half of antennomere width, length of antennomeres III–X increasing distally, branches of antennomeres III–X gradually decreasing, clypeus and genae protruding anteriorly, mandibles large, labrum reduced laterally, basally half as long as the distance of mandibular insertion points, extent of inner sulcus on internal margin of apical maxillary palpomere 1/2 or less, prothorax with ventral margin of hypomeron strongly sinuose, posterior corners of abdominal sterna V–VII rounded, median apical projection of pygidium wider than lateral projections, phallus 1/6 longer than parameres, apex of phallus in lateral view well delimited, ventroapical cleft absent, parameres simply straight, subcylindrical.

Etymology. The generic name is built from the root word "*Cladodes*" adding the prefix "*Ande*" indicating the genus geographic range. Gender is masculine.

Species included. Andecladodes cosangensis **gen.n.**, **sp.n.**, *Andecladodes ovalis* **sp.n.**

Distribution. Ecuador.

Andecladodes cosangensis **sp.n.**

(Figs. 3F, 4F, 5F, 6B, 7C, 8E–F, 9C, 10E1–E2)

Holotype, male, "ECUADOR, Napo Prov., Cosanga, 1900–2100 m, 0^{o} 36' S 77^{o} 53' W, Bolm lgt. 12–16. Dec 2010 (UPOL).

Diagnosis. Body black, only elytral apex brightly orange (Fig. 8), elytra arcuately acuminate distally, phallus apically bulbous.

Description. Whole body black, only apex of elytra, and a broad medial stain in basal half of abdomen orange. Margin between black and orange elytral coloration arcuate. Head with small eyes, interocular distance 1.5× longer than eye diameter. Antennae short, reaching humeral area, antennomere I stout, with a short horn-like extension as long as half of antennomere width, antennomeres II and III short, length of antennomeres III–X gradually increasing. Branches of antennomeres III–X very slender, lamella of antennomere III the longest, length of lamellae decreasing towards apex. Mandibles slightly falcate (Fig. 35). Labrum connate to frontoclypeus, tongue-shaped, forming small, rather translucent, median extension. Clypeolabral suture indistinct, absent. Maxillary palps slender, terminal palpomere elongate, with apex compressed. Labial palps 3-segmented, minute, terminal palpomere diminishing apically, both maxillary and labial palps setose. Pronotum trapezoidal, anterior and lateral margins moderately arcuate, anterior corners widely obtuse (Fig. 9). Discal area slightly elevated, almost glabrous, covered with fine primary pubescence, anterior and lateral edges of pronotum strongly punctured. Scutellum triangular with apex widely obtuse. Elytra about 2× longer than humeral width, widest in elytral quarter, moderately acuminate distally. Longitudinal costae largely obsolete, costa 1 present only in basal half, costa 2 and marginal costa fully developed, costae 3 and 4 unclear, sutural margins dehiscent in apical 1/5. Sternum VIII with median point short, slender (Fig. 44). Pygidium with lateral margins parallel-sided in distal half, median extension large, moderately longer than the lateral (Fig. 43), syntergite asymmetrical, tergum IX provided with a single, unpaired, spine laterally, suture between tergum IX–X visible, apex of sternum IX moderately emarginated (Fig. 45). Male genitalia with phallus long, broad in basal half, apex bulbous (Figs. 88–90). Body length: 12 mm, humeral width: 4.6 mm, width in elytral quarter: 5.2 mm. Female unknown.

Etymology. Named in reference to the location of finding.

Distribution. Ecuador.

Comments. *Andecladodes cosangensis* **sp.n.** resembles *Dodacles elegans* by the elytra acuminate distally. Nevertheless, the structure of antennae (antennomere I shortly horned, length of antennomeres increasing distally and length of branches decreasing distally) and the shape of male genitalia demonstrated *A. cosangensis* **sp.n.** is closely related to the following new species with broadly widened, oval elytra. Therefore, the acuminate shape of elytra of *A. cosangensis* **sp.n.** and *Dodacles elegans* is assumed to have evolved as a result of convergent evolution.

Andecladodes ovalis **sp.n.**

(Figs. 3E, 4E, 5E, 6C, 7D, 8G–H, 9D, 10F1–F2)

Holotype, male, “ECUADOR, Baron”, without other data (MNHN).

Diagnosis. Body oval, widest in elytral midlength, basal half of elytra laterally yellow (Fig. 10), antennae with slender lamellae, their length decreasing distally, posterior corners of pronotum obtuse.

Description. Body dark brown, only basal half of each elytron laterally yellow, and luminous spots on sternum VIII and pygidium pale. Head with small eyes, interocular distance 1.6× longer than eye diameter. Antennae short, reaching humeral areas. Antennomere I stout, triangular, with apex prolonged in a short blunt horn, as long as half of antennomere width. Antennomeres II and III very small, lamellae long, very slender. Length of antennomeres III–X increasing to apex, while length of their lamellae decreasing apically (lamella of antennomere III the longest). Mandibles stout, arcuate to falcate (Fig. 36), labrum connate to frontoclypeus, anterior margin weakened, clypeolabral suture inconspicuous. Maxillary palps with terminal palpomere broad, about 1.5× longer than subapical palpomere, more or less compressed, labial palps with terminal palpomere elongate, narrowed apically, both palps setose. Pronotum with anterior margin almost semicircular, lateral margins moderately divergent backwards (Fig. 11), discal area elevated, finely pubescent, anterior and lateral edges of pronotum with broad punctures, posterior corners obtuse. Scutellum triangular. Elytra broadly oval, about 1.8× longer than humeral width, widest in elytral half. Longitudinal costae largely obsolete, costa 1 absent in distal half, costa 2 fully developed, costae 3 and 4 indistinct, marginal costa present, as strong as costa 2, sutural margins dehiscent. Pygidium widened apically, median extension as long as the lateral (Fig. 46). Median point of sternum VIII broad, (Fig. 47), sternum IX emarginated distally (Fig. 49). Syntergite asymmetrical. Phallus broadly widened in basal third, gently extended in distal 1/5 (Figs. 91–93), apex inconspicuously cleft. Body length: 16 mm, humeral width: 6.7 mm, width in elytral midlength: 7.6 mm. Female unknown.

Etymology. Named in reference to the body outline.

Distribution. Ecuador.

