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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

MARC A. BRANHAM AND MIGUEL ARCHANGELSKY

(MAB) The Ohio State University, Museum of Biological Diversity, 1315 Kinnear Rd., Columbus, OH 43212-1192, U.S.A. (e-mail: branham.24@osu.edu); (MA) Centro Regional de Investigaciones Cientificas y Transferencia Tecnologica, CRILAR (CONICET—UNLaR) Entre Rios y Mendoza s/n, 5301, Anillaco, La Rioja, Argentina (e-mail: marchangelsky@crilar.com.ar)

Abstract.—The last larval and pupal stages of the widespread and common North American firefly, *Lucidota atra* (G. A. Olivier 1790), are described and illustrated. Last instar larvae were collected in rotting logs in the early spring and fed terrestrial snails from the same logs until the larvae pupated. The larva of *L. atra* was misidentifed in the literature and has subsequently been misidentified as a species in the genus *Photinus.* A discussion of the homology of abdominal sclerites in larval, pupal, and adult fireflies is provided.

Key Words: Lampyridae, *Lucidota atra, Photinus,* larva, pupa, morphology, firefly, lightningbug, glowworm, ventrite

The genus *Lucidota,* as defined by Laporte (1833) and fixed by Motschulsky (1853), is restricted to the New World and contains some 64 described species. The genus ranges from the United States to Argentina. *Lucidota atra* (G. A. Olivier) occurs from the northeastern United States to Central America (McDermott 1966). The larva of this species was first described by H. F. Wickham (1895), but because larvae in the tribe Photinini are difficult to distinguish (LaBella and Lloyd 1991), a more detailed larval description is required. Peterson (1951) apparently incorrectly identified the larva on which he based his drawing of "*Photinus* sp." in his book "*Larvae of Insects.*" Upon examining "*Photinus* sp." in Peterson's larval collection at The Ohio State University and comparing it with larvae reared by one of us (MAB), it was discovered that Peterson's larva is actually *L. atra.*

For this study, last instar larvae were collected in early spring and kept until eclosion, thus allowing a positive identification from the adult. No larval descriptions exist for other species of this genus, most likely due to difficulties in rearing firefly larvae (Archangelsky and Branham 1998).

MATERIALS AND METHODS

Seven last instar larvae were collected in a rotting log on April 6, 1993 outside of Lawrence, KS, and kept in a glass jar with damp wood from the log along with some terrestrial snails collected in the same wood. Empty snail shells were removed from the jar every few days. The wood inside the jar was inspected for moisture content periodically. When the wood appeared to be drying out, it was moistened with distilled water. To further simulate the inside of the log, the jar was wrapped with paper

to reduce light entering the jar. No special requirements were necessary for pupation.

Three larvae and one pupa were fixed in boiling water and transferred to 70%EtOH. In order to study the larval morphology, a specimen's head, mouthparts and antennae were dissected, cleared in lactic acid, and mounted on microscope slides using Hoyer's as the mounting medium. The descriptions and drawings were done using a Wild M5 dissecting microscope and a Zeiss Axioscope 20 compound microscope, both with a camera lucida.

Results

Lucidota atra (G. A. Olivier)

Description of last larval instar.—Length: 13.0 to 15.0 mm. Body elongate, fusiform, slightly flattened dorsoventrally (Fig. 1). Whitish ventrally with pink along sides of thorax and abdomen. Sclerotized regions uniformly light to dark brown and granulose. All tergites, except abdominal tergites 8 and 9, bearing 3 light colored stripes that are more or less parallel to the longitudinal axis of body.

Head capsule: Prognathous, subquadrate, dorsoventraly flattened, and robust (Fig. 2); retractable within thorax. Labrum and clypeus fused. Epicranial suture present as well as frontal sutures that extend to bases of antennae. One pair of lateral stemmata, posterior to base of antennae. Head capsule not fused ventrally (Fig. 3).

