

## 4.15. Lampyridae Latreille, 1817

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**Distribution.** 83 genera and approximately 2000 species are described. These are distributed worldwide with the greatest diversity of species occurring in the Oriental and the Neotropical regions. The two largest genera are the Old World *Luciola* Laporte and the New World *Photinus* Laporte (McDermott 1964, 1966). While species diversity is higher in regions that are relatively humid, a minority of species (e. g., *Microphotus* LeConte, some *Pleotomus* LeConte) are known to occur in arid habitats.

**Biology and Ecology, Adults.** Only a percentage of adult lampyrids are luminous and genera which lack the ability to glow as adults are generally restricted to basal clades within the family and rely solely on long range pheromones for mate attraction (Branham & Wenzel 2003). The luminous signals of adult males are produced from photic organs of various shapes (e. g., one spot, paired spots, stripe, entire surface of ventrite) located on abdominal ventrites 5–7 (true abdominal segments VI–VIII). The photic organs of adult females also appear on ventrites 5–7, though females generally possess photic organs of reduced size and have fewer luminous ventrites compared to males of the same species. Complex luminous sexual signals, consisting of single flashes or trains of multiple flashes, appear to be associated with more structurally complex photic organs, which have both increased innervation and increased tracheole supply (Buck 1948). These complex organs are large and commonly occupy the entire ventral surface of the abdominal segment on which they appear (Branham & Wenzel 2003). Luminescence in adults is typically used in sexual signaling to communicate species identity and facilitate pair formation. These photic emissions vary in complexity from glows produced by the female to attract non-luminescent males, to flash-answer dialogues between both sexes of the same species employing critical timing parameters (Lloyd 1966, 1971). While glows are used by some species as sexual signals, communication protocols that employ flash-answer signals are known to have evolved at least three times in the family (Branham & Wenzel 2003). “Intermittent flash synchrony” is sometimes known to occur in populations, or even in groups of males within a population of some *Photinus* species, which normally produce asynchronous flashes (Mast 1912; Blair 1915; Otte & Smiley 1977; Copeland & Moiseff 1995). The intermittent synchrony found in *Photinus* fireflies are produced by flying males. However, perhaps the most spectacular examples of synchronous flashing are produced by sedentary aggregations of several species of the Old World *Pteroptyx* Olivier, which occur in tropical southeast Asia,

from the Philippines to eastern India and Sri Lanka (Buck 1938). These synchronous aggregations of fireflies consist of both sexes, which are drawn to the aggregation sites from some distance and remain there, signaling at night, for weeks if not months on the same vegetation (Case 1980; Ohba 1984; Lloyd *et al.* 1989). Within Lampyridae, morphological structures adapted to form copulation clamps are known from only a few species of *Pteroptyx* and *Luciola*. A copulation clamp partially formed from the deflexed elytral apices, is restricted to males of *Pteroptyx* from New Guinea. To form the top of the clamp, the tips of the male’s elytra hook around the anterior edge of the female’s sixth abdominal tergite. The bottom of the clamp is formed from the distal margin of the male’s seventh sternite, which pushes upwards against the ventral surface of the female’s abdomen (Lloyd & Wing 1981; Wing *et al.* 1983; Ballantyne 1987 a). Males of non-New Guinea *Pteroptyx*, as well as *Luciola pupilla* E. Olivier, do not possess deflexed elytral apices but show clamp-like modifications to the end of the male abdomen (Ballantyne 1987 b). Interestingly, the modifications of the abdomen in non-New Guinean *Pteroptyx* do not appear to be homologous with those found in their New Guinea relatives (Ballantyne 1987 a, 1987 b). Aggressive mimicry is known to occur in females of the *pennsylvanica-versicolor* group of the genus *Photuris* LeConte. These females respond to the flash patterns of conspecific males with their own species specific signals during courtship (Barber 1951). The *Photuris* “femmes fatales” are capable of producing flashes that approximate the female response of sympatric *Photinus* or species of *Pyroctomena* Melsheimer, and, when these heterospecific males land near them to mate, the *Photuris* females quickly seize and devour them (Lloyd 1965, 1984). While it was first hypothesized that these aggressive mimics gained only valuable protein from feeding on other fireflies, Eisner *et al.* (1997) discovered that females of *Photuris versicolor* (Fabricius) also acquire defensive steroids called lucibufagins. High levels of lucibufagins are common in *Photinus* fireflies, but both *Photuris* males and females appear to lack lucibufagins upon emergence from the pupa. In addition, Eisner *et al.* (1997) cited evidence that *Photuris* aggressive mimics endow their eggs with the newly acquired defensive steroids. Spermatophores are found in some species of fireflies where females mate more than once. Nutrients derived from these spermatophores have been shown to be incorporated into developing oocytes. Conversely, in species where females mate only once, the eggs are fully developed immediately following female eclosion and males do not form spermatophores (Wing 1985; van der Reijden *et al.* 1997; Rooney & Lewis 1999, 2002).

