Life cycle and description of the immature stages of a terrestrial firefly endemic to Mexico: *Photinus extensus* Gorham (Coleoptera, Lampyridae)

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Abstract

The life cycle, morphology, and bionomy of *Photinus extensus* Gorham, 1881, an endemic species of Mexico, are described. Redescriptions of adults (male and female) are also presented. Larvae were reared to the adult stage from eggs laid by females collected at the El Pedregal de San Ángel Ecological Reserve, south of Mexico City. The activity period of adults of *P. extensus* begins at the end of July and finishes by the end of August. Females lay between 3 and 198 eggs. Larvae hatch from the eggs after a period of 11 to 71 days, undergo 6 larval instars and a pupal stage in an annual cycle. Morphological characters of the sixth larval instar of *P. extensus* are compared with those of several other genera assigned to the tribe Photinini. Knowledge of the natural history of firefly larvae is relevant since most species do not feed as adults and therefore depend on resources acquired during the larval stage.

Keywords

Bionomics, egg, larva, Photinini, pupa, redescription
Introduction

Fireflies belong to the family Lampyridae Rafinesque, 1815, and show a wide-ranging phenotypic and ecological diversity (Riley et al. 2021). Currently, there are more than 2400 described species with a worldwide distribution (Martin et al. 2019; Ferreira et al. 2020; Zaragoza-Caballero et al. 2020; Riley et al. 2021; Silveira et al. 2022). The highest species diversity is found in the Neotropical region (Costa 2000). Fireflies include nonluminous and luminous adults, luminous larvae and the females of some taxa are flightless (Branham 2010; Lewis et al. 2020). They inhabit wetlands, grasslands, forests, agricultural fields and urban parks (Lewis et al. 2020). Many fireflies are strongly associated with particular habitats and vegetation types (Faust 2017).

Firefly species can be either diurnally or nocturnally active. Diurnal species generally do not have light organs as adults and rely on pheromonal and visual cues (Ohba 2004; Branham 2010). Luminous species are nocturnal or crepuscular, with bioluminescent signals produced from photic organs of various shapes and sizes located on abdominal ventrites. These visual signals are typically used in sexual signaling to communicate species identity and facilitate pair formation (Branham 2010).

Firefly larvae can be aquatic, semiaquatic or terrestrial and can be found along the margins of streams and ponds as well as in leaf litter or rotten logs (Branham 2010). All known larvae are luminous and emit glows of varying duration. They are predatory on snails, earthworms and other soft-bodied prey (Lewis et al. 2020). The adults of most species do not feed and therefore rely on resources gathered during the larval stages (Lloyd 2002; Vaz et al. 2020). Multiple genera endemic to the Neotropical region have no larval or pupal descriptions. The few species that have been studied have different life histories (Vaz et al. 2020).

Currently, only the morphology of a small percentage of lampyrid larvae, at the generic or specific levels, of the approximately 144 genera and 2400 species, is known (Archangelsky 2010; Madruga and Branham 2020; Vaz et al. 2020; Zaragoza-Caballero et al. 2020; Riley et al. 2021; Silveira et al. 2022). There are a few studies describing the immature stages in the tribe Photinini. However, most of them have poorly detailed descriptions, composed only by the last larval stage (Riley et al. 2021). Besides, no tools to compare microstructures have been implemented. Of the 29 genera belonging to Photinini (Martin et al. 2019; Zaragoza-Caballero et al. 2020), there are detailed descriptions only for some species of *Pyractonema* Solier in Gay, 1849, *Pyropyga*, Motschulsky, 1852 *Lucidina* Gorham, 1883, *Lucidota* Laporte, 1833, *Phosphaenus* Laporte 1833 (Bugnion 1929; Beutel 1995; Branham and Archangelsky 2000; Archangelsky and Branham 2001; Archangelsky 2010, Kawashima 2017; Novák 2018b).

*Photinus* Laporte, 1833 is the most diverse genus of the subfamily Lampyrinae with more than 300 described species (McDermott 1964; Zaragoza-Caballero et al. 2020). Members of this genus live in a variety of habitats (from tropical dry forests to temperate and tropical montane cloud forests). Species range from the United States to Argentina. One species, recently collected in Spain, was described as new (Zaragoza-Caballero and Viñolas 2018) but then synonymized with the South American species *Photinus signaticollis* (Blanchard, 1846) (Koken et al. 2022).
In the past 20 years the number of known *Photinus* species has increased due to the description of new species from Mexico (Zaragoza-Caballero 2000, 2005, 2007, 2015, 2017; Zaragoza-Caballero et al. 2020). This fact contrasts with the lack of knowledge of the larval stages and the natural history of these organisms. Until now, no study has accurately documented the life cycle duration of a *Photinus* species. This lack of knowledge is the result of the difficulty of collecting mated females, as well as challenges associated with rearing larvae under laboratory conditions. Moreover, some species are known to spend several years in the larval stage, and the time fireflies need to complete their life cycle depends on the geographical region and the availability of larval food (Buschman 2017).

As for most genera in the family Lampyridae, *Photinus* larvae are poorly studied. Buschman (2017) observed that the first instars of this genus are smaller compared to those of *Photuris* Dejean, 1833, but no descriptions are provided. Most research documenting the natural history of *Photinus* focuses on the adult stage. These studies include courtship in males (flash communication) (Wing 1991; Viviani 2001; Faust and Weston 2009; Faust 2010), nuptial gifts (Lewis et al. 2004a, 2004b), the utilization of ejaculate-derived proteins to nourish developing oocytes in certain species (Demary 2005) and the size of signal detection and emission organs (López-Palafox et al. 2020).

This paper documents the life cycle and larval morphology of a *Photinus* species for the first time. *Photinus extensus* Gorham, 1881 is an endemic species of Mexico. Its known distribution includes the state of Chiapas, Hidalgo, Mexico, Morelos and Mexico City (Zaragoza-Caballero et al. 2020). A reduced population of this firefly was also found in El Pedregal de San Ángel Ecological Reserve, South of Mexico City. The life cycle of *P. extensus* is herein presented, with descriptions of larval instar 6. Some characteristics of instars 1 and 3 are mentioned; the adult was described as well.

**Methods**

**Collection**

Adults of *P. extensus* were collected in the buffer zone of the El Pedregal de San Ángel Ecological Reserve (19°19′28.82″N, 99°11′20.95″W); this zone is between the core zone and the urban area of Mexico City, it is totally in the territory of the Universidad Nacional Autónoma de México. El Pedregal de San Ángel Ecological Reserve is located at the Southeast of Mexico City in the central Campus of the (UNAM) (Fig. 1). This community developed on a basaltic lava substrate approximately 1,670 years ago (Lot and Camarena 2009); the type of vegetation corresponds to a xerophytic shrub (Rzedowski 1978). The climate is sub-humid tempered with summer rains and an annual average precipitation of 833 mm; the annual average temperature is 15.5 °C (Orozco-Segovia et al. 2009). Fourteen adult females and 70 adult males of *P. extensus* were collected on August the 3rd, 8th, and 10th of 2018, between 19:30 and 21 h. Adult specimens were located by their bioluminescence in the undergrowth, where
the dominant plant species is *Pittocaulon praecox* (Cav.) H. Rob. & Brettel (Asterales: Asteraceae). Other collections were made at the same site between June and July 2019, and five larvae were obtained. These developed into two female pupae and three males. Larvae, pupae, and adults were fixed in 70% ethanol for their preservation.

