

62. LAMPYRIDAE Latreille 1817

by James E. Lloyd

Family common name: The fireflies, lightningbugs, and glowworms

Family synonyms: Malacodermidae Latreille 1806, in part; Telophoridae Leach 1815, in part

Adult American fireflies will usually be recognized by their flashes in the night; by their lantern, in males commonly appearing as two pale ventrites beneath the posterior abdomen; and by their large, flattened and flanged pronota which typically cover the eyes like a sun-shade, unless the head and neck are extended as when walking or climbing. Common lanternless species active in daylight typically have marginless, black elytra, many with ridges (costae), and pronota marked with red or orange. The integument of adult fireflies is soft and pliable, and with handling sometimes releases droplets of pale blood, especially from the elytra, which in some species is known to be poisonous when ingested by some predators — even lethal in some instances. Odor is often plant-like, and taste, bitter, astringent. Larvae are most often found and recognized by the intermittent glows they emit, especially on damp nights.

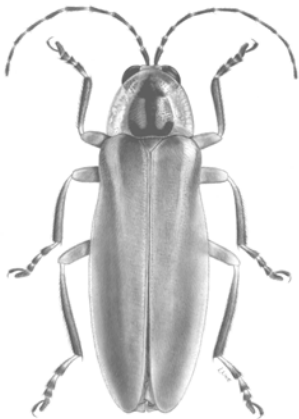


FIGURE 1.62. *Photuris pennsylvanica* (DeGeer) (*sensu* H. S. Barber 1951)*

Description: Shape, elongate or elongate oval, rarely oval; size, 4-18 mm.; color, variously, black, brown, tawny, charcoal, pearl, or olivaceous, with areas of pink, red, yellow, or salmon, especially on the pronotum, with color splashes below. Head deflexed/hypognathous; surface smooth or punctate, elongate. Antennae, with 8-13 but usually 11 antennomeres (in NA forms), filiform, serrate, sometimes with branches, and inserted above the mandibles. Labrum frequently indistinct, occasionally connate (fused at base) with

frons; mandibles often large and curved, sometimes abruptly narrowed at tip, occasionally greatly reduced; maxillae with galea and lacinia greatly reduced, palpi with 4 palpomeres, and variously modified, the terminal palpomere usually enlarged; labium with gular sutures separate, submentum partly membranous, and mentum reduced, ligula small, 3-segmented labial palpi, terminal segment usually enlarged, sometimes lunate (rather, mit-

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* For more than a century most *Photuris* spp. in NA were lumped under the name *P. pennsylvanica*, but Barber's work on flashing behavior led to recognition of several new and synonymized species, and to further research on the use of flash patterns in firefly taxonomy.

ten-shaped). Eyes lateral, often large and sometimes bulging and nearly or actually meeting below.

Pronotum distinctive, covering head when at rest; shield-like and variously semicircular, sub-pentagonal, sub-triangular, sub-trapezoidal, etc., with explanate margins and raised disk, occasionally with a midline groove, rarely a carinula; surface smooth, punctate, or granulate, median and lateral vittae often present and diagnostic (i.e. vittagrams); hypomera, large and not reaching anterior margin (i.e. "open") in most American species (see Key). Bright colors (apparently pterodine pigments) are often present in the pronotal and neck region, and are potentially of some taxonomic use. Prosternum short, prominent, procoxal cavities open, procoxae conical, prominent, and contiguous; mesosternum short, mesocoxae prominent, conical, contiguous; metasternum longer, broad, mesal margins of metepisterna straight or nearly so, not curved or sigmoid; metacoxal cavities open, metacoxae transverse and contiguous. Trochanters quadrate, interstitial, angularly joined to their femora. Femora flattened, somewhat swollen. Tibia stout, somewhat flattened, apical spurs present or absent; tarsal formula 5-5-5, slender, penultimate tarsomere with pads (pulvilli); claws simple or variously forked (bifid), occasionally with a basal protuberance. Scutellum evident and triangular. Elytra with explanate margins, sometimes with longitudinal ridges (costae), and sides variously nearly parallel, somewhat or considerably widest in middle, or tapering and narrowing in posterior third or so. Elytral bead and margin often pale in color, contrasting with disk. Elytral vestiture sometimes provides useful characters for species identification, e.g., *Pyraetomena*.

Abdomen of male with 7 visible ventrites, corresponding to abdominal segments 2-8 (except 6 in Luciolinae which may possibly be represented in North America), excluding the small genital segment ("clasper") which is occasionally absent. In some genera (e.g., *Phausis*) the distal abdominal dorsites (more or less equal tergites) at the sides extend over the pleural areas and are broadly visible from below (i.e. are lobed, foliate). The first abdominal segment is dorsal only, except in *Photinus granulatus* and

Phosphaenus hemipterus. Light organs are often present on ventral surface of the abdomen of one or both sexes, and in males of American lightningbug fireflies (*Aspisoma*, *Photinus*, *Photuris*, *Pyractomena*, *Micronaspis*, *Bicellonycha*) they completely occupy visible ventrites 5 and 6. Male genitalia consist of 2 lateral lobes, a median lobe, and a basal piece, and provide taxonomically useful characters variously at the generic, species, and/or species-group levels. In *Photuris* the basal piece has a pair of lateral filaments (Fig. 16), which remain outside the female during copulation and may have a proprioceptive function.