**Biology and Ecology, Larvae.** Lampyrid larvae are common in mesic environments, where they are found along the margins of streams and ponds, as

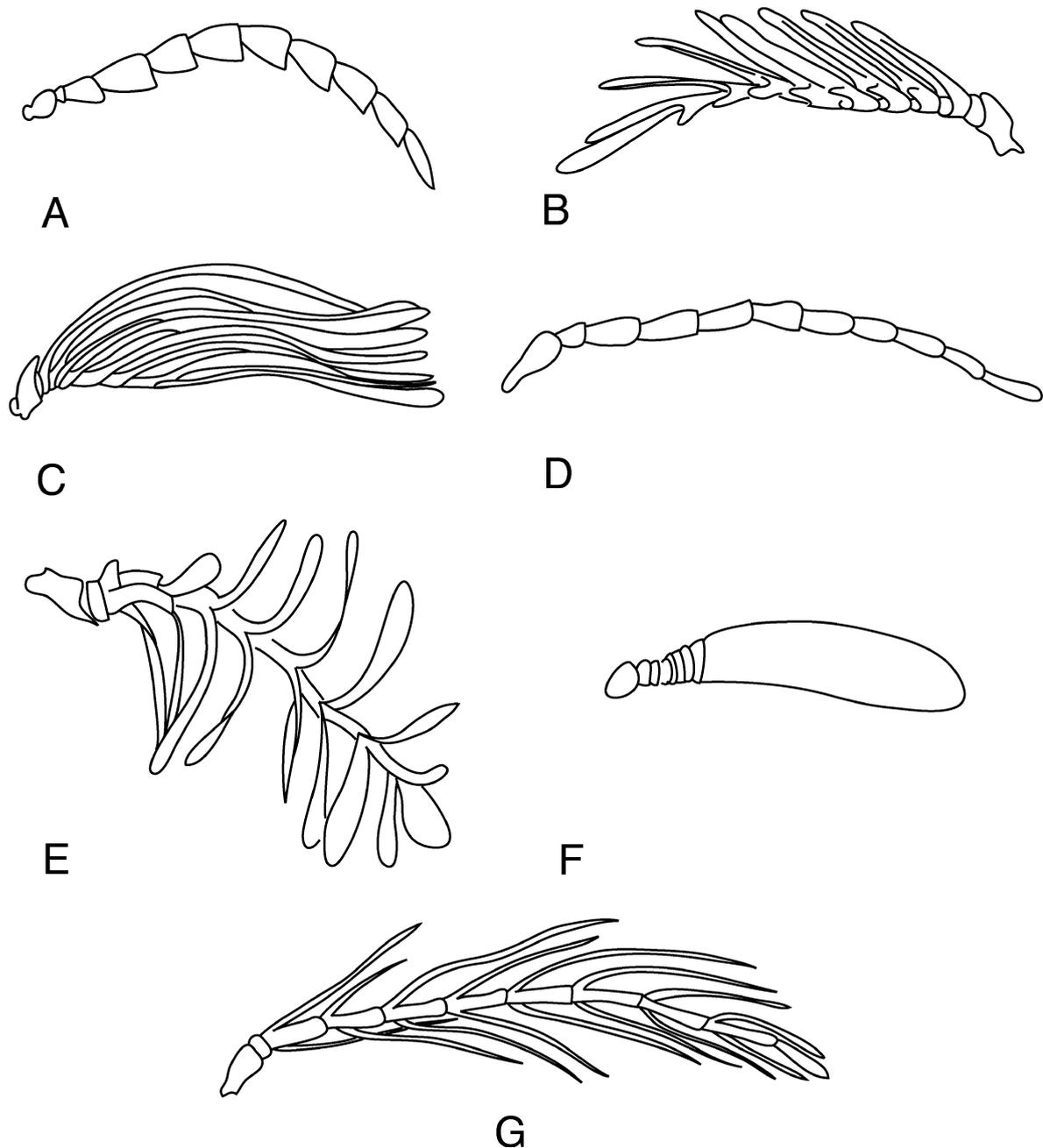


Fig. 4.15.1 A–G, Adult antennae. A, Serrate, *Pyrocoelia praetexta* E. Olivier, male, left antenna, ventral view; B, Biflabellate, *Lucio splendens* E. Olivier, male, right antenna, ventral view; C, Flabellate, *Dodacles plumosa* (Gorham), male, left antenna, ventral view; D, Filiform, *Photinus pyralis* (L.), male, left antenna, ventral view; E, Biflabellate, *Lamprocera* sp., male, left antenna, ventral view; F, “Capitate,” *Petalacmis praeclarus* E. Olivier, male, left antenna, anterior view; G, Bipectinate, *Psilocladus* sp., male, right antenna, dorsal view (A–G © M. Branham).