Key to genera of Cladodinae

1. Flabellum of antennomere III markedly shorter than IV, antennomeres III–X of same length or increasing in length up to midlength 2

– Flabellum of antennomere III the longest of all, length of lamellae of antennomeres III–X gradually decreasing towards apex, length of antennomeres III–X increasing distally. . . . . 6 (*Dodacles* lineage)

2. Outline parallel to slightly elliptic, elytral marginal costa facing downwards in ventral view 3

– Outline broadly elliptic, marginal costa facing outwards in ventral view 5

3. Clypeus connate to frons, pronotum anteriorly rounded 4

– Clypeus connected to frons by a membrane, pronotum almost triangular . . . . *Cladodes s.s.*

4. Flabellum of antennomere III up to half as long that of IV, syntergite with paired, horn-like appendages, phallus with paired, longitudinal dorsal keels . . . . *Cladodes ater*

– Flabellum of antennomere III slightly shorter than IV, syntergite lacking paired, horn-like appendages, phallus without paired, longitudinal dorsal keels . . . . *Ledocas*

5. Clypeus entirely connate to frons, anterolateral region of pronotum with well-delimited punctures of similar size (not forming rudimentary vitreous spots), phallus lacking paired, longitudinal dorsal keels . . . . *Cladodes gloriosus*

– Clypeus usually connected to frons by membrane – if connate, just at central third, anterolateral region of pronotum with punctures of different sizes that often fuse to form rudimentary vitreous spots, phallus with paired, longitudinal dorsal keels . . . . *Nyctocrepis*

6. Scape with inner margin acuminate, often forming a well-defined spine, mandibles arcuate 7

– Scape rounded, mandibles right-angled or almost so 8

7. Elytral inner margin straight to slightly dehiscent, pygidium with posterior corners longer and wider than median, sometimes with prosternum fused to hypomera, sometimes with phallus longer than paramere . . . . *Andecladodes* **gen.n.**

– Elytral inner margin moderate to strongly dehiscent, pygidium with posterior corners shorter and narrower than median, prosternum never fused to hypomera, phallus always shorter than paramere . . . . *Dryptelytra*

8. Pygidium transverse, posterior corners feebly developed and rounded, elytron never dehiscent . . . . *Brasilocladodes* **gen.n.**

– Pygidium as long as wide, posterior corners well-developed and acute, elytron very slightly to strongly dehiscent . . . . *Dodacles*

List of genera of Cladodinae subfam.n.

Cladodes Solier, 1849
= *Rhipidophorus* Solier, 1849
Ledocas Olivier, 1885
Nyctocrepis Motschulsky, 1853
    subgenus *Fenestratocladodes* Pic, 1935
Dodacles Olivier, 1885
Brasilocladodes **gen.n.**
Dryptelytra Laporte, 1833
Andecladodes **gen.n.**

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REFERENCES

Barber HS. 1923. A remarkable wingless glow-worm from Ecuador. *Insecutor Inscitiae Mentruus* **11**: 191–194.

Bocakova M, Bocak L, Hunt T, Teraväinen M, Vogler AP. 2007. Molecular phylogenetics of Elateriformia (Coleoptera): evolution of bioluminescence and neoteny. *Cladistics* **23**: 477–496.

Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CHC, Newton AF, Reid CAM, Schmitt M, Ślipiński SA, Smith ABT. 2011. Family-group names in Coleoptera (Insecta). *ZooKeys* **88:** 1–972.

Branham MA, Wenzel JW. 2003. The origin of photic behavior and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). *Cladistics* **84**: 565–586.

Bremer K. 1994. Branch support and tree stability. *Cladistics* **10**: 295–304.

Cicero JM. 1988. Ontophylogenetics of cantharoid larviforms (Coleoptera: Cantharoidea). *The Coleopterists Bulletin* **42**: 105–151.

Constantin R. 2010. Les genres de Cantharidae, Lampyridae, Lycidae et Telegeusidae de Guyane française (Coleoptera, Elateroidea). *ACOREP-France: Coléoptères de Guyane* II, 1–45.

Crowson RA. 1972. A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families, Cneoglossidae and Omethidae. *Revista de la Universidad de Madrid. Estudios de Entomologia* **21**: 35–77.

Goloboff PA. 1993. Estimating character weights during tree search. *Cladistics* **9**: 83–91.

Goloboff PA, Farris JS, Nixon K. 2008. TNT: a free program for phylogenetic analysis. *Cladistics* **24**: 774–786.

Green JW. 1959. Revision of the species of *Microphotus*, with an emendation of the Lampyrini (Lampyridae). *The Coleopterists Bulletin* **13**: 80–96.

Janisova K, Bocakova M. 2013. Revision of the subfamily Ototretinae (Coleoptera: Lampyridae), *Zoologischer Anzeiger* **252**: 1–19.

Jeng ML. 2008. Comprehensive phylogenetics, systematics, and evolution of neoteny of Lampyridae (Insecta: Coleoptera). PhD Dissertation. University of Kansas, Lawrence, KS, USA. 388 pp.

Jeng ML, Yang PS, Engel MS. 2007. The firefly genus *Vesta* in Taiwan (Coleoptera: Lampyridae). *Journal of the Kansas Entomological Society* **80**: 265–280.

Jeng ML, Yang PS, Satô M. 1998. The genus *Cyphonocerus* (Coleoptera, Lampyridae) from Taiwan and Japan, with notes on the subfamily Cyphonocerinae. *Elytra*, Tokyo **26:** 379-398.

Kazantsev S. 2010. Fireflies of Russia and adjacent territories (Coleoptera: Lampyridae). *Russian Entomological Journal* **19:** 187–208.

Kundrata R, Bocakova M, Bocak L. 2014. The comprehensive phylogeny of the superfamily Elateroidea (Coleoptera: Elateriformia). *Molecular Phylogenetics and Evolution* **76**, 162–171.

Lawrence JF, Newton AF. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references, and data on family-group names). *In* J. Lawrence, J. F., Pakaluk and S. A. Ślipiński (Eds.), Biology, phylogeny, and classification of Coleoptera. Museum i Instytut Zoologii PAN, Warzawa, pp. 779-1092.

Lewis PO. 2001. A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data. *Systematic Biology* 50(6):913–925.

Maddison WP, Maddison DR. 2018. Mesquite: a modular system for evolutionary analysis. Version 3.51. http://www.mesquiteproject.org

Martin GJ, Branham MA, Whiting MF, Bybee SM. 2017. Total evidence phylogeny and the evolution of adult bioluminescence in fireflies (Coleoptera: Lampyridae). *Molecular Phylogenetics and Evolution* **107**: 564–575.

Martin GJ, Stanger-Hall KF, Branham MA, Silveira LFL, Lower SE, Hall DW, Li X.-Y, Lemmon, AR, Lemmon EM, Bybee SM. 2019. Higher-Level Phylogeny and Reclassification of Lampyridae (Coleoptera: Elateroidea). *Insect Systematics and Diversity* 3(6): 11; 1–15.

McDermott FA. 1962. Illustrations of the aedeagi of the Lampyridae (Coleoptera). *The Coleopterists Bulletin* **16**: 21–27.

McDermott FA. 1964. The taxonomy of the Lampyridae (Coleoptera). *Transactions of the American Entomological Society* **90**: 1–72.

McDermott FA. 1966. Lampyridae. 1–149. In: Steel, W. O. (Ed.) Coleopterorum Catalogus Supplementa, pars 9. Uitgeverij Dr. W. Junk, Gravenhage, Netherlands.

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R. 2020. IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. *Molecular Biology and Evolution*, 37(5): 1530–1534.

Nascimento EA, Bocakova M. 2017. A revision of Neotropical genus Eurrhacus (Coleoptera: Lycidae). *Annales Zoologici* **67**: 689-697.

Nixon KC. 2002. WinClada ver. 1.0000. Published by the author, Ithaca, NY, USA.

