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A Possible Larva of *Lepicerus inaequalis* Motschulsky (Coleoptera: Myxophaga: Lepiceridae) from Panama

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Abstract

A larva is described which is presumed to be that of *Lepicerus inaequalis* Motschulsky based on several probable first instars and one later instar collected a few miles from and in a similar habitat to adult specimens of this species. The association is additionally based on several features also occurring in other known myxophagan larvae. A key is provided comparing these larvae with those of the other three families of Myxophaga.

Key words: Coleoptera, Myxophaga, Lepiceridae

Introduction

"How often have I said to you that when you have eliminated the impossible, whatever remains, however improbable, must be the truth?" Sherlock Holmes to Dr. Watson (Doyle 1890).

Thirty-seven years ago, one of us (AFN) discovered a short series of minute larvae extracted with a Tullgren funnel from wet leaves and flood debris along the banks of a stream near Gamboa, Canal Zone, Panama. Two adults of *Lepicerus inaequalis* Motschulsky were collected on the same date in a similar habitat along a nearby stream (see below). A permanent slide was made of one larva and several others were cleared, dissected and placed in ethanol or glycerine. These unusual larvae (Fig. 1) were compared with those myxophagan taxa with known immature stages, but a possible association with *Lepicerus* was rejected due to the complete lack of spiracular gills. These unusual breathing organs are present in Torridincolidae, Hydroscaphidae and Sphaeriusidae and were considered as a potential synapomorphy of the suborder (e.g., Beutel & Haas 1998). When various staphylinoid taxa were excluded as possible candidates by AFN, the assumption was that these specimens probably represented a species of Cucujoidea whose immature stages were as yet unknown. Given the diversity of the Panamanian beetle fauna, this possibility was pursued no further. In the intervening years, one of us (JFL) reexamined these larvae on several occasions, in connection with various projects, including keys to beetle larvae (Lawrence 1991; Lawrence *et al.* 1999), but it was only in the past few years that the myxophagan alternative was reconsidered. Although there is virtually no information on the life cycle of *Lepicerus* species, it has been assumed over the years by Hinton (1969) and others that the beetles are aquatic. This idea was supported by Reichardt (1976) who claimed that a ventral plastron occurs in *L. bufo* (Hinton). Navarrete-Heredia *et al.* (2005), who made a detailed study of this species and *L. inaequalis*, found that no plastron was present in either species. These authors also noted that adults of *L. inaequalis* were usually found near the edges of rivers in moist substrate just below the surface, but never below the water line or associated with algae or plants, while those of *L. bufo* were usually found in sandy areas further from the river's edge, often under stones. Shepard *et al*. (2005) collected *L. inaequalis* in numbers from various sites in Costa Rica; typical habitats were in sand relatively high up on stream banks, near where marginal vegetation meets bare sand, although many specimens were collected below the water line (A.E.Z. Short, personal

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communication). Adults of a third species, *L. pichilinguae* Flowers *et al.*, 2010, from western Ecuador, were found in leaf litter in pasture land about 200 meters away from the nearest stream. In a phylogenetic analysis of Myxophaga based on adult and larval morphology (Beutel 1999), *Lepicerus* was sister to the remaining myxophagan families, and Beutel *et al.* (1999) considered the hygropetric life style to be a probable groundplan feature of Myxophaga excluding Lepiceridae. In the light of these results, the "mystery" larva was reexamined and compared to other myxophagans with respect to characters not directly involving respiratory adaptations connected with aquatic habitats. The proximity of these larvae to an adult *L. inaequalis* and the occurrence of several myxophagan features mentioned below increases the likelihood of the association, but hopefully corroborating evidence will eventually be found.