well as in leaf litter or rotten logs and under rocks. In arid regions, larvae are commonly active above ground at night, immediately following rains. All known lampyrid larvae are luminous. The origin of larval luminescence appears to predate the origin of the family Lampyridae (Branham & Wenzel 2001, 2003). Larvae produce light via paired photic organs located on the ventral surface of the eighth abdominal segment. The only larvae that are known to vary from this photic organ morphology are *Lamprohiza delarouzei* Jacquelin DuVal, which

have two pairs of photic organs (one pair each on abdominal segments II and VI) (Balduf 1935), and *Lamprohiza splendidula* L., which have 3–12 luminous spots on abdominal segments II–VI (Schwalb 1960). Though luminescence is employed in the eggs, larvae and most pupae of lampyrid species, the adaptive significance of larval luminescence has received considerable attention (McDermott 1964; Crowson 1972; Siviniski 1981). The fact that fireflies are known to sequester defensive steroids and are commonly rejected by naïve predators suggests

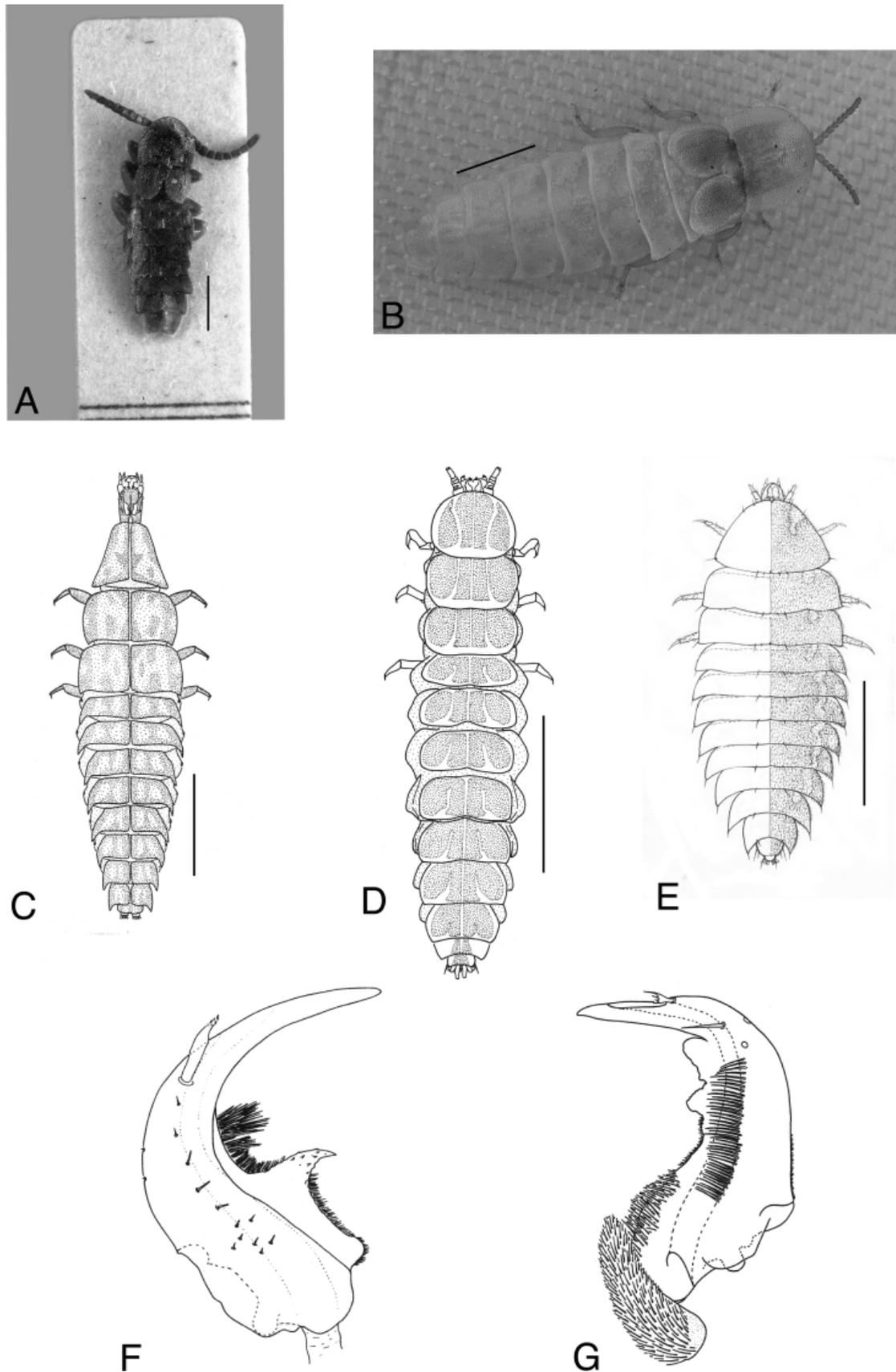


Fig. 4.15.2 A, *Phosphaenus hemipterus* (Fourcroy), brachypterous male, line = 2.5 mm; B, *Pleotomodes needhami* Green, brachypterous female, line = 2.0 mm; C, *Pyractomena borealis* (Randall), larva, line = 5.0 mm; D, *Luciola atra* (G.A. Olivier), larva, line = 5.0 mm; E, *Photuris* sp., larva, line = 5.0 mm (from Peterson 1951); F, *P. borealis*, left larval mandible, dorsal view; G, *L. atra*, right larval mandible, dorsal view. (A, B, © M. Branham; C, F, from Archangelsky & Branham 1998; D, G, from Branham & Archangelsky 2000)