Antenna: 3-segmented, partially retractable within membranous base (Fig. 4); originating on latero-apical edges of head capsule. Basal segment widest, attached to membranous base, median portion of dorsal surface covered with medium length setae pointing anteriorly, lateral pointing setae on anterior third of segment approximately 2 to 3 times a long as setae in medial region. Second segment shorter than third, narrower, evenly covered by long setae, carrying a large globular sensorium slightly longer than third antennomere. Third segment very short, stout with several short setae, an api-

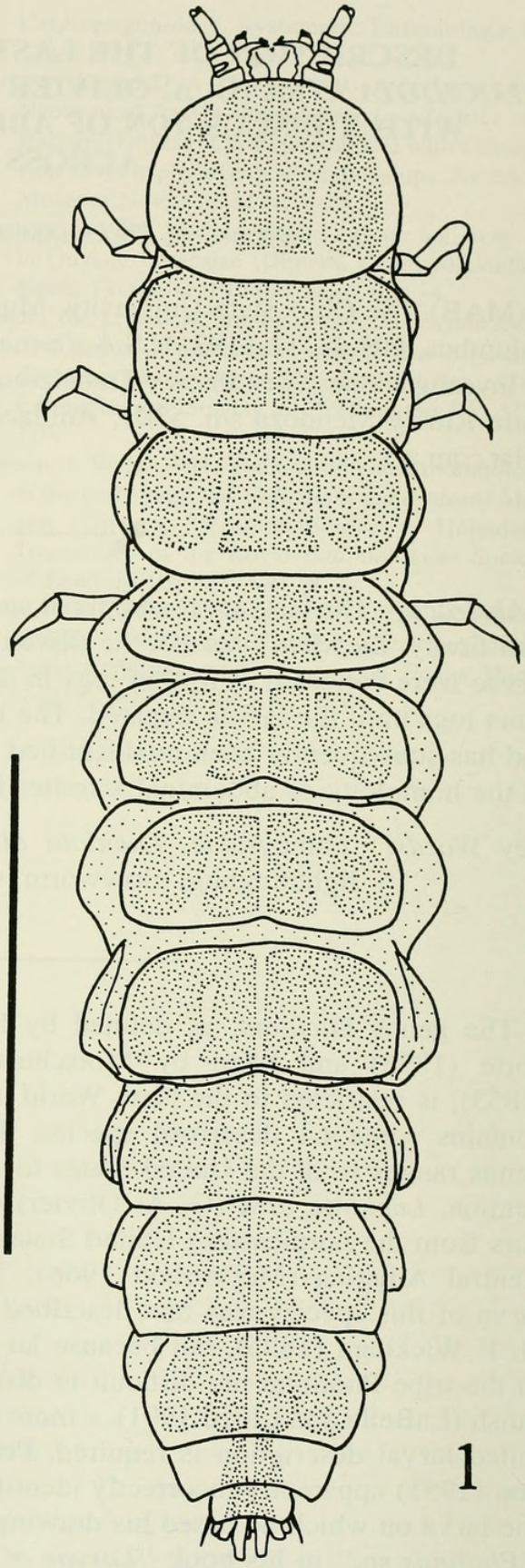
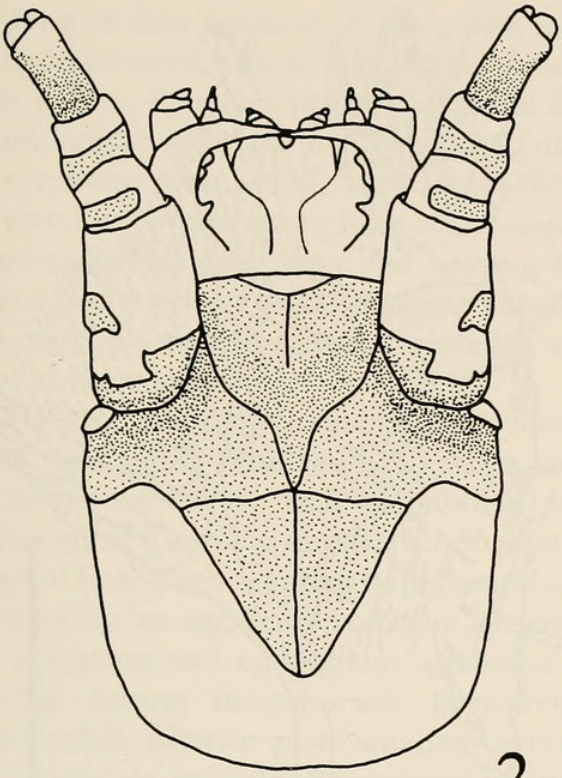
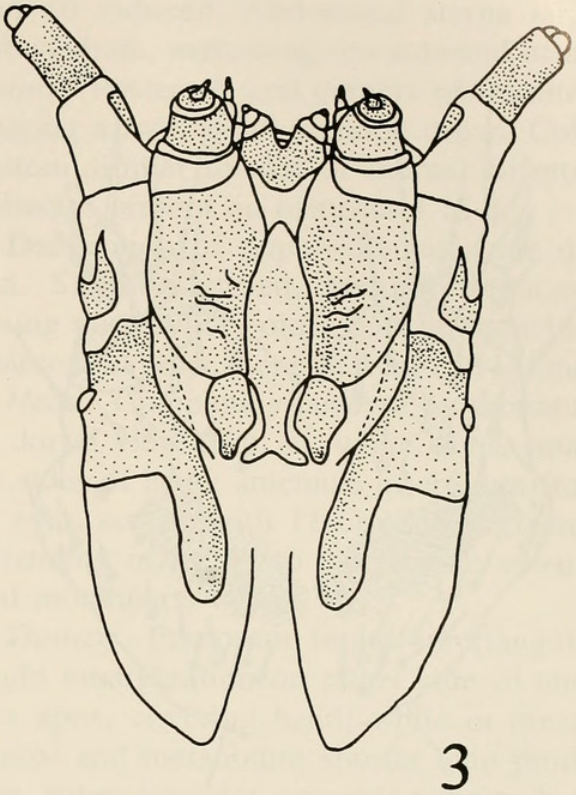
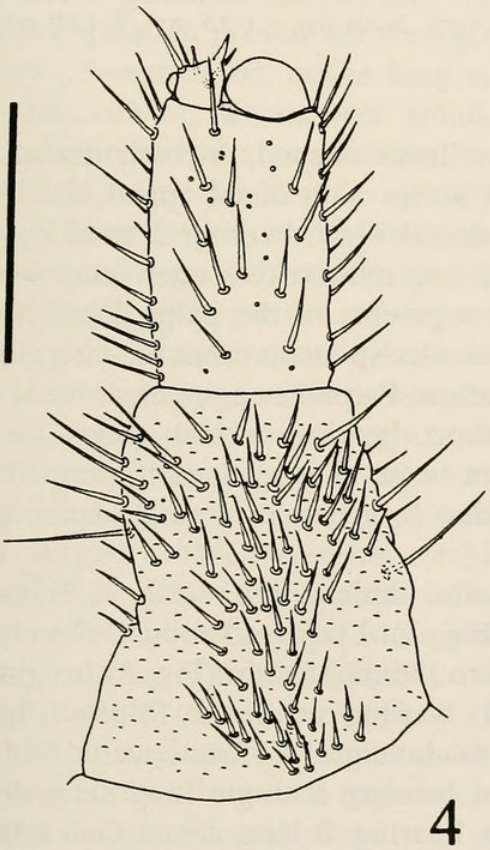
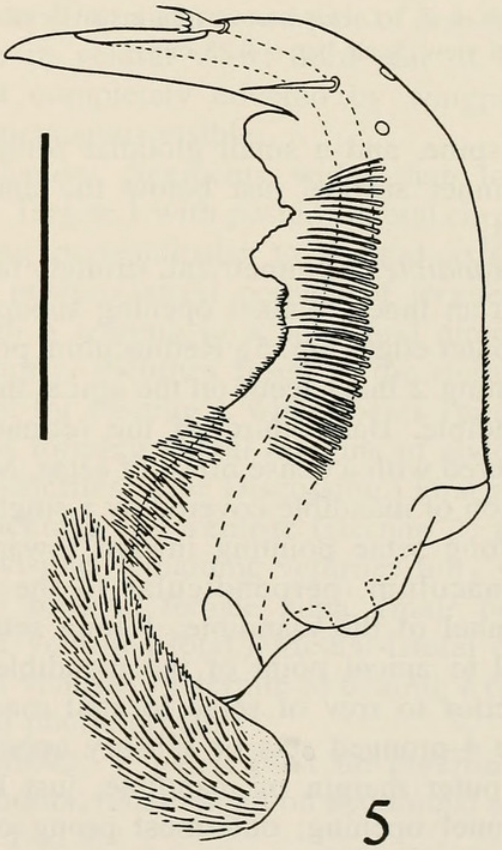