Noteworthy sexual dimorphism: females of several species (e.g. *Pleotomus* spp., *Pleotomodes* spp., *Lucidota luteicollis* LeConte, and several in *Photinus*) have shortened elytra and wings, and females or both males and females of *Pyropyga nigricans* (G. A. Olivier) from some sites have reduced wings and elytra (Lloyd 1999). Brachyptery is not known to occur in *Photuris*, *Ellychnia*, or *Pyractomena*. Females of some genera, such as *Microphotus* and *Phausis* are larva-like to some degree, but whether they are “larviform” is problematic (see Cicero 1988). The lanterns of females of flashing lampyrids differ topographically from those of their males. Those of *Photuris* females occupy the same two segments, but each has a nonluminous frame; those of *Pyractomena* occupy the 4 remote corners of the 2 ventrites; and the lantern of *Photinus* is a median, sub-semicircular plate on the (visible) 5th ventrite. Known *Phausis* females glow from pairs of lanterns that are visible dorsally along the abdomen, in addition to their retained larval lanterns.

Larva: Full-grown larvae of North American species are 12–25 mm in length, well sclerotized, onisciform, and dorsoventrally flattened, or fusiform, or cylindrical and elongate (Figs. 2-7). Color varies among species, and is black, slate gray, brown, reddish-brown, or tan, and some have pink areas between sclerites. As examples, those of *Photuris congener* LeConte are brick red, those of *Pyractomena borealis* (Randall) vary from brick red to dark brown and are sometimes variegated, and those of *Ellychnia corrusca* (L.) are charcoal with pink pleural areas. Larvae have 12 visible dorsal plates (terga). The head is elongate and sub-cylindrical with prognathous mouthparts, curved, falcate and channeled mandibles, and retractable 3-segmented antennae, each bearing a globular accessory structure on the third joint and having stemmata near the base.

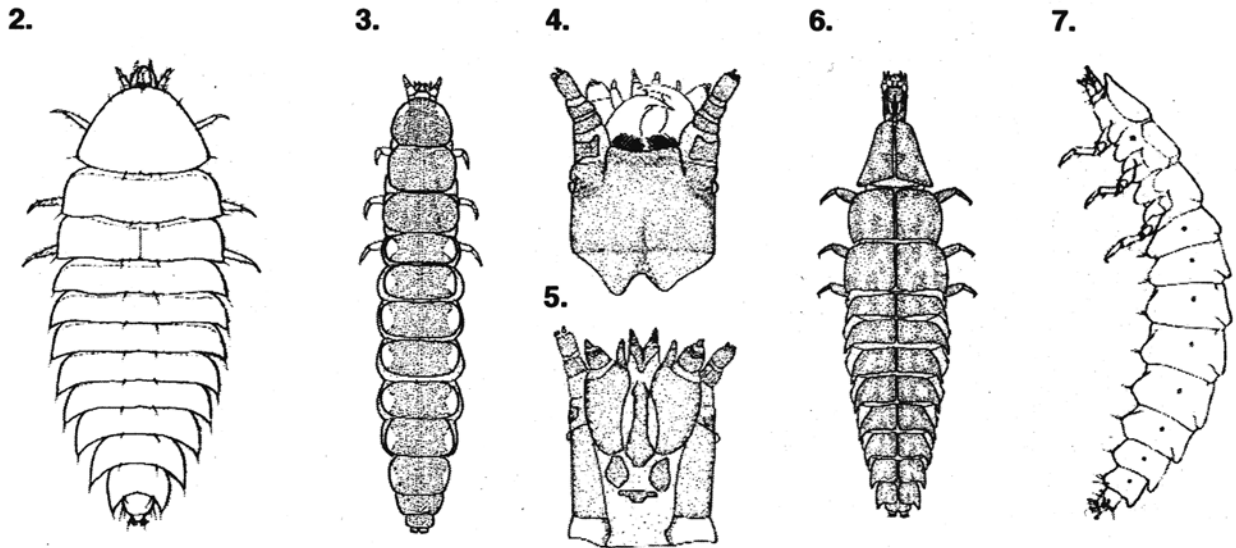
Though usually retracted within the prothorax except while walking, during feeding the head and neck are extended and inserted into the flesh of stunned (poisoned) prey (*Pyractomena* larvae in captivity have been found dead with greatly extended, limp, and perhaps even stretched necks, perhaps having been “strangled” by the powerful foot muscles of reviving snails.). Clypeus and labrum are not distinct; maxillae with a small cardo, large stipes, 3- or 4-segmented palpi, and 2-segmented mala; labium with mentum and submentum fused, ligula inconspicuous, and 2-segmented palpi.

Thorax with an elongate prothorax narrowing anteriorly, and as long as the meso- and metathorax combined; the meso- and metathoraces are sub-quadrangle, and slightly wider than long. Legs are 5-segmented with apical, claw-like tarsunguli. The abdo-

men is 10-segmented, with the ultimate dorsite concealed, and with paired lanterns ventrally evident on the epipleura of segment 8. An unusual eversible, 8-fingered, membraneous structure sometimes with many delicate teeth over its surface, occurs at the tail. This pygopodium is extruded and used for grooming (washing) after eating. Functional annular biforous spiracles are located in the mesipleura and the epipleura of abdominal segments 1-8 (Archangelsky and Branham 1998 and 2001; Branham and Archangelsky 2000; Labella and Lloyd 1991; Peterson 1951).