**Rearing in the laboratory**

To observe the reproductive activity of *P. extensus*, adult specimens collected were divided into 14 groups consisting of five males and one female were placed in an 8 × 15 cm plastic container; peat moss substrate was added to simulate their natural environment. After oviposition, eggs were placed over a gauze patch in a 50 × 100 mm

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**Figure 1.** Map of Mexico City. Location of the study area where adults of *P. extensus* were collected (indicated with a star).
Petri dish, and moistened every 48 hours with an antimycotic solution based on Ni- 
statine diluted in water (1/10). After eclosion, larvae were repartitioned into groups of 
five in separate Petri dishes (5×10 mm). To avoid dehydration, a filter paper layer 
was added and moistened every two days. This filter paper was replaced every week. 
Starting with the fourth larval instar, each larva was placed in a separate Petri dish 
(5×10 mm), with half of the dish covered with the filter paper, and the other half 
filled with sterilized dry sawdust. Following previous studies (Archangelsky and Bra-
nham 2001; Archangelsky 2010), larvae were fed small pieces of earthworm *Eisenia 
etida* (Savigny, 1826) (Haplotaxida: Lumbricidae). Dead or partially consumed prey 
were removed from the Petri dishes every two days to keep containers clean. Pupae 
were maintained in Petri dishes (5×10 mm) at room temperature with sterilized dry 
sawdust until they completed their development. Specimens representing the differ-
ent larval instars, pupae, and adults, were preserved in 70% ethanol for reference and 
subsequent study.

**Morphological study**

Adults were identified using original descriptions, literature (Zaragoza-Caballero et 
al. 2000), and by comparison with photographs of type specimens (Natural His-
tory Museum of London, BMNH) (Fig. 2A–F) and specimens identified by experts 
deposited at the Colección Nacional de Insectos (CNIN), Instituto de Biología, 
UNAM, terminology of internal genitalia of females followed Silveira et al. (2022). 
Juvenile stages and adults of *P. extensus* were examined under a Zeiss stereoscopic 
microscope (Discovery V8) with a 1× objective lens coupled with 16× eyepieces. Lar-
val heads of each instar were separated from the body and immersed in 10% KOH 
solution, the mouthparts were dissected under a stereoscopic microscope and placed 
glycerin on slides for observation. Description of the distribution of the setae was 
made for the last instar larva following Branham and Archangelsky (2000) and Arch-
angelsky (2010). Pygopodial structure for the last instar larva was interpreted using 
Fu et al. (2012). Redescription of the adult of *P. extensus* was made based on col-
lected material. For the morphological description of larval instars, we followed the 
terminology of Novák (2018a) and Fu et al. (2012). A table 1 was made to compare 
morphological larval characters of Photinini (*Pyraclonema, Pyropyga, Lucidota, Lu-
cidina, Phosphaenus and Photinus*) (Branham and Archangelsky 2000; Archangelsky 
and Branham 2001; Archangelsky 2010; Novák 2018b), after Archangelsky (2010) 
and Kawashima (2017).

Images were taken with an AxiocamMRC5 camera attached to a Zeiss Axio Zoom 
V16 microscope with an objective lens Plan NeoFluar Z, 1×10.25 FWD 56 at the 
Laboratorio de Microscopía y Fotografía de la Biodiversidad II, Instituto de Biología, 
UNAM. Larvae were examined and imaged with a Hitachi SU1015 scanning electron 
microscope at the Laboratorio de Microscopía y Fotografía de la Biodiversidad I, Insti-
tuto de Biología, UNAM.
Figure 2. Photinus extensus Gorham, type specimens NHM-London A general habitus of the adult male in dorsal view B ventral view C general habitus of the adult female in dorsal view D ventral view E male labels (lectotype) F female labels (paralectotype). Photos: Keita Matsumoto.
Results

*Photinus extensus* Gorham, 1881
Figs 3A–E, 4A–E [Adults]

Redescription. Adult male (Fig. 3A, B) \((n = 70)\). Length of body 16.1–20.3 mm; width 3.7–4.2 mm. Body brownish, except the pronotal disk with a central black spot and two red spots at the sides; protrochanters, coxae, seventh and eighth ventrites yellowish; light organ in sternites 5–6 and 7th sternite with diminished light spots.

**Head.** Intercocular space flat, almost parallel, shagreen-like integument, brilliant and pilose; frons vertical, interantennal distance \((0.17–0.22 \text{ mm}; 0.2 \pm 0.01 \text{ mm})\) slightly wider than the antennal fossae \((0.23–0.32 \text{ mm}; 0.28 \pm 0.04 \text{ mm})\); eyes finely faceted, semispherical, prominent, longer \((1.1–1.18 \text{ mm}; 1.17 \pm 0.03 \text{ mm})\) than wide \((0.62–0.98 \text{ mm}; 0.9 \pm 0.08 \text{ mm})\); antennae filiform, long \((5.7–7.11 \text{ mm}; 7.0 \pm 0.11 \text{ mm})\), one-and-a half times longer than pronotum, extending beyond the posterior coxae, scape claviform reaching a length of \((0.69–0.98 \text{ mm}; 0.79 \pm 0.10 \text{ mm})\), as long as the next two antennomeres together, the second short \((0.19–0.79 \text{ mm}; 0.28 \pm 0.05 \text{ mm})\), the third to the tenth \((0.54–0.71 \text{ mm}; 0.66 \pm 0.07 \text{ mm})\), the eleventh reaches \((0.51–0.73 \text{ mm}; 0.77 \pm 0.03 \text{ mm})\); frontoclypeal suture membranous, almost straight; clypeus trapezoidal, anterior margin concave, with setae along the margin; mandibles falcate, robust, with setae on the external base; maxillary palpmere ogival and robust, labial palpmere seciriform.

**Thorax.** Pronotum wider \((3.95–4.4 \text{ mm}; 4.04 \pm 0.08 \text{ mm})\) than long \((2.8–3.4 \text{ mm}; 3.01 \pm 0.27 \text{ mm})\), semicircular, with a longitudinal groove indistinct in the basal half, anterior margin rounded, posterior sinuate, posterior angles straight, sides narrowly explanate, with irregular glandular pores at the front and ordered on the posterior and lateral margins, surface brilliant, abundant pilosity, decumbent; scutellum spatulate, with the posterior margin rounded, surface brilliant, punctate and decumbent pilosity; long elytra, parallel, four and a half times longer \((12–13.5 \text{ mm}; 12.6 \pm 0.57 \text{ mm})\) than wide \((2.4–2.8 \text{ mm}; 2.58 \pm 0.19 \text{ mm})\), surface rugose, opaque, with two types of pilosity, one relatively long and erect, the other small and procumbent; mesothoracic respiratory spiracles not tubular; long legs, pro, meso and metalegs similar to each other, femurs fusiform, tibiae channeled, a little dilated at the apex, external margin crenulate, two symmetric tibial spurs present in pro, meso and meta legs, tarsomeres laterally compressed, first metatarsomere longer \((0.6–0.76 \text{ mm}; 0.73 \pm 0.03 \text{ mm})\) than the next two metatarsomeres together \((0.51–0.68 \text{ mm}; 0.63 \pm 0.08 \text{ mm})\), fourth bifid, covering the fifth, claws simple.