Fig. 1. *Lucidota atra,* fifth instar larva, habitus. Scale bar = 5 mm.

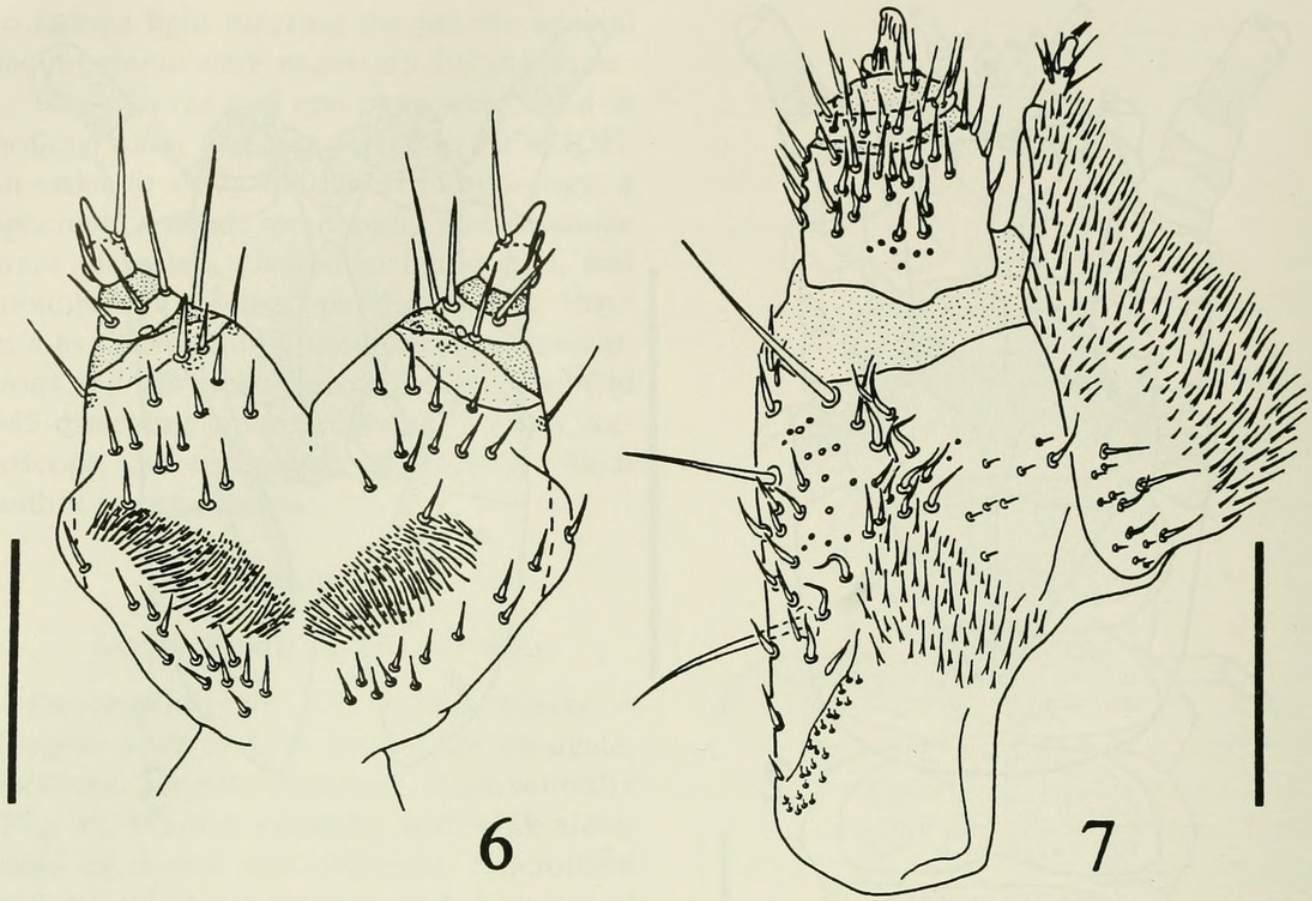








Figs. 2–5. *Lucidota atra,* head of fifth instar larva. 2, Dorsal view. 3, Ventral view. Scale bar = 1 mm. 4, Right antenna, dorsal view. 5, Right mandible, dorsal view. Scale bars = 0.2 mm.



Figs. 6–7. *Lucidota atra,* fifth instar larva. 6, Labium, dorsal view. Scale bar = 0.15 mm. 7, Left maxilla, dorsal view. Scale bar = 0.23 mm.

cal spine, and a small globular sensorium on inner surface just below the antennal apex.