Olivier E. 1907. 53me fascicule. Coleoptera. Fam. Lampyridae. 1–74. *In*: Wytsman P. A. (Ed.) Genera Insectorum. Vol. VIII. Verteneuil & Desmet, Bruxelles. [In French]

Olivier E. 1910. Lampyridae. 1–68. *In*: Schenkling, S. (Ed.) Coleopterorum Catalogus, pars 9. W. Junk, Berlin, Germany. 68 pp. [In French]

Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Ohna SH, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. *Systematic Biology*, 61(3):539–542.

Silveira LFL, Bocakova M, Mermudes JRM. 2015. Taxonomy of the Brazilian firefly *Cladodes illigeri* (Coleoptera, Lampyridae): morphology and new records. *Iheringia, Série Zoologia* **105**: 359–366.

Silveira LFL, Mermudes JRM. 2014. Systematic review of the firefly genus Amydetes Illiger, 1807 (Coleoptera: Lampyridae), with description of 13 new species. *Zootaxa* **3765**: 201–248.

Silveira LFL, Mermudes JRM, Bocakova M. 2016. Systematic review of the firefly genus *Scissicauda* (Coleoptera, Lampyridae, Amydetinae) from Brazil. *ZooKeys* **558**: 55–75.

Silveira LFL, Khattar G, Vaz S, Wilson VA, Souto PM, Mermudes JR, Stanger-Hall KF, Macedo MV, Monteiro RF. 2020. Natural history of the fireflies of the Serra dos Órgãos mountain range (Brazil: Rio de Janeiro)–one of the ‘hottest’ firefly spots on Earth, with a key to genera (Coleoptera: Lampyridae). *Journal of Natural History* **54**(5-6): 275-308.

Souto PM, Campello L, Khattar G, Mermudes JRM, Monteiro RF, Silveira LFL. 2018. How to design a predatory firefly? Lessons from the Photurinae (Coleoptera: Lampyridae). *Zoologischer Anzeiger*, **278**: 1-13.

Stanger-Hall KF, Lloyd JE, Hillis DM. 2007. Phylogeny of North American fireflies (Coleoptera: Lampyridae): Implications for the evolution of light signals. *Molecular Phylogenetics and Evolution* **45**: 33-49.

Captions

Figure 1. Tanglegram of Cladodinae parsimony (A - left) and Bayesian (B - right) topologies. A: Strict consensus of 22 unweighted shortest trees with unambiguous character changes mapped on branches in WinClada, black squares representing nonhomoplasious changes, white squares homoplasious changes. Squares are labeled with small character numbers on top and character states on the bottom. Bold red numbers in boxes are Bremer (top)/symmetric resampling support (black, bottom) values; B. Bayesian phylogeny of Cladodinae presenting nodes labeled with posterior probabilities (bottom) and IQ-TREE ultrafast bootstrapping supports (top).

Figure 2. Representatives of the Cladodinae; A, *Cladodes flabellatus* (photo: A. Reyes); B, *Cladodes cincticollis* (photo: V. Valdés); C, *Cladodes ater* (photo: M. Cid); D, *Ledocas remixtus* (photo: S. Quipildor-Sánchez); E, *Nyctocrepis demoulini* (photo: A. Madruga); F, *Nyctocrepis stellata* (photo: A. Katz); G, *Dodacles elegans* (photo: P. Smith); H, *Brasilocladodes illigeri* (photo: L. Silveira); I, *Brasilocladodes delalandei* (photo: A. Bouzan); J, *Ledocas proteus* (photo: M. Rojas-Quintero).

Figure 3. Habitus, dorsal view; A, *Cladodes flabellatus*; B, *Ledocas parallelus*; C, *Ledocas pikillactanus* **sp.n.**; D, *Nyctocrepis malleri*; E, *Andecladodes ovalis* **sp.n.**; F, *Andecladodes cosangensis* **sp.n.**, lamella of antennomere III damaged; G, *Brasilocladodes carinatus*; H, *Dryptelytra cayennensis*; I, *Dodacles elegans*; J, *Dodacles niger*; K, *Dodacles lateralis*; L, *Dryptelytra pampahermosae* **sp.n.** Scales: 5 mm.

Figure 4. Pronotum: A, *Cladodes cincticollis*; B, *Ledocas parallelus*; C, *Ledocas pikillactanus* **sp.n.**; D, *Nyctocrepis malleri*; E, *Andecladodes ovalis* **sp.n.**; F, *Andecladodes cosangensis* **sp.n.**, lamella of antennomere III damaged; G, *Brasilocladodes carinatus*; H, *Dryptelytra cayennensis*; I, *Dodacles elegans*; J, *Dodacles niger*; K, *Dodacles lateralis*; L, *Dryptelytra pampahermosae* **sp.n.** Scales: 1 mm.

Figure 5. Antenna: A, *Cladodes melanurus*; B, *Ledocas parallelus*; C, *Ledocas pikillactanus* **sp.n.**; D, *Nyctocrepis malleri*; E, *Andecladodes ovalis* **sp.n.**; F, *Andecladodes cosangensis* **sp.n.**,; G, *Dodacles elegans*; H, *Dryptelytra cayennensis*; I, *Dryptelytra pampahermosae* **sp.n.**; J, *Vesta chevrolatii*. Scales: 1 mm.

Figure 6. Head. A, ventral view; *Ledocas pikillactanus* **sp.n.**; B–C, dorsal view; B, *Andecladodes cosangensis* **sp.n.**; **C,** *Andecladodes ovalis* **sp.n.** Scales: 0.5 mm.

Figure 7. A, C–H, Abdomen, ventral view; A, *Ledocas pikillactanus* **sp.n.**; C, *Andecladodes cosangensis* **sp.n.**; D, *Andecladodes ovalis* **sp.n.**; E, *Nyctocrepis malleri*; F, *Dodacles niger*; G, *Dodacles lateralis*; H, *Dryptelytra pampahermosae* **sp.n.**; B, distal portion of hind tibia and tarsus, *Ledocas pikillactanus* **sp.n.**

Figure 8. A, C, E, G, I, K, M, O, Q, S, U, W, Sternum VIII; B, D, F, H, J, L, N, P, R, T, V, X, Pygidium; A–B, *Ledocas parallelus*; C–D, *Ledocas pikillactanus* **sp.n.**; E–F, *Andecladodes cosangensis* **sp.n.**; G–H, *Andecladodes ovalis* **sp.n.**; I–J, *Dryptelytra cayennensis*; K–L, *Dryptelytra pampahermosae* **sp.n.**; M–N, *Dodacles elegans*; O–P, *Dodacles niger*; Q–R, *Dodacles lateralis*; S–T, *Nyctocrepis malleri*; U–V, *Brasilocladodes illigeri*; W–X, *Brasilocladodes carinatus*. Scales: 1 mm.

Figure 9. Sternum IX and syntergite; A, *Ledocas parallelus*; B, *Ledocas pikillactanus* **sp.n.**; C, *Andecladodes cosangensis* **sp.n.**; D, *Andecladodes ovalis* **sp.n.**; E, *Dryptelytra cayennensis*; F, *Dryptelytra pampahermosae* **sp.n.**; G, *Dodacles elegans*; H, *Dodacles niger*; I, *Dodacles lateralis*; J, *Nyctocrepis malleri*; K, *Brasilocladodes illigeri*; L, *Brasilocladodes carinatus*. Scales: 1 mm.