that larval luminescence functions as an aposematic warning signal (Kloft *et al.* 1975; Eisner *et al.* 1978; Underwood *et al.* 1997; Knight *et al.* 1999; De Cock & Matthysen 1999, 2003). Some genera, such as *Photinus*, are subterranean as larvae while others (e. g., *Photuris*) are active on the surface in leaf litter and still others (e. g., *Pyrractomena*) are semi-aquatic and are able to stay submerged for a short period of time while foraging for food (Buschman 1984 a). Some species in the genus *Luciola* are fully aquatic, respiring through the use of tracheal gills (Annandale 1900; Blair 1927; Okada 1928; Jeng *et al.* 2003). The larvae, pupae and adults of both sexes of *Pleotomodes needhami* Green have been collected in the nests of several species of ants. *Pleotomodes needhami* are not thought to feed on the ants or their brood while the ants appear to ignore the fireflies (Sivinski *et al.* 1998). Schwab (1960) discovered that larvae locate prey via chemical cues and seemingly have the ability to not only follow old snail slime trails, but also determine the polarity of these trails in order to follow them in the correct direction. Once they locate the prey, but before feeding, larvae inject digestive juices from the midgut through a channel in each mandible into the prey. The digestive juices paralyze the prey and then liquefy its tissues, which are then ingested through the oral cavity (Fabre 1913; Vogel 1915). The abdominal segment X of all lampyrid larvae bear eversible tubular organs that are covered with minute hooks which adhere to all types of substrates; these are used as hold-fast organs, but also aid in locomotion and in the grooming of the larval head after feeding (Bugnion 1933; Domagala & Ghiradella 1984). The number of larval instars appears to vary in Lampyridae. While Archangelsky & Branham (1998) found five larval molts in *Pyrractomena borealis* (Randall), which were all reared under the same photoperiod, Buschman (1977) found instar number to vary from 4–9 in *Pyrractomena lucifera* (Melsheimer) under different photoperiod regimes. Higher numbers of larval instars seem to be present in larvae under shorter photoperiods. Naisse (1966) and Buschman (1977) found that the female larvae of *Lampyrus noctiluca* L. and *Pyrractomena lucifera* respectively, underwent an additional instar compared to male larvae of the same species. Larvae can take from several months to up to two years to reach pupation (Williams 1917; Hess 1920). Lampyrids pupate underground in excavated cells, on the surface in covered cells called igloos, or in natural cavities in dead logs (Hess 1920; Buschman 1984 b; Branham & Archangelsky 2000; Archangelsky & Branham 2001). Those species that are aquatic or semi-aquatic as larvae (some *Luciola* and *Pyrractomena* respectively) exit the water prior to pupation and construct mud cells. Some species of *Aspisoma* Laporte have arboreal larvae that construct cryptic pupae which hang like “Lepidoptera chrysalids” (LaBella & Lloyd 1991). Most pupae are known to be luminescent (even if they are not luminescent as adults) and increase the intensity of their glow when disturbed.

**Morphology, Adults** (Fig. 4.15.1 A–G; 4.15.2 A, B; 4.15.3 A–G; 4.15.4 A–T). 7–43 mm in length, elongate oval and generally flattened.

Head completely or partially concealed from above by pronotum. Posterior region of compound eyes usually not emarginated, but emarginations present in many Luciolinae. Ocelli absent. Antennal insertions flush with head capsule, approximate. Frontoclypeal suture absent or incomplete. Labrum sometimes visible, though frequently indistinct. Antennae filiform to serrate, bipectinate, flabellate, biflabellate or, very rarely, capitate (Fig. 4.15.1 A–G); antennae of males with 8–10 (*Microphotus*), 11, or 13 (*Pleotomus*) antennomeres, 11 being the most common. Basal antennal flagellomeres usually symmetrical with apical flagellomeres. Mandibles falcate; sometimes short and robust, those of several genera being completely setiferous except at apex; mola absent. Maxilla with distinct galea and lacinia; apex of the galea densely setose; lacinia without spines; palp 4-segmented with apical maxillary palpomere almost always securiform. Labial palp 3-segmented, with apical palpomere usually securiform.

