TAXONOMY AND BEHAVIOR OF *PHOTURIS TRIVITTATA* SP. N. (COLEOPTERA: LAMPYRIDAE: PHOTURINAE); REDESCRIPTION OF *ASPISOMA TRILINEATA* (SAY) COMB. N. (COLEOPTERA: LAMPYRIDAE: LAMPYRINAE: CRATOMORPHINI)

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ABSTRACT

Photuris trilineata (Say) is assigned to *Aspisoma* Laporte, and the type female is redescribed. *Photuris trivittata* sp. n. is described from behavior voucher specimens, and behavioral data are presented and discussed. Aspects of abdominal segmentation and aedeagal structure of *Aspisoma* and *Photuris* are described.

Key Words: flash patterns, ecology, predation, neotropical fireflies

RESUMEN

Photuris trilineata (Say) es asignado al *Aspisoma* Laporte, y el tipo de hembra es redescrito. *Photuris trivittata* sp. n. se describe de acuerdo a los comportamientos de los especímenes comprobantes y los datos de los comportamientos son presentados y discutidos. Aspectos sobre la segmentación abdominal y el edeago del *Aspisoma* y *Photuris* son descritas.

Translation provided by author.

Say (1835) described *Lampyris trilineata* from a female now housed in the Museum of Comparative Zoology at Harvard University. Olivier (1886) assigned *L. trilineata* to *Photuris* but did not examine the type and appears to have based his action on the similarity of the described color patterns. Lloyd tentatively assigned the behavior voucher specimens included here to *Photuris trilineata* (Say), but after locating and examining the type female of *L. trilineata* he determined that *trilineata* should be assigned to *Aspisoma* and that his specimens were of a new species. Olivier's collection in the Paris Museum was examined by Ballantyne in November 1993. Olivier's methodical collection often reflects the chronology of his published work, and standing in the Olivier collection under *Photuris trilineata* (Say) were specimens of *Photuris* which are conspecific with the specimens described below. *Lampyris trilineata* Say is assigned to *Aspisoma*; Olivier's firefly apparently has remained unnamed, and is herein described as *Photuris trivittata*. JEL provided the biological data; LAB provided the taxonomic framework.

Taxonomy

Taxonomic characters follow Ballantyne (1987a, 2000) with exception of abdominal segmentation and aedeagal structures, which are discussed separately below. Descriptions are ordered so that features on the dorsal surface are described in sequence from the anterior to posterior end, and then the ventral surface is described in the same manner. This facilitates handling under the microscope. Length, measured as median length of pronotum plus maximum length of an elytron, is sometimes a misleading representation since the pronotum droops in pinned specimens, and the specimen will always appear shorter than the figure given. The length of the head, which may protrude to a variable extent in males, is not included. Measurements (i.e., lengths) taken at the longest and widest areas respectively, such as pronotal width, greatest head width in anterior aspect, are used on a comparative rather than absolute basis (Lampyrids being soft bodied are subject to much distortion)—for example the distance between the antennal sockets is given as a function of the nearest convenient point of reference, the width of an antennal socket.

McDermott (1964) distinguished the Photurinae with a "membranous labrum arising from the ventral surface of a strongly sclerotized clypeus." The nature of the labrum was reinterpreted by John Lawrence (1987): in the cantharoids there is probably never a well-developed clypeus separated from the frons by a complete frontoclypeal suture. In most Lampyridae the labrum is at least slightly sclerotized and separated from the clypeus

by a strip of membrane. The anterior strongly sclerotized plate on the Photurinae head is here interpreted as the labrum.

While specimens were still soft and flexible many aedeagi were extruded by the collector (JEL), and remain attached to the specimen, usually with the basal piece still encased between ventrite 9 and tergite 9 (the "aedeagal sheath" of Ballantyne 1987a, b), and often hidden. Some aedeagi were removed and mounted on transparent points, using transparent glue, and remounted beneath the specimen (specimens were softened for 2-3 days in a humid atmosphere in an airtight container with moist sand with a few drops of Lysol® to retard mold).

The two specimens selected for scanning electron microscopy were dried pinned specimens which had the aedeagus extended. They were mounted on aluminum stubs using double sided semitransparent tape and coated with gold in a Denton Vacuum Desk II Cold Sputter Etch Unit, and examined in a Hitachi 570 scanning electron microscope at an accelerating voltage of 15 KV. The operation was carried out as part of a class exercise in the Department of Entomology and Nematology at the University of Florida in Gainesville, under the direction and assistance of Prof. Harvey Cromroy. The type female of *Lampyris trilineata* Say was not dissected, and drawings represent the specimen in its actual state at the time of examination. Specimens are currently housed in the JEL collection in Gainesville (JELC), or the Florida State collection of Arthropods (FSCA).

Abdominal segmentation. Abdominal segmentation is interpreted from Ballantyne (1987a, 1992). Terminology of the ventral abdominal plates has varied. Green (1956) used "sternite" for the median half of each ventral segment in *Photinus* and considered the lateral area on each side the pleurite, which is narrowly inflexed dorsally and bears the spiracles. Crowson (1972) called the ventral abdominal plates "ventrites" but (page 39) referred the spiracles to the "inflexed edges of the sternal plates." A refinement of the definition of the term "ventrite" in the Lampyridae was proposed (Branham & Archangelsky 2000).