Materials and methods

The description and illustrations were based on one later instar 3 mm in length and four early instars 1.2 to 1.35 mm in length with the following collection data: **PANAMA:** Canal Zone: Río Frijoles, 4.1 miles northwest of Gamboa, 19.ii.1976, Berlese wet leaves and flood debris, A. F. Newton coll. The collecting site was located along Pipeline Road, and the name of the stream has been changed to Río la Seda. The nearby stream where adults were collected was called Río Frijolito (now changed to Río Mendosa) and is 6.7 miles northwest of Gamboa. The largest specimen was first illustrated (Fig. 1) and then cleared and dissected; the body, head capsule, ventral mouthparts and mandibles were placed in alcohol and studied in glycerine. A permanent slide was made of one of the smaller larvae, and a scanning electron micrograph of the left mandible of the largest specimen is shown in Fig. 1B. The remaining specimens were stored alcohol for many years, examined at various times, and transferred to different vials, especially during the senior author's move to Australia. Unfortunately, the mandibles and ventral mouthparts of the largest specimen were lost and the smaller specimens became depigmented by a chemical released from the plastic vial caps previously used by CSIRO. The images in Figs. 2 and 3 were photographed in open glycerine slides using a Micropublisher 5 digital camera mounted on a Leica M205C microscope. All images were edited with Adobe Photoshop. Material has been deposited in the following collections: Australian National Insect Collection, CSIRO Ecosystem Sciences, Canberra, ACT, Australia (specimens in glycerine and alcohol) and Field Museum of Natural History, Chicago, Illinois, USA (permanent slide).

Description of the Larva

Length: 1.2–3 mm (most specimens 1.2–1.35 mm). Body (Fig. 1A) with thorax and first eight abdominal segments about equal in width, but each segment laterally rounded and somewhat lobate; segment VIII and tergum IX gradually narrowed posteriorly, the latter forming a narrowly acute process; slightly flattened and lightly pigmented with weakly sclerotized head and tergal plates; vestiture of sparsely distributed long setae. Head (Figs. 1A, 2A–D) slightly transverse (about 0.8 times as long as wide), not emarginate posteriorly above occipital foramen; ecdysial lines weakly indicated with epicranial stem very short and frontal arms more or less U-shaped and contiguous at base. Stemmata relatively large, well separated and with well-developed lenses, six on each side, an anterior curved row of four and two lying behind them, located on elevated area. Antennae more than half as long as head width, located on raised, membranous antennifer; ratio of antennomere lengths 1: 3.8: 1.9; first antennomere 0.75 times as long as wide, second about 3 times as long as wide and about as wide as first; third about 3 times as long as wide and much narrower than the second; sensorium at apex of antennomere 2 about half as long as antennomere 3, outwardly directed and narrowly conical with subacute apex; antennal insertions separated from mandibular articulations by strip of cuticle about half the diameter of antennifer. Frontoclypeal suture absent. Labrum about 0.4 times as long as wide with sides weakly rounded and apex truncate. Mandibles (Figs 1B, 2A, 2C, 3B) asymmetrical, short and broad, slightly longer than wide, without accessory ventral process; ventral condyle located at about middle of mandible; apex quadridentate with teeth more or less perpendicular to plane of movement; incisor edge with two weak serrations; mola large, surface composed of tightly packed, sclerotized papillae, which do not extend onto ventral surface; dorsal surface of mandibular base without rows of microtrichia; inner edge without lobe or setal tuft at base of mola; prostheca absent from both mandibles. Ventral