Figure 10. Male genitalia, ventral, lateral and dorsal views; A, *Cladodes flabellatus*; B1–B2, *Ledocas parallelus*; C1–C2, *Ledocas pikillactanus* **sp.n.**; D1–D2, *Nyctocrepis malleri*; E1–E2, *Andecladodes cosangensis* **sp.n.**; F1–F2, *Andecladodes ovalis* **sp.n.**; G1–G2, *Dodacles niger*; H1–H2, *Dodacles lateralis*; I1–I2, *Brasilocladodes illigeri*; J1–J3, *Brasilocladodes carinatus*.; K1–K3, *Dodacles elegans*; L1–L3, *Dryptelytra cayennensis*; M1–M3, *Dryptelytra pampahermosae* **sp.n.**; N1–N2, *Vesta chevrolatii*. Scales: 0.5 mm.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Data matrix of 66 morphological characters used in the cladistic analysis.

Table S2. Character list and comments.

Figure S1. Phylogeny of Cladodinae: single tree obtained in implied weighted parsimony analyses with concavity constants: A. k=1–5 showing bootstrap support under k=3; B. k=6–25 with symmetric resampling support under k=10.

Figure S2. Comparison of fast and slow optimizations using (A) accelerated (ACCTRAN) and (B) delayed (DELTRAN) transformations on the strict consensus of 22 unweighted parsimony trees.

Figure S3. The majority-rule consensus of the 22 shortest trees from the initial unweighted parsimony analysis of Cladodinae.

Figure S4. Branch support using standard bootstrapping (left) and symmetric resampling (right) applied on the unweighted Cladodinae dataset.

Figure S5. Phylogenetic relationships among major lineages of Cladodinae using IQ-TREE maximum likelihood with ultrafast bootstrapping support on branches.

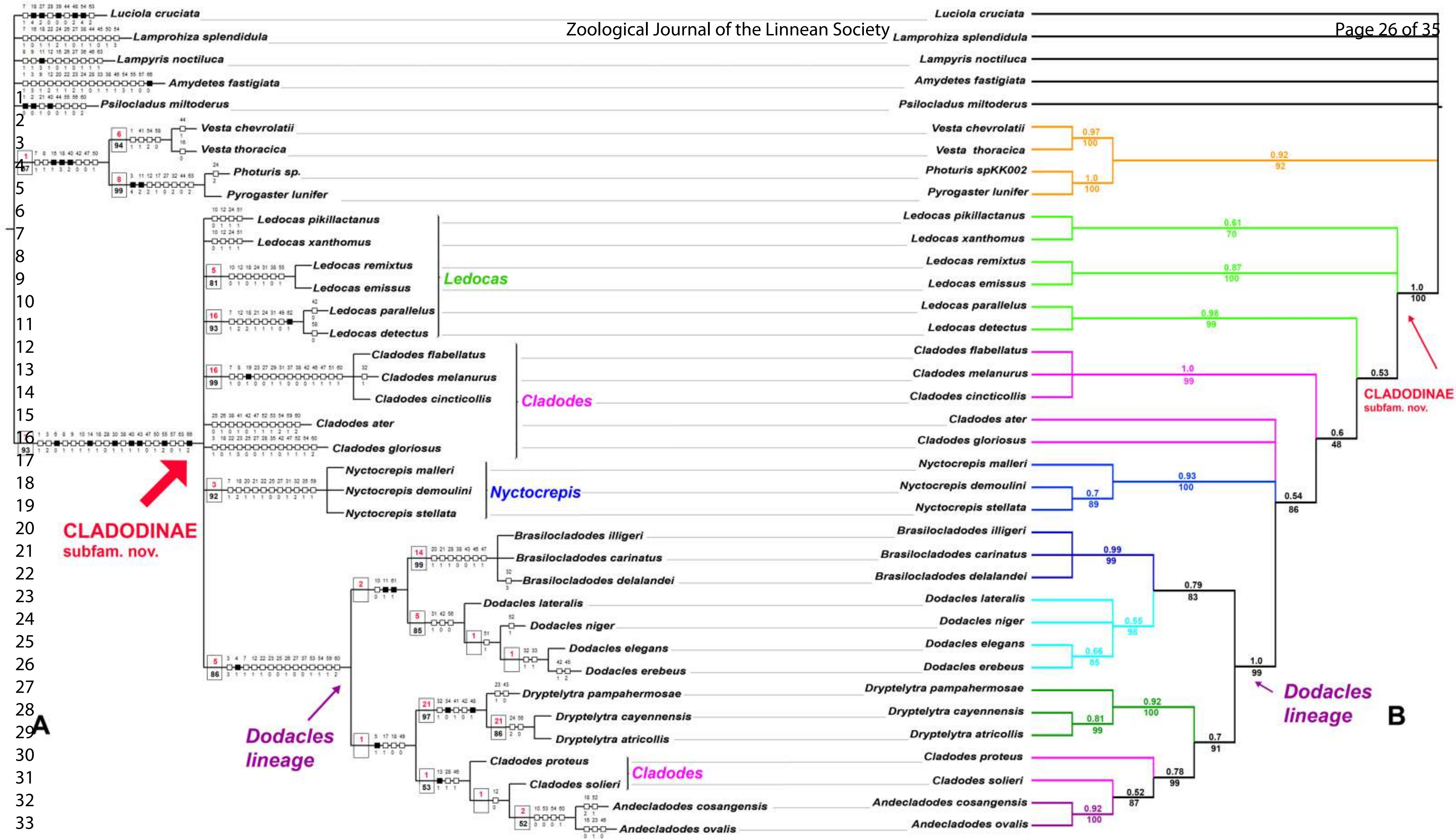
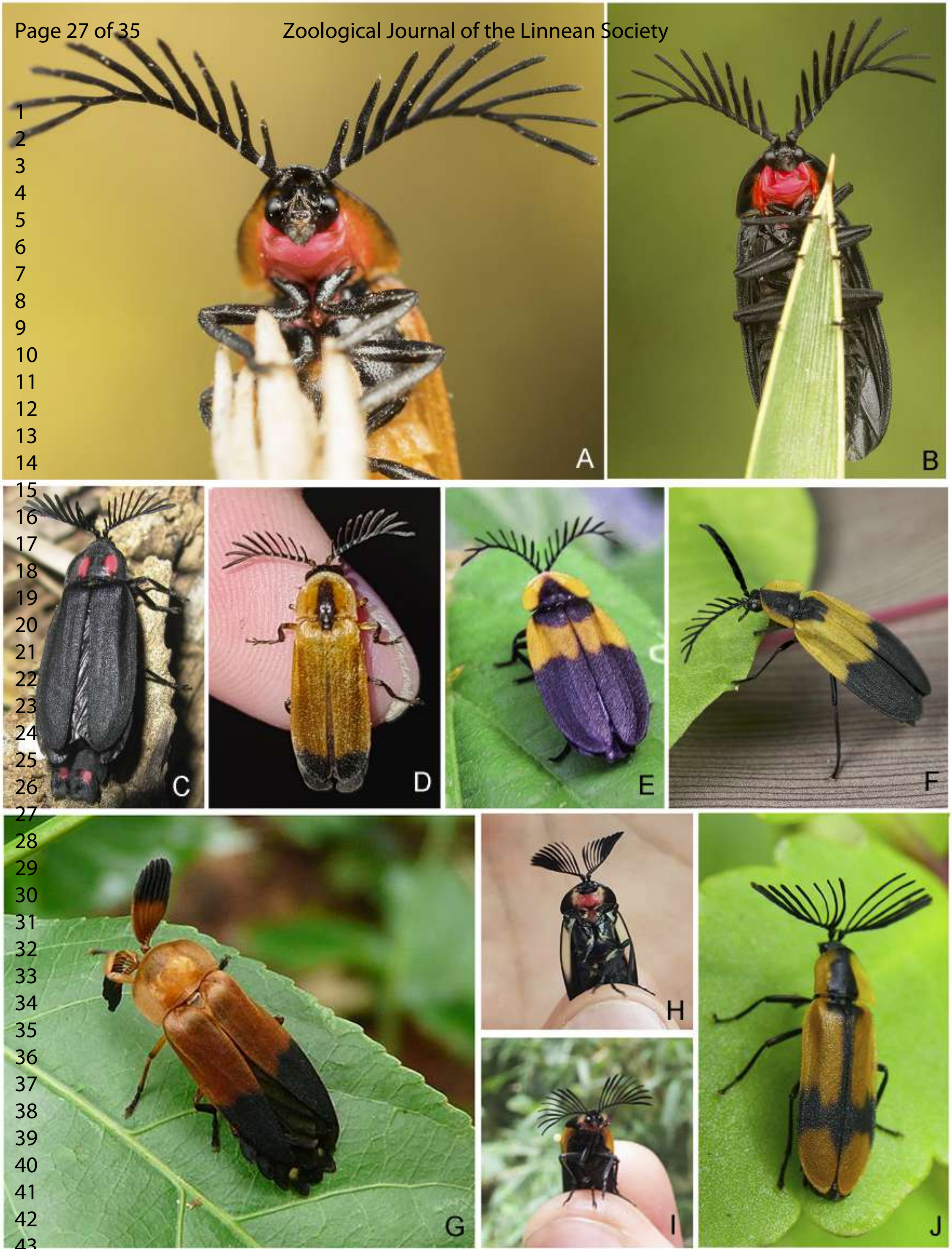