The abdomen of *Aspisoma* and *Photuris* males (Figs. 4 and 15) consists of 8 visible tergites, although the first may be difficult to distinguish. Segments 2-8 are distinguishable ventrally. The light organs occupy the ventral plates of segments 6 and 7. Ventrite 8 is well developed although it is usually shorter than 7. Ventrite 9 (which surrounds the aedeagus) is usually visible externally, protruding beyond the posterior margin of ventrite 8, and completely covered dorsally by the relatively large tergite 8.

The *Aspisoma* abdomen is broad, flattened, tapering at front and behind (Figs. 3 and 4); the dorsally reflexed lateral margins of the ventrites bear the spiracles which are covered by the lateral tergal margins and difficult to see in pinned specimens; the light organ in males and females occurs in ventrites 6 and 7 (Figs. 3 and 4) but may be considerably retracted from the lateral areas in females; depressions in lateral areas of ventrites 6 and 7 probably house sense organs (Lloyd & Ballantyne, pers. obs.); ventrite 8 is transverse, about half as long and wide as 7, with the median posterior margin emarginate; aedeagal sheath (= ventrite and tergite 9) when visible externally is turned on its side; tergite 8 about as long as, but narrower than, tergite 7.

The male *Photuris* abdomen (Fig. 15) has ventrites 6 and 7 often medially emarginate posteriorly; ventrite 8 always tapers posteriorly, is usually about half as long as 7, although sometimes retracted beneath 7; the median posterior margin of ventrite 7 always has a pointed projection of varying length; tergite 8 often has lateral margins reflexed; aedeagal sheath ventrite and lateral projections of aedeagus sometimes visible behind ventrite 8. The female abdomen has light organs apparently contained in ventrites 6 and 7; ventrite 8 tapers posteriorly and may be medially incised (Fig. 16).

Aedeagal structure. The aedeagus of *Aspisoma* most closely approaches that of the Luciolinae (Ballantyne 1987a, b, 2000), in having a clearly defined median lobe, lateral lobes (which may be slightly longer or shorter than the median lobe), and an elongate well defined basal piece. The median lobe is elongate, slender, and often medially carinate along the dorsal surface; lateral margins of the median lobe can expand and are variably developed. Small hooks may arise from the inner face of the lateral lobes and in *A. physonotum* they engage against the median dorsal carina of the median lobe (Ballantyne 1992).

The aedeagus of *Photuris* spp. consists of median and lateral lobes and a basal piece, and paired long slender processes extending from the sides of the basal piece (Figs. 17 and 18). These pieces "splay" to varying degrees in pinned specimens, and the full extent of the basal piece is not always visible in specimens where the aedeagus is still attached to the abdomen.

Barber (1951) described the *Photuris* aedeagus: "sides of the 'basal piece' are produced into long slender, clubbed, lateral processes extending beyond the apex of a slender median lobe". McDermott (who completed Barber's manuscript after his death), included figures (Figs. 2 and 3) of *Photuris lucicrescens* aedeagus which was unlabeled but described in the text as having "the lateral lobes fuse with the dorsal surface of the median lobe at about basal third, and are armed internally opposite this point with a strong transverse ridge, which is sharply angulate at inner third". McDermott (1962) figured 3 unlabeled *Photuris* spp. aedeagi and (1964) referred to the *Photuris*

aedeagus with 2 long slender lateral processes, but did not determine their origin. Lloyd (1979, 1981) pictured a copulating *Photuris* spp. pair, and attributed the lateral processes of the aedeagus to the basal piece (as Ballantyne does here) (Lloyd 2002); the picture shows that these pieces remain outside the female during intromission.

Photuris trilineata was used (as *Photuris* sp.) as the outgroup in a cladistic analysis of Australian Luciolini (Ballantyne & Lambkin 2000).

Aspisoma trilineata (Say) comb. n.
Figs. 1-3

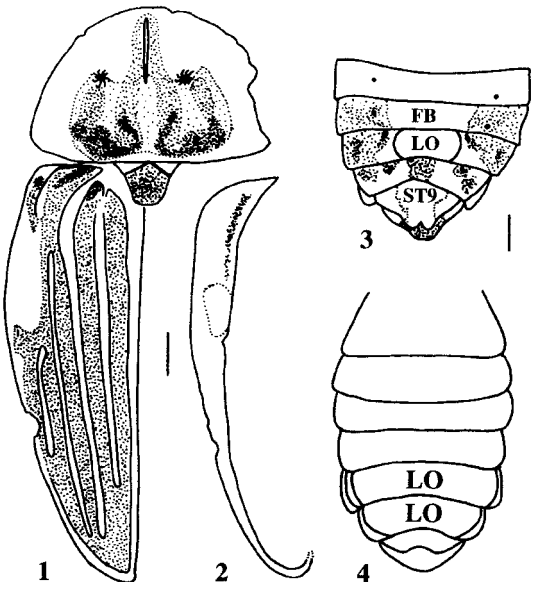
Lampyris trilineata Say, 1835, p. 157.

Photuris trilineata (Say).Olivier, 1886, p. 232; 1910, p. 52. McDermott, 1966, p. 92 (misidentification).

Type. Holotype female, Mexico (Museum of Comparative Zoology, Harvard University).