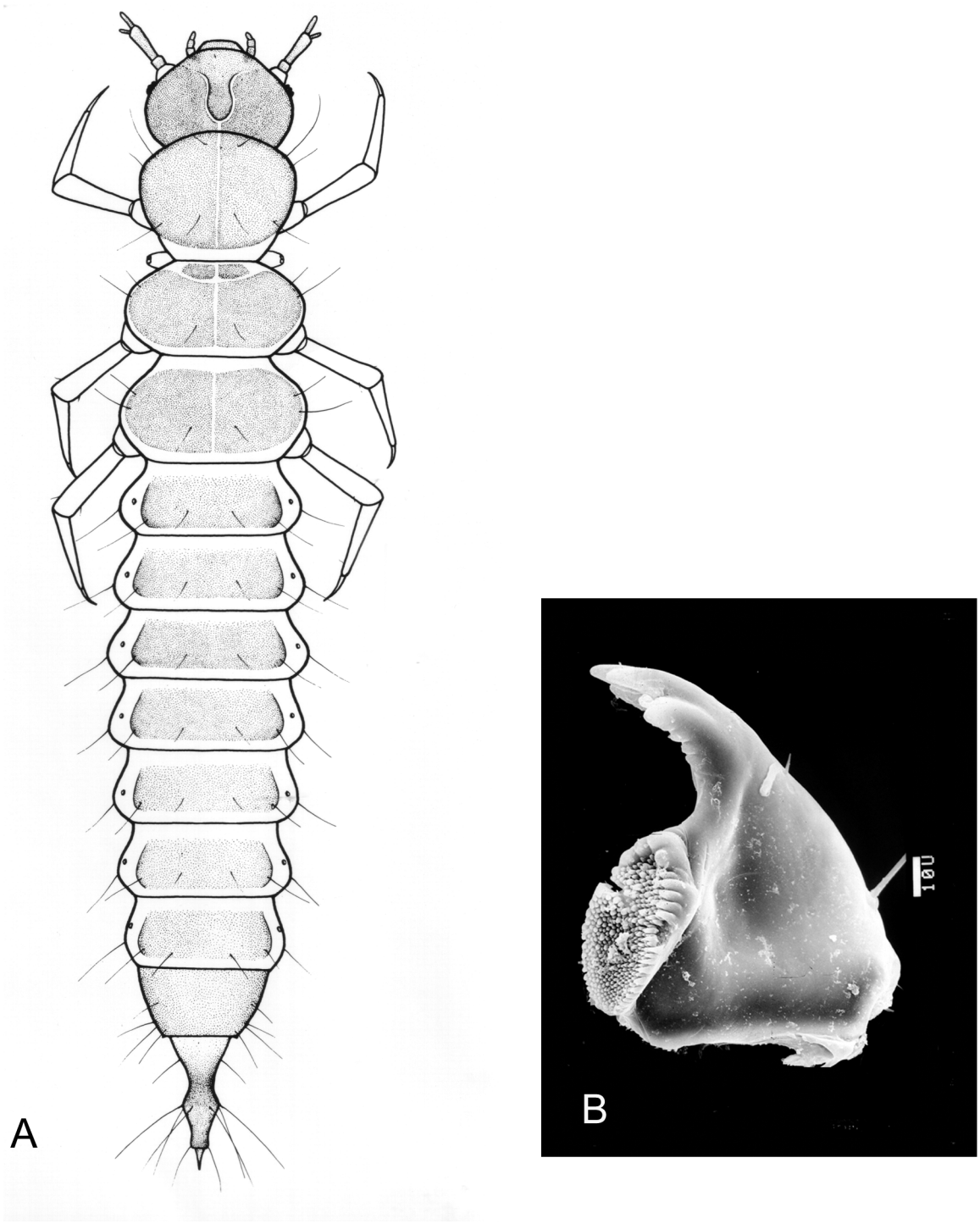

FIGURE 1. Presumed larva of *Lepicerus inaequalis* Motschulsky: A, habitus, dorsal, length = 3 mm; B, left mandible, dorsal.

mouthparts retracted; cardines not clearly delimited; maxillary articulating area absent; stipes slightly elongate; mala (Fig. 3B) slightly elongate, slightly curved mesally and apically rounded; maxillary palps well developed and 3-segmented with distinct palpifer; palpomere 1 strongly transverse, 2 about 1.4 times as long as wide, 3 about twice as long as wide, narrowly rounded at apex. Ligula bilobed and covered with small papillae; labial palps 2-segmented and well separated. Hypostomal rods (Figs 2C–D) long and diverging; gula elongate. Hypopharyngeal sclerome absent; hypopharynx with central dense cluster of microtrichia flanked by shorter spicules. Tentorial bridge moderately broad, curved, with 2 slender anterior arms attached. Thorax relatively long, about half as long as abdomen; each thoracic tergum with pair of very long setae. Legs long and slender, widely separated, coxae subglobular, slightly projecting laterally so that they are partly visible from above; procoxae separated by about 1.5