Mandible: Symmetrical, strongly falcate, with an inner channel opening subapically on outer edge (Fig. 5). Retinaculum present, forming 2 inner teeth on the apical third of mandible. Basal third of the retinaculum covered with a dense brush of setae. Medial region of mandible covered by a single row of long setae pointing inward toward the retinaculum, perpendicular to the inner channel of the mandible; 1 long seta parallel to apical point of the mandible, just anterior to row of setae located medially. One 4-pronged seta or sensory appendage on outer margin of mandible, just before channel opening; outermost prong of this seta longer than the other 3.

Labium: Closely attached to maxilla, formed by a short and strongly sclerotized prementum, mentum (distally membranous) and submentum (fused to mentum). Prementum heart shaped, in both dorsal and ventral views with distal apical cleft (Fig. 6); in dorsal view, bearing 2 basal regions of very fine setae with longer setae present on the segments of the palp; 2 brushes of fine cuticular spines present on each side of prementum. Palpus 2-segmented; basal segment short, bearing several spines, second segment twice as long as first, pointed and somewhat forked with a single spine (Fig. 6).

Maxilla: Apical region (Fig. 7). Basal region (Fig. 3). Long and robust, closely attached to labium. Cardo (Fig. 3) irregularly shaped, bearing no setae. Stipes (Fig. 7) very broad, ventral surface covered with setae and bearing a single long seta; dorsal surface bearing 2 long setae. Galea large, 2-segmented, basal segment very long, 3 times as long as second segment and lacking setae; distal segment short, conical and bearing several short setae with 1 seta on distal apex of segment. Lacinia large, twice

as long as first segment of the galea, inner surface covered with a thick brush of cuticular spines. Palpus 3-segmented, basal segment largest, subquadrate, longer than other 2 segments combined, distal two-thirds covered with medium to long setae; second segment wider than long and bearing medium length setae; distal segment subconical without setae, bearing a globular sensorium-type structure.

Thorax: Prothorax subcircular, wider at base, containing retracted head when larva is in repose. Meso- and metathorax subrectangular. Thoracic tergites subdivided by sagittal line. Each segment with pleural area formed by an upper laterotergite, below it an epimeron and episternum separated by pleural suture; mesothoracic laterotergite subdivided, anterior plate smaller, carrying mesothoracic spiracle. Prosternum medium sized; meso- and metasterna smaller, narrow, subdivided into an anterior basisternum and a posterior sternellum. 1 pair of biforous spiracles present on mesopleuron.

Legs: 5-segmented, coxae long and cylindrical, robust; trochanters small, subtriangular in lateral view; femora long and cylindrical, widening slightly apically, with a single long seta in medial inner portion; tibiotarsi as long as femora, tapering towards distal end; pretarsi strong, simple, with a pair of stout setae at base. Double row of strong setae on inner margin of tibiotarsi, lacking on inner margin of femora.

Abdomen: 10-segmented, segments 1 to 8 similar in shape, tapering toward end; each tergite subrectangular, tergites 1 through 8 divided by a sagittal line and 2 lighter colored lines parallel to sagittal line; lateral portions of tergite 8 lightly colored; lateral portions of tergite 9 lightly colored and without sagittal line; segment 10 a narrow ring surrounding anal region, carrying holdfast organ. Pleural areas well developed, segments 1 to 7 subdivided, upper plate large, suboval, carrying spiracles, lower plate small, narrowly subtriangular; pleuron 8 with only 1 suboval plate carrying a spiracle; pleural areas of segments 9 and 10 reduced. Abdominal sterna large, subquadrate, narrowing towards end of abdomen. Postero-lateral corners of sternite 8 bearing a twin spotted photic organ. Color pattern similar to that of thorax. Biforous spiracles present on pleurites 1 to 8.

Description of pupa.—Female, one day old. Slightly curved, ventrally concave; young pupa white, older pupa approaching charcoal in color. Length: 10.0 to 11.0 mm.

Head: Completely covered by pronotum in dorsal view (Fig. 9), white. Eyes small, on sides of head; antennae inserted in front of eyes, serrate with 11 obvious segments, extending in length to metacoxae; antenna and mouthparts white.