Habits and habitats: Comparatively few studies have been made on the juvenile biology of fireflies (Archangelsky and Branham 1998; Buschman 1984a, 1984b, 1987; Lloyd 1997a; Wing 1989, 1991). In some species eggs are deposited a few at a time over several days or weeks. This is probably the case in *Photinus pyralis* (L.), and in several *Photuris* species which acquire nutritional substances as well as defensive compounds for their eggs from their predation on other fireflies (Eisner *et al.* 1997). In others, eggs may be laid together at one time, as in *Photinus collustrans* LeConte in which the brachypterous females live and die in their burrows (Wing 1989). The eggs of some North American species glow very dimly briefly after deposition, from luminous material that is placed on the eggs in the egg canal; in some the light organs of developing embryos may later begin to glow.

As far as known, larvae of all lampyrid species are luminescent, and emit glows of varying duration, nearly always from a pair of relatively simple lanterns at the tail (abdominal segment 8). Glowing larvae are most often seen in damp situations, for examples, herbaceous soggy ground along roadside verges, around ponds and marshes, at seeps of earthen dams, and along streams. Old fields, cattail marshes, and low wet pastures are especially rich habitats in the northeast and northern midwestern states. *Photuris* larvae are the emitters of the most commonly seen glows, and on damp and rainy nights especially, *Pyractomena* larvae sometimes glow several feet above ground on woody vegetation. Glowing larvae of *Micronaspis floridana* Green are found at the landward edges of the black needle-rush zone of saltwater marshes around the coastline of Florida. Larvae of some *Pyractomena* species are found on emergent vegetation of ponds and marshes. *Photinus* larvae are subterranean and seldom seen, and *Ellychnia* and *Lucidota* inhabit rotting logs, and glow when their logs are pulled apart and crumbled. In western states and Florida a few species occur in very dry habitats; those of *Pleotomodes* are inquilines of various ant species (Sivinski, *et al.* 1998), but adaptations of *Lucidota luteicollis* LeConte for Florida’s dry scrub and sandhill habitats remain unknown. There has long been interest and speculation about the function of larval luminescence (Sivinski 1981); experimental evidence indicates that the light has aposematic value. As far as known, all lampyrid larvae are predaceous, with *Pyractomena* and *Photinus* possibly specializing on (“favoring”) gastropod mollusks and earthworms respectively; *Photuris* larvae are omnivorous, predators of soft-bodied prey, and scavengers of dead insects and fallen berries. *Pyractomena lucifera* (Melsheimer) hunts snails underwater and brings them to the surface to eat (Buschman 1984a).



4. head, dorsal view, 5. head, ventral view (from Archangelsky and Branham 2001, with permission). 6. *Pyractomena borealis* (Randall) larva, dorsal view (from Archangelsky and Branham 1998, with permission). 7. *Lucidota atra* (G. A. Olivier) (not *Photinus*, see Branham and Archangelsky 2000) larva, lateral view (modified from Peterson 1951).

Lampyridae larvae and other luminous worm-form insects in the US are referred to by the term “glowworm,” including Phengodidae larvae and females, and larval fungus gnats (Mycetophilidae: Diptera); the lampyrid *Lampyrus noctiluca* (L.) in Britain and northern Europe has been called the glowworm for centuries.

Pupation occurs in earthen underground or surface cells in most species, and takes from one to three weeks depending upon ambient temperature and species. *Pyractomena* and apparently other Cratomorphini pupate on herbaceous and woody vegetation, which may keep them above rising flood water. *Pyractomena borealis* (Randall) in Florida often pupates next to vines, twig stubs, and other pupae, and in bark crevices, strongly favoring a southern exposure which provides increased warmth from insolation, accelerating winter development and eclosion, and mating follows immediately (Lloyd 1997a). In the northeast *Ellychnia corrusca* pupates in dead logs in autumn, then ecloses; during winter adults are sometimes found on tree trunks, though mating does not occur until spring.

Lampyrids whose adult males emit bioluminescence in “neurologically precise” flashing patterns (lightningbug fireflies, e.g. *Photinus*, *Pyractomena*, *Photuris*; Figs. 1, 25-27, 31-32) are common east of the Rocky Mountains but are presently known only from scattered western localities, in Arizona, Colorado, Idaho, Montana, Oregon, and British Columbia (Cicero 1982; Fender 1961b). Lampyrids in which only the females emit light, and males, with rare exception, are lightless with huge eyes (glowworm fireflies, a behavioral appellation with strong taxonomic/generic correlation, e.g., *Phansis*, *Microphotus*, *Pleotomus*; Figs. 22, 28), occur across North America and are well represented in western states — females of these species are typically brachypterous, apterous or

“larviform,” and apparently most live in burrows, but as noted, those of *Pleotomodes* (Fig. 33) live in ant nests (Fender 1961a,b; Sivinski et al 1998). Also common in the west, but well represented in the eastern and middle states, are several nonluminescent species (daytime dark fireflies). Some of these are known to use pheromones for sexual communication (e.g., *Lucidota atra* (G. A. Olivier) (Fig. 35), *Photinus indictus* (LeConte), *Pyropyga nigricans* (Say) (Fig. 34)), and probably most others do also, excepting perhaps *Photinus cookii* Green. Recent phylogenetic analyses using cladistic methods bring new insight into the evolution of sexual communication in fireflies, and also the evolution of bioluminescence in Coleoptera (Branham and Wentzel 2001, and in prep.).