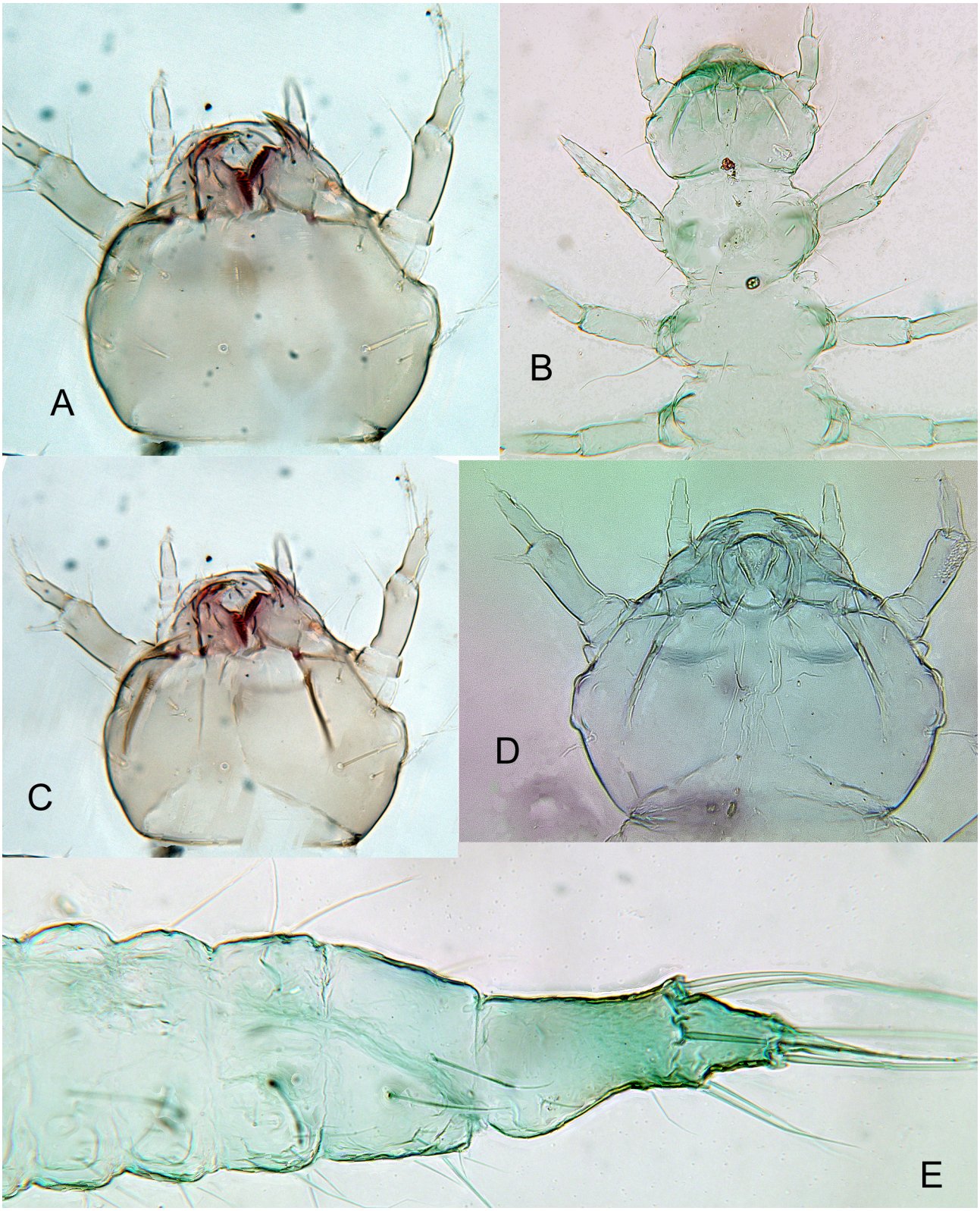

FIGURE 2. *L. inaequalis* larva: A, head, showing frontal arms (vaguely indicated) and stemmatal elevation; B, head and thorax, showing thoracic spiracular tubes; C, head, showing hypostomal rods and gula; D, head, ventral, showing antennal sensorium and tentorium; E, abdominal apex, lateral, showing terminal process and anal opening.