**Abdomen.** Sternites 5–6 longer than the preceding, with stigmatiform pores, posterior margin of sternite six cleaved, the seventh concave, the eighth ojival; posterior margin of pygidium convex; aedeagus short, robust, with symmetrical basal piece \((0.67–0.7 \text{ mm}; 0.68 \pm 0.05 \text{ mm})\), as long as lateral lobes \((0.66–0.7 \text{ mm}; 0.67 \pm 0.45 \text{ mm})\), with posterior margin concave, lateral lobes apically acute and convergent, median lobe cylindrical, with dorsal part membranous and ventral part with sclerosed base and apical half membranous, dorso-basal excrescences as long, oblique lobes, median orifice apical, lateral lobes narrowing towards the apex, apex blunt and wide (Fig. 3C, D, E).
Adult female (Fig. 4A, B) (n = 14). Length: 11.1–20.3 mm; width: 3.2–6.5 mm. Body brownish, except the pronotal disk with a central black spot and two red spots at the sides; procoxae, protrochanters, meso-coxae, meta-coxae, seventh and eighth sternites yellowish; light organ in fifth sternite.

Figure 3. Photinus extensus Gorham A general habitus of the adult male in dorsal view B ventral view; Aedeagus: C dorsal view D lateral view E ventral view.
Life cycle and immatures of *Photinus extensus*

**Head.** Interocular space flat, more or less parallel, shagreen integument, brilliant and pilose, frons vertical, interantennal distance (0.16–0.37 mm; 0.25 ± 0.10 mm) wider than antennal fossae (0.16–0.37 mm; 0.44 ± 0.16 mm); eyes small, finely facet-ed, semispherical, longer (0.65–0.94 mm; 0.67 ± 0.25 mm) than wide (0.45–0.76 mm; 0.54 ± 0.15 mm), antennae filiform, short (4.16–5.52 mm; 5.23 ± 0.96 mm), as long as the length of pronotum, without extending beyond the posterior margin of metasternum; scape reaching a length of (0.57–0.64 mm; 0.58 ± 0.34 mm), longer than the two next antennomeres together, the second short (0.2–0.39 mm; 0.37 ± 0.06 mm), from the third to the tenth (0.35–0.58 mm; 0.44 ± 0.07 mm), the eleventh reaches (0.54–0.69 mm; 0.68 ± 0.05 mm); frontoclypeal suture membranous, almost straight; clypeus trapezoidal, anterior margin concave, with setae along the margin; mandibles falcate, robust with setae on the external base; maxillary palpmere ogival and robust, labial palpmere securiform.

**Thorax.** Pronotum wider (3.27–4.97 mm; 4.21 ± 0.86 mm) than long (2.21–2.6 mm; 2.2 ± 0.2 mm), semicircular, with a longitudinal groove indistinct on the basal half, anterior margin rounded, posterior margin straight, posterior angles straight, sides narrowly explanate, with glandular pores irregular at the front and ordered on the posterior and lateral margins, surface brilliant, pilosity abundant, decumbent, scutellum spatulate, with the posterior margin rounded, surface brilliant, punctate and pilosity decumbent; elytra short, without covering the abdomen, two-and-a-half times longer (4.62–6.5 mm; 5.2 ± 0.62 mm) than wide (1.91–2.71 mm; 2.22 ± 0.42 mm), surface rugose, opaque, pilosity decumbent; divergent in the median margin, epipleura reduced, mesothoracic respiratory spiracles not tubular; legs similar to each other; tibiae and femurs flat, fusiform, tibiae channeled, a little dilated at the apex, external margin crenulate, tarsomeres laterally compressed, first metatarsomere (0.41–0.64 mm; 0.62 ± 0.22 mm) slightly longer than the next two together (0.46–0.58 mm; 0.53 ± 0.06 mm), the fourth bifid, covering part of the fifth, claws simple.

**Abdomen.** Sternites 5–6 longer than the preceding, without stigmatiform pores, posterior margin of sternite six almost straight, the seventh cleaved, the eighth with a notched; posterior margin of pygidium convex. Internal genitalia with a short and rounded spermatophore-digesting gland, longer than spermatheca, bursa copulatrix with an elongated and weakly sclerotized plate. Ovipositor with valvifers free, two-and-a-half times longer (2.41–3.10 mm; 2.75 ± 0.48 mm) than coxites (1–1.12 mm; 1.06 ± 0.08 mm); coxites divergent posteriorly; styli minute, sclerotized; proctiger plate short with rounded posterior margin, well-sclerotized (Fig. 4C, D, E).

**Description of pre-imaginal stages.**

**Egg (Fig. 5A, B).** Semispherical shape, whitish, with a diameter of approximately 290–300 µm (Fig. 5A). Surface with concavities that differ in size and shape (4–10 µm), evenly distributed, some present in aggregations (Fig. 5B). As time elapsed, the surface of the eggs became more transparent, allowing the observation of the larvae before hatching.
Figure 4. *Photinus extensus* Gorham A general habitus of the adult female in dorsal view B ventral view C internal genitalia D ovipositor dorsal view E internal anatomy of the reproductive tract: spermatophore digesting (SDG) and spermateca (SPT).
Sixth instar larva (Figs 6A, B, 7A–H, 8A–G, 9A–F). Description. Elongate, tapering body, dorso-ventrally flattened, length 12.27–18.18 mm; integument of granular appearance; tergites from protergum to abdominal segment IX divided by sagittal line in dorsal view. Tergites with two lateral pale stripes that run throughout the body to the VIII segment, more sclerotized than the sternites, with clearly visible setae on the posterior margin of tergites VII to X; the last tergum completely dark except the lateral margins paler; anterior margin of the first head segment with two fossae (sensorial or glandular) paler and bigger than the rest of the punctations of the segment. Membranous pleura except for a dark sclerotized area around the spiracles, without apparent setae. The ventral surface is flexible due to the intersegmental membranes. Mesothoracic and abdominal pleural areas of segments I–VIII with bilabiate spiracles.

Head capsule. Prognathous; slightly visible when retracted into prothorax due to the transparency of the protergum; extensible neck membrane covered in extremely short spines forms a two-layer envelope around the head; partially retractable within the prothorax; completely sclerotized, small, wider (0.88–1.54 mm; 1.2 ± 0.27 mm) than long (0.68–1.09 mm; 0.92 ± 0.17 mm), flat, sides almost parallel; stemmata on each side, with an almost transparent spot located posteriorly to the stemmata; clypeus and labrum fused forming the clypeo-labrum covering base of the mandibles in dorsal view; maxillae and labium connate forming maxillolabial complex covering most of the ventral cephalic area; epicranial suture dark, U-shaped, with a very short epicranial stem, frontal arms V-shaped (Figs 7A, 8A). Epipharynx formed by two oval plates, without setae, that project centrally beyond the anterior margin of the head. Hypopharynx with short setation.