Redescription of type female. Length:13.7 mm. Color: Pronotum dingy yellow with dark brown markings on median area of dorsal surface (Fig. 1); pronotum largely semitransparent, and pale pink and yellow fat body visible through the cuticle; mesonotum light brown; mesoscutellum dark brown, darker in posterior area; elytra medium brown, with lateral, apical and sutural margins, and longitudinal interstitial lines dingy yellow (Fig. 1); head yellow; antennae, palpi and labrum light brown; ventral surface of pro- and mesothorax medium brown, of metathorax moderately dark brown; legs medium brown with dark brown tarsi; abdominal ventrites yellow with brown mottling; compact light organ material defined in median area of ventrite 7 only, although ventrite 6 bears a diffuse median area of fat body (Fig. 3).

Body covered with fine short pale setae, which have been abraded in certain areas. Pronotum (Fig. 1) 4.2 mm long, 6 mm wide; with dense covering of short fine pale setae; setal swirls originate in positions marked (Fig. 1); dorsal surface with median ridge extending posteriorly from anterior margin for about ⅓ length of the pronotum; anterolateral corners of pronotum rounded obtuse; posterolateral corners rounded; lateral margins diverging posteriorly along most of their length, and widely flattened especially in the posterior half. Elytra (Fig. 1) 9.5 mm long; convex-sided when closed; laterally explanate margins well developed, especially in anterior ½ (Fig. 2); 4 interstitial lines present, of which the most lateral line is evanescent anteriorly and posteriorly; epipleuron and sutural ridge extending to and around apex of elytron. Head small, completely retracted into and beneath pronotum in resting condition; greatest head width 2.2 mm; smallest interocular width 0.8 mm; antennal sockets separated by more than width of an antennal socket; head not depressed between eyes; mouthparts well developed. Terminal ventrites as figured (Fig. 3).



Figs. 1-4. (1-3) *Aspisoma trilineata* holotype female: (1) dorsal aspect of pronotum and left elytron (position of hair swirl pattern indicated on pronotum); (2) ventral surface of epipleural margin of left elytron; (3) ventral surface of terminal abdomen. (4) *Aspisoma physonotum* male: ventral surface of terminal abdomen. Scale lines are 1 mm. FB, fat body; LO, light organ; ST9, ventrite 9.

Photuris trivittata sp. n.
(Fig. 23 habitus)

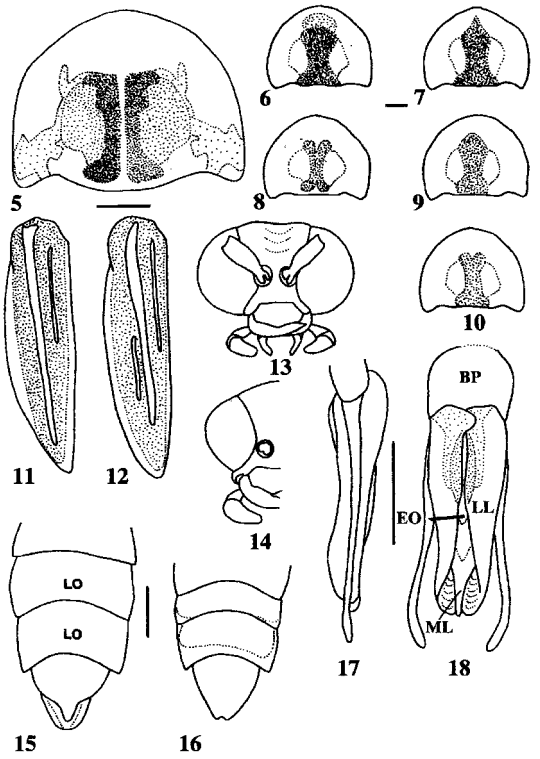
Type Specimens (Currently housed in JELC, Gainesville). Holotype male: MEXICO. Tabasco: 27 km w Cardenas at CSAT, 1980, J E Lloyd (M805*). Paratypes: same locality as holotype, 16.X.1980, 3 males (M809*, M8010*, M8015*); 18.X.1980, 1 male (M8027* used for SEM); 23.X.1980, 1 male (M8048*); 28.X.1980, 3 males, 1 female (M80104*, M80108*, M80103*, M80116); same locality and collector as for holotype, 1980: 16.X.1980, 1 female (M8050), 1 male (M803, CSAT); 17.X.1980, 1 female (M8025); 20.X.1980, 1 male (M8037); 21.X.1980, 2 males (M8044 macerated, M8047), 1 female (M8046); 23 X.1980, 3 males (M8052, 8053, 8055), 1 female (M8049); 28.X.1980, 2 males (M80109, 80114), 5 females (M80106, M80111-113, 80115). Cardenas, nr hotel Siglo XX, 27.X.1980, J E Lloyd, 1 male (M8093*), 1 female (M8059) (JELC). Cancun, Quintana Roo State, D Thomas & J Burne, 10.VIII.1990, 1 male (FSCA). Chiapas: Palenque, D. Thomas, 16-20.V.1985, 1 male, 2 females (FSCA); Parque Lag. Belgica, D Thomas, J Burnie, 5-6. VII.1989, 1 female (FSCA); 5 mi N Ixhuatan, B Ratcliffe, C Messenger, 9-16.IX.1985, 1