In eastern and middle North America, males of flashing species often fly in conspicuous thousands over meadows and fields, beginning with *Photinus pyralis* (L.) (Fig. 31) shortly after sunset, and a little later various *Photuris* species continue well into the night during their peak mating season. Noteworthy conspicuous flashers include *P. tremulans* Barber, *P. versicolor* (Fabricius), *P. v. quadrijulgens* Barber, and *P. lucicrescens* Barber. These fireflies also fly at higher altitudes, over forest canopies and especially over the crowns of trees adjacent to and within grassland. *Photuris lucicrescens* seems to be most common along streams. Although populations of *Pyractomena angulata* (Say) (Fig. 26) are occasionally seen in roadside marshes, more often and on any late spring or summer evening individuals or a few males will be seen emitting their distinctive amber flicker as they weave around ecotonal shrubs and high boughs of trees. The flashing of some species in the *Photuris frontalis* group (Fig. 25) is often eye-catching, because males fly a meter or so above the ground emitting

continuous trains of short flashes at short intervals, and at high densities they emit their flashes in synchrony.

In the sexual signaling of most Nearctic lightningbug firefly species, males emit species-typical flash patterns which their females answer with flashes. In general, the bioluminescence of *Photinus* is yellow, that of *Photuris* is green, and *Pyraclomena*, orange-yellow or amber, but there are exceptions, a few being quite remarkable. Generic diagnosis in the field via color will often err because judgement is confused, apparently by variations in the dark adaptation of the observer's eyes and the color of background illumination. When firefly luminescence appears white it is apparently because dim light has not adequately stimulated human cone (color) receptors. As far as known, fireflies cannot discriminate color, but are differentially sensitive to different wavelengths — e.g., twilight *Photinus* spp. to yellow, the later active *Photuris* spp. to green.

Male flash patterns show considerable variation among species, and sometimes a range of distinct patterns within species. Several flash patterns consist of single flashes or groups of short flashes of various timing characteristics; these are repeated at fairly regular but temperature dependent (advertising) intervals. Other variations in species-typical flash patterns include intensity modulations within single pulses of light, resulting in flickers, crescendos, and bimodal twinkles. Flash patterns can often be used to identify the species of flying males at a distance, and in some cases, and in particular in the genus *Photuris*, flash patterns provide the only reliable character for identification (Barber 1951; McDermott 1914; Lloyd 1969a, 1990, 2001). Female response flashes are typically single flashes, with various timing characteristics in response-delay and duration, but in a few species, especially those in the *Photinus ardens* group and probably some *Photuris* species, female responses are more complex (Lloyd 1966a).

Males of several *Photuris* species use two or more distinctively different flash patterns. For examples, males of *Photuris tremulans* Barber emit a short flash and a flicker pattern, the latter explaining Barber's choice of epithet; and, in some populations during early evening, males of *Photuris pennsylvanica* (DeGeer) (sensu Barber 1951) emit a short flash, but within a half hour all have switched to the short-long (dot-dash) flash pattern described by Barber (1951). When flickering *P. tremulans* males and short-flashing *P. pennsylvanica* males receive a flashed answer (female or penlight) they switch (default) to their other (species-identifying) pattern, *P. tremulans* to the short flash and *P. pennsylvanica* to the dot-dash pattern, and continue their approaches toward respondents (Lloyd 1997b). During the approach of male fireflies to a female, after they have landed, patterns sometimes become more variable, and without specific knowledge, may become unreliable for identification.

Many fireflies emit light in contexts other than sexual communication, but little is known about these flashes, or whether they have special significance in the lives of fireflies. Some flashing in *Photuris* females and those of the *Photinus ardens* group clearly provides illumination at landing and takeoff, and others may be aposematic. A listing of situational emissions presently records 21 “varieties,” such as “caught in spider-web”, “walking

through grass”, and “grasped by wolf spider.” Finally, *Photuris* females of many species take perches in the activity spaces of other species and flash deceptive, female-mimicking responses to passing males, attract them, and eat them. *Photuris* females (*fairbaldi*?) were found to use defensive compounds from their prey for their own and their eggs' protection. In several cases, the “supernumerary” flash patterns of *Photuris* males closely match, except for color, those of their females' prey.

Status of the classification: In the last three decades, following the extensive and outstanding revisionary work by J. W. Green (1948-1961), and cataloging and organizational work and study by McDermott (1964, 1966), there has been extensive field study and collection of the lightningbug genera *Photinus*, *Photuris*, and *Pyraclomena*, and a revisionary study of *Photuris* is nearly complete. About 40 new species will be named in the mentioned genera, raising the total count of United States Lampyridae to about 150 species, but it is expected that there are probably 50 additional species yet to be discovered throughout North America (Lloyd 2001 in press). DNA studies have recently been initiated and may establish methods for the DNA analysis from single legs of the several thousand flash-behavior-voucher specimens now archived.

Recent phylogenetic study has made a few significant changes in the composition of the family Lampyridae: the Matheteini (*Mathetens* and *Ginglymocladius*) have been removed to Omethidae (Crowson 1972), and the Pterotini (*Pterotus*) placed in limbo as *incertae sedis* (Branham and Wentzel 2001). It would appear that revisionary studies are needed for *Ellychnia* and *Phausis* accompanied by focused field collection and associated ecological/behavioral observation. Authors and dates for higher lampyrid categories are not given here; though these names occasionally appear in restricted usage, their authors and dates are absent from even highly structured and formal taxonomic treatments. I retain some reservation about the author of the family name itself.