Anterior edge of pronotal shield rounded. Base of prothorax approximating elytral bases. Procoxal cavities contiguous. Scutellar shield never abruptly elevated. Elytra reduced in males of *Phosphaenus hemipterus* (Fourcroy) (Fig. 4.15.2 A) and reduced (Fig. 4.15.2 B) or absent in females of various groups; without reticulate pattern; epipleura distinct and usually wide at base. Mesal edges of metanepisterna straight or nearly so. Metacoxal cavities contiguous or nearly contiguous. Hind wings present, reduced or absent. Radial cell usually well-developed. Anal notch of hind wing absent. Tibial spurs usually indistinct or absent; tarsal formula 5-5-5; claws paired and simple or toothed or bifid, without setae near base.

Abdomen hologastrous in most adult males, bearing seven or eight visible ventrites corresponding to sternites II–VIII or IX. Sternite VIII highly reduced in Luciolinae and both VIII and IX withdrawn into segment VII, leaving only six ventrites exposed. Brachypterous males of the European *Phosphaenus hemipterus* Laporte with larval type of abdomen with sternites I–IX visible. In most species, females with one less ventrite than males. Segment I represented by tergite only (except in *P. hemipterus* and *Photinus granulatus* Fall). Spiracles present on dorsally reflexed lateral portions of sternites or in emarginations in their lateral edges. Photoc organs present in one or both sexes of some species; when present, generally located on ventrites 5, 6 and 7 (segments VI, VII, and VIII). Aedeagal sheath composed of segments IX and X; aedeagus of trilobate type with phallobase, parameres, and penis; tips of parameres may form sharp “hooks” (*Tenaspis* LeConte, *Erythrolychnia* Motschulsky and *Macrolampis* Motschulsky); paramere tips in *Diaphanes* Motschulsky “hooked” but blunt rather than sharp; in *Tenaspis*, parameres robust basally

but with apical halves becoming greatly narrowed and curved, forming long, slender hook-like extensions; aedeagus of *Photuris* with two long, thin, apically bulbous lateral filaments attached to phallobase; two similar filaments in species of *Vesta* Laporte arise from medial region on the outside surface of each of the two parameres. Ovipositor with distal styli. [McDermott 1964; Lloyd 2002.]

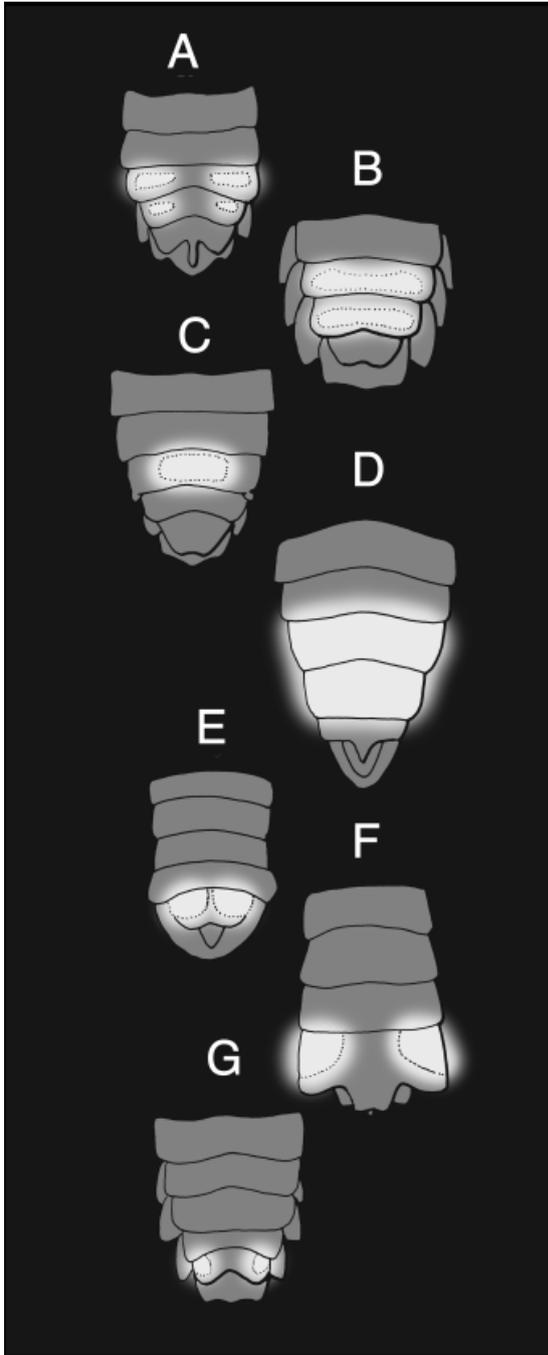


Fig. 4.15.3 A–G, Representative adult photic organ morphologies. A, *Cratomorphus diaphanus* (Germar); B, *Pyrocoelia rufa* E. Olivier; C, *Erythrolychnia oliveri* Leng & Mutchler; D, *Bicellonycha amoena* Gorham; E, *Robopus* sp. 2; F, *Pteroptyx tener* E. Olivier; G, *Pleotomus pallens* LeConte. (Modified from Grimaldi & Engel 2005 and Branham & Wenzel 2003)

**Morphology, Larvae:** (Figs. 4.15.2 C–G) 5–65mm in length. Body onisciform, fusiform, or subparallel. Tergal margins explanate in some taxa (e. g., *Atyphella* Olliff, *Lamprigera* Motschulsky, *Photuris*) (Fig. 4.15.2 E), but not in others (e. g., *Photinus*, *Pyractomena*, *Luciola*, *Lucidota* Laporte, *Pteroptyx*, *Colophotia* Dejean) (Figs. 4.15.2 C, D). Tergites more or less heavily sclerotized and pigmented.