Antenna. Trimerous, located on the distal margin of the epicranial plate; partially retractable into the antennal socket; three-segmented, basal antennomere and second antennomere (0.42–0.55 mm; 0.48 ± 0.05 mm) elongated, and a third segment (the flagellum) short (0.24–0.31 mm; 0.26 ± 0.03 mm); adjacent sensorial cone present; basal antennomere with two long setae in the anterior mid, almost entirely covered by moderately dense, second antennomere with long setae close to apex and entirely covered by dense smaller finer setae, third antennomere with long setae from base to apex, with short setae on the anterior margin (Fig. 7B, 8B).
**Maxilla.** Consisting of five parts, attached to lateral margins labium forming a maxillo-labial complex. Cardo elongate, irregular shape, with four setae in ventral surface, on long setae in posterior margin. Stipes elongated, ventrally covered with erect setae, with three long stout setae placed radially on the ventral apical region. Galea present, with two segments, the first longer and stouter than the apical, which is triangular (Fig. 7C, D). Lacinia covered with brush of long setae on outer lateral margin. Maxillae with three-segmented palpi, basal segment long (0.57–0.71 mm; 0.66 ± 0.06 mm) covered by setae in mid-region, segment II wider (0.30–0.40 mm; 0.35 ± 0.04 mm) than long (0.12–0.16 mm; 0.14 ± 0.01 mm); apical segment cylindrical (0.10–0.14 mm; 0.12 ± 0.01 mm) with numerous setae from base to mid region; (Figs 7E, F, 8C, D).
**Labium.** Closely attached to maxilla, formed by prementum, mentum and postmentum. Prementum heart-shaped, surface covered with numerous short setae and two long setae close apex; labial palpi with two segments, basal palp subquadrate with few setae in mid-region, distal palp conical without setae; mentum with one pair of setae on anterior third and one pair of setae on posterior third; postmentum elongate, slightly sclerotized at the medial base, laterally united by membranes to the cardines; with a setae on each side near the base.

**Mandible.** Symmetrical, falcate, strongly sclerotized, with an internal channel opening subapically on outer edge. Penicillus well-developed. Retinaculum short and rounded, present only as a blunt protuberance on basal third of the mandible. Densely covered by fine setae on the external margins basely, basal half on inner margin of mandible covered with a brush of stout setae, being longest on the retinaculous protuberance (8E, F); mesal margin serrate.

**Thorax.** Protergum wider (2.43–3.81 mm; 3.14 ± 0.57 mm) than long (1.54–2.59 mm; 2.11 ± 0.43 mm), subsemicircular, wider posteriorly, rounded at postero-lateral corners, covering the retracted head. Meso- and metatergum subrectangular three times wider than long, delimited by a pleural suture elongate barely evident from the laterotergites. Lateral areas of meso and metathorax scarcely sclerotized, composed of two laterotergites, the anterior with a well-developed spiracle on the mesothorax. Episterna extending from the anterior part to the lateral part of the coxae; epimeron forming a little sclerotized stripe, parallel to the coxae.

**Legs.** Pentamerous, the first pair of forelegs slightly shorter than the second and third. Coxae short (0.76–1.16 mm; 0.98 ± 0.18 mm), cylindric, widely separated at the base, decumbent; coxal-trochanteric membrane reaching about 1/3 of the coxal length. Trochanters pentagonal, joining the femur obliquely (0.51–0.82 mm; 0.71 ± 0.13 mm). Femur narrow and cylindrical in lateral view. Tibiotarsus narrowing distally with stout setae. All legs with a double row of long setae in the inner margin, numerous short setae in the outer margin: pretarsus claw-like with two setae at base (Figs 7G, H, 8G).

**Abdomen.** Tergites III–IX of similar length (0.86–1.36 mm; 1.09 ± 0.17 mm), width almost constant; segments I–VIII (or I–VII) wider than long, bearing a pair of long stout setae posterolaterally, with laterotergites at each side, with sclerotized plates containing the spiracles; ventral area of segments I–VIII with sternal areas almost squared, slightly pigmented, sternites with two long setae in mid-region; sternal medial area margined by laterosternites – sometimes pigmented, elongate, narrow, and paired, delimited by laterotergites dorsally, and ventrally by a medial sternal plate; ventral area of segment IX with a simple plate, without area differentiation; light organ present and segment VIII indistinct; abdomen ending with a series of eversible filaments (pygopodia) bifurcate at the apex, at least 30 pygopodia arise from 12 basal stalks which may branch more than once (the dorso and ventrolateral stalks branch into three); densely packed recurved hooks occur on the ventrolateral surface of each exerted pygopod and completely covering at apex, with toothed scales on the dorsolateral surface only on anterior half. (Fig. 9A–G).
Figure 7. Sixth instar of *Photinus extensus* Gorham A SEM image of the head retracted and anterior part of prothorax in lateroanterior view B antennae C prementum, maxillary palpus and galea (lateroventral) D distal part of galea E, F maxillary palpi in ventrolateral view G right metathoracic leg in ventrolateral view H pretarsus.
Third instar larva (Fig. 6C, D). Description. Similar to sixth instar. Length 11.45–13.78 mm. **Head capsule.** Wider (0.82–0.96 mm; 0.92 ± 0.05 mm) than long (0.57–0.85 mm; 0.71 ± 0.12 mm). **Antenna.** Basal antennomere and second antennomere (0.28–0.35 mm; 0.32 ± 0.02 mm), and a third segment (the flagellum) (0.15–0.21 mm; 0.18 ± 0.02 mm). **Maxilla.** Maxillae with three-segmented palpi, basal segment long (0.34–0.54 mm; 0.43 ± 0.07 mm) covered by setae in mid region, segment II wider (0.30–0.43 mm; 0.36 ± 0.06 mm) than long (0.12–0.17 mm; 0.14 ± 0.02 mm); apical segment cylindrical (0.10–0.13 mm; 0.11 ± 0.01 mm). **Thorax.** Protergum wider (1.36–1.53 mm; 1.4 ± 0.06 mm) than long (1.18–1.68 mm; 1.3 ± 0.20 mm), trapezoidal. **Legs.** Coxae short (0.77–0.97 mm; 0.86 ± 0.08 mm), femur obliquely (0.43–0.60 mm; 0.52 ± 0.07 mm). **Abdomen.** Tergites III–IX (0.68–0.85 mm; 0.77 ± 0.045 mm) ventral area of segments I–VIII with sternal areas almost squared, slightly pigmented, sternites with two long setae in mid-region.