Figure 1. Tanglegram of Cladodinae parsimony (A - left) and Bayesian (B - right) topologies. A: Strict consensus of 22 unweighted shortest trees with unambiguous character changes mapped on branches in WinClada, black squares representing nonhomoplasious changes, white squares homoplasious changes. Squares are labeled with small character numbers on top and character states on bottom. Bold red numbers in boxes are Bremer (top)/symmetric resampling support (black, bottom) values; B. Bayesian phylogeny of Cladodinae presenting nodes labeled with posterior probabilities (bottom) and IQ-TREE ultrafast bootstrapping support values (top).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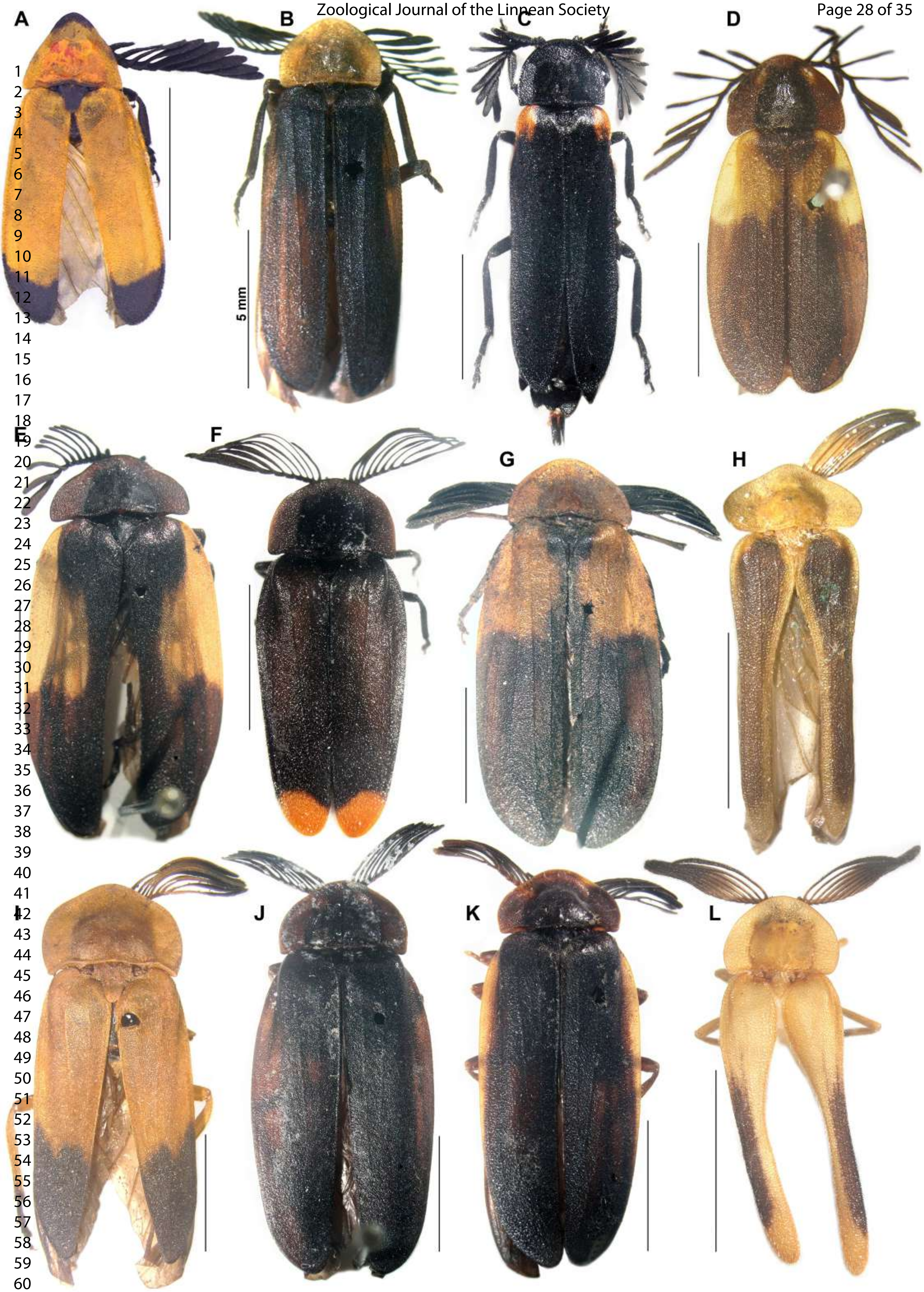
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B