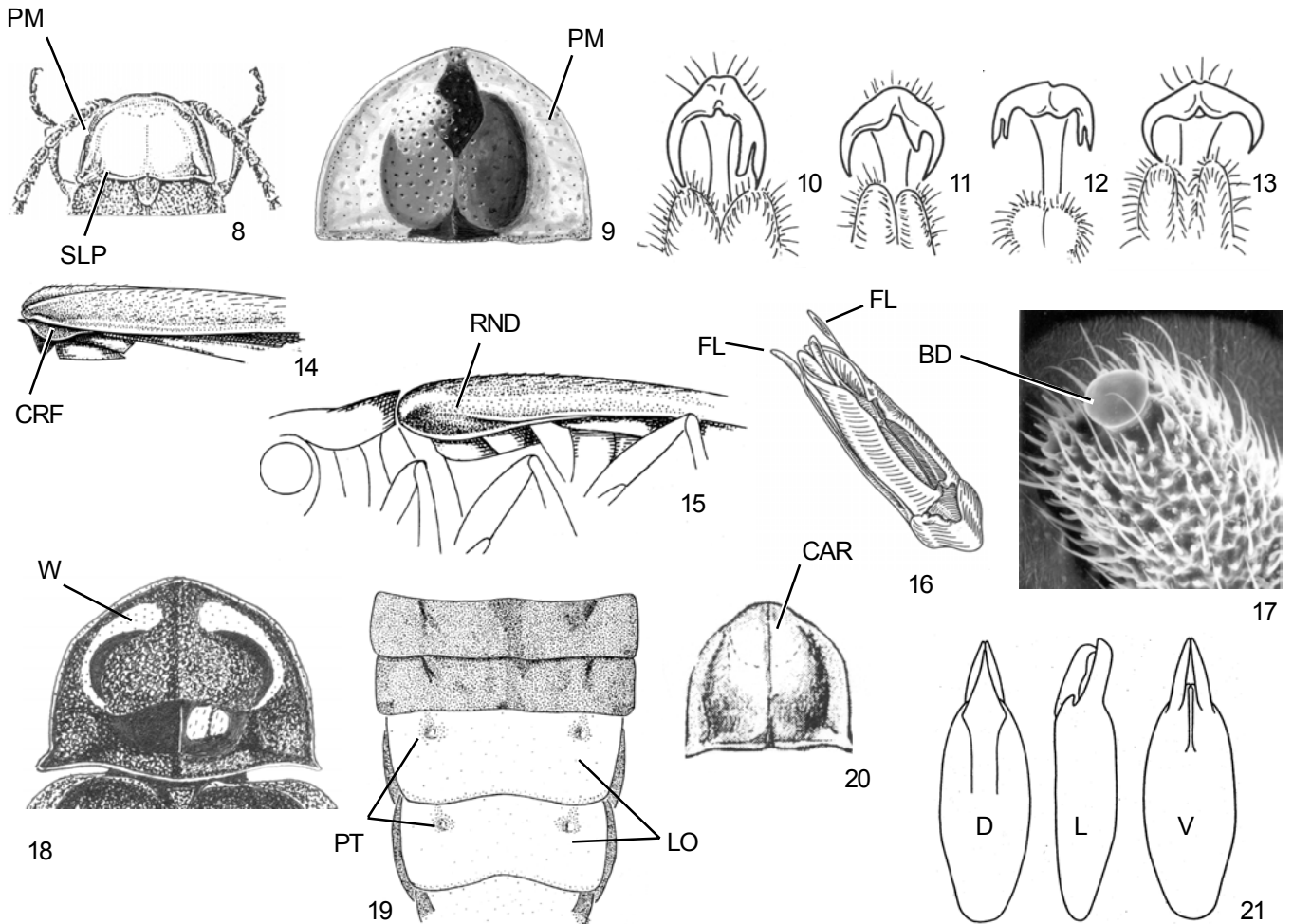
Distribution: Fireflies occur throughout the world on all continents except Antarctica, with tropical America having more than half of the described 2000 species (McDermott 1966). Probably two or three times this many remain to be described, with thousands of unworked and undetermined specimens presently archived in museums and private collections, but in nature extinction rate may be especially high in this family because of habitat loss in tropical regions throughout the world. Crowson (1972) noted that “the family has endemic representatives in all the main zoogeographical regions except New Zealand; one or two endemic species are recorded from islands of an apparent oceanic type, such as Palau and Yap in Micronesia.” Eighty to 85 genera have been described worldwide; 16 genera are known with certainty to occur in America north of the Rio Grande, and three others could be present. West coast species are daytime or glow-worm fireflies, with only occasional unsubstantiated reports of flashing (lightningbug) species, except for recent reports from British Columbia. A European genus (*Phosphaenus*) was found in Nova Scotia in the 1950s, presumably having arrived in ballast around the beginning of the 1800s with waifs of a number of plant and insect species. (And representatives of two Asian gen-

era, *Luciola* and *Lamprigera*, were introduced into Hawaii for the biocontrol of snails in the 1950s, but there have been no subsequent reports of their survival or occurrence there).