**First instar larva (Fig. 6E, F).** Description. Similar to sixth instar. Length 3.72–8.80 mm; after hatching, the first instar body does not appear sclerotized to the degree found in later instars. **Head capsule.** Wider (0.48–0.72 mm; 0.6 ± 0.10 mm) than long (0.24–0.51 mm; 0.38 ± 0.12 mm), s (Figs 6A and 7A).

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**Figure 8.** *Photinus extensus* Gorham, head structures of sixth instar larva A head capsule ventral view B right antenna, dorsal view C maxillary palpus and galea, ventral view D maxillary palpus, ventral view E mandible dorsal view F mandible ventral view and G leg dorsal view.
Antenna. Basal antennomere and second antennomere (0.12–0.28 mm; 0.19 ± 0.06 mm) elongated, and a third segment (the flagellum) short (0.08–0.17 mm; 0.12 ± 0.03 mm). Maxilla. Maxillae with three-segmented palpi; basal segment long 0.24–0.47 mm; 0.31 ± 0.08 mm) and well-defined, segment II wider (0.12–0.17 mm; 0.15 ± 0.01 mm) than long (0.05–0.07 mm; 0.06 ± 0.007 mm); apical segment (0.03–0.047 mm; 0.037 ± 0.007 mm). Labium. Postmentum elongate, slightly sclerotized at the medial base, laterally united by membranes to the cardines; with a setae on each side near the base.

Figure 9. Sixth instar of *Photinus extensus* Gorham A, B SEM image of pygopodium in general view and detailed C–F detail of the surface of pygopodium.
Life cycle and immatures of Photinus extensus

Thorax. Protergum wider (0.73–1.47 mm; 0.94 ± 0.21 mm) than long (0.51–0.75 mm; 0.53 ± 0.09 mm). **Legs.** Coxae short (0.44–0.65 mm; 0.53 ± 0.08 mm), femur obliquely (0.21–0.34 mm; 0.27 ± 0.05 mm). **Abdomen.** Tergites III–IX (0.31–1.2 mm; 0.74 ± 0.28 mm).

**Pupa, male** (Fig. 10A, B). Length 17–23 mm; width 6–7 mm. Body elongate, curved, ventrally concave, pale yellowish (sternites I–VIII slightly pigmented at the ends).

**Head.** Totally covered by the pronotum in dorsal view. Large eyes, located at the sides of the head; antennae in front of the eyes, nearer the frontal center, mouthparts visible in ventral view.

**Thorax.** Pronotum wider than long, semicircular, totally covering the head. Meso and metanotum shorter, subrectangular, bearing the elytra sidewards. All pairs of legs free, visible in ventral view. Spiracles present in the pleural areas of mesothorax.

**Abdomen.** Abdominal segments subrectangular, wider than long, spiracles present on abdominal pleural areas of segments I–VIII. Light organ on sternites V–VI.

**Life cycle** (Fig. 11). In their natural habitat, adults of *P. extensus* are active from early July, when the first males can be observed. Bioluminescent activity begins at dusk,
at approximately 20:00 h, and diminishes considerably an hour later. Male flight does not exceed 2 m in height. Females are brachypterous and perch in the undergrowth approximately 50 cm from the ground. Males flash every 4.5 seconds, flying in an arc when illuminated. When males detect a female, they wait for an intense flash as a response, which is brief. The flash intervals are of 10 to 20 seconds. Males react by flying lower and towards the female. Groups of 3 to 5 males commonly compete with each other to get the female first, to mate with her. Two types of competition were observed among males: 1) a mating ball: four or more males cover the copulating pair and try to dislodge the copulating male to gain access to the female, and 2) males using their pronotum as a lever to pry a copulating male from the female. In the laboratory, copulation was observed to last from between 2 to more than 4 hours.

During oviposition, females bend their abdomen and place the apical part of it on the substrate. Eggs are laid superficially or buried, randomly distributed, individually,
or in groups (up to aggregates of 50). The number of eggs deposited by each female varied from three to 198. Eggs emit a faint bioluminescence since they are oviposited, which is only perceptible to the human eye in complete darkness. In total, 956 eggs from 13 females were obtained.

Under lab condition *P. extensus* completed its development in approximately 12 months, from oviposition to imago. The egg stage under laboratory conditions had a duration of 11 to 70 days, with mortality of n = 144 eggs (15%).

*Photinus extensus* undergoes six similar larval instars that differ in both size and color (Fig. 4). Cannibalism among larvae during rearing was not observed. The only food larvae consumed was the earthworms provided. There was no synchronization among larvae during the progression of larval instars, which started at the end of August until the beginning of July. In captive conditions, the process of ecdysis from one stage to the other varied among individuals. The first larval instar had a duration of 14 to 153 days, where mortality was 60% (n = 491) among the eggs that hatched. The second larval instar had a duration of 14 to 172 days, with mortality of 61% (n = 199). The third larval instar had a duration of 15 to 140 days; mortality was 71% (n = 87). The fourth larval instar had a duration of 17 to 140 days, with a mortality of 52% (n = 20). The fifth larval instar had a duration of 24 to 192 days (n = 18) and the last larval instar had a duration of 53 days (n = 8). Pupation had a duration of 7 days in July, and according to the observations in the field, pupae were found under pyroclastic rocks.

**Discussion**

*Photinus extensus* has six instars; they are very similar and only differ in size, color and the degree of the body sclerotized and presence of setae. Instar III differs from I and VI by a trapezoidal pronotum (Fig. 5) and an exposed head. The periods of time of the instar I–V are variable in different specimens, ranging from 14 and 192 days; the last instar period in different specimens is constant, approximately 50 days; the pupa is completely developed in seven days.

Frequently, the identification and description of larvae in the tribe Photinini is based on the characters present in the final larval instar, mostly body shape, color pattern, head capsule features, and the morphology of mouthparts (Archangelsky 2010). There are both similarities and differences between larvae belonging to the tribe Photinini, including *P. extensus* (see Table 1). The larval character suite found in *P. extensus* is most similar to those found in *Pyractonema, Lucidota*, and *Pyropyga*. The major exception to this is the number of segments in the maxillary palp. Although this last character is shared with the genus *Phosphaneus*, it differs in the opening of the mandible channel. *P. extensus* differs from *Lucidina* in the number of segments in the maxillary palp, and the number of retinacula of the mandible. There are some patterns among the larvae described in Photinini; the shape of the body is narrow and parallel and the pronotal shape is semicircular or semioval and the opening of the mandible channel is at the inner margin subapical.
The distribution of the setae is different between genera (Table 2), chaetotaxy will be useful in Lampyridae as a tool to distinguish between immatures, also as a source of informative phylogenetics characters (Ballantyne et al. 2019; Riley et al. 2021; Vaz et al. 2021). However, the few studies on the morphology of immatures in Lampyridae and the lack of knowledge of chaetotaxy hinder comparison between fireflies and makes the elaboration of more detailed hypotheses very difficult.

