

THE EVOLUTION OF BIOLUMINESCENCE IN CANTHAROIDS (COLEOPTERA: ELATEROIDEA)

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ABSTRACT

We present the first cladistic analysis of genera in the family Lampyridae and other closely related beetles. A monophyletic concept of Lampyridae is established. The phylogenetic positions of the luminous cantharoid families [Omalisidae, Rhagophthalmidae and Phengodidae] in relation to Lampyridae are discussed, as well as the implications of the evolution of bioluminescence and photic signaling in this group of beetles. The Rhagophthalmidae appears to include *Dioptoma* and *Diplocladon* (formerly located in Phengodidae) and the Phengodidae apparently includes *Stenocladus* (formerly of Lampyridae). *Harmatelia*, *Drilaster* and *Pterotus* are transferred to Elateroidea *insertae sedis* and not included in Lampyridae where they were sometimes placed.

Key Words: Bioluminescence, Lampyridae, Omalisidae, Phengodidae, Rhagophthalmidae, Harmatelia, Drilaster, Pterotus

RESUMEN

Presentamos el primer análisis cladístico de los géneros en la familia Lampyridae y otros escarabajos muy relacionados. Se establece un concepto monofilético de Lampyridae. Se discuten las posiciones filogenéticas de las familias luminosas "cantharoid" [Omalisidae, Rhagophthalmidae y Phengodidae], y su relación con Lampyridae es discutida, al igual que las implicaciones de la evolución de la bioluminiscencia y señalamiento de luz en este grupo de escarabajos. La familia Rhagophthalmidae parece incluir *Dioptoma* y *Diplocladon* (antes localizados en Phengodidae) y la Phengodidae aparentemente incluye *Stenocladus* (anteriormente de Lampyridae). *Harmatelia*, *Drilaster* y *Pterotus* son transferidos *insertae sedis* a Elateroidea y no se incluyen en Lampyridae donde a veces han sido colocados.

The common and conspicuous bioluminescent displays of adult fireflies have been marveled at by man throughout history and have long been recognized, as displays of courtship. In 1647, Thomas Bartholin related an observation of Carolus Vintimillia that "nature had endowed them [female fireflies] with a vigorous light in order that they could call the males at night with their shine" (Harvey 1957). Bishop Heber in his *Tour through Ceylon* remarks: "Before beside us and above, the firefly lights his torch of love" (Harvey 1940). However, the less conspicuous bioluminescent emissions of less well-known beetles seem to have escaped notice by most. This phylogenetic analysis focuses on the origin of luminous habit and the evolution of luminescence. Therefore, the taxa chosen for this analysis most heavily represent the breadth of Lampyridae with an equal number of luminous and non-luminous genera in the cantharoid lineage. This analysis establishes the limits of a monophyletic Lampyridae, places other luminous taxa that are thought to be closely related to fireflies, and investigates possible origins and losses of luminescence in taxa related to Lampyridae.

The superfamily Cantharoidea was combined into the Elateroidea when Lawrence (1988) rede-

finied Elateriformia. Our analysis includes most of the families that formerly composed the Cantharoidea of Crowson (1955, 1972) (his included Brachypsectridae, Omalisidae (= Omalysidae, Homa-lisidae), Karumiidae, Drilidae, Phengodidae, Telegeusidae, Lampyridae, Cantharidae, Lycidae, Cneoglossidae, Plastoceridae and Ometthidae). We refer loosely to the taxa used in this analysis as "cantharoids," as they have been treated historically as a monophyletic group within the Elateroidea (Lawrence 1988).

MATERIALS AND METHODS

Eighty-five exemplar taxa were selected to represent a diversity of Lampyridae and outgroup families. Selection of taxa included as many subfamilies and tribes as possible within Lampyridae, based on the classification schemes of Crowson (1972) and Lawrence & Newton (1995), and 11 subfamilies within 9 other families, based on Lawrence & Newton (1995) (Appendix 1). We did not include any members of Elateridae in this analysis as they are too distantly related to the taxa considered here (Lawrence 1988). Seventy four male morphological characters with a total of

212 character states were used in the analysis. Inapplicable characters were coded as "-", while missing characters were coded as "?". All characters were analyzed under equal weights with 20 multistate characters as additive (see Appendix 2, 3). Plastoceridae was designated as the root of the tree based on Lawrence's (1988) phylogenetic analysis of the Elateriformia. The parsimony ratchet (Nixon 1999) (consisting of 100 iterations, weighting 12% of the characters) was implemented in Nona (Goloboff 1993), run within Winclada (Nixon 2000). The most parsimonious trees discovered were used as the starting place for a more exhaustive search using the "max*" command within NONA. The "best" command was then used to eliminate sub-optimal trees. A strict consensus tree was then calculated from these most parsimonious trees. Bremer support (Bremer 1988, 1994) was calculated using NONA, and the search was set to a Bremer support level of 5, with four runs, each with a buffer of 5000 trees.

RESULTS

The parsimony ratchet returned trees of 818 steps. Starting from these 52 trees, "max*" and "best" gave 280 most parsimonious trees of 818 steps. A strict consensus (Fig. 1) of these 280 trees collapsed 13 nodes and produced a consensus tree of 848 steps ($ci = 0.16$, $ri = 0.57$). Bremer values listed in Figure 2 indicate the number of steps that are required, up to 5, to find the closest tree that does not contain that particular node. Lampyridae is monophyletic with the exception of a few taxa that have been of controversial affinity (*Harmatelia*, *Drilaster*, *Pterotus*, and *Stenocladius*.) Two genera currently classified as phengodids (*Diopstoma* and *Diplocladon*) were placed with rhagophthalmids in this phylogenetic analysis. The families Drilidae, Omalidae, Lycidae, Omethidae, Teleguesidae and Phengodidae appear to be monophyletic. The monophyly of Cantharidae is not supported.

DISCUSSION

Testing the Monophyly of Existing Families

Lampyridae.

In view of our phylogeny, Lampyridae as defined by Crowson (1972) and Lawrence and Newton (1995) is not monophyletic. The three synapomorphies that define the base of Lampyridae are: covered head position, oblique attachment of trochanter to femora, and wing vein CuA1 intersecting MP above fork (Kukalova-Peck & Lawrence 1993). The genera *Harmatelia*, *Pterotus*, *Drilaster* (*Ototreta*) and *Stenocladius* are currently classified as lampyrids (Lawrence & Newton 1995; after Crowson 1972) though in our

analysis they are clearly placed outside of the family Lampyridae. This is not entirely unexpected, as several previous authors (LeConte 1859; McDermott 1964; Crowson 1972) who have examined some of these taxa have viewed them as possessing questionable affinities to existing families. LeConte (1859) placed *Pterotus obscuripennis* in Drilidae and then later (1881) moved it to Phengodidae. Of the genus *Pterotus*, LeConte (1859) stated, "A singular genus, which I have described at length from my inability to place it properly. It seems to have a mixture of characters belonging to the Lampyrides, Telephorides and Drilids, but from the small size of the posterior coxae is probably better placed with the latter." McDermott (1964) also mentions the difficulty he encountered in trying to place some of these taxa, "Both *Pterotus* and *Harmatelia* share a large degree of similarity between some characters. Also neither fits strictly to the accepted lampyrid characteristics and both have some suggestion of phengodid affinities. Combining these two genera in the subfamily Pterotinae is admittedly arbitrary but nevertheless serves to bring them together as transitional forms." Crowson (1972) wrote that the genera *Pterotus* and *Ototretadrilus* were the most phengodid-like and probably the most primitive firefly genera he had studied. (Specimens of *Ototretadrilus* were not available to us.)

The genus *Drilaster* was originally described in the family Drilidae by (Kiesenwetter 1879), and *Ototreta* was originally described in the family Lampyridae. The synonymy between *Drilaster* and *Ototreta* was noticed by Nakane (1950) (see also Sato 1968). However, Asian workers continued to use the older name (*Drilaster*) but moved it to Lampyridae. American and European workers continued using *Ototreta* as it appeared to be the valid name in McDermott 1964 and 1966. Therefore, not only should American workers discontinue the use of the name "*Ototreta*," but these taxa should no longer be associated with the family Lampyridae. For a short history of the taxonomic placement of *Drilaster* and *Ototreta*, see Table 1.

According to our phylogeny (Fig. 1), if *Harmatelia*, *Pterotus*, *Drilaster* and *Stenocladius* continue to be considered fireflies, the families Lycidae, Cantharidae, Phengodidae, Omethidae and Teleguesidae would need to be synonymized with Lampyridae. This seems drastic given the peripheral significance of the genera and the traditional affection for the families. *Harmatelia*, *Pterotus*, and *Drilaster* should be removed from Lampyridae and given the taxonomic label of "Elateroidea *incertae sedis*" awaiting further study to place them properly. *Drilaster* may not be monophyletic. Our analysis clearly places *Stenocladius* sp. in the family Phengodidae. Ohba et al. (1996) studied the external morphology of *Stenocladius* larvae and found that they did not possess an epicranial suture on the dorsal surface of the