female (FSCA); Lago Montebello, D Thomas, J Mackley, 15.VI.1985, 1 female (FSCA); Simojovel, D Thomas, 23.VIII.1987, 1 female (FSCA); Chicoasen Dam area, D & A Thomas, 10.IX.1988, 1 female (FSCA). Comitan, 31 mi SE of Chis, Burke et al., at light, 17.VI.1965, 2 females. Veracruz, Dos Amates Mun. Catemaco, P Hubbell, 4-14.XI.1972, 1 female. BELIZE. Orange walk, Sept 1986, D Thomas, 1 male, 1 female (FSCA). COSTA RICA. Guanacaste, 2.7 mi NE La Cruz on Pan Amer. Hwy, 27.IX.1961, Hubbell et al., 1 female (pink), GUATEMALA. Dept. Isabel, Quirigua, 11.I.1937, 240 ft C. Roys, 1 male (pink); Peten, Pasion River at Cambio, 20.IV.1935, Hubbs-Vander Schalie, 1 female (pink); Suchitepe-quez, Dept. E of Cocales, 400-500 m, 2.XII. 1983, flsh on grnd, J Schuster, 2 females (JELC); Peten Tikal, 100 ft, I. Cantrall, 1 female 7.II.1956, at light at camp (pink), 1 female 17.II.1956 (pink), 1 female 13.III.1956 (pink), 1 female 31.III.1956 (pink). HONDURAS. Dept. Morazán, Esc. Agr. Pan. Zamborano, T. Hubbell, 2550 ft 18.VIII.1948 (vega Yeguare R., 1 female (pink); 2600 ft (hortaliza), 13.VII.1948, 2 females (pink); 2600 ft (creek bank) 19.VII.1948, 2 males (pink); 2600 ft 30.VII.1948, 1 female (pink). Tela, 6.IV.1923, T Hubbell, 1 male, 1 female (pink).

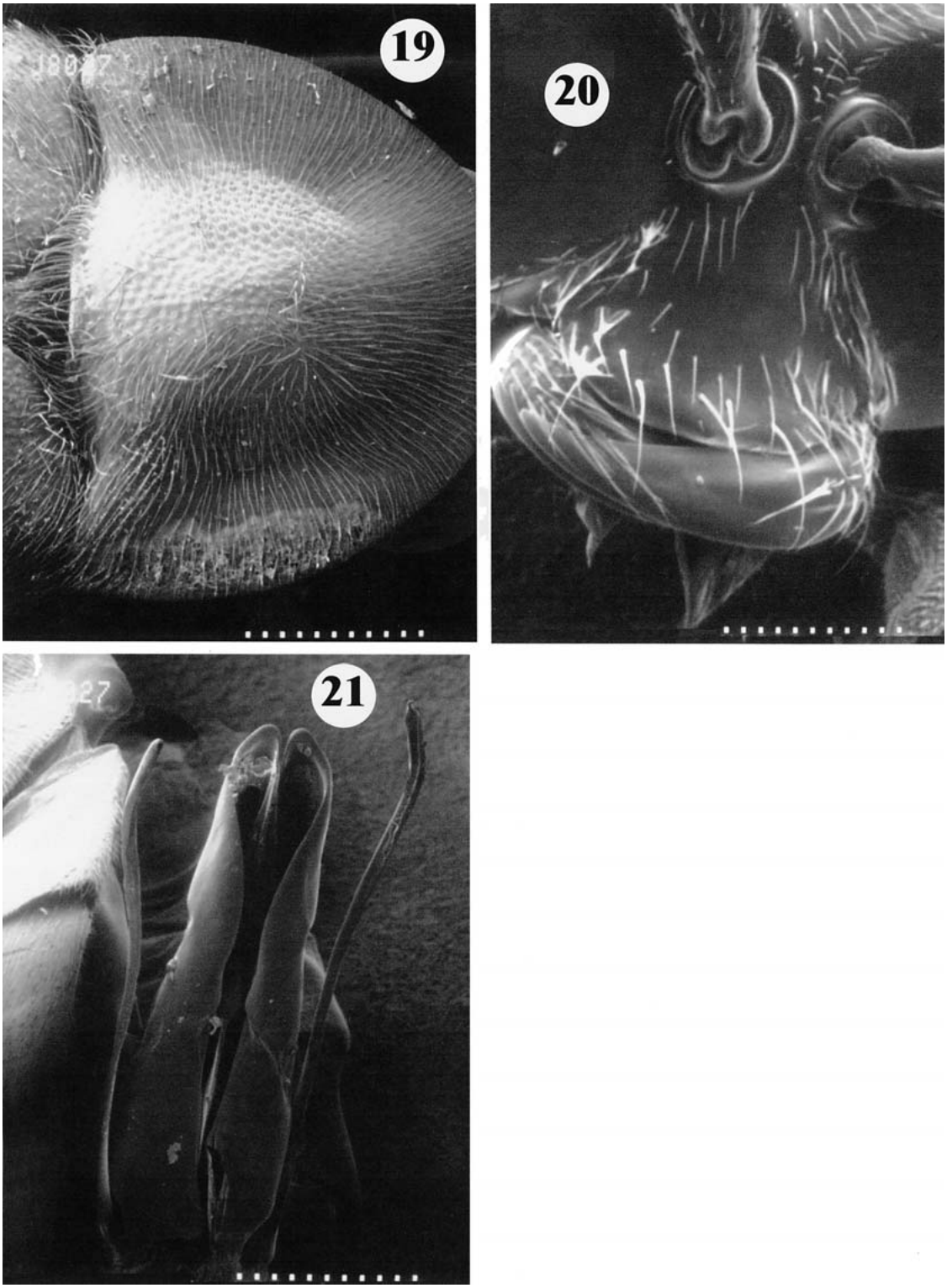
(Specimens "*" in the collection of JEL may bear a green label "semiosystematic voucher specimen, James E Lloyd". A further lettered and numbered label on each specimen relates to field records kept by the collector.)