Table 1. Morphological larval characters of known Photinini genera (after Archangelsky 2010, Kawashima 2017 and Novák 2018b).

| Character                  | Pyroctonema nigripennis Solier | Pyropyga nigricans (Say) | Lucidota atra Olivier | Lucidina accensa Gorham | Phosphaenus hemipterus Goeze | Photinus extensus Gorham |
|----------------------------|--------------------------------|--------------------------|-----------------------|--------------------------|------------------------------|--------------------------|
| Body shape                 | Narrow, parallel               | Narrow, parallel         | Narrow, parallel       | Wide, suboval 4.2× longer than narrow | Oblong and narrow ~4.5× longer than narrow | Narrow, parallel 5.7–6.1× longer than narrow |
| Ratio: body length/thoracic length | 2.8–3.1                       | 3.4–3.7                  | 3.4–3.7               | 2.6                      | 3.14                         | 2.9                      |
| Cephalic capsule           | Short and wide, retractable into the thorax | Short and wide, retractable into the thorax | Short and wide, retractable into the thorax | Subquadrate, moderately flattened dorso-ventrally. | Rectangular, retractable into the thorax | Short and wide, retractable into the thorax |
| Antennae                   | Wide, partially retracted into the head | Wide, partially retracted into the head | Wide, partially retracted into the head | Long and thin, completely retracted into the head | Long and thin, partially retracted into the head | Long and thin, partially retracted into the head |
| Opening of the mandible channel | At the exterior margin, subapical | At the exterior margin, subapical | At the exterior margin, subapical | At the exterior margin, subapical | At the exterior margin, subapical | At the exterior margin, subapical |
| Number of retinacula of the mandible | 1                             | 1                         | 2                     | 4                        | 1                           | 1                        |
| Maxillar palp              | Three palpomere                | Three palpomere           | Three palpomere        | Two palpomere             | Tew palpomere                | Four palpomere            |
| Shape of pronotum          | subcircular                    | subcircular               | subcircular            | subcircular               | subcircular                 | subcircular               |
| Shape of mesonotum         | sub oval                       | sub oval                  | sub oval               | trapezoidal               | sub oval                    | rectangular               |
| Shape of metanotum         | sub oval                       | sub oval                  | sub oval               | rectangular               | sub oval                    | rectangular               |
| Thorax color               | Dark with three pale, longitudinal, and subparallel lines | Dark with three pale, longitudinal and subparallel lines | Dark with three pale, longitudinal and subparallel lines | Almost blackish brown, lateral and hind margins more or less paler than the ground Subrectangular | dorsally dark reddish-brown, ventrally pink/ochre/light brown with darker plates on laterotergites and sternum | Dark, with pale stripes |
| Shape of the abdominal tergites | Subrectangular, except VII–IX subsquared | Suboval                  | Suboval, posterior margin of tergites V–VIII straight | Subrectangular            | I–VII, IX subrectangular, VIII suboval | Subrectangular            |
| Abdomen color              | With a clear line on each side. Dark segments VII–IX. | Dark with pale lateral areas (segments I–VIII) | Dark with three pale longitudinal and subparallel lines, at the inner interior margin | Almost blackish brown, lateral and hind margins more or less paler than the ground I–VI, segments VII–X pale yellowish to milky white | pink/ochre/light brown | Pale with a little pink stripe in the second third in segments I–V, the rest of them pale |
The larval characters have shown to be important to clarify the phylogenetic relationships as Archangelsky (2010) mentioned. However, it seems to be a difficult task to get a good dataset of larval characters of Lampyridae.

The life cycle, morphology, and behavior of the species of *Photinus* are similar. *Photinus carolinus* Green, 1956, *P. ignitus* Fall, 1927, *P. marginellus* LeConte, 1852, *P. pyralis* (Linnaeus, 1767), *P. greeni* Lloyd, 1969, and *P. extensus* are the known species that produce spermatophores due to the prolonged time of copulation (Cratsley et al. 2003; South and Lewis 2012).

The length of the pupal stage varies slightly in *Photinus*. The pupal stage of *P. extensus* has a duration of six days (Faust 2010). Nevertheless, the pupa of *P. carolinus* is present during May, while that of *P. extensus* is present in July. Another difference is that the pupae of *P. extensus* observed in the field were found under pyroclastic rocks, in contrast with *P. carolinus*, which has been reported to occur under leaf-litter, near rotten logs, or moss (Faust 2010). Until now, little information has come to light about the pupae in other genera of Photinini (Archangelsky and Branham 2001). In other genera like *Aspisoma* Laporte, 1833, of Cratomorphini, the pupal stage is similar, occurring during a short period between six and ten days (Costa et al. 1988; Archangelsky 2004).

### Table 2. Chaetotaxy larval characters.

|                     | *Photinus extensus* Gorham | *Pyraconema nigripennis* Solier | *Lucidota atra* Olivier |
|---------------------|----------------------------|---------------------------------|-------------------------|
| **Hypopharynx**     | Margin covered by dense pubescence. | Surface covered by dense pubescence. | No information.         |
| **Mandible**        | With patches of dense pubescence in the basal part in ventral Margin covered by dense pubescence. With patches of dense pubescence in the basal part in ventral view. Mid-region covered by a single row of long setae. | With patches of dense pubescence in ventral view. Mid-region covered by only one row of long setae. One long seta close to the apex. |                                           |
| **Cardo**           | With 4 long setae in ventral surface and one long seta in the posterior margin. | With 13–15 setae in ventral surface. | Without setae.          |
| **Maxillary palpomeres** | Basal palp covered by setae in the mid region. Distal palp with setae from base to mid region. | Basal palp covered by setae. Palp II with some setae. Last palp without setae. | Basal palp with long setae from the mid region to the apex. Palp II with shorter setae. Distal palp without setae. |
| **Labial palpomeres** | Basal palp with few setae in mid region. Distal palp without setae. | Basal palp with some setae. Distal palp without setae. | Basal palp with few long setae. Distal palp with one long seta. |
| **Prementum**       | Surface with many setae. Two long setae close to apex. | Dorsal and ventral surface with many setae. | With two basal regions of very fine setae, with longer setae on the palp segment. |
| **Submentum**       | With two long setae in mid region. | With two long setae in the basal middle. | No information.         |
| **Antennomeres**    | Apex with two long setae. Antennomere III with long setae from base to apex. | All antennomeres covered by setae. Antennomere III with many short setae. | Basal antennomere with mid region covered by setae. Antennomere III with longer setae. Antennomere II covered evenly by long setae. Antennomere III with short setae. |
| **Legs**            | With a double row of long setae in the inner margin. Outer margin with many setae. Pretarsus with two setae at the base. | With a double row of long setae in the inner margin. Pretarsus with two setae at the base. | With a double row of long setae in the inner margin. Pretarsus with two setae at the base. |
| **Abdomen**         | Sternites with two long setae in mid-region. | Sternites with two long setae in mid-region. | No information.         |
Conclusion

The complete life cycle of *Photinus extensus*, including descriptions of egg, larvae, and pupa, was documented for the first time. Larvae were reared in laboratory conditions to the adult stage from eggs. The six instar of *P. extensus* are very similar; they differ only in size and in the sclerotized degree.