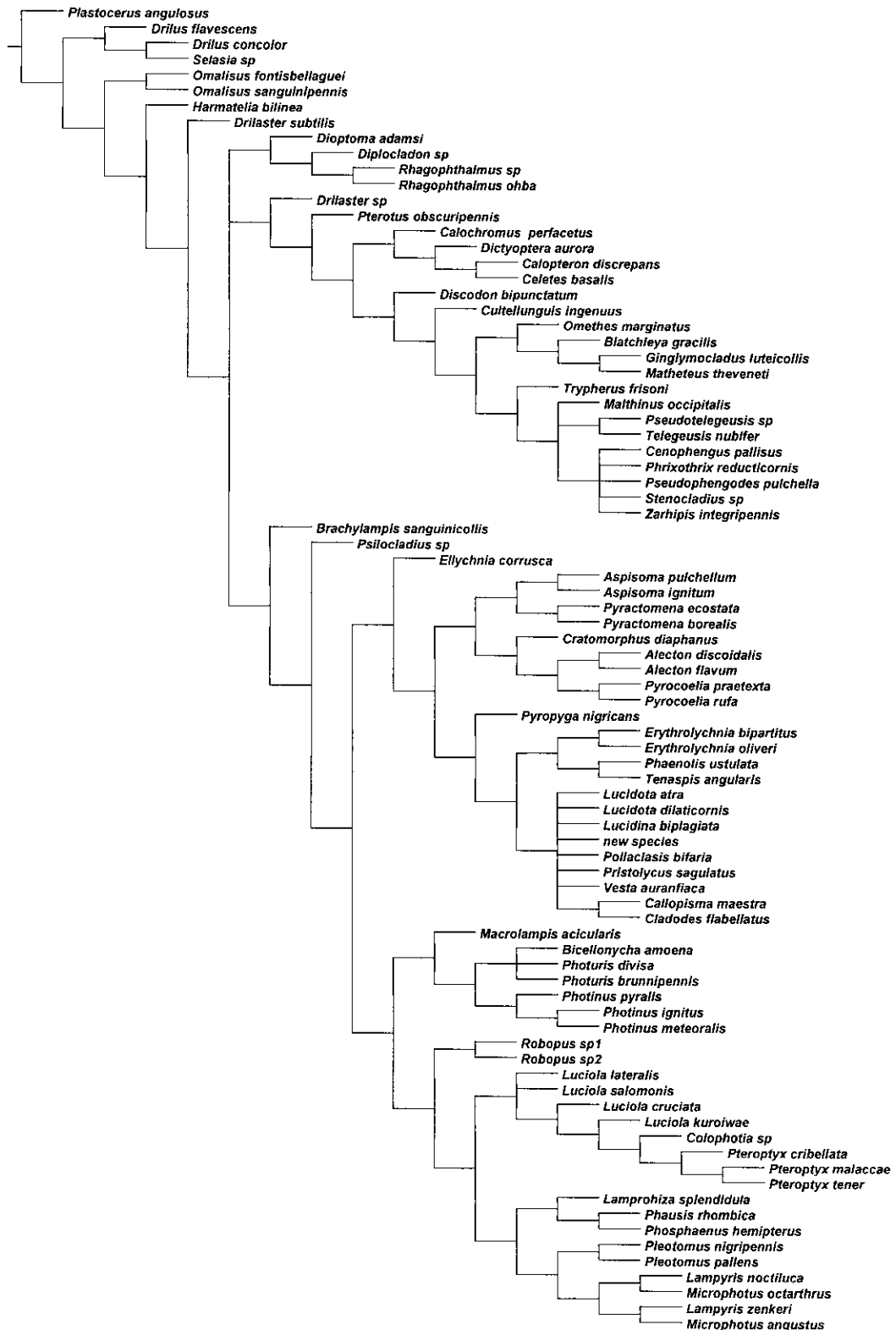


Fig. 1. Strict consensus of 280 most parsimonious trees (848 steps, C.I. 0.16, R.I. 0.57). The node at which *Brachylampis sanguinicollis* is the basal defines the base of the lampyrid clade.

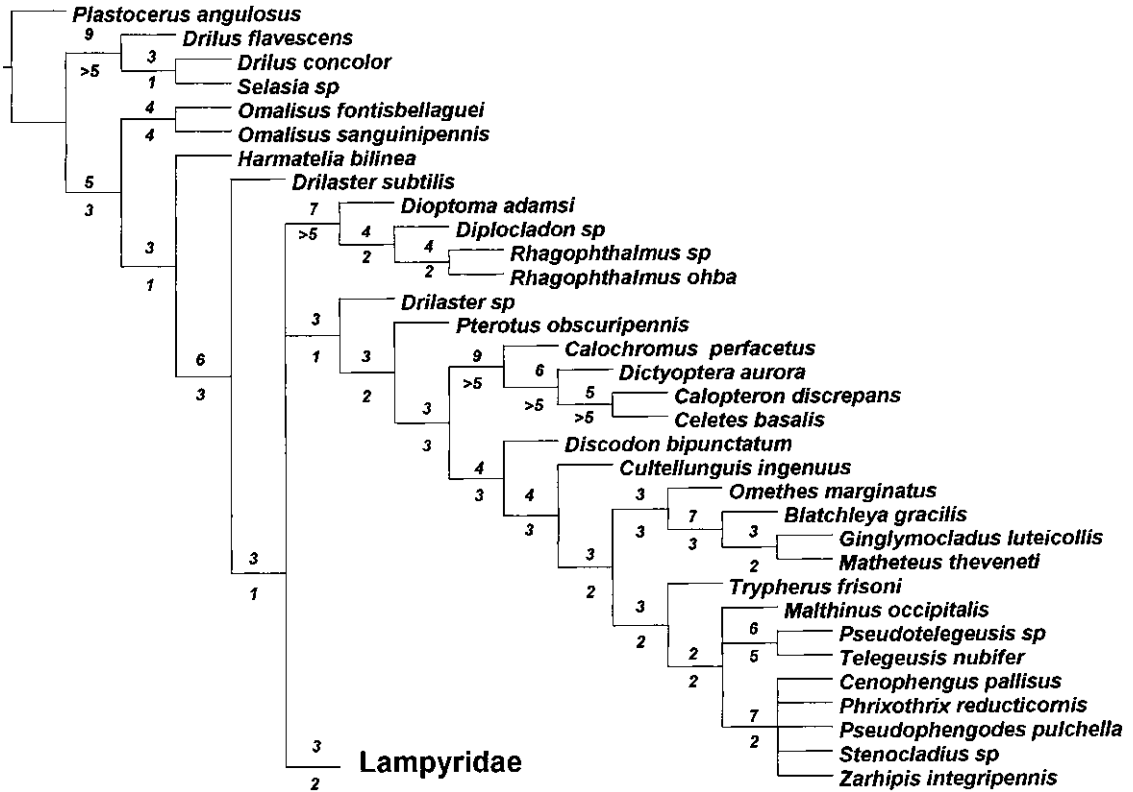


Fig. 2. The strict consensus with the lampyrid clade collapsed and represented by Lampyridae. Numbers located under the nodes are Bremer Support values (set at a max. Bremer value of 5.) Numbers located above the nodes present the number of synapomorphic characters at that node.

larval head. This suture is well developed in larvae of Lampyridae. They hypothesized that the fused dorsal surface of the larval head in *Stenocladus* is more closely allied with Phengodidae than Lampyridae. Our analysis supports this association. Because the clade containing these taxa in our analysis is unresolved, there is no information concerning which subfamily of Phengodidae *Stenocladus* should be placed within (Fig. 2).

Other Cantharoid families.

The families Plastoceridae, Drilidae, Omalidae, Rhagophthalmidae, Lycidae, Omethidae, and Teleguesidae are supported as being monophyletic in our analysis including very few representatives. Phengodidae and Cantharidae are not supported as being monophyletic. With the exception of *Diopstoma adamsi* and *Diplocladon* sp., the four other phengodid taxa used in this analysis are a monophyletic clade. Our analysis placed *Diopstoma* and *Diplocladon* at the base of the clade containing the family Rhagophthalmidae. The Bremer support value for the base of this clade (Fig. 2) is high (>5), indicating strong support. The seven synapomorphies that define this clade

are: twelve antennomeres in male antennae, third antennomere long, basal antennal flagellomeres not symmetrical with apical flagellomeres, mandible apices acute (inside angle < 90 degrees), emarginate eyes, eyes posterior-ventrally approximated, and wing vein MP3 not contacting MP1+2. Therefore, we propose moving the genera *Diopstoma* and *Diplocladon* out of Phengodidae and into Rhagophthalmidae. On the other hand, Cantharidae does not seem to be supported as monophyletic in this analysis, and none of the four cantharid taxa included in the analysis form a clade. Cantharidae needs to be further examined in relation to other taxa and sampled more thoroughly within a phylogenetic context before a taxonomic change is made.

Phylogenetic Relationship
Between Lampyridae and Phengodidae

The family Phengodidae is composed of bioluminescent species that commonly resemble fireflies in their general appearance and are usually also found to be sympatric with many firefly species. Even though phengodid beetles share aspects of their biology with lampyrids (larviform

TABLE 1. SOME NOTABLE PAPERS SHOWING THE PREVIOUS TAXONOMIC PLACEMENT OF TAXA THAT THIS STUDY RELEGATES TO “*INCERTAE SEDIS*” STATUS.

Early Work	E. Oliver (1910) a, b	F. McDermott (1964) (1966)	Lawrence & Newton (1995) (after Crowson 1972)	Branham & Wenzel (this analysis)
Lampyridae <i>Ototreta</i> {E. Olivier 1900} <i>Stenocladus</i> {Fairmaire 1878}	Lampyridae (a) Luciolinae <i>Ototreta</i> Megalophthalminae <i>Harmatelia</i>	Lampyridae Ototretinae (1964) and Luciolinae (1966) <i>Ototreta</i> (= <i>Drilaster</i>)* Pterotinae (1964,1966) <i>Pterotus</i> <i>Harmatelia</i>	Lampyridae Ototretinae <i>Ototreta</i> (= <i>Drilaster</i>)* <i>Harmatelia</i> <i>Stenocladus</i> Pterotinae <i>Pterotus</i>	Elateriodesa Incertae Sedis <i>Drilaster</i> * <i>Harmatelia</i> <i>Pterotus</i> Phengodidae <i>Stenocladus</i>
Drilidae <i>Drilaster</i> {Kiesenwetter 1879} <i>Pterotus</i> {LeConte 1859}	Drilidae (b) <i>Drilaster</i> <i>Stenocladus</i>	Rhagophthalminae (1964, 1966) <i>Diopstoma</i> {Pascoe 1860}	Phengodidae Rhagophthalminae <i>Diopstoma</i> <i>Diplocladon</i> {Gorham 1883}	Rhagophthalmidae <i>Diopstoma</i> Diplocladon
Elateridae <i>Harmatelia</i> {Walker 1858}				

*McDermott (1964,1966) synonymized *Drilaster* and *Ototreta*, retaining the name *Ototreta*. Sato (1968) confirmed this synonymy while pointing out that *Drilaster* has priority over *Ototreta*. Crowson (1972) as well as Lawrence and Newton (1995) retained McDermott's use of "*Ototreta* (= *Drilaster*)". The varied use of these generic names has led to some confusion: the genus *Drilaster* is used in Asia without reference to *Ototreta*, while "*Ototreta* (= *Drilaster*)" is used in Europe and the United States. We refer to this genus as *Drilaster* based on the priority of the name *Drilaster* and to eliminate further confusion. Additionally, we propose that *Drilaster* be removed from Lampyridae and be given Elateriodesa *Incertae Sedis* status.

females, the use of pheromones and luminescence), phengodids have historically been seen as a group taxonomically distinct from Lampyridae. However, it is probably the similarities between Lampyridae and Phengodidae, with bioluminescence being one of the most obvious, which have linked them as closely related taxa in the eyes of many cantharoid workers. "Within Cantharoidea, Phengodidae and Lampyridae appear to be directly related, so that the luminosity of both groups can plausibly be attributed to inheritance from a common ancestor . . ." (Crowson 1972). Our phylogeny provides evidence that Phengodidae is not sister to, or basal to, Lampyridae. In addition, it shows that Rhagophthalmidae and Omalidae are the bioluminescent families that are sister, or basal to Lampyridae, respectively (Fig. 3).