KEY TO MALES OF NEARCTIC GENERA

- 1. Pronotum with explanate lateral borders absent or very narrow (Fig. 8, pm); hypomera closed, i.e. reaching anterior margin of pronotum, or nearly so 2
- Pronotum with lateral borders explanate (i.e., flanged, flared out each side of disk; e.g., Fig. 9, pm); hypomera open anteriorly, i.e. not reaching anterior margin 4
- 2(1). All antennomeres without branches 3

- All except terminal antennomeres of flagellum with one (elongate, strap-like) branch; West Coast (CA, OR); superficially resembling phengodids *Pterotus*
- Antennomeres 3-10 each with two branches; eastern U.S. *Pollaclasis*
- 3(2). Locality in California; posterolateral corners of pronotum projecting and ridged, and hind margin with a sub-lateral pit (Fig. 8, SLP); length <5 mm *Brachylampis*
- Locality in southcentral Texas (see Classification); pronotum corners not projecting, ridged, etc., and length probably >6mm near *Luciola*
- 4(1). Antennae robust with antennomeres 3-10 each with two leaf-like branches that are fused at their bases (Fig. 22) *Pleotomus*
- Antennae not as above, instead unbranched, usually filiform or serrate, rarely compact, robust. 5



FIGURES 8.62-21.62. 8. Pronotum, etc. of *Brachylampis* (PM, pronotal margin, SLP, sub-lateral pit; from VanDyke 1939). 9. Pronotum of *Photuris* sp (PM, pronotal margin). 10. Sub-symmetrical fork of anterior tarsal claw of *Photuris* males. 11. Asymmetrical fork of anterior tarsal claw of *Micronaspis* males. 12. Forked anterior and posterior tarsal claws of *Bicellonycha*. 13. Simple tarsal claws of *Photinus* spp. and those of many other genera. 14. Folded and creased humeral area of left elytral epipleuron (CRF). 15. Rounded humeral area at base of left elytral epipleuron (RND). 16. Genitalia of *Photuris* spp. with filaments (FL) attached to the basal piece. 17. Bead on terminal antennomere of *Phausis reticulata* (Say) antenna. 18. Pronotum of *Phausis reticulata* (Say) with windows (W) over eyes. 19. Posterior ventrites of *Photinus concisus* Lloyd, showing two ventrites with lantern (LO) and pits (PT). 20. Pronotum of *Pyraetomena* with mid-line carinula (CAR). 21. Genitalia of *Pyropyga nigricans* (Say), dorsal, lateral, and ventral views, showing general form found in genus, from Green 1961.

- 5(4). Anterior claws of fore and mid (pro and meso) tarsi bifid (2-pronged) (Figs. 10-12) 6
 — Anterior claws of fore and mid tarsi simple, not bifid (e.g., Fig. 13) 8
- 6(5). Posterior claw of all tarsi bifid (Fig. 12); locality in Arizona; pygidium with pink or red (habitus, Fig. 23) *Bicellonycha*
 — Posterior claw of all tarsi simple not bifid; locality not in Arizona; pygidium without pink or red, instead pale, dusky, or dark 7
- 7(6). Pronotal disk contoured and transparent over dorso-lateral surfaces of eyes (Fig. 24); two prongs of anterior claw of fore-tarsi strongly asymmetrical, one basal and one apical (Fig. 11); epipleurae folded and creased basally (Fig. 14, CRF); basal piece of genitalia without lateral filaments (only known localities on Florida coastline); habitus Fig. 24) *Micronaspis*
 — Pronotal disk not as above, instead rounded but not conforming to shape of eyes and opaque (Figs. 1, 25, 27); two prongs of anterior claw of fore-tarsi nearly symmetrical, both apical as in Fig. 10; epipleura rounded basally (i.e. at humerus, Fig. 15, RND); basal piece of genitalia with lateral filament (Fig. 16, FL) *Photuris*
- 8(5). Terminal antennomere with a tiny sub-spherical, smooth, glabrous, sometimes vitreous (glass-like) bead (Fig. 17, BD, sometimes collapsed) 9
 — Terminal article of antennae without such a bead 11
- 9(8). Antennae with 10 or fewer antennomeres (excluding terminal bead); abdominal spiracles ventral (occurrence almost exclusively western and southwestern US, i.e. AZ, CA, NM, UT, CO, WTX) *Microphotus*
 — Antennae with 11 antennomeres (i.e., excluding terminal bead); abdominal spiracles dorsal (broad US occurrence, except AZ, SCA, CO, NV, UT) 10
- 10(9). Pronotum with two anterior somewhat transparent (glassy) windows over eyes (one rare California exception) (Figs. 18, 28); eyes touching or nearly so below; head deeply concave above; pygidium not predominately yellow *Phausis*
 — Pronotum without windows; eyes distant below; head rounded above; pygidium predominately yellow (only reported occurrence southeastern Arizona) *Paraphausis*
- 11(8). Body outline broadly oval; pronotum distinctly transverse and sub-triangular; epipleurae very wide (habitus neotropical in appearance, Figs. 29, 30) 12
 — Body outline normal, i.e., narrowly oval or elongate; pronotum not distinctly transverse; epipleurae normal, not exceptionally wide (except in *Lamprohiza* which has pronotal windows) 13
- 12(11). Light organ (yellow or white enamel-like cuticle) occupying two posterior ventrites of abdomen; antennae filiform (Fig. 29) — (locality records, excepting airport quarantine interceptions, only southern-most points of USA, Florida Keys and near Brownsville, Texas) *Aspisoma*
- Light organ absent; antennae strongly serrate (Fig. 30). —(localities broadly arcing around Gulf states) *Tenaspis*
- 13(11). Light organ (yellow or pale, commonly enamel-like cuticle) present on 2 or 3 ventrites of abdomen 14
 — Light organ as described not present on 2 or 3 ventrites of abdomen, instead either completely absent or merely a small, median spot on one ventrite 16
- 14(13). Light organ occupying entire surfaces of the two ventrites (Fig.19, LO); two pits present on each light-organ-bearing ventrite (Fig. 19, PT); pronotum without transparent (“glassy”) spots (“windows”) over eyes 15
 — Light organ not occupying entire surfaces of the two ventrites, instead margin of each lantern-bearing ventrite with nonluminous border (“frame”); pits not present on light-organ-bearing ventrites; pronotum with transparent (glassy, tear-shaped) windows over eyes *Lamprohiza*
- 15(14). Median line of pronotum with a distinct though low keel (i.e., a ridge, carina, carinula) along most or all of its length (Figs. 20, CAR, 26); pronotum sub-pentagonal *Pyractomena*
 — Median line of pronotum without such a keel — instead flat, or with a shallow, often discontinuous groove (Figs. 31, 32); pronotum not distinctly sub-pentagonal (or if so then elytra shortened leaving most of abdomen exposed; rare exotic, only eastern maritime Canada, see *Phosphaenus*) *Photinus* (part)
- 16(13). Eyes large, approximate (actually or nearly touching) beneath head; tip of mandibles abruptly narrowing (habitus Fig. 33) *Pleotomodes*
 — Eyes small and well separated; tip of mandibles not abruptly narrowing 17
- 17(16). Second antennal article very short, wider than long, about one-quarter as long as third; first antennal article shorter than third 18
 — Second antennal article short but not wider than long, at least one-third as long as third; first antennal article longer than third 20
- 18(17). Antennae compressed, flattened in cross-section, and serrate or sub-serrate; elytra usually covering all or most of abdomen (except *P. nigricans* in a few and isolated localities; abdomen not lobed; localities occurring across North America) 19
 — Antennae not compressed, not serrate or sub-serrate; elytra very short, leaving at least 5 abdominal dorsites exposed and all strongly lobed; locality only maritime Canada *Phosphaenus*
- 19(18). Antennae delicate, only feebly compressed and serrate; pronotum sub-semicircular or hexagonal in outline, usually not more narrowly rounded in front; genitalia of general form in Fig. 21 (habitus of one common species Fig. 34) *Pyropyga*
 — Antennae coarse and distinctive, strongly compressed and serrate; pronotum sub-pentagonal or -triangular in outline, its anterior margin usually more narrowly rounded than other rounded angles of outline; genitalia variable, not resem-