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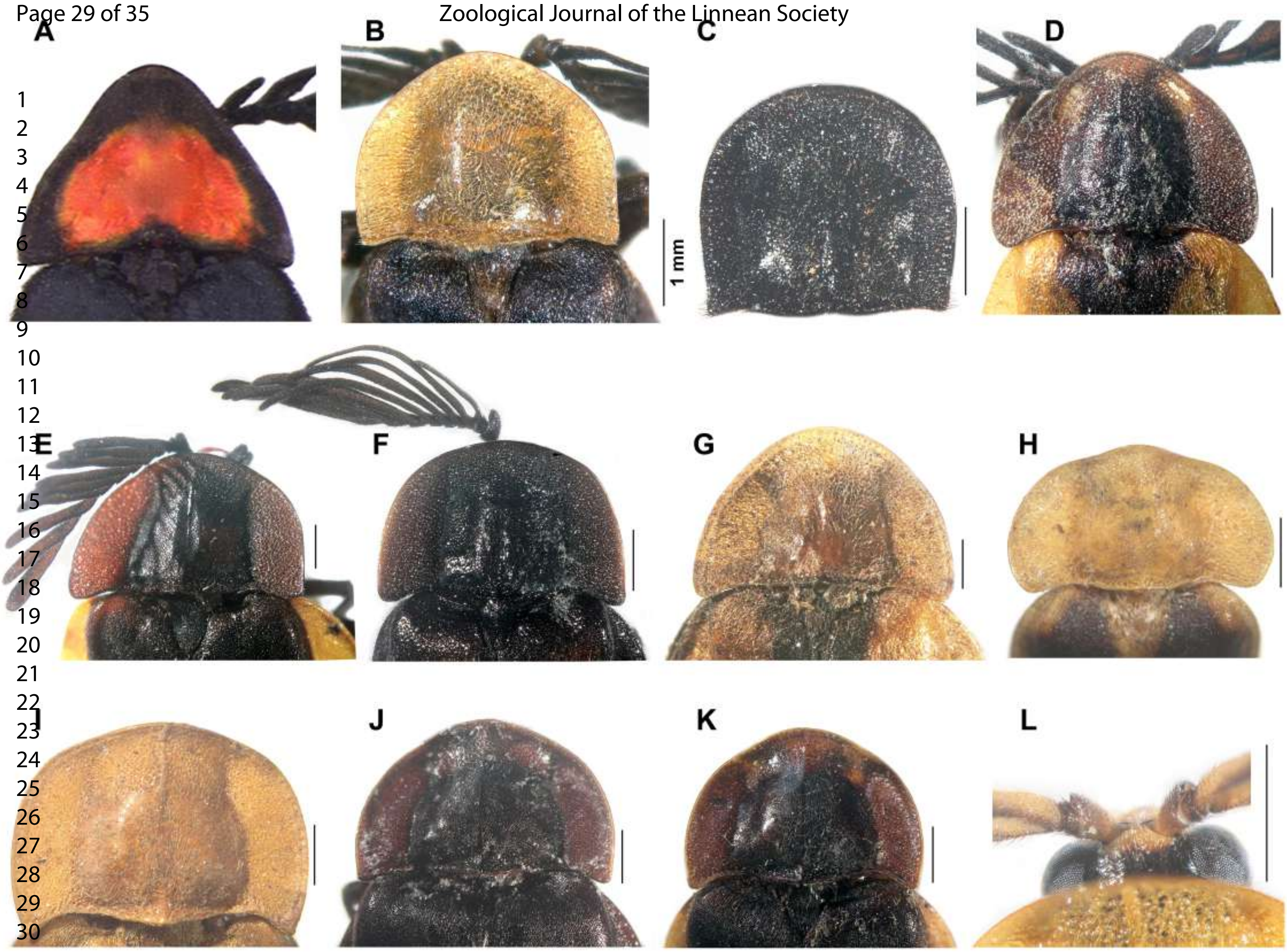
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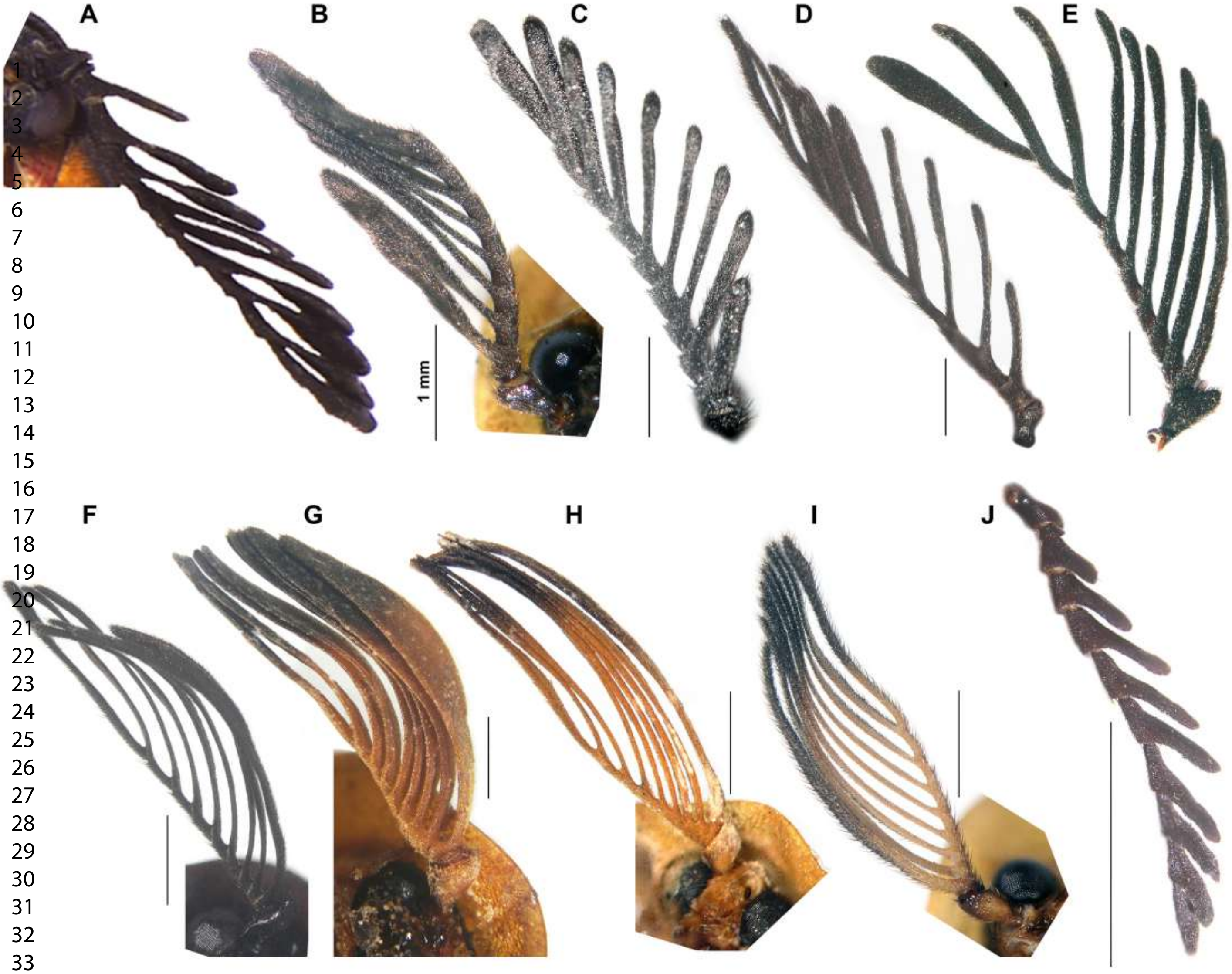
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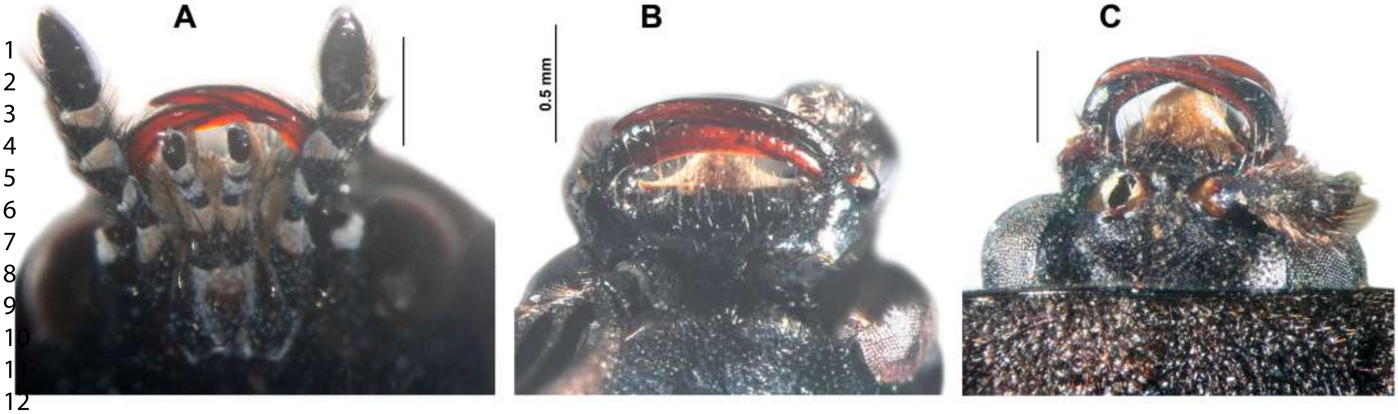
A
B
0.5 mm
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A