The Evolution of Bioluminescence in Non-lampyrid Cantharoids

Bioluminescence in the order Coleoptera is known to occur in Elateridae, Staphilinidae (Costa et al. 1986) and four cantharoid families: Omalidae, Rhagophthalmidae, Phengodidae and Lampyridae (Lloyd 1978). Several recent studies have provided hypotheses concerning the evolutionary relationships within or around Cantha-

roidea (Crowson 1972; Potatskaja 1983; Beutel 1995) using a variety of techniques, characters and exemplar taxa. Plotting luminescence (larval or adult) onto these different trees, supports interpretations ranging from three origins, to one origin and three losses. However, these studies treat families as single units. Therefore, if luminescence arises only once in each of the three luminescent families, (Omalidae, Phengodidae, and Lampyridae, with *Rhagophthalmus* species treated as phengodids), three separate origins would be the maximum number of steps. Conversely, a single origin would be the minimum number of steps if all families were treated as being monophyletic. Crowson (1972) proposed a dendrogram for the relationships between the cantharoid families (Omethidae, Cantharidae, Plastoceridae, Lycidae, Omalidae, Drilidae, Telegeusidae, Phengodidae, and Lampyridae). This scheme predicts two character optimizations of three steps each. One optimization poses three origins for bioluminescence, while the second poses two origins and one loss of bioluminescence. Potatskaja (1983) proposed a dendrogram for the relationships between the cantharoid families (Brachyspectridae, Cantharidae, Phengodidae, Drilidae, Omalidae, Lycidae and Lampyridae) based on larval mouthpart characters. Potatskaja

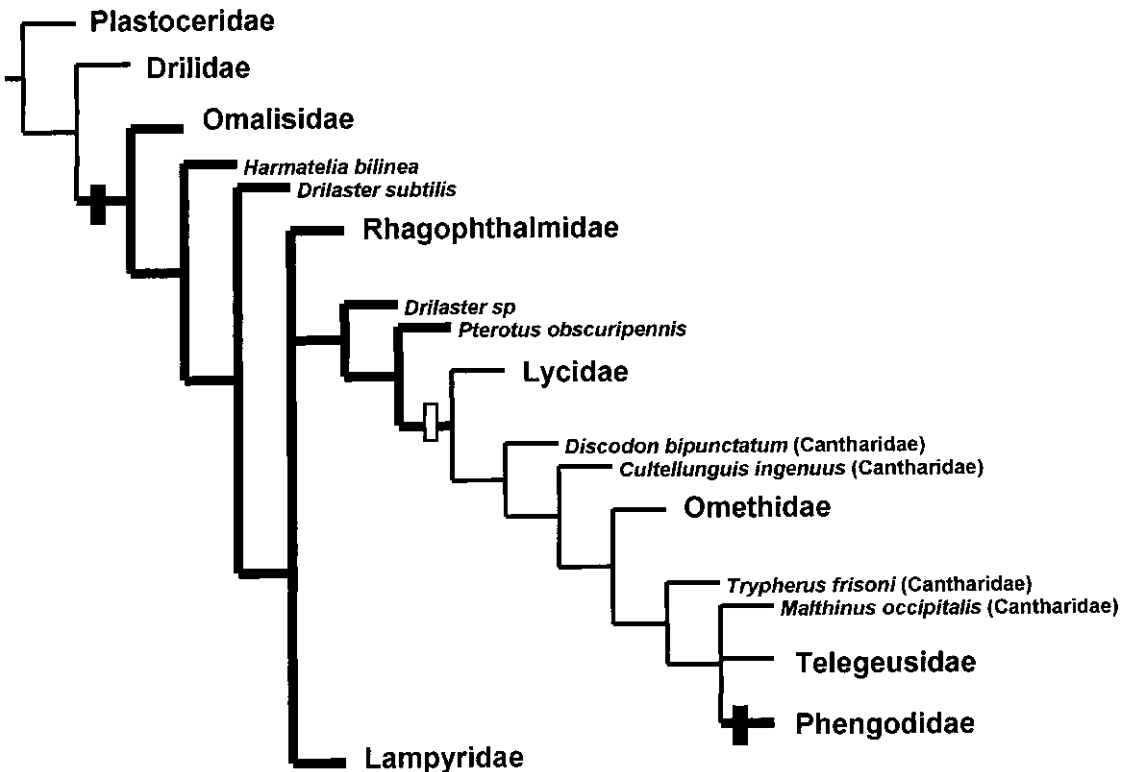


Fig. 3. The evolution of bioluminescence in cantharoids. The condensed strict consensus tree with two origins of luminescence and one loss plotted.

concluded that two lineages, one termed "cantharid" (composed of Phengodidae, Drilidae, Omalisidae, Brachyspectridae, and Cantharidae) and the other "lycid" (composed of Lampyridae and Lycidae) originated from a phengodid ancestral form. No specific taxon was designated as the root. In reference to the origin of bioluminescence, this topology predicts two optimizations of three steps each: three separate origins, or two origins and one loss. In 1995, Beutel proposed a phylogenetic analysis of Elateriformia based on 27 larval characters (33 states). Within this analysis Cantharoidea was represented by seven taxa, one species per each of Brachyspectridae, Cantharidae, Drilidae, Omalisidae, Phengodidae, Lampyridae, and Lycidae. All of the cantharoid taxa were placed in the same clade except for Cantharidae, which was placed close to Elateridae, rather than with the rest of the cantharoids. The clade containing the bioluminescent cantharoid taxa was poorly resolved in the consensus tree and predicts a single topology of one origin and three losses.

Our analysis suggests a single solution, considering a taxon to be luminescent if any life stage is luminescent. There are two origins of bioluminescence with one loss: luminescence arose once basally, early in the evolutionary history of the cantharoid clade, and was subsequently lost and then later regained in the phengodids, see Fig. 3. Taxa in which luminescence was regained under this scenario are currently classified as belonging to the family Phengodidae, (*Cenophengus pallisus*, *Phrixothrix reducticornis*, *Pseudophengodes pulchella*, and *Zarhipis integripennis*), as well as *Stenocladus* sp. which we consider to be a phengodid and propose its inclusion in this family. The seven synapomorphies that define Phengodidae are: tibial spurs are absent, bipectinate antennae, distal margin of antennal flagellomeres approximating proximal margin in width, antennal lobes produced from basal region of flagellomere, two elongated antennal lobes per flagellomere, narrow juncture between flagellomere and antennal lobe, and juncture between lateral and hind margins of pronotum are truncate (= 90 degrees). Therefore, all luminescence in the cantharoid lineage is homologous except for that of Phengodidae, which is a reversal to luminous habit. Additionally, all known luminescent cantharoid taxa have luminous larvae, and in Omalisidae the larvae are luminous, but not either adult (Crowson 1972). The fact that Omalisidae is the most basal of all the bioluminescent cantharoids indicates that luminescence arose first in the larvae and then subsequently in the adults (Fig. 4).

Photic Organ Evolution in Non-lampyrid Cantharoids

Larvae.

Only the larval photic organs of Phengodidae and Lampyridae have been studied in detail. The

larvae of Omalisidae have never been studied, and the larvae of Rhagophthalmidae have been studied and described only recently (Wittmer & Ohba 1994), though no morphological, physiological or histological work has been published on this group. Therefore, from what is currently known from evidence scattered among the taxa, the pattern of two luminous spots per segment on larvae is the most ancient and common larval photic organ pattern in the cantharoid lineage (Fig. 4). The number of luminous segments varies, but all known luminous cantharoid larvae bear pairs of luminous photic organs. While most lampyrid larvae bear only a single pair of photic organs on the eighth abdominal segment, larvae of the other taxa generally possess a pair of photic organs on each abdominal segment with additional pairs sometimes present on the larval thorax (Table 2). While the larvae of many genera of luminous cantharoids are not yet known, all species known to be luminous as adults are also luminous as larvae. Therefore, while only some larvae are known from the families Omalisidae, Rhagophthalmidae, Phengodidae and Lampyridae, the larvae of all species in these families are hypothesized to be luminous (Fig. 4). Crowson (1972) hypothesized that Barber's (1908) luminous larva from Guatemala, described as *Astraptor* sp., could have been a large female larva or a larviform female of *Telegeusis*. Sivinski (1981) points out that in a later unpublished manuscript Schwarz and Barber identified the single specimen as the phengodid *Microphenus gorhami*. Therefore, as far as is known, the family Teleguesidae does not contain any luminous taxa. Barber (1908) mentions that there was a single photic organ in the head which produced a red light that was thrown directly forward and hence was not easily seen from above. This specimen seemed to have no other photic organs, though it was observed in the daytime and not for long. A red head-light is known only in other phengodid larvae (Viviani & Bechara 1997).

Adult Females.

Females of luminous cantharoid taxa, excluding Lampyridae, generally possess the same photic organ morphology as their larvae, which is generally paired, luminous spots on the post-lateral margins on some of the thoracic and each of the abdominal segments (Table 2). Females, and males of the family Lampyridae vary in photic organ morphology (Lloyd 1978), perhaps due to sexual selection as the females of many firefly species attract mates via a luminescent sexual signal system (McDermott 1917; Schwab 1960; Lloyd 1978 and 1979; Branham & Greenfield 1996; Venzl & Carlson 1998). While the luminescent sexual signals of fireflies have received considerable attention, pheromones are the dominant sexual signals used in courtship in most cantharoids, including

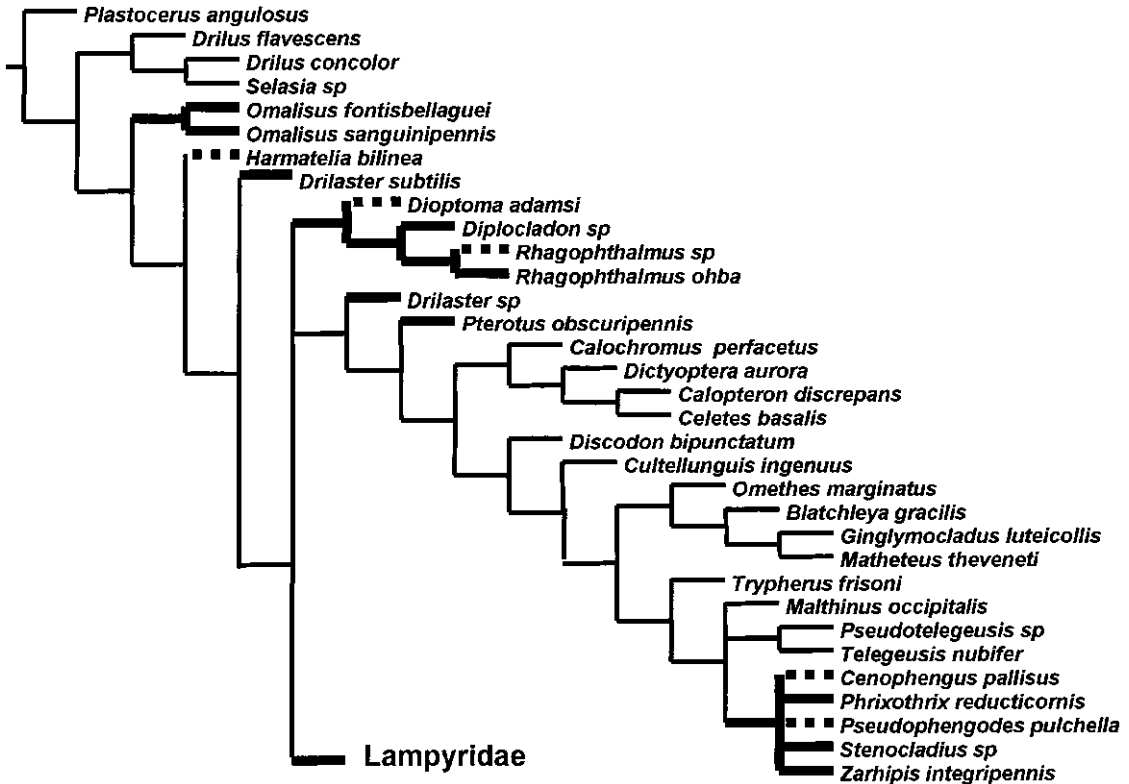


Fig. 4. The evolution of larval bioluminescence in cantharoids. The strict consensus tree with the lampyrid clade collapsed. The known presence of larval luminescence is indicated by bold branches, with the hypothesized presence of larval luminescence indicated by dotted branches.