Male. Length: 13-15 mm long (holotype 14 mm). Color: Pronotum yellow with median brown markings (Figs. 5-10), semitransparent; fat body visible through cuticle in posterolateral corners is yellow, in median area is pink; mesoscutellum and metanotal plates yellow; elytra brown, with broad lateral, narrow apical and narrow sutural margins yellow, and 2-3 longitudinal yellow interstitial lines; (Figs. 11 and 12 show variation; the coloration gives the appearance of 3-4 brown stripes); head yellow, anterior margin of labrum dark brown; antennae brown, basal portion of all segments narrowly yellow; maxillary palpi mostly brown, penultimate segment yellow at base, enlarged terminal segment yellow on inner face; labial palpi yellow; ventral prothorax yellow; legs 1 yellow with brown tarsi, brown apices of tibiae, and brown markings on femora at inner and outer basal and apical surfaces; mesopleura brown, mesosternum yellow; legs 2 marked as for legs 1 except for basal tarsomere which is brown at apex only; ventral metathorax brown; basal abdominal ventrites dingy to brownish yellow, semitransparent and fat body is visible through cuticle; light organ in ventrites 6 and 7 creamy yellow; ventrite 8 yellow; basal abdominal tergites medium brown, terminal 3 tergites pale yellow.

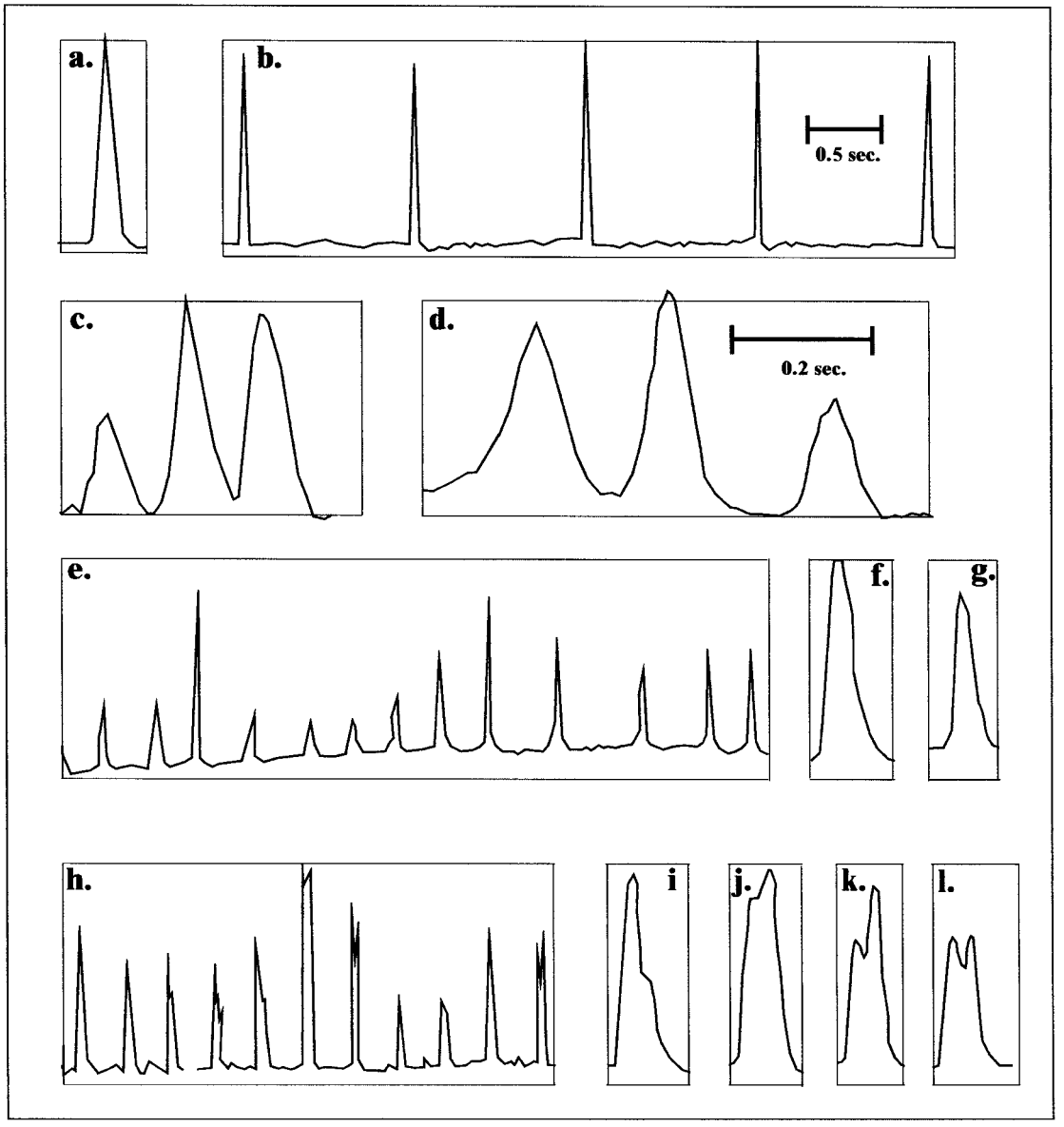
Pronotum 3.3-3.9 mm long; 5.2-5.9 mm wide; setal swirl pattern distinctive (Fig. 19); pronotal punctures small, shallow, separated by up to their width and evenly distributed over dorsal surface; hypomera open in front; lateral pronotal margins diverging along anterior half or more with some convergence in posterior area; anterolateral corners obliterated; posterolateral corners rounded obtuse; anterior margin narrowly explanate; lateral margins widely flattened along their length and anterior area as wide as posterior area; outline as figured (Figs. 5 and 19). Elytra with 3 interstitial lines well defined by their pale color but not well elevated relative to the sutural ridge (Fig. 23); epipleuron not extending posteriorly beyond mid point of elytron; sutural ridge evan-