bling form in Fig. 21 (habitus of the most common species Fig. 35) *Lucidota*

- 20(17). Margins and sutural beads of elytra yellow or pale, contrasting with dark color of elytral disks; lateral margins of pronotal flanges always without dark (black, charcoal) stripe *Photinus* (part)
- Margins and beads of elytra concolorous with elytral disks; lateral margins of pronotal flanges with dark stripe in most and most common species (Fig. 36) *Ellychnia*

CLASSIFICATION OF THE NEARCTIC GENERA

Lampyridae Latreille 1817

Lampyrinae

Lampyrini

Microphotus LeConte 1866, 7 spp., Arizona, California, New Mexico, and Texas (key to spp., Green 1959).

Paraphausis Green 1949, 1 sp., Arizona.

Pleotomini

Pleotomodes Green 1948 (Fig. 33), 3 spp., Florida and Arizona (tribal position and removal from synonymy with *Lampyrus*, Geisthardt 1986).

Pleotomus LeConte 1861 (Fig. 22), 3 spp., Arizona and northeastward to Maryland. (Key to spp., LeConte 1881 [The three species are legitimate and warrant distinction.]

Lamprocerini

Tenaspis LeConte 1881 (Fig. 30), 1 sp., *T. angularis* (Gorham 1880), broadly around the Gulf states.

Cratomorphini

Aspisoma Laporte 1833 (Fig. 29), 1 sp., *A. ignitum* (Linnaeus 1767), southernmost Florida and Texas.

Micronaspis Green 1948 (Fig. 24), 1 sp., *M. floridana* Green 1948, Florida peninsular coastline.

Pyractomena LeConte 1845 (Fig. 26), 16 US spp., 2 to be named, all but sw NA, with only scattered localities w of Kansas (description and biology of juveniles, Archangelsky and Branham 1998; key to spp., Green 1957). This generic name is sometimes misspelled, often as *Pyractonema*, which is a South American genus.

Photinini

Ellychnia Blanchard 1845 (Fig. 36), 12 spp.+, but in need of revisionary field work, widely distributed in US (key to western species, Fender 1970).

Lamprobizza Motschulsky 1853, 1 sp. [two specimens voucher LeConte's 19th century IL and MD records, but none since; other reports apparently from misidentified native *Phausis reticulata*, spurious reports and museum IDs to the contrary]

Lucidota Laporte 1833 (Fig. 35), 3 spp., widely distributed US (description and homologies of lampyrid juveniles, Branham and Archangelsky 2000; key to spp., LeConte 1881; additional species descriptions, LeConte 1878).

Phausis LeConte 1851 (Fig. 28), 7+ spp., but in need of revisionary field work, widely distributed except sw US (key to spp., Fender 1961a).