Phengodidae, and are also used by many lampyrids (McDermott 1964; Lloyd 1971). Therefore, (with the exception of the family Omaliscidae and the genus *Drilaster*), the pattern of bioluminescent evolution in the larvae (Fig. 4) and the pattern found in the females of luminous taxa (Fig. 5) is very similar. The fact that Omaliscidae is the basal-most luminous cantharoid taxon and both adult males and females are not bioluminescent suggests that bioluminescence first arose in larvae and later in adults.

Rhagophthalmus ohbai females, in addition to retaining the larval pattern of photic organs, also possess a novel photic organ on the eighth ventrite, which is used in courtship, see Table 2 (Ohba et al. 1996a). After using the ventral photic organ on the eighth ventrite for courtship, females curl around their eggs and glow from ten sets of paired photic organs located at the lateral margins of the ten luminous body segments, (see Table 2), which serve as an aposematic warning display (Ohba et al. 1996a; Chen 1999). Rhagophthalmidae appears to be the sister of Lampyridae, which is the only other cantharoid family known to contain females that employ photic signals in courtship. In addition, based on the pres-

ence of extremely well developed eyes in rhagophthalmid males and the lack of greatly elaborate bipectinate antennae, such as those found in Phengodidae, we believe that photic signals are the primary mode of sexual signaling.

Crowson (1972) incorrectly cited Green (1912) as reporting that the female of *Harmatelia* is apterous and larviform. Green (1912) states that, "I have not yet succeeded in determining the female of this beetle, and it remains uncertain whether the other sex is an apterous grub-like creature, or whether it is in the form of another beetle."

Adult Males.

All known bioluminescent adult cantharoid males are restricted to the families Lampyridae, Rhagophthalmidae (as defined here) and Phengodidae (as defined here) as well as the genus *Harmatelia*. While the exact number and position of the photic organs varies, they are generally found in pairs on one or more of the thoracic segments, and on each of the first eight abdominal segments. Male photic organs, like those of larvae and females, are found near the lateral margins of these body segments (Table 2). The more dorsal

TABLE 2. A COMPARISON OF CANTHAROID TAXA INCLUDED IN THIS ANALYSIS WITH SPECIAL REFERENCE TO PHOTIC ORGAN MORPHOLOGY ACROSS LIFE STAGES AND THE PRESENCE OF NEOTENIC CHARACTERISTICS IN ADULT FEMALES.

	<i>Larvae:</i> Photic Organ Morphology	<i>Females:</i> Larviform or Alate	<i>Female:</i> Photic Organ Morphology	<i>Males:</i> Photic Organ Morphology
Plastoceridae	Unknown	Wingless, elytra shorter than abdomen (Crowson 1972)	None	None
Drilidae	None	Wingless, elytra shorter than abdomen (Lawrence 1991a). Females of <i>Selasia unicolor</i> are "larviform" (Barker 1969)	None	None
Omalisidae	Paired p. organs on sides of abdomen (Lawrence 1991b)	Wingless, elytra shorter than abdomen (Crowson 1972)	None	None
Rhagophthalmidae <i>Dioptoma</i>	Unknown	Neotenic: larviform with the exception of adult antennae and legs (tarsi subdivided into tarsomeres and claws) (Lawrence & Newton 1995)	Roundly quadrate p. organ, almost completely occupying the venter of penultimate abd. segment (Green 1912)	4 p. organs along dorsal hind margin of prothorax. One pair on lateral margins of all 8 abd. segments, and one pair of dorsal organs on each abd. seg.5-7 (Green 1912)
<i>Diplocladon</i>	A medial dorsal and two lateral p. organs on each body segment except head and last body segment (Halverson et al. 1973)	Larviform: possessing larval antennae and legs (Lawrence & Newton 1995)	A medial dorsal and two lateral p. organs on each body segment except head and last body segment (Haneda 1950)	None
<i>Rhagophthalmus</i>	A median dorsal and two postlateral p. organs on each segment: from mesothorax to 8th abdominal segment (10 sets total) (Ohba et al. 1996a)	Neotenic: larviform with the exception of 8-seg. antennae, tarsi subdivided into tarsomeres and claws (Costa et al. 1986)	Ten sets of paired p. organs on postlateral margins of mesothorax and abdomen; single p. organ on ventrite of abd. seg. 8 (Wittmer et al. 1996a)	Weak light visible from sets of paired p. organs on lateral margins of each abd. seg. and pronotum with an additional central organ on mesonotum (Chen 1999)
Lycidae	None	Nearly always alate	None	None
Cantharidae	None	Alate	None	None
Omethidae	Unknown	Alate, occasionally reduced wings (Lawrence 1991)	None	None
Teleguesidae	Unknown	Unknown	Unknown	None
Phengodidae <i>Cenophengus</i> <i>Phrixothrix</i>	Unknown	Larviform Larviform	???	None
	Two medial organs on head and eleven pairs of p. organs in the posterolateral margins of 2nd thoracic through the 9th abd. segment (Viviani & Bechara 1997; Halverson et al. 1973; Harvey 1952)		Two medial organs on head and eleven pairs of p. organs in the posterolateral margins of 2nd thoracic through the 9th abd. segment (Halverson et al. 1973; Harvey 1952)	A single dorsomedian p. organ on prothorax and paired p. organs located dorsolaterally on thoracic and abd. segments (Viviani & Bechara 1997)

TABLE 2. (CONTINUED) A COMPARISON OF CANTHAROID TAXA INCLUDED IN THIS ANALYSIS WITH SPECIAL REFERENCE TO PHOTIC ORGAN MORPHOLOGY ACROSS LIFE STAGES AND THE PRESENCE OF NEOTENIC CHARACTERISTICS IN ADULT FEMALES.

	<i>Larvae:</i> Photic Organ Morphology	<i>Females:</i> Larviform or Alate	<i>Female:</i> Photic Organ Morphology	<i>Males:</i> Photic Organ Morphology
<i>Pseudophengodes</i>	Unknown	Unknown	Unknown	Large p. organs on ventral surface of 8th abd. segment (Viviani & Bechara 1997; M. Branham, pers. obs.)
<i>Zarhipis</i>	11 luminous bands: 1 each at base of meso- and metathroax, and on all but the last abd. tergites. Paired p. organs (1 spot per side): on upper lateral surfaces of abd. segs. 1-9 (Tiemann 1967)	Larviform	11 luminous bands: 1 each at base of meso- and metathroax, and on all but the last abd. tergites. Paired p. organs (1 spot per side): on upper lateral surfaces of abd. segs. 1-9. Also, 1-3 luminous spots on abd. sterna 2-9 (Tiemann 1967; Rivers 1886)	None
<i>Stenocladius</i>	Paired p. organ on 7th abd. segment (Ohba et al. 1996b)	Neotenic: larviform with the exception of tarsi subdivided into tarsomeres and claws (Ohba et al. 1997)	A diffuse glow emitted from entire body—no specific photic organs present (Ohba et al. 1997)	When present, paired p. organs on 6th abd. segment (Ohba et al. 1997)
“Incertae Sedis” <i>Harmatelia</i>	Unknown	Unknown	Unknown	One p. organ on each side of mesothorax with 1 pair of p. organs on dorsum of each of 8 abd. seg. (One each near posterolateral margin) (Green 1912; McDermott 1965)
<i>Drilaster</i>	Paired p. organs on 8th abd. seg. (Ohba 1983)	Alate (some larviform?)	None	None
<i>Pterotus</i>	Paired p. organ on 7th abd. segment (Dean 1979)	Larviform? Dean (1979) states that females are fully larviform. However, his Plate II indicates the presence of compound eyes, adult antennae and paired claws on each leg.	Paired p. organ on 7th abd. segment (Dean 1979)	None

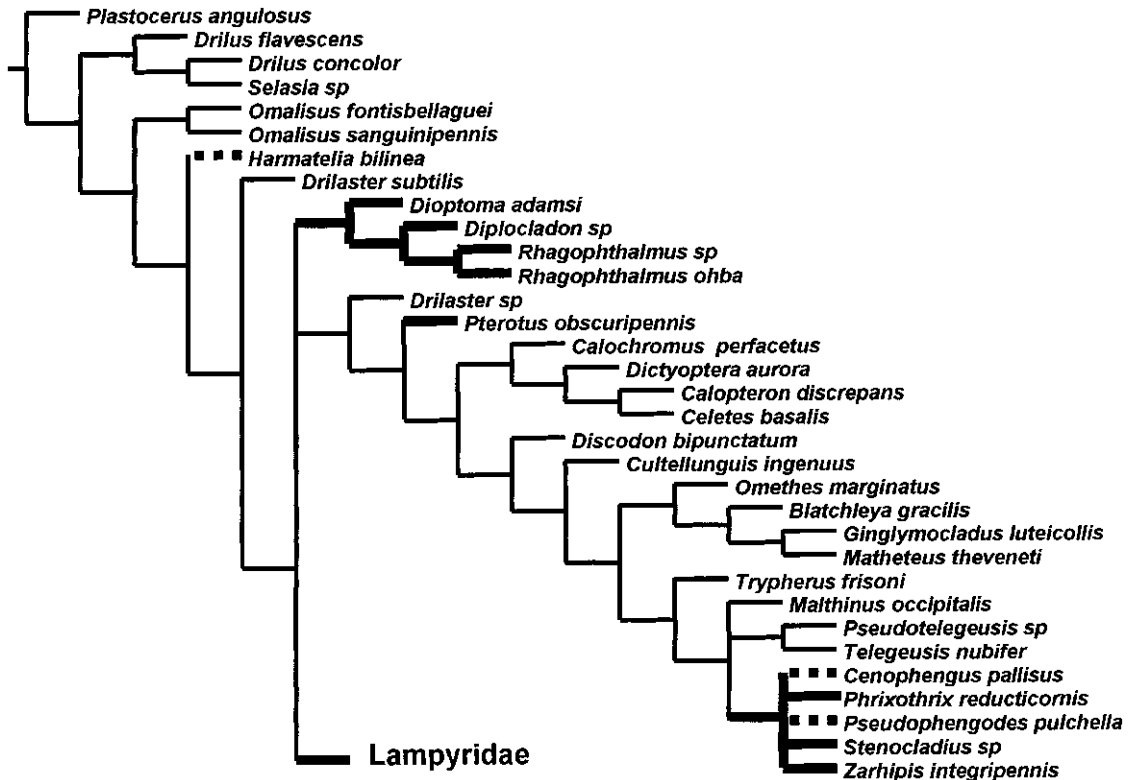


Fig. 5. The evolution of bioluminescence in female cantharoids. The strict consensus tree with the lampryrid clade collapsed. The known presence of luminescence in females is indicated by bold branches, with the hypothesized presence of luminescence in females indicated by dotted branches.