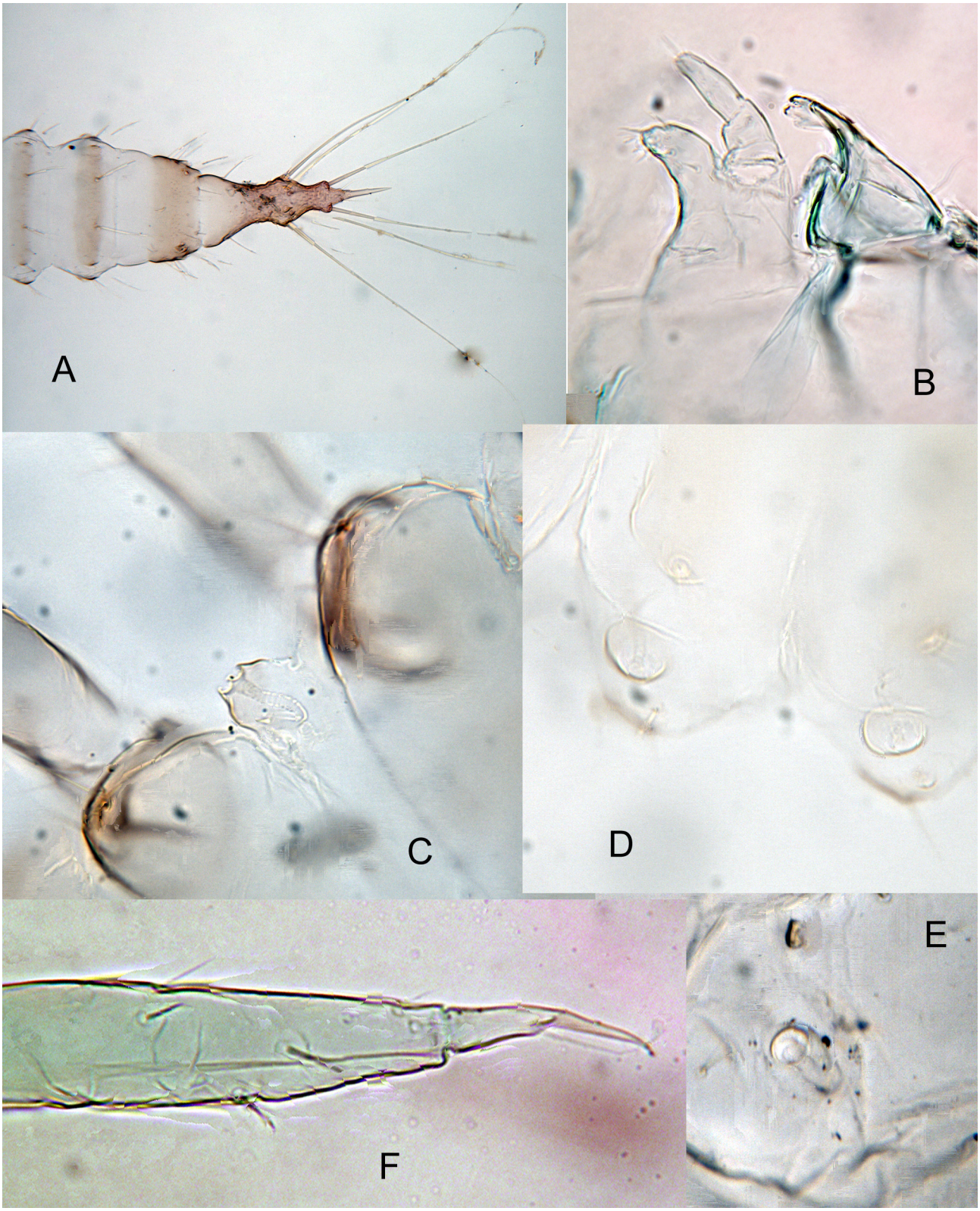

FIGURE 3. *L. inaequalis* larva: A, abdominal apex, dorsal, showing terminal process and posterolateral location of 8th spiracles; B, mandible and maxilla; C, thoracic spiracle, showing paired openings; D, abdominal segments I and II, showing spiracles; E, first abdominal spiracle; F, tibiotarsus and pretarsus.

coxal diameters, meso- and metacoxae by more than two coxal diameters; trochanter about as long as coxa; femur long, parallel-sided, apically truncate, with few setae only; tibiotarsus (Fig. 3F) slightly shorter than femur, narrowed apically, with few setae; pretarsus slender, narrowly acute, with 1 moderately long seta located just beyond middle. Abdominal segments I–VIII each with short lateral tergal lobe; terga I–VII each with strongly transverse, very lightly pigmented tergal plate; terga VII and VIII more or less evenly pigmented; segment IX (Figs 1A, 2E, 3A) about twice as long as VIII, with tergum extending well onto ventral surface, narrowing posteriorly and laterally sinuate, with 4 long setae beyond middle and another 2 at apical fourth; apex narrowly acute; paired urogomphi absent. Sternite IX strongly transverse, broadly rounded at apex; segment X membranous and concealed. Spiracles (Figs 3C–E) annular-biforous with long accessory chambers and closing apparatus, those on thorax (Figs 1A, 3C) located at end of moderately long spiracular tubes, those on abdominal segments borne on shorter tubes; spiracles on segments I–VII located above lateral tergal lobes, those on segment VIII located at posterolateral edges of tergum, facing posteriorly.