Figs. 5-18. *Photuris trivittata* sp. n. (5-10) Dorsal surface of pronotum (5) M805 detail—dense stippling represents dark brown markings, less dense stippling represents pink fat body, least dense stippling represents yellow fat body; (6) M80116 female; (7) M809 male; (8) M8010 male; (9) M80104 female; (10) M8015 male (single dotted line represents extent of fat body visible through cuticle). (11, 12) dorsal surface of left elytron (11) M8027 male; (12) M809 male. (13, 14) anterior aspect of head (13) M8048 male; (14) right side only M80116 female. (15, 16) ventral view of terminal abdominal segments (15) M8027 male; (16) M80116 female. (17, 18) aedeagus (17) left lateral M805 holotype male; (18) dorsal M805 holotype male. Scale lines are 1 mm. BP, basal piece of aedeagus; EO, ejaculatory orifice; LL, lateral lobe aedeagus; LO, light organ; ML, median lobe aedeagus.



Figs. 19-21. *Photuris trivittata* sp. n. Electron micrographs. (19) M8027 male, dorsal surface of pronotum, dotted scale line 1.36 mm; (20) M80108 male, anterior aspect of head, antennal sockets, dotted scale line 0.5 mm; (21) M8027 male, dorsal aspect of aedeagus, dotted scale line 0.75 mm.



Figs. 22a-l. Chart traces of *Photuris trivittata* flashes, except for "d" an *Aspisoma* sp., detected in the field with a photomultiplier system, recorded on magnetic tape, then chart traced at two different speeds. Horizontal axis is time; vertical axis, relative intensity. Time scale is indicated by bars: bar in "b" applies to b, e, h; bar in "d" applies to all others. (a) Single flash of male; (b) five single flashes in sequence emitted by a perched male; (c) modulated flash of about 8.3 Hertz (Hz, cps); (d) modulated flash of co-active *Aspisoma* sp. with form similar to that of certain flashes emitted by *P. trivittata*, but at a much slower modulation rate, averaging 4.8 Hz (5.3 and 4.2 Hz); (e) flashes of female with short train of rapid flashes; (f, g) individual female flashes; (h) train of bimodal rapid flashes of a perched male; (i-l) male flashes from train in "h".

escent before elytral apex. Head slightly to moderately exposed in front of pronotum in withdrawn condition; gently excavated between eyes; eyes widely separated on ventral surface; greatest head width 2.8-3.3 mm; antennal sockets close but not contiguous (Figs. 13 and 20); mouthparts well developed, apical segment of labial palpi lunate (Figs. 13 and 20); labrum wider than long, well sclerotized, separated from head by an inflexible suture and bearing short rounded projections along its anterior margin; antennal length 2-3 times greatest head width; flagellar segment 1 short, half as long as flagellar segment 2, remaining flagellar segments long, slender,

Fig. 23. Habitus of *Photuris trivittata* male from near Cardenas, Tabasco, Mexico. Note the distinctive and diagnostic (for the present) elytral vittae. The split, median pronotal vitta in Cardenas specimens differs considerably from vittae occurring in North American *Photuris* species. This is a carbon dust drawing by Laura Line.

simple, much longer than wide, and narrowing towards apex. Abdomen with median posterior margin of ventrite 8 narrowly prolonged and apically rounded (Fig. 15). Aedeagus (Figs. 17, 18, and 21) with median lobe narrowing at apex, not projecting posteriorly beyond apices of lateral lobes; lateral lobes closely approximate dorsally, narrowly overlapping at base in ventral aspect, and shallowly excavated in apical 1/5; aedeagus bearing elongate slender projections bearing sense organs on their apical inner surface (Fig. 21).

Female. Length: 13 mm long. Macropterous; colored as for male; head slightly smaller than that of male (Fig. 14); light organ in ventrites 6, 7; ventrite 8 narrowing posteriorly, median posterior margin emarginate (Fig. 16).

Flashing and Ecology

Photuris trivittata was observed on the campus of the Agriculture School at Cardenas, Tabasco, Mexico, at the edge of small woods along an irrigation ditch and mowed roadside. Occurring with it at this site were about a dozen flashing species of *Photinus*, *Photuris*, and *Aspisoma*. Female *trivittata* hunted males of at least one other *Photuris* species in an adjacent field, and an *Aspisoma* species near the woods, via aggressive mimicry (sensu Wickler 1968; Pasteur 1982; Lloyd 1964, 1984). At a nearby site near an irrigation canal, this same firefly displayed a sedentary flashing-feeding behavior previously unreported for *Photuris* fireflies.