position of these lateral photic organs in the adult males versus larval males is probably due to the lateral tergites, found as plates in the dorsal region on the side of the larval abdomen, becoming fused to the larval tergites to form a single large plate covering the entire dorsal surface of the adult male abdomen. One exception is *Pseudophengodes pulchella*, which bears a large photic organ on the ventral surface of the eighth ventrite that seems to be used in courtship. Until recently, the only phengodid genus that was known to contain adult luminescent males was *Pseudophengodes*. However, Viviani and Bechara (1997) discovered through rearing experiments that phengodid males in the tribe Mastinocerini (*Brasilocerus*, *Euryopa*, *Mastinocerus*, *Mastinomorphus*, *Phrixothrix*, *Stenophrixothrix*, and *Taxinomastinocerus*) are luminous throughout the adult stage and that the luminescent emissions seem to serve a defensive rather than courtship function. No adult phengodid males in the North American tribe Phengodini (*Phengodes* and *Zarhipis*) are known to be continuously luminescent through the entire stage. Even though there is little variation found in male photic organs outside of Lampryridae, the scattered occurrence of photic

organs in males clearly seems to indicate multiple origins (Fig. 6).

J. W. Green's first published observations (1911) of live *Harmatelia bilinea* males did not include any notice of luminescence, even though Green was specifically looking for evidence that this insect was luminescent. The following year (1912), Green published that he had observed two specimens that "exhibited a distinct light when examined in a dark room." The fact that Green had examined many *Harmatelia* specimens without noticing any photic emission may be an indication that these males are not luminescent throughout their entire adult life. It is well known (McDermott 1965; Lloyd 1978; Viviani & Bechara 1997; Branham & Archangelsky 2000) that some lampryrid species which are not luminescent as adults retain the ability to glow via larval photic organs for a short time after they have eclosed and are still teneral. McDermott (1965) hypothesized that the males of both *Pterotus* and *Harmatelia* might have the ability to produce light only briefly after eclosion as does the firefly *Lucidota atra*. McDermott also mentioned in this same work that H. S. Barber (unpublished observation, confirmed by J. E. Lloyd) observed that

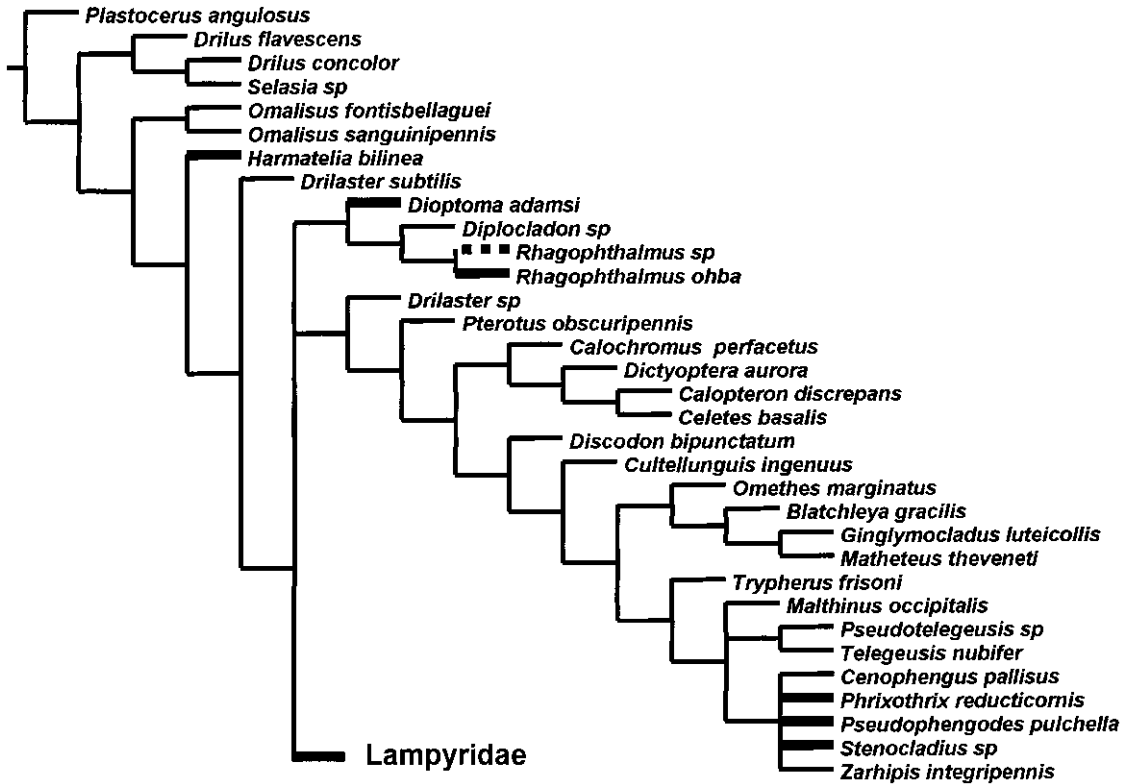


Fig. 6. The evolution of bioluminescence in male cantharoids. The strict consensus tree with the lampyrid clade collapsed. The known presence of luminescence in males is indicated by bold branches, with the hypothesized presence of luminescence in males indicated by dotted branches.

Phengodes males also have the ability to produce light shortly after eclosion. This photic carry-over into the adult, while only temporary in some taxa, is suggestive of a larval origin of the photic organ and its carry over into the adult.

Some *Rhagophthalmus ohbai* males are known to be luminous from paired spots along the lateral edges of ten body segments, (see Table 2). These males are weakly luminous (Chen 1999) and evidently are not always observed (Ohba et al. 1996a). It seems likely that *Rhagophthalmus* males have only a temporary ability to produce light immediately following eclosion and luminescence is not used in courtship (Ohba et al. 1996a).

Luminescence and Life Stages.

The phengodid genus *Phrixothrix* is the only luminous non-lampyrid cantharoid in which larvae, adult males, and adult females are known to be luminescent throughout all life stages (Table 2). Luminescence throughout all life stages of *Phrixothrix hirtus* is essentially the same. The photic organ morphology appears to be identical between all life stages with the exception that the head lantern is lacking in the adult

males. Therefore the lateral lanterns of all stages appear identical and the head lanterns of the larvae and females are identical. In addition, the photic emission spectra is essentially the same for each type of photic organ regardless of life stage (Costa et al. 1999). An additional example of similarity in the emission spectra and a possible connection between larval and adult luminescence was found by Viviani and Bechara (1997) who argued that, "Continuance of the same bioluminescent color in the lateral lanterns of larval, pupal, and adult stages of *Mastinomorphus* sp.1 and *P. heydeni* suggests conservation of the same luciferase iso-form throughout its life cycle." The pattern of photic organ morphology appearing more or less identical across life stages along with similar photic emission spectra being emitted from these organs supports the hypothesis by Crowson (1972) that luminescence first evolved in larvae and was then "carried over into adults."

Evolution of Photic Signaling in Non-firefly Cantharoids

Sivinski (1981) provides a detailed synopsis of the various theories that have been proposed for the function of larval luminescence and the evi-

dence supporting each. While it is now generally accepted that lampyrids are chemically defended and larval photic emissions probably function as aposematic displays (Lloyd 1973; Sydow & Lloyd 1975; Eisner et al. 1978, Belt 1985, Underwood et al. 1997; Knight et al. 1999; De Cock 2000), there exists much less information concerning whether other larval cantharoids are distasteful as well, though it appears that at least some phengodids are chemically defended (Burmeister 1873; Harvey 1952; Sivinski 1981). It is interesting that almost all larval photic organs are paired and are located on the sides of the abdomen or on the eighth abdominal ventrite where the photic emissions are readily seen from the side or from above. This is most consistent with the aposematic warning display hypothesis. The exception to this rule is the pair of medial photic organs on the head of some phengodid larvae such as *Phrixothrix* (Table 1). The photic emissions from these organs were measured by Viviani and Bechara (1997) and were found to be in the range of 574–636nm, well into the red range. Electroretinograms of *Phrixothrix* larvae showed that these larvae have a spectral sensitivity shifted to the red (V. R. Viviani, E. J. H. Bechara, D. Ventura and A. Lall unpublished data; Viviani & Bechara 1997). Viviani and Bechara (1997) hypothesize that these red-emitting head-mounted photic organs provide an illumination function, which may help in locating prey that do not possess spectral sensitivity shifted to the red, and that the lateral photic organs serve an aposematic defensive function.

As the basal luminescent taxa only possess lateral photic organs, it is probable that the first function of larval luminescence was as an aposematic warning display. Larval photic organs where then lost in Lycidae, Omethidae and Cantharidae, and then reappear in Phengodidae. In some phengodids, a photic organ arose on the head and produced red light which was used for illuminating prey (Viviani & Bechara 1997).

The function of luminescence in the adult phengodids is not well understood. Available data suggest that bioluminescence produced by the lateral organs of the adult males and females in this family, seems to serve an aposematic defensive role rather than mate attraction (Rivers 1886, Tiemann 1967, Sivinski 1981). However, the continuous glow produced by the ventral photic organ on the eighth abdominal ventrite in *Pseudophengodes* is also consistent with use as either illumination of the surroundings during flight or intersexual communication (Viviani & Bechara 1997).

The function of luminescence in *Rhagophthalmus ohbai* was studied by Ohba et al. (1996a) who provide evidence that the emissions of the lateral photic organs in females serve an aposematic warning function, illumination while the females

guards her eggs, while the ventral photic organ on the eighth abdominal segment seems to function exclusively in a courtship context. Hence, in this family the paired lateral and the ventral photic organs are used independently in separate contexts: defense and courtship. Across all luminescent cantharoid taxa, photic organs used to produce sexual signals seem to be exclusively restricted to the ventral regions of the body. It is also interesting to note that the eighth abdominal segment is consistently associated with the location of such photic organs. The reason for this association remains unknown.