Discussion

The combination of 5-segmented legs, with tibia and tarsus fused, and well-developed, tuberculate mandibular mola excludes this larva from members of the Archostemata and Adephaga, but not from numerous polyphagan groups. The presence of large stemmata with well-developed lenses and located on a pair of elevated projections appears to be a myxophagan feature (e.g., Beutel *et al.* 1999: figs 1, 5–8), but no member of this suborder has a full complement of six stemmata, a condition known in most Adephaga and also in a number of basal polyphagan taxa. Anton & Beutel (2006) emphasized the similarities between Myxophaga and Polyphaga with respect to the complex microphagous feeding systems present in both larvae and adults. Certainly the feeding systems of the two groups are similar, including a pair of basal mandibular molae, often associated with a variety of brushes, and sometimes fields of linear microtrichia or tooth-like asperities, but perhaps more attention should be given to the differences between these systems in the two suborders. Myxophaga, for instance, lack a hypopharyngeal bracon which connects the two mandibular sockets and supports the labium-hypopharynx and associated structures; basal mandibular molae combined with a hypopharyngeal bracon and some type of sclerotized hypopharyngeal armature occur in all known archostematan larvae and in those of various polyphagan groups, including Agyrtidae, Leiodidae, Eucinetidae, Clambidae, Scirtidae, Derodontidae, Nosodendridae, Jacobsoniidae, Lymexylidae, many Cucujoidea and Tenebrionoidea, and the curculionoid family Nemonychidae. The archostematan mola, in contrast to those of most polyphagan families, is either simple or, in the case of *Micromalthus*, armed with a few transverse ridges. Features often associated with the bracon in Polyphaga include 1) rows of slender, linear microtrichia on the dorsal surfaces of the mandibles (which interact with similar rows on the pharynx), 2) fields of tooth-like asperities on the ventral mandibular surfaces, often continuous with the molar armature, and 3) a sclerotized, flattened or molar-like hypopharyngeal sclerome, which interacts with the ventral mandibular armature (Lawrence 1989, 1991; Lawrence *et al.* 2011; Lawrence & Ślipiński 2013). Another feature, often associated with the bracon and sclerome, is the so-called accessory ventral process, which is attached to the base of the mandible and projects mesally towards the molar area. It occurs in many of the families above, but is absent in Agyrtidae, Leiodidae, Jacobsoniidae, Lymexylidae, some of the more derived groups of Cucujoidea, all Tenebrionoidea and in Nemonychidae; it was coded as present in Hydroscaphidae by Lawrence *et al.* (2011), but this was an error based on a misinterpretation of the mesally displaced ventral condyle (Beutel & Haas 1998). The possible larva of *Lepicerus*, like those of all known Myxophaga, lacks the bracon and all associated structures, including the accessory ventral process. A feature strongly suggesting myxophagan affinities of the larva is the presence of papillae on the labial ligula. This feature is also found in larvae of the other three families (Beutel *et al.* 1999: figs 2, 18, 22) but is almost generally absent in other groups of beetles (with the exception of Hydraenidae).

The spiracular openings, although very small, appear to be of the annular-biforous (bicameral) type with relatively long accessory spiracular chambers. In this respect, the larva differs from those of Archostemata, Myxophaga and most Adephaga, which have annular spiracles, and resembles those of the adephagan family Haliplidae and a large number of polyphagan groups, including the hydrophilid subfamilies Helophorinae and Georissinae, the staphylinoid families Agyrtidae and Leiodidae, the dascilloid family Rhipiceridae, Derodontidae and Nosodendridae, a small selection of Cleroidea, many families of Cucujoidea and Tenebrionoidea, a few

Chrysomeloidea and a number of Curculionoidea. The biforous type of spiracle, in which the main spiracular opening is replaced by a stigmatic scar, occurs in a few Scarabaeoidea, schizopodine Buprestidae and almost all Byrrhoidea and Elateroidea. In some polyphagan families the annular-biforous type has evolved into the annular type in derived subgroups, while in others (e.g., some Cerambycidae, a few Chrysomelidae and Curculionidae), spiracles are annular-biforous in first-instars but annular in later instars. Since annular-biforous spiracles are not known in other insect orders, but are common in more basal polyphagan groups, they are usually considered to be a part of the polyphagan groundplan. Their presence in a myxophagan larva and also in the adephagan family Haliplidae suggests that they could be part of the coleopteran groundplan.