Among Photinini larvae there are not many differences, differing in the number of segments in the maxillary palp and in the number of retinacula of the mandible; the shape of the body and pronotum, and the opening of the mandible channel follow a similar pattern. Life cycle information is essential to carry out protection and conservation actions for insects that are very sensitive to environmental changes, like fireflies. For example, the species that do not produce light are easily overlooked and the information about their life cycle is deficient. This results in “Data Deficient” categorization in evaluations of extinction risk. Thus, more studies are needed in which the life history, habitat associations, and microhabitat are detailed (Fallon et al. 2021). Also, it is necessary to understand that requirements of larvae are different to those of adults to have an integral vision in the actions of protection of the fireflies.

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References

Archangelsky M (2004) Description of the last larval instar and pupa of *Aspisoma fenestrata* Blanchard, 1837 (Coleoptera: Lampyridae) with brief notes on its biology. Tijdschrift voor Entomologie 147(1): 49–55. https://doi.org/10.1163/22119434-900000138

Archangelsky M (2010) Larval and pupal morphology of *Pyractonema nigripennis* Solier (Coleoptera: Lampyridae: Photinini) and comparative notes with other Photinini larvae. Zootaxa 2601(1): 37–44. https://doi.org/10.11646/zootaxa.2601.1.3
Archangelsky M, Branham MA (2001) Description of last instar and pupa of *Pyropyga nigricans* (Coleoptera: Lampyridae, Photinini) and comparison with larvae of other Photinini genera. Canadian Entomologist 133(2): 155–164. https://doi.org/10.4039/Ent133155-2

Ballantyne LA, Lambkin CL, Ho J-Z, Jusoh WFA, Nada B, Nak-Eiam S, Thancharoen A, Wattanachaiyingcharoen W, Yiu V (2019) The Luciolinae of S. E. Asia and the Australopacific region: a revisionary checklist (Coleoptera: Lampyridae) including description of three new genera and 13 new species. Zootaxa 4687(1): 1174. https://doi.org/10.11646/zootaxa.4687.1.1

Beutel RG (1995) Phylogenetic analysis of Elateriformia (Coleoptera: Polyphaga) based on larval characters. Journal of Zoological Systematics and Evolutionary Research 33(3–4): 145–171. https://doi.org/10.1111/j.1439-0469.1995.tb00969.x

Branham MA (2010) Lampyridae Latreille, 1817. In: Leschen RAB, Beutel GR, Lawrence JF (Eds) Coleoptera, Beetles. Volume 2: Morphology and Systematics (Elateroidea, Bostrochiiformia, Cucujiformia partim). Walter de Gruyter, Berlin, Germany, 141–149. https://doi.org/10.1515/9783110911213.141

Branham MA, Archangelsky M (2000) Description of the last larval instar and pupa of *Lucidota atra* (G.A.Olivier, 1790) (Coleoptera: Lampyridae), with a discussion of abdominal segment homology across life stages. Proceedings of the Entomological Society of Washington 102(4): 869–877.

Bugnion E (1929) Le ver-luisant provencal et la Luciole nicoise. Association des Naturalistes de Nice et des Alpes-Maritimes; Memoire Supplement au “Riviera Scientifique”, 131 pp.

Buschman LL (2017) Analysis of courtship flash behaviour in two *Photuris* fireflies (Coleoptera: Lampyridae) with field validation and rearing notes. In: Day JC (Ed.) Lampyrid: The Journal of Bioluminescent Beetle Research. Abingdon, CreateSpace Independent Publishing Platform, 1–19.

Costa C (2000) Estado de conocimiento de los Coleoptera neotropicales. In: Martín-Piera F, Morrone JJ, Melic A (Eds) Hacia un proyecto CYTED para el inventario y estimación de la diversidad entomológica en iberoamérica: Pribes 2000. Sociedad Entomológica Aragonesa, Zaragoza, 99–114.

Costa C, Vanin SA, Casari-Chen SA (1988) Larvas de Coleoptera do Brasil. Museu de Zoologia, Universidad de Sao Paulo, Brazil, 282 pp. https://doi.org/10.5962/bhl.title.100233

Cratsley CK, Rooney JA, Lewis SM (2003) Limits to nuptial gift production by male fireflies, *Photinus ignitus*. Journal of Insect Behavior 16(3): 361–370. https://doi.org/10.1023/A:1024876009281

Demary K (2005) Sperm storage and viability in Photinus fireflies. The Journal of Physiology 7: 837–841. https://doi.org/10.1016/j.jinsphys.2005.04.001

Fallon CE, Walker AC, Lewis S, Cicero J, Faust L, Heckscher CM, Pérez-Hernández CX, Pfeiffer B, Jepsen S (2021) Evaluating firefly extinction risk: Initial red list assessments for North America. PLoS ONE 16(11): 1–18. https://doi.org/10.1371/journal.pone.0259379

Faust LF (2010) Natural history and flash repertoire of the synchronous firefly *Photinus carolinus* (Coleoptera: Lampyridae) in the great Smoky Mountains National Park. The Florida Entomologist 93(2): 208–217. https://doi.org/10.1653/024.093.0210
Faust LF (2017) Fireflies, glow-worms, and lightning bugs: identification and natural history of the fireflies of the Eastern and Central United States and Canada. Athens (GA), University of Georgia Press, USA, 356 pp.

Faust LF, Weston PA (2009) Degree-day prediction of adult emergence of *Photinus carolinus* (Coleoptera: Lampyridae). Environmental Entomology 38(5): 1505–1512. https://doi.org/10.1603/022.038.0519

Ferreira VS, Keller O, Branham MA (2020) Multilocus phylogeny support the nonbioluminescent firefly Chespirito as a new subfamily in the Lampyridae (Coleoptera: Elateroidea). Insect Systematics and Diversity 4(6): 1–13. https://doi.org/10.1093/isd/ixaa014

Fu X, Ballantyne LA, Lambkin CL (2012) The external larval morphology of aquatic and terrestrial Luciolinae fireflies (Coleoptera: Lampyridae). Zootaxa 3405(1): 1–34. https://doi.org/10.11646/zootaxa.3405.1.1

Kawashima I (2017) Larval morphology of the lampyrine species, *Lucidina accensa* Gorham (Coleoptera: Lampyridae: Lampyrinae) from Honshû, Japan. Japanese journal of systematic entomology = 日本昆虫分類学会会報, 23(1): 129–134.

Koken M, Guzmán-Álvarez JR, Gil-Tapetado D, Romo Bedate MA, Laurent G, Rubio L, Rovira Comas S, Wolffler N, Verfaille F, De Cock R (2022) Quick spreading of populations of an exotic firefly throughout Spain and their recent arrival in the french Pyrenees. Insects 13(2): e148. https://doi.org/10.3390/insects13020148

Lewis SM, Cratsley CK, Demary K (2004a) Mate recognition and choice in *Photinus* fireflies. Annales Zoologici Fennici 41: 809–821.