CONCLUSION

Our phylogenetic analysis suggests that bioluminescence arose twice within the cantharoid lineage and was lost once. The first origin of luminescence in the lineage was ancient and luminescence first arose in larvae where it served as an aposematic warning display. Luminescence was retained in the larvae of the Rhagophthalmidae and Lampyridae and was likely carried over through the pupae into the adult stage where it became functional in some taxa and not in others. While photic signals are used in mate attraction in the Rhagophthalmidae, adult photic signals reached their greatest sophistication in the adults of the family Lampyridae, where photic signals are used in intraspecific communication and both photic organs and photic signals became greatly elaborated under the context of sexual selection. The second origin of luminescence occurred in the family Phengodidae where its function in both larvae and adults is as an aposematic warning display. In some phengodid taxa, luminescence has become elaborated to serve possibly as an illumination device for locating prey. In addition, males of the genus *Pseudophengodes* possess a lampyrid-like photic organ on the eighth abdominal ventrite, which glows continuously and likely serves to either illuminate potential landing sites or functions in courtship. While some researchers have previously hypothesized that the families Lampyridae and Phengodidae were close relatives and shared the charismatic ability to produce bioluminescent signals, these two families are perhaps more interesting than previously thought because they are not closely related and their bioluminescence is convergent.

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APPENDIX 1. LIST OF TAXA USED IN THE ANALYSIS.

Material studied was borrowed from the following institutions: California Academy of Sciences, San Francisco, CA [CASC]; Field Museum of Natural History, Chicago, IL [FMNH]; Florida State Collection of Arthropods, Gainesville, FL [FSCA]; Collection of author [MABC]; Museum of Comparative Zoology, Harvard University, Cambridge, MA [MCZC]; Ohio State University Collection, The Ohio State University, Columbus, OH [OSUC]; Snow Entomological Museum Collection, University of Kansas, Lawrence, KS [SEMC]; Museum of Zoology, University of Michigan, Ann Arbor, MI [UMMZ]; National Museum of Natural History, Smithsonian Institution, Washington, D.C. [USNM].

List of Species Studied: The higher classification used here is based on Lawrence & Newton (1995), and in the case of Rhagophthalmidae, Wittmer and Ohba (1994).

Plastoceridae	<i>Plastocerus</i> (= <i>Ceroplatus</i>) <i>angulosus</i> (Germar) [FMNH]
Omalisidae	<i>Omalisus</i> (= <i>Omalysus</i> , <i>Homalisus</i>) <i>fontisbellagui</i> (Fourar.) 1785 [FMNH] <i>O. sanguinipennis</i> Cast. 1840 [FMNH]
Drilidae	<i>Drilus concolor</i> Ahr. 1812 [FMNH] <i>D. flavescens</i> G.A. Olivier 1790 [USNM] <i>Selasia</i> sp. [FMNH]
Omethidae	
Matheteinae	<i>Matheteus theveneti</i> LeConte 1874 [CASC] <i>Ginglymocladius luteicollis</i> Van Dyke 1918 [CASC]
Omethinae	<i>Omethes marginatus</i> LeConte 1861 [CASC] <i>Blatchleya gracilis</i> Blatchley 1910 [OSUC]
Phengodidae	
Phengodinae	<i>Cenophengus pallidus</i> Schaeffer 1904 [FSCA] <i>Phrixothrix reducticornis</i> Wittmer 1963 [UMMZ] <i>Zarhipis integripennis</i> LeConte 1874 [MABC], [UMMZ]
Rhagophthalminae	<i>Diopoma adamsi</i> Pascoe 1860 [USNM] <i>Diplocladon</i> sp. [CASC]
Rhagophthalmidae	<i>Rhagophthalmus ohbai</i> Wittmer and Ohba 1994 [MABC] <i>Rhagophthalmus</i> sp. [SEMC], [CASC]
Telegusidae	<i>Pseudotelegeusis</i> sp. [SEMC] <i>Telegeusis nubifer</i> Martin 1931 [SEMC]
Lycidae	
Calochrominae	<i>Calochromus perfacetus</i> (Say) 1825 [OSUC]
Lycinae	<i>Calopteron discrepans</i> (Newman) 1838 [OSUC] <i>Celetes basalis</i> LeConte 1851 [OSUC] <i>Dictyoptera aurora</i> (Herbst) 1789 [OSUC]
Erotinae	
Cantharidae	
Cantharinae	<i>Cultellunguis ingenuus</i> LeConte 1881 [OSUC]
Silinae	<i>Discodon bipunctatum</i> Schaeffer 1908 [OSUC]
Malthininae	<i>Malthinus occipitalis</i> LeConte 1851 [OSUC]
Chauliognathinae	<i>Trypherus frisoni</i> Fender 1960 [OSUC]
Lampyridae	
Pterotinae	<i>Pterotus obscuripennis</i> LeConte 1859 [UMMZ]
Cyphonocerinae	<i>Pollaclasis bifaria</i> (Say) 1835 [MCZC], [FSCA]
Otoretinae	<i>Brachylampis sanguinicollis</i> Van Dyke 1939 [CASC] <i>Drilaster subtilis</i> (E. Olivier) 1908 [CASC] <i>Driliaster</i> sp. [MABC] <i>Harmatelia bilinea</i> Walker 1858 [CASC] <i>Stenocladus</i> sp. [MABC]
Amydetinae	<i>Cladodes flabellatus</i> Solier 1849 [CASC] <i>Psilocladus</i> sp. [MABC]

APPENDIX 1. (CONTINUED) LIST OF TAXA USED IN THE ANALYSIS.

Material studied was borrowed from the following institutions: California Academy of Sciences, San Francisco, CA [CASC]; Field Museum of Natural History, Chicago, IL [FMNH]; Florida State Collection of Arthropods, Gainesville, FL [FSCA]; Collection of author [MABC]; Museum of Comparative Zoology, Harvard University, Cambridge, MA [MCZC]; Ohio State University Collection, The Ohio State University, Columbus, OH [OSUC]; Snow Entomological Museum Collection, University of Kansas, Lawrence, KS [SEMC]; Museum of Zoology, University of Michigan, Ann Arbor, MI [UMMZ]; National Museum of Natural History, Smithsonian Institution, Washington, D.C. [USNM].

List of Species Studied: The higher classification used here is based on Lawrence & Newton (1995), and in the case of Rhagophthalmidae, Wittmer and Ohba (1994).

Lampyriinae	<i>Vesta aurantiaca</i> E. Olivier 1886 [USNM]
	<i>Alecton discoidalis</i> Laporte 1833 [MCZC]
	<i>A. flavum</i> Leng et Mutch. 1922 [MCZC]
	<i>Aspisoma ignitum</i> (Linnaeus) 1767 [OSUC]
	<i>A. pulchellum</i> (Gorham) 1880 [FSCA]
	<i>Callophisma maestra</i> Mutch. 1923 [CASC]
	<i>Cratomorphus diaphanus</i> (Germar) 1824 [USNM]
	<i>Ellychnia corrusca</i> (Linnaeus) 1767 [MABC]
	<i>Erythrolychnia bipartitus</i> (E. Olivier) 1912 [FSCA]
	<i>E. olivieri</i> Leng et Mutch. 1922 [FSCA]
	<i>Lamprohiza splendidula</i> (Linnaeus) 1767 [CASC]
	<i>Lampyris noctiluca</i> Linnaeus 1767 [CASC], [FSCA]
	<i>L. zenkeri</i> Germar 1817 [FMNH]
	<i>Lucidina biplagiata</i> (Motsch.) 1866 [MABC]
	<i>Lucidota atra</i> (G. A. Olivier) 1790 [MABC]
	<i>L. dilaticornis</i> (Motschulsky) 1854 [FMNH]
	<i>Macrolampis acicularis</i> (E. Olivier) 1907 [CASC]
	<i>Microphotus angustus</i> LeConte 1874 [FMNH]
	<i>M. octarthrus</i> Fall 1912 [MABC]
	New Species [MABC]
	<i>Phaenolis ustulata</i> Gorham 1880 [FSCA]
	<i>Phausis rhombica</i> Fender 1962 [MABC]
	<i>Photinus ignitus</i> Fall 1927 [OSUC]
	<i>P. meteoralis</i> (Gorham) 1881 [CASC]
	<i>P. pyralis</i> (Linnaeus) 1767 [MABC]
	<i>Phosphaenus hemipterus</i> (Fourcroy) 1785 [CASC]
	<i>Pleotomus nigripennis</i> LeConte 1885
	<i>P. pallens</i> LeConte 1866 [MABC]
	<i>Pristolycus sagulatus</i> Gorham 1883 [CASC]
	<i>Pyractomena ecostata</i> (LeConte) 1878 [FSCA], [UMMZ]
	<i>P. borealis</i> (Randall) 1828 [MABC]
	<i>Pyrocoelia praetexta</i> E. Olivier 1911 [MABC]
	<i>P. rufa</i> E. Olivier 1886 [MABC]
<i>Pyropyga nigricans</i> (Say) 1823 [MABC], [CASC]	
<i>Robopus</i> sp. #1 [MABC]	
<i>Robopus</i> sp. #2 [MABC]	
<i>Tenaspis angularis</i> (Gorham) 1880 [CASC], [MCZC]	
Lucioliinae	<i>Colophotia</i> sp. [MABC]
	<i>Luciola cruciata</i> Motschulsky 1854 [MABC]
	<i>L. kuroiwae</i> Matsumura 1918 [MABC]
	<i>L. lateralis</i> Motschulsky 1860 [CASC]
	<i>L. salomonis</i> (E. Olivier) 1911 [CASC]
	<i>Pteroptyx cribellata</i> (E. Olivier) 1891 [MABC], [UMMZ]
Photurinae	<i>P. malaccae</i> (Gorham) 1880 [MABC]
	<i>P. tener</i> E. Olivier 1907 [MABC]
	<i>Bicellonycha amoena</i> Gorham 1880 [FSCA]
	<i>Photuris brunnipennis</i> Jacq.-Duv. 1856 [OSUC]
	<i>P. divisa</i> LeConte 1852 [MABC]

APPENDIX 2. CHARACTERS AND CHARACTER STATES.

Multistate characters treated as ordered are specified below. Values for Consistency Index (C.I.) and Retention Index (R.I.) for each character in the analysis as they appear on the consensus tree are indicated after the last character state (C.I., R.I.). The character-taxon matrix is presented in Appendix 3. The morphological terminology of Lawrence & Britton (1991) and Snodgrass (1993) was used. Wing venation scheme follows that used in Kukulova-Peck & Lawrence (1993).