Head distinctly prognathous, parallel-sided, subcylindrical, narrower than thorax, and when fully retracted generally concealed from above by pronotum. Anterior prothoracic collar with cervical muscles (Labella & Lloyd 1991: “muscular sheath”) enclosing large parts of the head, unless head is fully extended. Exposed anterior part of head capsule sclerotized and pigmented on dorsal side and laterally; considerable parts on ventral side membranous; retracted posterior part of head capsule represented by strongly enlarged postoccipital region, mostly semimembranous and unpigmented, deeply incised ventromedially, less strongly so dorsomedially (Beutel 1995 [*Phosphaena*]). Epicranial stem (coronal suture) and frontal sutures usually present; length of epicranial stem variable (not recognizable in *Phosphaena*; Beutel 1995). One stemma located on each side of the head. Frontoclypeal suture absent. Labrum completely fused to head capsule; labral muscles absent (Beutel 1995 [*Phosphaena*]); anterior epipharynx densely pubescent. Antennae 3-segmented, retractable. Sensorium on preapical antennomere shorter than or equal in length to apical antennomere; extrinsic muscles originate on head capsule. Mandibles falcate, with internal channel running from the mandibular base to anterior opening just before apex (Fig. 4.15.2 F, G); posterior opening on proximal dorsal mandibular surface between secondary mandibular joint and large, densely pubescent extension of mesal mandibular base; viewed in cross section, internal channel located within chitinous wall of dorsal mandibular surface (Vogel 1915: fig. 23); incisor edge of mandible usually bearing one or two heavily sclerotized retinacula; mesal region of mandibular base bearing microtrichia or spines; flexor of mandible very strongly developed, its origin occupying large parts of the posterior head capsule (Beutel 1995: fig. 10b). Ventral mouthparts closely connected; maxillolabial complex forms main part of ventral closure of head; connected with ventrolateral wall of head capsule by fairly wide membrane; maxillary and labial parts not fused but connecting membrane very narrow. Cardo sclerotized and distinct; stipes broad and elongate, with extensive membranous apical part; galea 2-segmented; lacinia represented by extensive, densely pubescent structure connected with dorsomesal stipital edge (Vogel 1915; Beutel 1995); palp 3- or 4-segmented; *M. craniocardinalis* absent; *M. tentoriocardinalis* strongly developed, nearly vertical, originating on sclerotized ventral wall of prepharyngeal tube; *M. tentoriostipitalis* also strongly developed, composed of a nearly vertical and a smaller longitudinal