Evening flashing activity at the ditch site began about one-half hour after sunset (x-bar = 33 min, 1.5 crep (i.e., civil twilight duration, see Neilsen 1963); range = 24-40 min, 1.1-1.8 crep; n = 6, 17-28 Oct 1980), in the shrubs and understory, and quickly moved up and around the canopy foliage of the trees. The most common male flashing pattern observed at this site was a short flash (base duration ca 52 mSec, Fig. 22a), that was emitted in continuous sequence at 1.2-1.4 sec, quite-regular intervals (Fig. 22b; 27.2°C; Table 1). Perched males also emitted this pattern, and they as well as flying males could be attracted (via penlight) close from 20-30 meters above ground, by flashing a short flash immediately after each of their flashes. On one occasion about 15 males were seen perched in a low tree, each facing outward with head and neck extended, flashing this pattern. This pattern was also emitted amongst and around the tips of the fronds of oil palms at the second site.

Males high in the trees at the first site occasionally appeared to emit a bimodal flash pattern, with the two peaks appearing 20-30 mSec apart. However, photo-multiplier recordings of what were verbally noted as this “fast double”, showed that it was a short flicker of 3-4 modulations (Fig. 22c) with a mean modulation rate of ca 8.0 Hertz. The mean pattern period of this signal was 2.4 sec (27.2°C; Table 1). This pattern is similar in form to that of a co-active *Aspisoma* species at this ditch site, but the modulation rates of the two are different (cf. Figs. 22c, d). Male *P. trivittata* sometimes emitted a longer flash, which had an estimated duration of about 300 mSec.

Across campus at the second site, near a large irrigation canal, male and female *Photuris* of two species perched in aggregations on the seedheads of a tall Bahia grass, *Paspalum virgatum*. They “mouthed”, chewed or licked, the seeds, which were coated with a sticky material. Each of the two mixed groups observed numbered 20-30 individuals and extended along the canal about 30 ft. The groups were about 200 ft apart and a few isolated individuals perched and flashed in the grass extending along the canal bank between them. Males and females on the grass heads emitted sequences (trains) of short flashes, and fireflies in these aggregations had a tendency to flash together in bouts of up to about 1 minute duration, separated by relatively dark periods.

TABLE 1. FLASH DATA FROM ELECTRONIC RECORDING AND STOPWATCH MEASUREMENTS. FLICKER MODULATION RATES ARE EACH FOLLOWED BY THE NUMBER OF MODULATIONS USED TO CALCULATE THE RATE INDICATED. MEANS ARE INDICATED BY "$\bar{x}$"; STANDARD DEVIATION BY "s". NUMBERS IN BRACKETS ARE ID NUMBERS OF INDIVIDUAL MALES ON CHART RECORDS THAT ARE ARCHIVED WITH THE VOUCHER SPECIMENS AND FIELD NOTE BOOKS.

A. Data from photo-multiplier recordings

Male no.	Observations	$\bar{x}$	s.d.	Temp.
Short flash period				
1.	1.35, 1.35, 1.36	1.35	0.01	26.1°C
3.	1.19, 1.18, 1.18, 1.18, 1.18, 1.17, 1.14, 1.16	1.17	0.02	25.8°C
4.	1.27, 1.23, 1.24, 1.22, 1.20, 1.20, 1.20, 1.21, 1.22, 1.22, 1.22, 1.23, 1.23, 1.24, 1.24, 1.22, 1.22 (perched)	1.22	0.02	27.2°C
5.	1.25, 1.24, 1.23, 1.25, 1.25, 1.23	1.24	0.01	27.2°C
6.	1.25, 1.25, 1.24, 1.24	1.25	0.01	27.2°C
7.	1.24, 1.26, 1.25, 1.18, 1.19, 1.11, 1.19, 1.23, 1.23, 1.23	1.21	0.05	27.2°C
8.	1.28, 1.28, 1.27, 1.27, 1.25, 1.27, 1.23, 1.20, 1.22, 1.24, 1.23, 1.22, 1.21, 1.21, 1.21	1.24	0.03	27.2°C
	Combine 5 males @ 27.2°C: $\bar{x}$ = 1.23 Sec., s.d. = 0.02			
Flicker pattern period				
9.	1.80, 2.26, 1.94	2.00	0.24	25.8°C
10.	2.30			27.2°C
11.	2.48			27.2°C
	Combine 2 males @ 27.2°C: $\bar{x}$ = 2.39 Sec., s.d. = 0.13			
Flicker modulation rate				
9.	9.6/3, 9.6/2, 8.9/3, 8.8/3, 9.0/3	9.2	0.4	25.8°C
10.	8.5/3, 8.2/3	8.4	0.2	27.2°C
11.	7.5/4, 7.4/4	7.5	0.1	27.2°C
	Combine 2 males @ 27.2°C: $\bar{x}$ = 8.0 Sec., s.d. = 0.6			

Short flash duration

Σ = 70 flashes (8 males) pm-recorded; 64 flashes from 8 males usable:
8 flashes, 2 males: $\bar{x}$ = 53 mSec, r = 51-56 mSec, 26.1°C, 23-X-80.
6 flashes, 1 male: $\bar{x}$ = 48 mSec, r = 46-51 mSec, 25.8°C, 26-X-80.
50 flashes, 5 males: $\bar{x}$ = 52 mSec, r = 48-62 mSec, 27.2°C, 28-X-80.