0. *Head position*: 0-exposed; 1-partially exposed; 2-covered. (C.I. 0.18, R.I. 0.72)
1. *Head shape*: 0-deflexed between eyes; 1-partially deflexed; 2-not deflexed. (C.I. 0.8, R.I. 0.52)
2. *Antennal insertions* (ordered): 0-widely separated; 1-moderately approximated; 2-approximated. (C.I. 0.8, R.I. 0.61)
3. *Antennal sockets*: 0-prominent; 1-flush. (C.I. 0.5, R.I. 0.33)
4. *Number segments (antennomeres) in male antennae* (ordered): 0-eight; 1-ten; 2-eleven; 3-twelve; 4-thirteen. (C.I. 0.44, R.I. 0.50)
5. *Antennal seg. #3 (flagellomere #1)* (ordered): 0-short, 1-same as #4; 2-long. (C.I. 0.7, R.I. 0.52)
6. *Antennal features (general)*: 0-filiform; 1-serrate; 2-flabellate; 3-pectinate; 4-bipectinate. (C.I. 0.25, R.I. 0.63)
7. *Distal antennal flagellomeres* (ordered): 0-longer than wide; 1-about as long as wide; 2-much wider than long. (C.I. 0.14, R.I. 0.29)
8. *Basal antennal flagellomere/s*: 0-not symmetrical with apical flagellomeres; 1-symmetrical with apical flagellomeres. (C.I. 0.14, R.I. 0.53)
9. *Distal margins of flagellomeres*: 0-straight; 1-concave. (C.I. 0.11, R.I. 0.46)
10. *Distal margin of antennal flagellomeres*: 0-approximating proximal margin in width; 2-wider than proximal margin. (C.I. 0.7, R.I. 0.38)
11. *Antennal flagellomere #2* (ordered): 0-not compressed; 1-slightly compressed; 2-greatly compressed (C.I. 0.8, R.I. 0.60)
12. *Lateral margins of the distal antennal flagellomeres*: 0-parallel; 1-non-parallel. (C.I. 0.5, R.I. 0.52)
13. *Antennal lobes produced from* (ordered): 0-basal region of flagellomere; 1-medial region of flagellomere; 2-apical region of flagellomere. (C.I. 0.25, R.I. 0.62)
14. *Number of elongated antennal lobes per segment*: 0-one lobe; 1-two lobes. (C.I. 0.25, R.I. 0.62)
15. *Antennal lobes*: 0-compressed; 1-not compressed. (C.I. 0.20, R.I. 0.33)
16. *Length of antennal lobes* (ordered): 0-less than length of flagellomere; 1-approximating length of flagellomere; 2-greater than length of flagellomere. (C.I. 0.50, R.I. 0.66)
17. *Antennal lobe / flagellomere juncture*: 0-broad; 1-narrow (C.I. 0.16, R.I. 0.44)
18. *Antennal lobes*: 0-not bearing a sensory depression at apex; 1-bearing a sensory depression at apex (C.I. 1.0, R.I. 1.0)
19. *Mandibles* (ordered): 0-prominent; 1-normal sized; 2-reduced; 3-very reduced. (C.I. 0.14, R.I. 0.68)
20. *Mandible tooth*: 0-absent; 1-present. (C.I. 1.0, R.I. 1.0)
21. *Mandible width*: 0-stout; 1-slender. (C.I. 0.12, R.I. 0.68)
22. *Mandible shape*: 0-apices acute (inside angle <90 degrees); 1-apices non-acute(inside angle near 180 degrees). (C.I. 0.5, R.I. 0.56)
23. *Mandible type*: 0-normal type (arcuate, regularly narrowing to tips); 1-specialized type (tips slender and glabrous with discontinuous curvature). (C.I. 0.25, R.I. 0.84)
24. *Hypomera*: 0-not extending to anterior edge of pronotal shield; 1-narrowly extending to anterior edge of pronotal shield; 2-broadly extending to anterior edge of pronotal shield; 3-lacking. (C.I. 0.30, R.I. 0.82)
25. *Hypomera space around head (side view)*: 0-head (eyes) not able to retract between hypomera; 1-head (eyes) partially enclosed (up to half width of eyes); 2-head (eyes) retractable (less than half eye width exposed). (C.I. 0.11, R.I. 0.65)
26. *Maxillary palpi*: 0-filiform; 1-clavate compressed; 2-clavate; 3-modified. (C.I. 0.12, R.I. 0.57)
27. *Maxillary palp apical seg*: 0-filiform; 1-securiform; 2-elongate; 3-greatly elongate and flattened; 4-conical. (C.I. 0.4, R.I. 0.5)
28. *Labial palpi*: 0-filiform; 1-clavate compressed; 2-clavate; 3-modified. (C.I. 0.16, R.I. 0.44)
29. *Labial palp apical seg*: 0-filiform; 1-securiform; 2-elongate; 3-greatly elongate and flattened. (C.I. 0.20, R.I. 0.52)
30. *Eyes*: 0-oval; 1-emarginate. (C.I. 1.0, R.I. 1.0)
31. *Eyes posterior-ventrally* (ordered): 0-separated; 1-approximated; 2-contiguous. (C.I. 0.25, R.I. 0.66)
32. *Pronotum border*: 0-smooth; 1-margined; 2-explanate. (C.I. 0.22, R.I. 0.46)
33. *Hind angles of pronotum*: 0-truncate (junction between lateral and hind margin = 90 degrees); 1-acute (junction < 90 degrees); 2-laterally expanded (junction > 90 degrees); 3-notched (junction <90 degrees due to deep notch in hind margin). (C.I. 0.13, R.I. 0.58)
34. *Overall surface area of hypomeron* (ordered): 0-absent; 1-small; 2-large/broad. (C.I. 0.22, R.I. 0.58)
35. *Scutellum shape*: 0-distinct; 1-poorly developed. (C.I. 0.25, R.I. 0.40)
36. *Scutellum*: 0-membranous, 1-sclerotized. (C.I. 1.0, R.I. 1.0)

APPENDIX 2. (CONTINUED) CHARACTERS AND CHARACTER STATES.

Multistate characters treated as ordered are specified below. Values for Consistency Index (C.I.) and Retention Index (R.I.) for each character in the analysis as they appear on the consensus tree are indicated after the last character state (C.I., R.I.). The character-taxon matrix is presented in Appendix 3. The morphological terminology of Lawrence & Britton (1991) and Snodgrass (1993) was used. Wing venation scheme follows that used in Kukulova-Peck & Lawrence (1993).