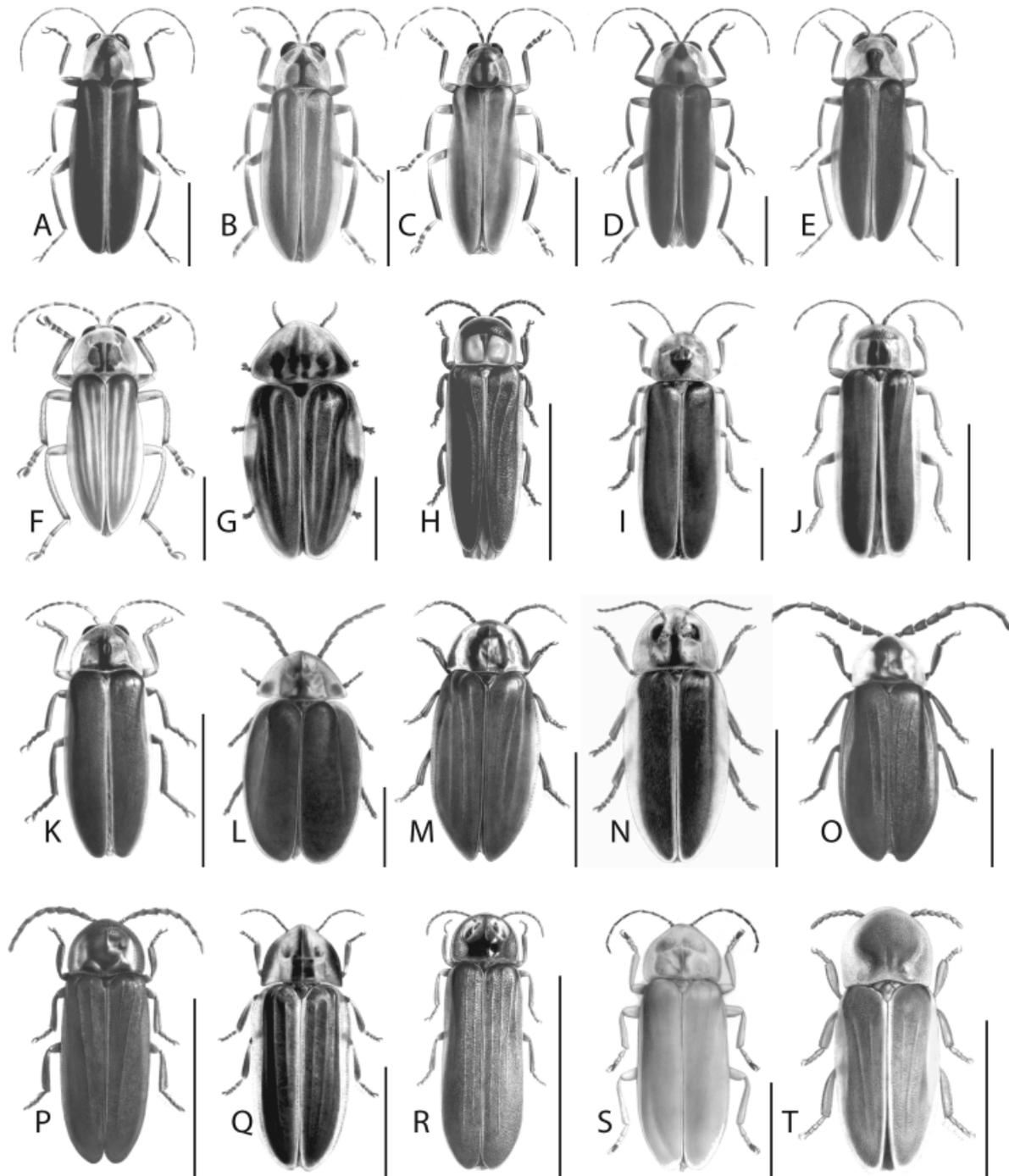


Fig. 4.15.4 A–T, Some representative North American Lampyridae, line = 5.0 mm. A, *Photuris versicolor* (Fabr.); B, *Photuris lloydi* McDermott; C, *Photuris pennsylvanica* (De Geer); D, *Photuris lineaticollis* (Motch.); E, *Photuris frontalis* LeConte; F, *Photuris trivittata* Lloyd and Ballantyne; G, *Aspisoma ignitum* (Linn.); H, *Photinus tanytoxus* Lloyd; I, *Photinus pyralis* (Linn.); J, *Photinus macdermotti* Lloyd; K, *Bicellonycha w. wickershamorum* Cicero; L, *Tenaspis angularis* (Gorham); M, *Ellychnia corrusca* (Linn.); N, *Micronaspis floridana* Green; O, *Luciola atra* (G. A. Olivier); P, *Pyropyga nigricans* (Say); Q, *Pyractomena angulata* (Say); R, *Phausis reticulata* (Say); S, *Photinus pallens* (Fabr.); T, *Pleotomodes knulli* Green (Carbon dust drawings by L. Line, courtesy of J. E. Lloyd.)

subcomponent; vertical subcomponent originating on ventral prepharyngeal wall, longitudinal bundle on gular sclerite; *M. craniolaciniialis*, *M. stipitogalealis* and *M. stipitopalpalis* externus present (Beutel 1995). Labium composed of elongated mental plate

between maxillae and narrow prementum; ligula absent; labial palp 2-segmented; *M. submentopraementalis* absent; *Mm. tentoriopraementalis* inferior and superior well developed (Beutel 1995). Gula wider than long. Tentorium vestigial. Posterior

epipharynx and hypopharynx laterally fused, forming a short prepharyngeal tube. Pair of conspicuous sclerotized dorsolateral plates embedded in pharyngeal wall immediately posterad of anatomical mouth opening; connected with caudal part of furcate hypopharyngeal suspensorium by short semi-membranous zone (Beutel 1995); pharyngeal tube long; *M. frontobuccalis* posterior very strongly developed. Brain and suboesophageal ganglion completely shifted to prothorax (Beutel 1995).

Protergum subelliptical and narrowed anteriorly. Thoracic terga generally divided by sagittal line. Meso and metathoracic terga subquadrate, slightly wider than long. Legs 5-segmented (including simple pretarsus), either long and slender or short and stout; femur and tibiotarsus often bearing one or two rows of strong setae on inner margin. One pair of biforous spiracles present on mesothorax.

Abdominal terga I–VIII generally divided by a sagittal line, which is lacking on tergum IX (Fig. 4.15.2 C). Segment X often concealed from above and reduced to a short sclerotized ring bearing ever-visible, tubular, filamentous holdfast organs, which are covered with minute hooks. Spiracles biforous, located on abdominal laterotergites I–VIII. Sac-like tracheal gills present on sides of abdominal segments I–VIII in many fully aquatic larvae. Segment VIII bearing a photic organ with one luminous spot appearing on each of the two laterotergites. *Lamprohiza* larvae bear additional paired photic organs on ventrites anterior to segment VIII. [Labella & Lloyd 1991; Beutel 1995; Branham & Archangelsky 2000; Archangelsky & Branham 2001.]