B. Flash pattern period data from stop watch records

3 males: 1.4 1.4 1.4; $\bar{x}$ = 1.4, 26.1°C
3 males: 1.4 1.4 1.4; $\bar{x}$ = 1.4, 26.1°C
6 males: 1.4, 1.3-1.4; $\bar{x}$ = 1.4, 26.1°C
2 males: 1.6 1.6; $\bar{x}$ = 1.6, 24.4°C
1 male: 1.3, 26.7°C

Flash rate within an individual's train was not constant. A few (5-15) rhythmic flashes were emitted in rapid succession, then rate slowed and became much less regular (Fig. 22e). Brief (ca 10-sec, 25.8°C) recordings of the flashes of several individuals on seeds suggest that there may be sexual differences. In a sample of four males and four females, the flashes of two males are nearly all bimodal, while those of females are all unimodal (Figs. 22e-l). Male flashes are longer on average (duration 91 mSec versus 75 mSec for females). In the short bouts of regular, rhythmic flashing, the flash rate of males is lower (x = 2.8 Hz versus x = 3.4 for females; Table 1). However, no overt sexual behavior such as mounting or rapproachment was observed.

Several kinds of insects occurred on the grass, including mosquitoes, crane flies, leaf beetles, roaches, grasshoppers, and moths, all apparently feeding on the seeds, except for a cone-headed katydid that was eating another insect. *Photuris trivittata* captured and fed upon mosquitoes, crane flies and beetles. To our knowledge, this is the only time that adult *Photuris* have been found eating prey other than Lampyridae in the field,

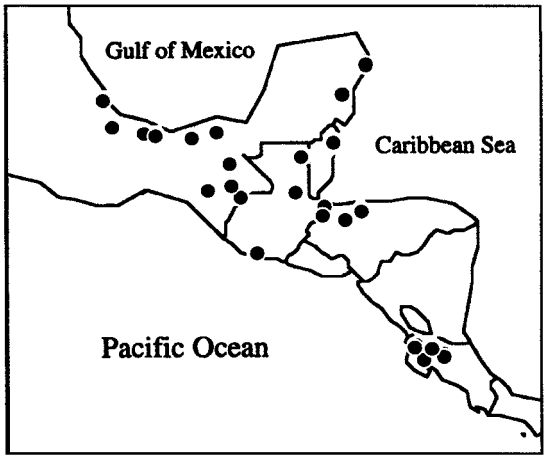


Fig. 24. Known distribution of *P. trivittata* as presently recognized, from specimens located in several collections.

though captive specimens have fed upon other insects. Firefly prey (*Photinus*, *Pyractomena*) provides defensive chemical substances that *Photuris* fireflies use in their own defense (Eisner et al. l997 and refs). However, non-firefly prey may also be captured by Nearctic *Photuris*, but because they don't glow while being eaten, go unnoticed. In the field adjacent to the first site, female *P. trivittata* perched down in dense grass within a foot of the ground, flashed responses to flash patterns of *Photuris* males of another species and attracted them to within 1 meter distance. *Photuris trivittata* occurs broadly through Central America, from southern Mexico to Costa Rica (Fig. 24), and its predation certainly has had an important influence on the signaling behavior of other lampyrids, and perhaps the behavior of other insects as well.

ACKNOWLEDGMENTS

Ballantyne thanks Prof. Harvey Cromroy and Mr. Bill Carpenter of the Department of Entomology and Nematology at the University of Florida in Gainesville for helpful advice, criticism, and patience during the preparation of specimens for SEM work; Dr. John Capinera for accommodation within the Department of Entomology and Nematology; Dr. Robert Ballantyne for support and encouragement and critical comments. Ballantyne undertook this project while on sabbatical leave at the University of Florida in 1993. Lloyd thanks the curators and collection managers for the loan of specimens: D. Furth, Harvard University, whom he especially wishes to thank for bringing the recently rediscovered neotropical insect collection of Thomas Say—which included Say's *L. trilineata*—to his attention; M.F. O'Brien and R.D. Alexander, The University of Michigan; N. Ladkin, M.A. Houck, and R.W. Sites, Texas Tech University; V. Scott, The University of Colorado; Drs. Awinash Bhatkar and Stitzer-Bhatkar for the invitation to visit the Cardenas campus (CSAT = Colegio Superior de Agricultura Tropical), and for locating and guiding him to various firefly localities; John Sivinski, Skip Choate, Joseph Cicero, Scotty Long, Tom Walker, and Marc Branham for reading part or all of the manuscript at various stages of development; Flora MacColl, Pamela Howell, Seth Ambler, and Mike Sanford, for considerable technical assistance in preparing the manuscript and computer enhancement of the figures; Laura Line for preparing the carbon dust habitus drawing (Fig. 23); Sara Díaz-Barreto for preparing the Resumen; and several students in his Honors firefly classes for finding the latitudes and longitudes of various collection localities. Approved for publication as Florida Agriculture Experiment Station Journal Series Number R-08250.

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