Thorax: Pronotum large, subtriangular, slight emargination on either side of anterior apex, covering head; white or cream. Meso- and metanotum shorter than pronotum, subrectangular, carrying wing pads on sides; posterior medial portion of mesonotum coming to a point, point lacking on metanotum. First and second pair of legs fully visible in ventral view; third pair of legs almost completely covered by wingpads, only metatarsus visible.

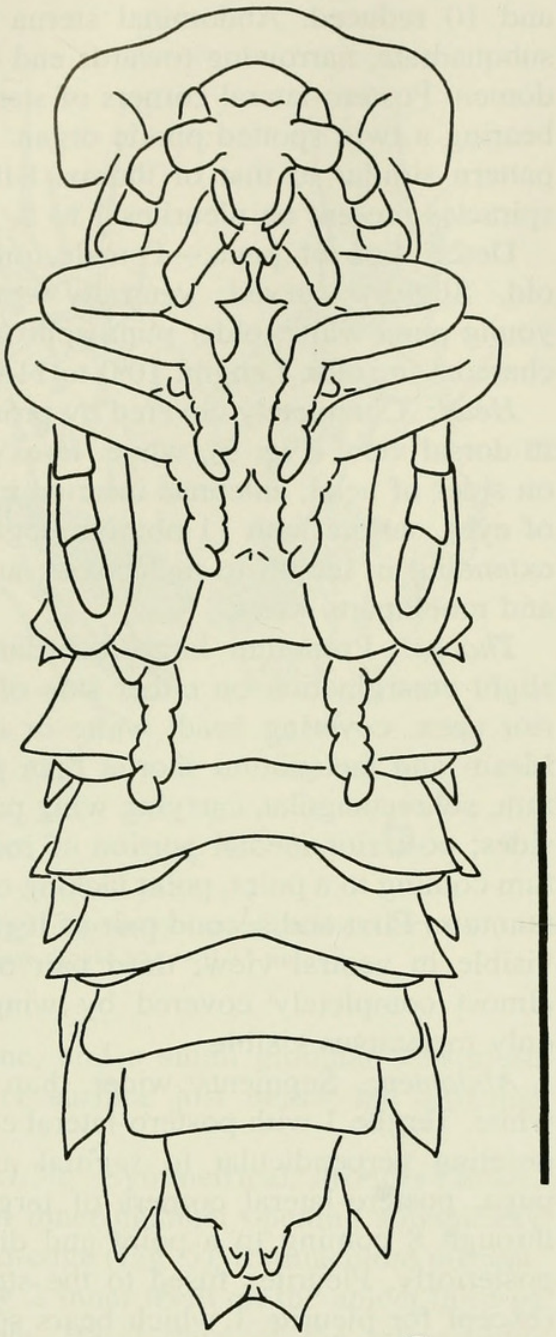
Abdomen: Segments wider than long, white. Tergite 1 with postero-lateral corners pointing perpendicular to sagittal axis of pupa; postero-lateral corners of tergites 2 through 8 coming to a point and directed posteriorly. Pleurites fused to the sternites (except for pleurite 1 which bears spiracle 1) thus forming lateral margins of abdominal "ventrites" (see Discussion.) First sternite lacking, first ventrite (sternite 2) partially visible, remaining ventrites fully visible, 7 total in female pupa, (male pupa with 8 ventrites total.) Medial-lateral corners of ventrite 7 (sternite 8) bearing a twin spotted photic organ.