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37. *Prosternum* (ordered): 0-small; 1-medium; 2-large. (C.I. 0.22, R.I. 0.53)
38. *Mesosternum* (*ant. margin*): 0-straight; 1-emarginate. (C.I. 0.50, R.I. 0.75)
39. *Mesal margins of metepisterna*: 0-sigmoid; 1-straight or nearly so. (C.I. 0.33, R.I. 0.83)
40. *Anterior coxae* (ordered): 0-contiguous; 1-nearly contiguous; 2-separate at base. (C.I. 0.33, R.I. 0.42)
41. *Anterior coxal shape*: 0-conical; 1-subconical; 2-triangular; 3-broad; 4-bulbous. (C.I. 0.19, R.I. 0.54)
42. *Middle coxae* (ordered): 0-contiguous; 1-nearly contiguous; 2-separate. (C.I. 0.22, R.I. 0.63)
43. *Hind coxae* (ordered): 0-contiguous; 1-nearly contiguous; 2-separate. (C.I. 0.09, R.I. 0.33)
44. *Hind coxae / femoral plates* (ordered): 0-plates obsolete; 1-< length of coxae; 2-entire length of coxae. (C.I. 0.16, R.I. 0.74)
45. *Trochanter attachment to femora*: 0-oblique; 1-very oblique; 2-interstitial. (C.I. 0.22, R.I. 0.82)
46. *Middle trochantins*: 0-setiferous; 1-glabrous. (C.I. 0.10, R.I. 0.47)
47. *Femora*: 0-slender; 1-normal; 2-flattened; 3-swollen. (C.I. 0.22, R.I. 0.56)
48. *Tibiae*: 0-slender; 1-normal; 2-flattened; 3-swollen. (C.I. 0.14, R.I. 0.50)
49. *Tibial spurs* (ordered): 0-absent; 1-small; 2-well developed. (C.I. 0.06, R.I. 0.42)
50. *Hind tarsal segment one*: 0-normal; 1-elongate. (C.I. 0.22, R.I. 0.53)
51. *Tarsal segment three*: 0-simple; 1-lobed beneath. (C.I. 0.25, R.I. 0.66)
52. *Tarsal segment four*: 0-simple; 1-lobed beneath. (C.I. 0.25, R.I. 0.0)
53. *Claws*: 0-simple; 1-cleft. (C.I. 0.50, R.I. 0.66)
54. *Male elytra* (ordered): 0-fully covering abdomen; 1-somewhat reduced; 2-greatly reduced. (C.I. 0.28, R.I. 0.54)
55. *Elytra surface*: 0-slight punctures with no costae; 1-slight punctures with longitudinal costae; 2-deep window-shaped punctures with longitudinal costae; 3-coarse punctures with no costae; 4-slightly coarse punctures with longitudinal costae. (C.I. 0.26, R.I. 0.54)
56. *Elytral epipleural fold* (ordered): 0-absent; 1-narrow; 2-broad at base. (C.I. 0.22, R.I. 0.84)
57. *Abdominal ventrite #* (*including pygidium*) (ordered): 0-six visible; 1-seven visible; 2-eight visible. (C.I. 0.20, R.I. 0.72)
58. *Male ninth abdominal tergite*: 0-not emarginated behind; 1-emarginate behind. (C.I. 0.11, R.I. 0.75)
59. *Setae on claws*: 0-absent; 1-present. (C.I. 0.50, R.I. 0.85)
60. *Abdominal segment 6, shape of photic organ / s*: 0-two spots; 1-one spot; 2-all; 3-center strip; 4-none. (C.I. 0.57, R.I. 0.85)
61. *Abdominal segment 7, shape of photic organ / s*: 0-two spots; 2-strip; 3-all; 4-none. (C.I. 0.37, R.I. 0.73)
62. *Abdominal segment 8, photic organ's*: 0-absent; 1-present. (C.I. 0.08, R.I. 0.47)
63. *Paired photic organs on segments 1-7*: 0-absent; 1-present. (C.I. 0.50, R.I. 0.0)
64. *Wing vein r3*: 0-absent; 1-present. (C.I. 0.08, R.I. 0.26)
65. *Wing vein r4* (ordered): 0-absent; 1-partial; 2-complete. (C.I. 0.09, R.I. 0.42)
66. *Wing Radial Cell*: 0-open; 1-closed; 2-not present. (C.I. 0.13, R.I. 0.23)
67. *Wing vein MP3*: 0-contacting MP1+2; 1-not contacting MP1+2. (C.I. 0.07, R.I. 0.27)
68. *Wing 1st Cubito-Anal Cell*: 0-absent; 1-present. (C.I. 0.16, R.I. 0.54)
69. *Wing 2nd Cubito-Anal Cell*: 0-absent; 1-present. (C.I. 0.05, R.I. 0.55)
70. *Wing CuA1(cross-vein)*: 0-absent; 1-partial; 2-complete. (C.I. 0.11, R.I. 0.30)
71. *Wing CuA1 vein intersecting MP vein*: 0-above fork (MP3a&MP3b); 1-at fork 2-below fork; 3-other (no fork present). (C.I. 0.16, R.I. 0.21)
72. *Wing CuA2(cross vein)*: 0-absent; 1-partial; 2-complete. (C.I. 0.23, R.I. 0.67)
73. *Wing AA3+4 vein*: 0-absent; 1-present. (C.I. 0.08, R.I. 0.5)
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Character Number (10)	1	2	3	4	5	6	7
Character Number	01234567890123456789012345678901234567890123456789012345678901234567890123						
<i>Plastocerus angulosus</i>	02002130101012002100?	00010000000122012011420211111100003111-143000211112221					
<i>Drilus flavescens</i>	1000223000111200200000101000000022201111031021111001100012014300100-100-00						
<i>Drilus concolor</i>	12002212011111-----000001000000022201111011021121000100022?14300100-000-00						
<i>Selasia</i> sp.	11012221000001002100?0001001000012201111011021011000100022014300100-000-00						
<i>Omalisus fontisbellagui</i>	1210200010101-----1?0101001010012201211011121122010100311-043001111112031						
<i>Omalisus sanguinipennis</i>	1210200010101-----1?0101021210012201211011121122010100311-043001210102000						
<i>Harmatelia bilinea</i>	110020301010020021000010100101001220111102002012101010011200----10211112221						
<i>Drilaster subtilis</i>	1201200010010-----1001010210100222010110100210221101001120043?01210112221						
<i>Dioptoma adamsi</i>	1211321200110-----0010011011112220101102002112201010001200----11211112321						
<i>Diplocladon</i> sp.	12013211000112011010010011040011221010110000010222101001120043000211102201						
<i>Rhagophthalmus</i> sp.	10113210000102010010010011040012222010110000210222101001220043000201112220						
<i>Rhagophthalmus ohba</i>	101132100001120100100100100400122201011011210221011001220043001211112220						
<i>Drilaster</i> sp.	1201201010121-----0011001210100222010110111211202101001120043001110112221						
<i>Pterotus obscuripennis</i>	12002230100001002000010011000000212010?10111211222101001120043001210102201						
<i>Calochromus perfacetus</i>	2201211010111-----001101001010021110010321021222011001020043000001100-01						
<i>Dictyoptera aurora</i>	2220201000111-----0011010212100212010011321020222011002020043001100102101						
<i>Calopteron discrepans</i>	2220201010121-----101001011100211110012321020221011002020043001210102001						
<i>Celetes basalis</i>	1220201011121-----1010010212100212110012322020220011002020043000111100-00						
<i>Discodon bipunctatum</i>	1201210010110-----0011000001010021201010010001011110100102-043001210102001						
<i>Cultellunguis ingenuus</i>	0200210010100-----0011010010100001010100002010111210100102-043001210100-00						
<i>Omethes marginatus</i>	0200200010101-----011001001010023101010020021011211100001-043001110012200						
<i>Blatchleya gracilis</i>	1101200000101-----010101000000023101011000001000111100001?043001110102201						
<i>Ginglymocladus luteicollis</i>	1100203000000200110110101101010013101010020021020211100101-043001110112221						
<i>Matheteus theveneti</i>	21002030000101001000101000010100232110100200010000211100110043001210112221						
<i>Trypherus frisoni</i>	0111200010100-----001003001010013101010010101011110101002-043000010100-00						
<i>Malthinus occipitalis</i>	0201200010101-----101001000000013101010000101011110101302-043000100100-00						
<i>Pseudotelegeusis</i> sp.	02002110101011011000010020020000130100?00000101011??01002004300003-000-00						
<i>Telegeusis nubifer</i>	0101200010101-----0?1002033330013010010000001010210101002004300000-000-00						
<i>Cenophengus pallisus</i>	02213040011010102100010020010100000011100000010100101020020043001110000-00						
<i>Phrixothrix reducticornis</i>	02003140010000102100001010000000102010102001010112100020020043000231102300						
<i>Pseudophengodes pulchella</i>	02002050100000112100010010000000131010?00000010200001010020043100100100-00						
<i>Stenocladus</i> sp.	12112030100000002101001011000000001010110021110000100000120043000130100-00						
<i>Zarhipis integripennis</i>	02003040010010112100010010000002110101002000101101011121043001210112221						
<i>Brachylampis sanguinicollis</i>	2200210010110-----00110012210000222010110200201221101000220043001110102021						
<i>Psilocladus</i> sp.	22112040100000112101011011210000212010110200200220101001120043001210112021						
<i>Ellychnia corrusca</i>	2211211010110-----1001001111100212010110200200221101001221043001210111021						

APPENDIX 3. (CONTINUED) MORPHOLOGICAL CHARACTER MATRIX.

Character Number (10)	1	2	3	4	5	6	7
Character Number	01234567890123456789012345678901234567890123456789012345678901234567890123						
<i>Pyractomena ecostata</i>	2211210010110	-----	2011102111100202010110200201220001001221122001210112221				
<i>Pyractomena borealis</i>	2111210010110	-----	2011102111100202010110200201221001001221122001210112221				
<i>Aspisoma pulchellum</i>	2121210010010	-----	2011101211100212010110200100221001001220122101210102221				
<i>Aspisoma ignitum</i>	2211210010110	-----	2010102111100212011110200200221001001220122101210102021				
<i>Cratomorphus diaphanus</i>	2021211010110	-----	201110210?101212010110211200221101001221000001210112221				
<i>Pyrocoelia praetexta</i>	2121201011121	-----	2011102111100212010110401200220101001221031001211112221				
<i>Pyrocoelia rufa</i>	2021211111121	-----	2011101111100212010110401200220101001221031001210112221				
<i>Alecton discoidalis</i>	2121211210101	-----	2010102111100212010110101200221101001220043001210112221				
<i>Alecton flavum</i>	2121211210111	-----	201010211110021201011020110201200221101001220043001210112221				
<i>Pyropyga nigricans</i>	2201211010120	-----	1010002111100212010110200200221100001221043001210112221				
<i>Phaenolis ustulata</i>	2221204010120210200001110211010020201110101200220101001211043001200102021						
<i>Tenaspis angularis</i>	2211201011121	-----	1011102210100212010110100200221001001211043101210112021				
<i>Erythrolychnia bipartitus</i>	2021211010121	-----	1010102212100202010110200200221101001211013001210012220				
<i>Erythrolychnia oliveri</i>	2021201010121	-----	1010102112100202010110200200221101001211013001211112220				
<i>Lucidota atra</i>	2121201011121	-----	1010002210100212010110200100220101001221043101210112221				
<i>Lucidota dilaticornis</i>	2121201011121	-----	0010001210100212010110201200221101001220043101201112221				
<i>Lucidina biplagiata</i>	2211201011121	-----	0010001212100212010110400200220101001221043001100112221				
<i>new species</i>	2221211011121	-----	0010001112100212010110200200220101000220043101210112221				
<i>Pollaclasis bifaria</i>	21112140111010102100010012010100212010110201210210101001221043100210112221						
<i>Pristolycus sagulatus</i>	2211201011121	-----	2010012112100221010110301210220101004101043001011112221				
<i>Vesta auranfiaca</i>	2221?01011121	-----	001000111010022201011020020022110100122104310111112021				
<i>Callopisma maestra</i>	2220201010120	-----	0011001212100212010110200200220101001221043001210100-01				
<i>Cladodes flabellatus</i>	22212020110212002100011002212100212010110201200220101001221043101210110-21						
<i>Macrolampis acicularis</i>	2011210010110	-----	0001001112100202010110201200221101001220043001210112021				
<i>Photinus pyralis</i>	2111210010020	-----	000100121010020201011010020022101001220022001210101011				
<i>Photinus ignitus</i>	2101220010010	-----	1001001110100212010110100200221101001221022101210112121				
<i>Photinus meteoralis</i>	2201210010020	-----	1001001211100212011110101200221010012210221010012210112121				
<i>Bicellonycha amoena</i>	2021200010100	-----	0001001110100222010110200210222101101220022001110101321				
<i>Photuris divisa</i>	1020200010100	-----	0000000112100212010110200210222101100220022001210110-20				
<i>Photuris brunnipennis</i>	2021200010100	-----	0001000010100212010110200210222101101220022101210102201				
<i>Robopus sp1</i>	2121210010020	-----	1011001110100202010110200200220101001220043101210110-11				
<i>Robopus sp2</i>	2121210010020	-----	0011001110100202010110200200220101001220043101210111221				
<i>Luciola lateralis</i>	2011210010111	-----	1011011010101222010110200201211101001200021-01210112220				
<i>Luciola salomonis</i>	2021220010111	-----	1011011210101212010110200200211101000200021-01210112221				
<i>Luciola cruciata</i>	1220210010111	-----	0001011112101222010110200210220101001200022-01210112221				
<i>Luciola kuroiwae</i>	1021220110101	-----	101101111210120201011020020?220101001200022-01211002200				

APPENDIX 3. (CONTINUED) MORPHOLOGICAL CHARACTER MATRIX.

Character Number (10)	1		2		3		4		5		6		7	
Character Number	0	1	2	3	4	5	6	7	8	9	0	1	2	3
<i>Colophotia</i> sp.	2	1	1	1	2	0	0	0	0	0	0	0	0	0
<i>Pteroptyx cribellata</i>	1	0	0	1	1	1	1	0	1	0	0	2	2	1
<i>Pteroptyx malacca</i>	1	0	1	0	2	1	0	1	1	0	2	0	2	0
<i>Pteroptyx tener</i>	1	0	1	1	2	1	0	1	1	0	2	0	2	1
<i>Lamprohiza splendidula</i>	2	0	1	1	0	1	0	1	0	1	2	2	1	0
<i>Phausis rhombica</i>	2	1	0	2	1	0	1	0	2	1	0	1	0	0
<i>Phosphaenus hemipterus</i>	2	0	2	2	0	1	0	1	0	0	0	1	0	2
<i>Pleotomus nigripennis</i>	2	0	1	4	0	2	0	1	0	1	0	1	2	1
<i>Pleotomus pallens</i>	2	0	1	4	0	2	0	1	0	1	0	1	2	1
<i>Lampyris zenkeri</i>	2	0	1	2	0	0	1	0	1	1	0	1	0	1
<i>Microphotus angustus</i>	2	0	1	1	0	2	1	0	1	1	0	2	0	1
<i>Lampyris noctiluca</i>	2	0	1	2	1	0	1	2	0	2	0	1	0	1
<i>Microphotus octarthrus</i>	2	0	1	2	1	0	0	2	2	0	1	0	1	1