Phosphaenus Fourcroy 1785, 1 sp. [a single specimen from 1950s in Nova Scotia, presumably arriving in ballast around 1800]

Photinus Laporte 1833 (Figs. 31-32), 34 spp., 13 in prep., widely distributed in NA, but only scattered or riparian localities w of Texas and Kansas (key to species, Green 1956; key update, Lloyd 1966b, 1968, 1969b.)

Pyropyga Motschulsky 1852 (Fig. 34), 4 spp., widely distributed in US (description and comparison of juveniles, Archangelsky and Branham 2001; key to spp., Green 1961).

Photurinae

Bicellonycha Motschulsky 1853 (Fig. 23), 1 sp., *P. wickershamorum* Cicero 1982, Arizona.

Photuris LeConte 1851 (Figs. 1, 25, and 27), 22 spp., 28 in prep., eastern US west to Colorado, sw Texas (keys to spp., Barber 1951 and McDermott 1967, should not be relied upon).

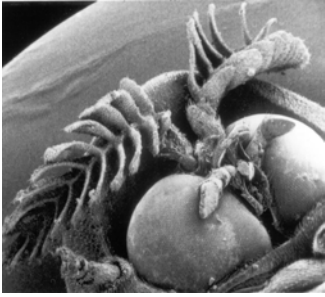
Luciolinae

Luciolini

Luciola Laporte 1833 (= near *Luciola*) [1 sp. possibly, in southcentral Texas but actual occurrence equivocal, one specimen reported but as possibly mislabeled].

Ototetrinae

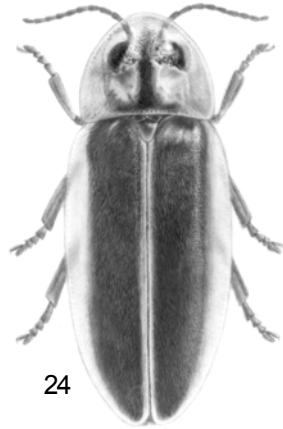
Brachylampis Van Dyke 1939, 2 spp. California (key to species, Van Dyke 1939).



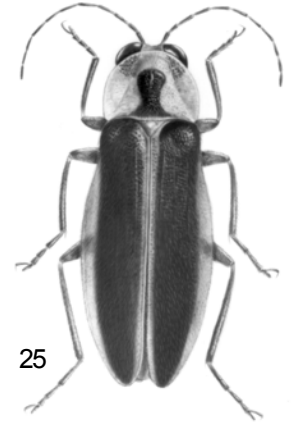
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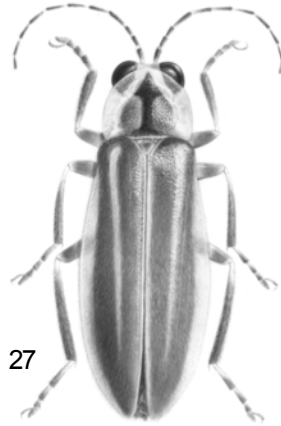
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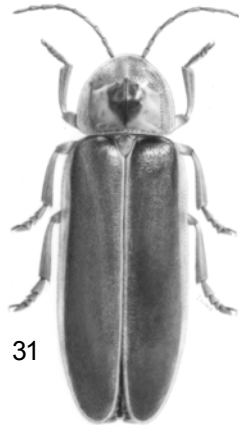
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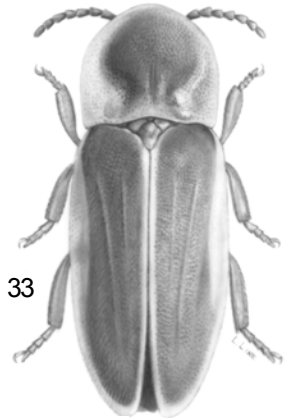
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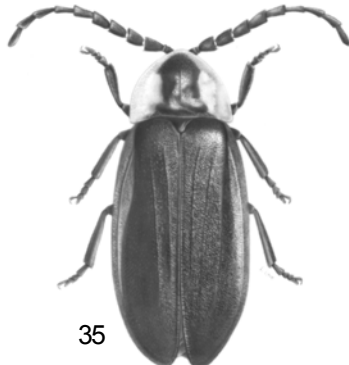
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35



36

Cyphonocerinae

Pollaclasis Newman 1838, 1 sp., *P. bifaria* (Say) 1835, widely scattered localities in eastern half of US.

Incertae sedis

Pterotus LeConte 1859, 2 spp., western U.S. (northern California and southern Oregon).

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FIGURES 22.62-36.62. 22. Ventral view of head and pronotum of *Pleotomus pallens*. LeConte, showing biramous antennae, and also huge glowworm-type eyes, with open hypomeron at lower left. 23-36. Carbon-dust habitus drawings of various fireflies, by Laura Line. 23. *Bicellonycha wickershamorum*. Cicero. 24. *Micronaspis floridana* Green. 25. *Photuris frontalis* LeConte. 26. *Pyractomena angulata* (Say). 27. *Photuris lloydii* McDermott. 28. *Phausis reticulata* (Say). 29. *Aspisma ignitum* (L.). 30. *Tenaspis angularis* LeConte. 31. *Photinus pyralis* (L.). 32. *Photinus macdermotti* Lloyd. 33. *Pleotomodes knulli* Green. 34. *Pyropyga nigricans* (Say). 35. *Lucidota atra* (G. A. Olivier). 36. *Ellychnia corrusca* (L.).

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