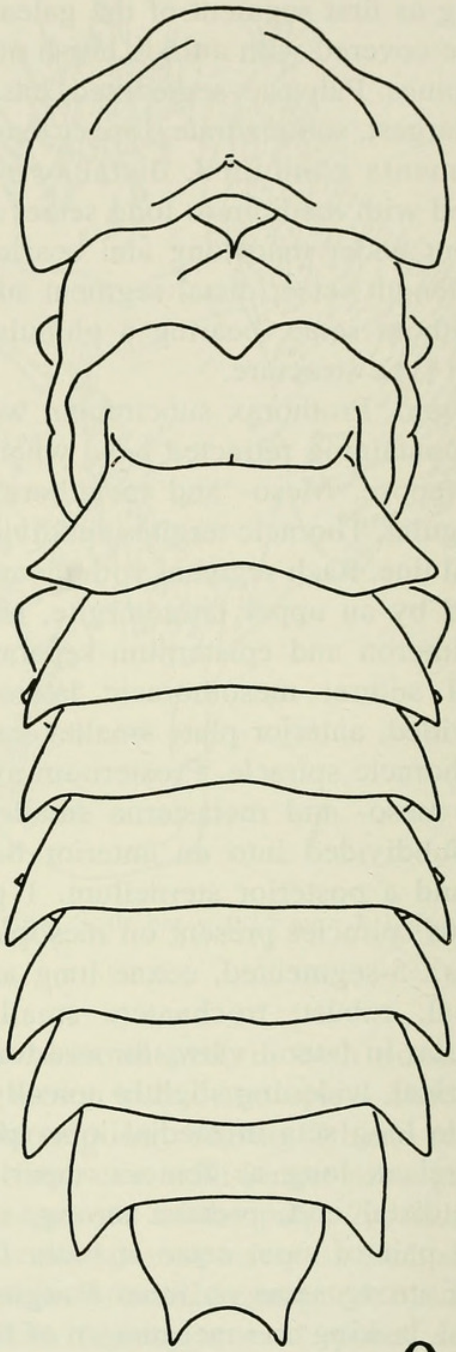
Spiracles: 9 pairs; First on pleuron of mesothorax, remaining 8 on abdominal segments 1 to 8.

Discussion

Biology

The activity period of *L. atra* adults range from early June to July, and the larval





Figs. 8–9. *Lucidota atra,* pupa. 8, Ventral view. 9, Dorsal view. Scale bar = 4 mm.

life is suspected to be approximately two years long, since both large and small larvae have been found together during midsummer (Balduf 1935). However, as this species has not been successfully reared from egg to adult, the two year life cycle remains speculative. Because *L. atra* larvae are typically found in rotten logs and stumps from the fall through early spring, it is assumed that these are the larvae that overwinter (Williams 1917; MacDermott 1964; MAB, personal observation). It should be noted, however, that stumps and logs are places where many coleopterists typically look for beetle larvae. Both larvae and pupae produced a glow from a two-spotted photic organ when disturbed. The two-spotted photic organ is located on the eighth sternite of the larvae and seventh ventrite (eighth sternite) of the female pupa. Therefore, it is expected that male pupa would also have a similar organ on its sev-

enth ventrite as the seventh ventrite of adult males of this species bare such an organ, though the ability to luminesce seems to diminish shortly after eclosion (MAB, personal observation). Since no *L. atra* larvae have been found foraging in the open, they may be subterranean in habit. Adults usually fly during the day, and males follow pheromone plumes to the females (Lloyd 1972). The female is typically up to a third larger than the male.

Traditional Perspective, and Modern View

Peterson (1951) included a side view drawing of a lampyrid larva along with a mandible and antennae which was labeled "*Photinus* sp." This same drawing was included by LaBella and Lloyd (1991) and has thereafter been used as an example of a *Photinus* larva. Upon comparing our *L. atra* larvae with the actual specimen upon which Peterson based his drawing (in the Peterson Larval Collection, The Ohio State University, Columbus, Ohio), they are identical matches. Additionally, Peterson's determination label in the vial with this specimen reads "*Photinus* sp.? ." This question mark on the determination label, evidently put there by Peterson himself, was most likely accidentally overlooked, and, thus for some 49 years, the specimen has been misidentified as *Photinus* sp., rather than *Lucidota atra.* This mistake is very easy to make due to the great morphological similarity between genera in the tribe Photinini, in which both *Photinus* and *Lucidota* are assigned. The only definitive method to associate larvae and adults is to rear the larvae.

Abdominal Sclerites in Lampyridae

Considerable confusion has occurred concerning the number of abdominal sclerites in discussions of adult firefly abdomen morphology. We believe that this confusion has been caused largely by the fact that lampyrids posses a varying number of visible ventral abdominal sclerites and there is a lack of accuracy in defining the terms used in descriptions and discussions of the abdomen. Without both an understanding of the homology among abdominal sclerites and the use of accurate terminology, morphological investigations of lampyrids are bound to remain confused.

The description of both larval and pupal states of *L. atra* is instructive for following the reduction and fusion of various abdominal segments and sclerites from the larval stage, where all abdominal sclerites are present and obvious, to the pupal stage, where the effect of internalization, reduction and fusion can be first detected. In all firefly larvae currently known, there are ten abdominal segments, with the tenth being quite small and, therefore, commonly overlooked. Each abdominal segment bears a tergite, distinct pleurites that bear the spiracles (segments one through eight) and a sternite. Identification of abdominal segments and sclerites in the larvae is not difficult. Reduction of abdominal segments and the internalization of sclerites in the adults however, can make it difficult to determine homology among abdominal segments.