**Phylogeny and Taxonomy.** Two recent phylogenetic studies have been published that have included a sampling of lampyrid taxa not limited to one geographic region and enough outgroup taxa to address higher level taxonomic questions within this lineage (Branham & Wenzel 2001, 2003; Bocakova *et al.* 2007). Branham & Wenzel (2001) conducted a phylogenetic analysis of morphological characters of Lampyridae (52 ingroup taxa) using outgroups representing all lineages within the traditional Cantharoidea (i. e., Plastoceridae, Drilidae, Cneoglossidae, Omalisidae (= Homalisidae), Rhagophthalmidae, Lampyridae, Lycidae, Omethidae, Telegeusidae, Phengodidae and Cantharidae) with the exception of Cneoglossidae. This matrix was assembled in order to test the monophyly of the family (Branham & Wenzel 2001) and to reconstruct the phylogenetic relationships and signal system evolution within Lampyridae (2003). The phylogeny indicates Lampyridae is not monophyletic as defined by Crowson (1972) and Lawrence and Newton (1995) as it places the lampyrid genera *Harmatelia* Walker, *Pterotus* LeConte, *Drilaster* (*Ototreta*) Kiesenwetter, and *Stenocladius* Fairmaire outside of the family. This is not surprising as these taxa are known to possess questionable affinities to existing cantharoid families and their placement within

Lampyridae appears arbitrary (LeConte 1859; McDermott 1964; Crowson 1972). Therefore, to preserve the monophyly of Lampyridae, Branham & Wenzel (2001) removed these genera from Lampyridae and placed *Drilaster* (*Ototreta*), *Harmatelia*, and *Pterotus* in “Elateroidea *Incertae Sedis*.” (see 2–XX.X). Under this new arrangement, the synapomorphies defining the base of Lampyridae include: head covered by pronotum, oblique attachment of the trochanter to femora, and wing vein CuA<sub>1</sub> intersecting MP above fork (Kukalová-Peck & Lawrence 1993). The monophyly of only two (Photurinae and Luciolinae) of the seven lampyrid subfamilies is supported by this analysis (Branham & Wenzel 2003). This finding supports the views of McDermott (1964) and Crowson (1972), who considered the taxonomy of Lampyridae to be helpful in the identification of taxa though not in delineating natural groups. Recently, Bocakova *et al.* (2007) conducted a molecular phylogenetic analysis (18S, 28S, 16S and COI) of Elateriformia in the broad sense (Lawrence & Newton 1995) to address the evolution of bioluminescence and neoteny. This analysis did not recover Lampyridae (17 lampyrid terminals) or the Cantharoidea (sensu Crowson 1972) as monophyletic groups. *Drilaster* was placed within Lampyridae and the soft-bodied condition which united Cantharoidea appears to have arisen multiple times. Bocakova *et al.* (2007) did not recommend any taxonomic changes as the result of their analysis.

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#### 4.16. Omethidae LeConte, 1861

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**Distribution.** The three subfamilies of Omethidae occur in eastern Asia and North America. The family is a small one, with a total described global fauna consisting of only eight genera and 33 species. While the greatest generic diversity exists in the United States, the Asian component of the family is far more speciose. The family exhibits a relictual, disjunct distribution in temperate North America, with species divided between eastern and western forested regions and absent from the continent's interior. In Asia, the group is mainly tropical and is more widely distributed. The exclusively Asian subfamily Driloniinae includes *Drilonius* Kiesenwetter with 22 described and numerous undescribed species from India, Sri Lanka, Southeast Asia, the Greater Sunda Archipelago, the Philippines, China and Japan. Matheteinae is endemic to California and Oregon and includes *Matheteus theveneti* LeConte, *Ginglymocladus discoidea* Van Dyke and *G. luteicollis* Van Dyke. Omethinae exhibit a Nearctic-Eastern Palearctic, trans-Beringian disjunct distribution, with two species (*Blatchleya gracilis* (Blatchley) and *Omethes marginatus* LeConte) in the eastern United States, five species (*Malthometes oregonus* Fender, *Symphymethes blandulus* Wittmer, *S. californicus* Wittmer, *Troglomethes leechi* Wittmer and *T. oregonensis* Wittmer) in the western United States, and a single species (*Omethes rugiceps* (Lewis)) in Japan. [Kiesenwetter 1874; Lewis 1895; Pic 1911, 1921, 1925, 1927, 1929, 1930, 1942, 1943; Van Dyke 1918; Wittmer 1941, 1944, 1948, 1956, 1957, 1960, 1995; Nakane 1950; Fender 1961, 1969, 1975; Sâto 1989; Ramsdale 2002.]