The differences between the possible *Lepicerus* larva and those previously described for Torridincolidae, Sphaeriusidae and Hydroscaphidae may be summarized in the following key based in part on the works of Böving (1914), Britton (1966), Reichardt (1974), Reichardt & Hinton (1976), Beutel (1998), Beutel & Haas (1998), Beutel *et al*. (1999), Vanin & Costa (2001), Beutel (2005) and Hájek & Fikáček (2008):

1. Body elongate and more or less parallel-sided; abdomen about twice as long as thorax; stemmata on each side six; antenna 3-segmented with slender sensorium about half as long as terminal antennomere and directed apicolaterally; mandible with well-developed quadridentate apex and no prostheca; maxillary palp extending well beyond apex of mala; spiracular gills absent; tergum IX forming elongate, subacute process; segment X concealed possible. . . . . **Lepiceridae**
- Body widest anteriorly or at middle, with sides distinctly curved; abdomen not or only slightly longer than thorax; stemmata on each side five or fewer, antenna 2-segmented with sensorium either palpiform and apically directed or very short, flattened and embedded in excavation of antennomere 2; mandible either with well-developed, subapical prostheca or with highly reduced apex; maxillary palp not extending to apex of mala; spiracular gills present; tergum IX not forming elongate, subacute process; abdominal segment X more or less exposed **2**
2. Abominal segments I–VIII each with pair of lateral or dorsolateral, articulated, segmented spiracular gills; stemmata on each side four; antenna moderately long and slender, 2-segmented, with small, flattened sensorium embedded in a subapical impression on antennomere 2; frontoclypeal suture absent and labrum free, small and transverse; apex of maxillary mala more or less truncate with fixed tooth and several articulated spines; urogomphi present or absent; segment X represented by paired flaps lying behind sternite IX, lacking paired hooks . . . . . **Torridincolidae**
- Abdomen without segmented spiracular gills; thoracic terga and abdominal terga I–VII or VIII each with posterior row of lancet-shaped setae; stemmata on each side four or five; antenna relatively short, 2-segmented, with long, slender sensorium extending beyond apex of antennomere 2; frontoclypeal suture present and labrum fused to clypeus to form large clypeolabrum; apex of maxillary mala falciform with two or three fixed apical teeth; urogomphi absent; segment X with one or three pairs of hooks **3**
3. Body short and broad, widest at anterior third and gradually narrowing posteriorly; abdominal terga I–VII each with pair of posteriorly-directed processes, each bearing a thin-walled, sac-like spiracular gill; antennal sensorium arising from near middle of antennomere 2; stemmata four on each side; mandible with reduced apex and no prostheca; abdominal segment VIII without paired elongate, posteriorly-directed processes; segment X bearing three pairs of hooks . . . . . **Sphaeriusidae**
- Body more elongate, with thorax distinctly wider than abdomen and the latter more strongly narrowed posteriorly; posterior edge of protergum, sides of abdominal tergum I and apex of tergum VIII each with pair of sac-like or tufted spiracular gills, those on tergum VIII at the ends of paired, posteriorly-directed processes; antennal sensorium arising from apex of antennomere 1; stemmata five on each side; mandible with distinct apex and well-developed prostheca; segment X bearing one pair of hooks . . . . . **Hydroscaphidae**

If the larva we describe here is indeed that of *Lepicerus inaequalis*, the new data would add strong support to the hypothesized sister-group relationship between Lepiceridae and the remaining myxophagan families. This would include the following larval synapomorphies of Torridincolidae, Hydroscaphidae, and Sphaeriusidae: abdomen as short as or shorter than the thorax, number of stemmata reduced to five or fewer, antennae 2-segmented or extremely shortened, mandible with well-developed subapical prostheca (groundplan), and spiracular gills.

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