In Coleoptera, the adult abdomen is usually composed of ten segments in the male (with the tenth often being highly reduced or fused with the ninth), and nine in the female (with the ninth being modified to form the genital segment) (Lawrence and Britton 1991). As was pointed out by Green (1956), the first abdominal segment in adult Lampyridae is indicated only by the first abdominal tergite, except females of *Photinus granulatus* (Green, p. 597). However, investigation concluded that the pleurite bearing the first abdominal spiracle is also present, though in reduced form, in pupal *L. atra* and the adults of some lampyrids. In the adult, the first visible ventral sclerite actually is of the second abdominal segment, as the ventral portion of the first abdominal segment is usually so internalized and reduced, it is not visible ventrally. This condition is termed a "hologastrous type abdomen" (Nichols 1989). Additionally, in

adult lampyrids the abdominal pleurites are fused to the sternites, thus forming a continuous ventral plate. The median half of this ventral plate was the larval sternite and the lateral regions on each side were the pleurites. Green (1956), therefore suggested "... it would be incorrect to refer to the ventral segments of the abdomen as sternites." Lawrence and Britton (1991) use the term "ventrites" to denote sternites that are externally visible.

In light of these two situations: sternite one lacking and the fusion of sternites with pleurites, while also keeping with Green (1956) and Lawrence and Britton (1991), we adopt the term "ventrites" to denote the visible ventral sclerites in the *L. atra* pupa, which like other firefly species, has the same abdominal morphology as the adult. In most firefly species, the female has one ventrite fewer than the male, with species in the Luciolinae being the exception, the male having six and the female having seven ventrites. McDermott (1964) stated that "The Lampyridae may be defined as that family of the Cantharoidea having usually seven visible ventral abdominal segments in the male." Apparently, McDermott did not count the ninth abdominal segment when visible, as a visible ventral segment. This may be due to the small size if the ninth ventral sclerite in relation to the other ventral sclerites and the fact that it is usually the terminal ventral sclerite. It is our present conclusion that the sclerite of the ninth abdominal segment (ventrite eight) needs to be counted as a "ventrite" when visible. Depending upon whether the eighth ventrite is concealed under ventrite seven or exposed, adult males will have either seven or eight ventrites (MAB, personal observation), with eight ventrites being found in the majority of genera family-wide, examined by MAB. Therefore, in males of most firefly species, ventrites one through eight correspond to abdominal segments two through nine. The only known exception is for members of the subfamily Luciolinae, which bear only six ventrites (McDermott 1964; Ballentyne 1987a, b) and the paedomorphic brachypterous male of the European species *Phosphaenus hemiperus* Laporte (MAB, personal observation). In the Luciolinae, the last segment exposed in the male is ventrite six (abdominal segment seven), with segment eight apparently reduced, or altogether lost, with segment nine forming part of the aedeagal sheath which is retracted into the abdomen (Ballentyne 1992). The male of *Phosphaenus hemiperus* more or less retains a larviform type abdomen. Therefore, it is no surprise that Torre-Bueno's (Nichols 1989) definition of "sternite = ventrite" is insufficient in conveying the homology of ventral abdominal segments in adults of Lampyridae.

Even though "segmental fusion" does not seem to occur in the firefly abdomen, the use of the term "ventrite" should be used with care to avoid confusion of the homology of various abdominal segments. However, the use of the term "ventrite" to denote only visible abdominal segments in the adult, while also keeping in mind (and mentioning a point of reference) that "ventrite one" is actually the ventral sclerite of the second abdominal segment (in almost all cases), is simply good nomenclature and serves to avoid confusion concerning which adult abdominal segment is being referred to.

Conclusion

The firefly larva labeled as "*Photinus* sp." by Peterson (1951) is actually the larva of *Lucidota atra,* which is herein redescribed in greater detail than the original description (Wickham 1895) in order to facilitate larval identification. Through rearing this species from larva to adult, it was possible to investigate the homology of abdominal segments and track possible fusion or reduction events that lead to a decrease in number of visible ventral abdominal sclerites in the adult. Fusion of both abdominal segments and "ventrites" are not known to occur in currently studied lampyrid taxa.

Acknowledgments

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