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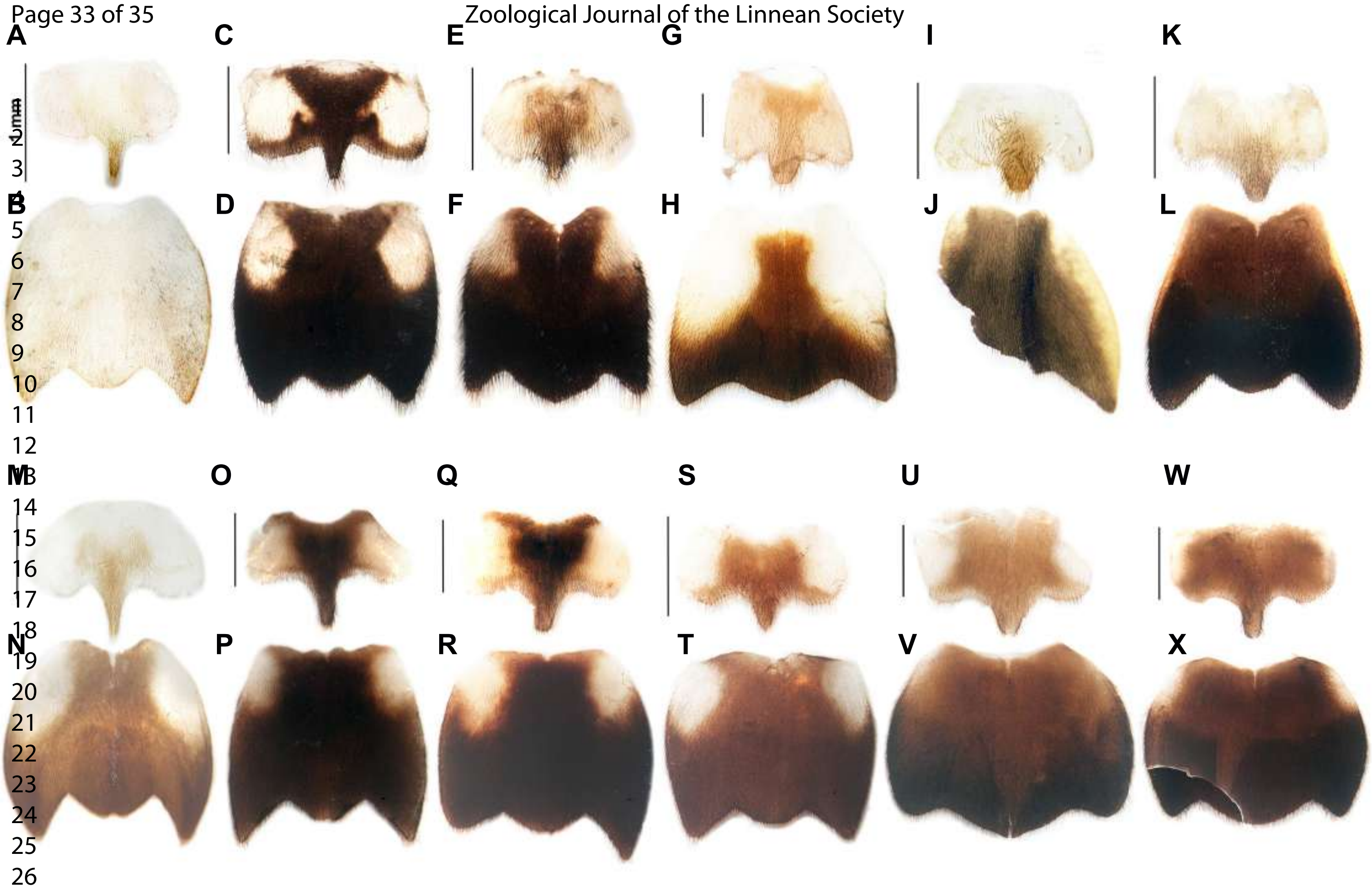
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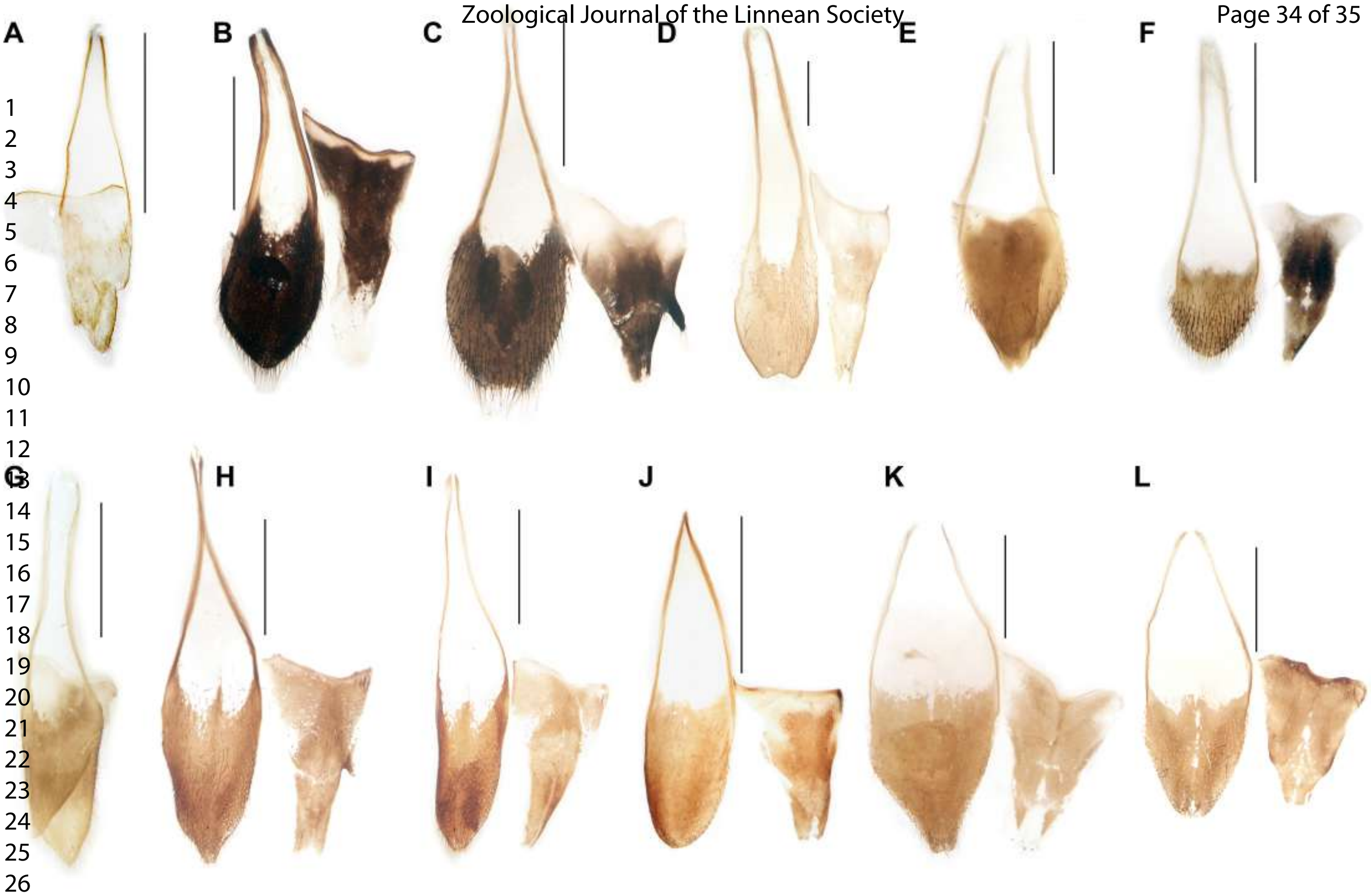
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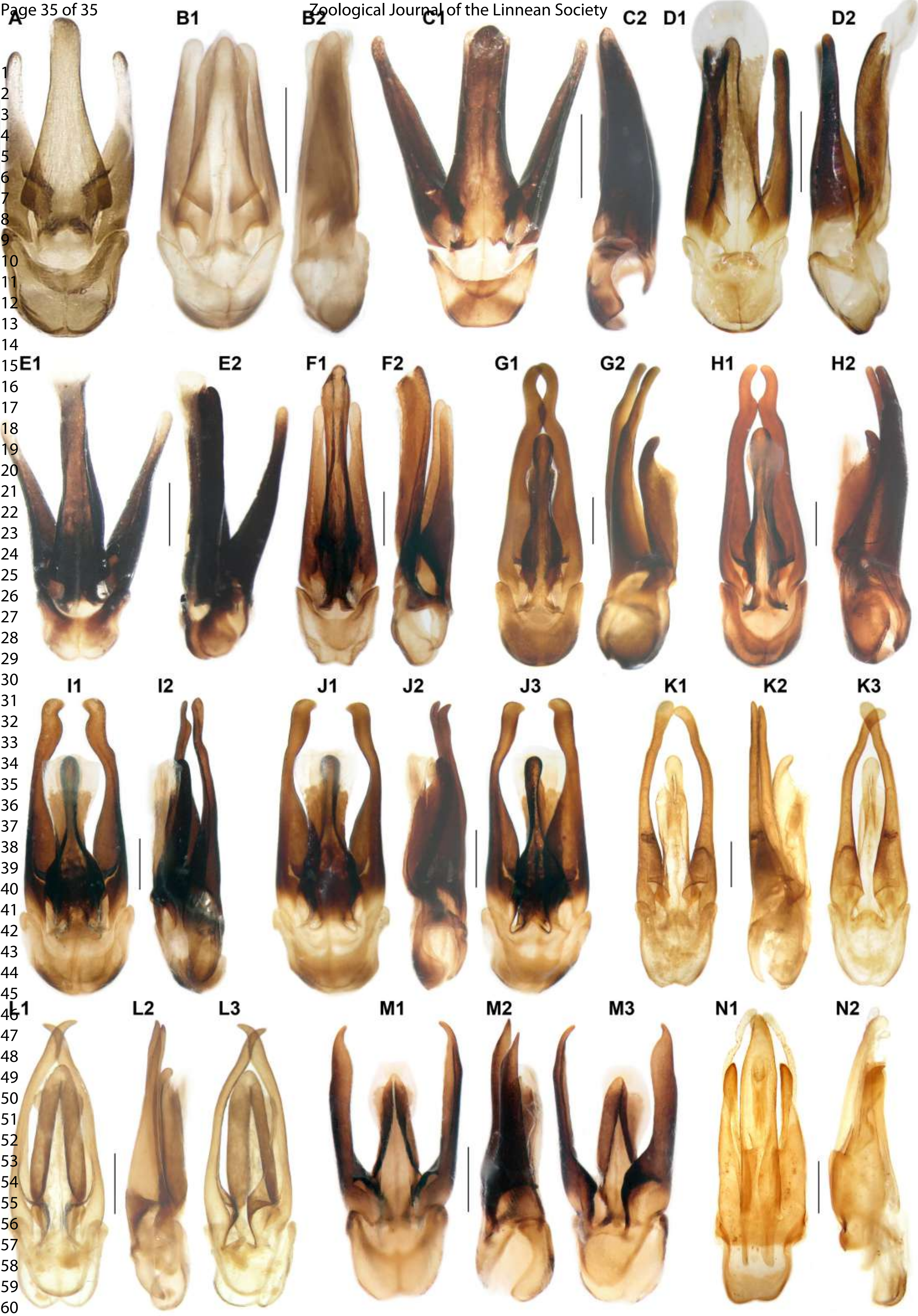
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B2
C1
C2
D1
D2
E1
E2
F1
F2
G1
G2
H1
H2
I1
I2
J1
J2
J3
K1
K2
K3
L1
L2
L3
M1
M2
M3
N1
N2