Lewis SM, Cratsley CK, Rooney JA (2004b) Nuptial Gifts and Sexual Selection in *Photinus* Fireflies. Integrative and Comparative Biology 44(3): 234–237. https://doi.org/10.1093/icb/44.3.234

Lewis SM, Wong CH, Owens A, Fallon C, Jepsen S, Thancharoen A, Wu C, De Cock R, Novák M, López-Palaxox T, Khoo V, Reed JM (2020) A Global Perspective on Firefly Extinction Threats. Biodiversity 70(2): 157–167. https://doi.org/10.1093/biosci/biz157

Lloyd JE (2002) Family 62. Lampyridae. In: Arnett Jr RH, Thomas MC, Skelley PE, Frank JH (Eds) American Beetles vol. 2: Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton, Florida, 187–196.

López-Palafox T, Macías-Ordóñez R, Cordero CR (2020) The size of signal detection and emission organs in a synchronous firefly: Sexual dimorphism, allometry and assortative mating. PeerJ 8: e10127. https://doi.org/10.7717/peerj.10127

Lot A, Camarena P (2009) El Pedregal de San Ángel de la ciudad de México: reserva ecológica urbana de la Universidad Nacional. In: Lot A, Cano-Santana Z (Eds) Biodiversidad del ecosistema del Pedregal de San Ángel. Libro conmemorativo del 25, 19–25.

Madurga O, Branham MA (2020) Description of life cycle and preimaginal stages of *Alecton discoidalis* Laporte, 1833 (Coleoptera: Lampyridae) under laboratory conditions. Zootaxa 4816(1): 81–91. https://doi.org/10.11646/zootaxa.4816.1.4

Martin GJ, Stanger-Hall KF, Branham MA, Da Silveira LFL, Lower SE, Hall DW, Li XY, Lemmon AR, Lemmon EM, Bybee SM (2019) Higher-Level Phylogeny and Reclassification of Lampyridae (Coleoptera: Elateroidea). Insect Systematics and Diversity 3(6): 1–15. https://doi.org/10.1093/isd/ixz024
Life cycle and immatures of *Photinus extensus*

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

Novák M (2018a) Redescription of immature stages of central European fireflies, Part 2: *Lamprohiza splendidula* (Linnaeus, 1767) larva, pupa and notes on its life cycle and behaviour (Coleoptera: Lampyridae). Zootaxa 4378(4): 516–532. https://doi.org/10.11646/zootaxa.4378.4.4

Novák M (2018b) Redescription of immature stages of central European fireflies, Part 3: *Phosphaenus emipterus* (Goeze, 1777) larva, pupa and notes on its life cycle and behavior, with a key to three Central European lampyrid larvae (Coleoptera: Lampyridae). Zootaxa 4382(3): 450–464. https://doi.org/10.11646/zootaxa.4382.3.2

Ohba N (2004) Flash communication systems of Japanese fireflies. Integrative and Comparative Biology 44(3): 225–233. https://doi.org/10.1093/icb/44.3.225

Orozco-Segovia A, Gamboa de Buen A, Barrandas-Miranda VL (2009) La diversidad funcional de los ecosistemas. In: Lot A, Cano-Zantana Z (Eds) Biodiversidad del Ecosistema en el Pedregal del San Ángel. Universidad Nacional Autónoma de México, México, 295–316.

Riley WB, Rosa SP, Lima da Silveira LF (2021) A comprehensive review and call for studies on firefly larvae. PeerJ 9: 1–24. https://doi.org/10.7717/peerj.12121

Rzedowski J (1978) Vegetación de México, Limusa, México, 247–273.

Silveira LFLd, Lima W, Fonseca CRVd, McHugh J (2022) *Haplocauda*, a new genus of fireflies endemic to the Amazon rainforest (Coleoptera: Lampyridae). Insects 13(1): e58. https://doi.org/10.3390/insects13010058

South A, Lewis SM (2012) Effects of male ejaculate on female reproductive output and longevity in *Photinus* fireflies. Canadian Journal of Zoology 90(5): 677–681. https://doi.org/10.1139/z12-031

Vaz S, Lima da Silveira LF, Policena RS (2020) Morphology and life cycle of a new species of *Psilocladus* Blanchard, 1846 (Coleoptera, Lampyridae, Psilocladinae), the first known bromeliad-inhabiting firefly, Papéis Avulsos de Zoologia 24(special issue): 1–15. https://doi.org/10.11606/1807-0205/2020.60.special-issue.24

Vaz SNC, Guerrazzi MC, Rocha M, Faust LF, Gabriel Khattar G, Mermudes JRM, Silveira LFLd (2021) On the intertidal firefly genus Micronaspid Green, 1948, with a new species and a phylogeny of Cratomorphini based on adult and larval traits (Coleoptera: Lampyridae). Zoologischer Anzeiger 292: 64–91. https://doi.org/10.1016/j.jcz.2021.01.002

Viviani VR (2001) Fireflies (Coleoptera: Lampyridae) from Southeastern Brazil: habitats, life history, and bioluminescence. Annals of the Entomological Society of America 94(1): 129–145. https://doi.org/10.1603/0013-8746(2001)094[0129:FCLFSB]2.0.CO;2

Wing SR (1991) Timing of *Photinus collarans* reproductive activity: finding a mate in time (Coleoptera: Lampyridae). Coleopterists Bulletin 45: 57–74.

Zaragoza-Caballero S (2000) Cantharoidea (Coleoptera) de México. IV. Nuevos *Photinus* (Lampyridae) del estado de Morelos. Dugesiana 7(1): 1–17.

Zaragoza-Caballero S (2005) Nuevas especies de *Photinus* (Coleoptera: Lampyridae: Photinini) de Jalisco, México. Folia Entomologica Mexicana 44(1): 75–82.

Zaragoza-Caballero S (2007) A new species of *Photinus* (Coleoptera: Lampyridae: Photinini) from Jalisco, Mexico, with comments on intraspecific aedeagal variability and a key to the species of the subgenus *Paraphotinus*. Zootaxa 1437(1): 61–67.
Zaragoza-Caballero S (2015) Nuevas especies de *Photinus* (Coleoptera: Lampyridae: Photinini) del bosque tropical caducifolio de Pacífico mexicano. Revista Mexicana de Biodiversidad 86(3): 638–651. https://doi.org/10.1016/j.rmb.2015.08.001

Zaragoza-Caballero S (2017) Nuevos *Photinus* Laporte, 1832 (Coleoptera: Lampyridae: Photinini). Dugesiana 24(2): 221–230. https://doi.org/10.32870/dugesiana.v28i2.7161

Zaragoza-Caballero S, Viñolas A (2018) *Photinus immigrans* sp. nov. (Coleoptera: Lampyridae: Photinini): Primer registro del género *Photinus* en Cataluña, España. Revista gaditana de Entomología 9(1): 273–286.

Zaragoza-Caballero S, López-Pérez S, Vega-Badillo V, Domínguez-León DE, Rodríguez-Mirón GM, González-Ramírez M, Gutiérrez-Carranza IG, Cifuentes-Ruiz P, Zurita-García ML (2020) Luciérnagas del centro de México (Coleoptera: Lampyridae): descripción de 37 especies nuevas. Revista Mexicana de Biodiversidad 91(0): 1–70. https://doi.org/10.22201/ib.20078706e.2020.91.3104