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Larvae of *Abachrysa eureka* (Banks) (Neuroptera: Chrysopidae: Belonopterygini): descriptions and a discussion of the evolution of myrmecophily in Chrysopidae

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Abstract

Here we describe the first and third instars and the egg of the New World chrysopid *Abachrysa eureka* (Banks). Like other members of the tribe Belonopterygini, this species is myrmecophilic. Comparisons of *Abachrysa* larval and egg characteristics with those reported from four other belonopterygine genera indicate that *Abachrysa* more closely resembles the Old World *Calochrysa* and *Italochrysa* than the New World *Vieira* and *Nacarina*. The three genera *Abachrysa*, *Calochrysa* and *Italochrysa* all have large eggs, accelerated embryonic development, and an elaborate set of morphological modifications for larval debris carrying, an important defense against ant attack. This pattern of shared features is consistent with the phylogenies recovered in recent molecular studies that place the New World genera *Vieira* and *Nacarina* basal to *Abachrysa* and the Old World genera. Our assessment of current morphological information in relation to the molecular studies indicates the following sequence: (i) The form of belonopterygine myrmecophily that is currently expressed in the basal lineages (*Nacarina* and perhaps *Vieira*) originated in the New World and does not involve elaborate larval modifications for debris carrying. (ii) Myrmecophily that is based on a correlated set of developmental and morphological traits subserving debris carrying evolved in the New World when *Abachrysa* diverged. (iii) Subsequently, the debris-carrying clade of Belonopterygini underwent a significant radiation in the Old World, but not in the New World.

Key words: Debris carrying, egg size, embryonic development, phylogeny, geographic distribution

Dedication

We dedicate this article to the memory of Ellis G. MacLeod (1928–1997, University of Illinois), a devoted educator and student of Neuroptera. In 1968, his student Joseph Sheldon collected a gravid female of *Abachrysa eureka* (Banks) and sent it to Ellis for rearing. Ellis was successful and today remains as the first and only person known to have reared a belonopterygine chrysopid from egg to adult. However, he never published the results of that work. Upon his death his fine drawing and photographs of the *A. eureka* egg and third instar, along with his notes and an early draft of a manuscript on this species, passed to JDO at Texas A&M University. His results are now included here with our findings on the first instar and egg.

Introduction

The cosmopolitan Belonopterygini is one of five tribes now included in the green lacewing subfamily Chrysopinae (Garzón-Orduña *et al.* 2019, Winterton *et al.* 2019). This tribe has several distinctive features, the most interesting of which is its reported use of ant brood as prey, a feature that has not been associated with any other group of green

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lacewings. Belonopterygini is a relatively small tribe; currently, it consists of 15 genera. Four of these are known from the New World (North and South America), and eleven occur in the Old World (loosely defined here as Europe, Asia, Africa, and Australia) (Brooks & Barnard 1990, Tauber *et al*. 2006, Tauber 2007, Winterton & Brooks 2015, Sosa & Tauber 2017, Oswald 2019).

Belonopterygine larvae are rarely encountered in the field. Indeed, until this report the mature larvae of only two species were described. Both were found in association with ant nests, and both are from the genus *Italochrysa*: the European *Italochrysa italica* (Rossi) described by Principi (1943, 1944, as *Nothochrysa italica* Rossi) and the Australian *Italochrysa insignis* (Walker) described by Tauber & Winterton (2014). In addition, larval associations with ants were reported for two New World belonopterygine genera: *Nacarina* and *Abachrysa* (Weber 1942, MacLeod's unpublished notes). Unfortunately, specimens associated with these two reports are not known.

Field-collected belonopterygine females occasionally oviposit when they are held in vials or cages; consequently, over the years, first instars from three genera have become available for morphological study. As demonstrated by Tauber *et al*. (2006, 2014) and Monserrat & Díaz-Aranda (2012), the comparative morphology of first instar chrysopids can provide considerable systematic and phylogenetic information. The initial descriptions of belonopterygine first instars came from New (1983, 1986): *I. insignis* and *Calochrysa extranea* (Esben-Petersen); Díaz-Aranda & Monserrat (1995): *Italochrysa stigmatica* (Rambur); and Tsukaguchi (1995): *Italochrysa japonica* (McLachlan). Subsequently, Tauber *et al*. (2006) described the first instar of *Vieira elegans* (Guérin-Méneville) [as *Berchmansus elegans* (Guérin-Méneville)], and Monserrat & Díaz-Aranda (2012) added detailed information for *I. stigmatica*.

Here, we describe and present comparative data from the first and third instars of the New World *Abachrysa eureka* (Banks). The information on the first instar is derived from specimens obtained by the second and third authors (SKK, JDO), and that on the third instar stems from MacLeod's drawing, photos, and notes. In addition to descriptions, our report evaluates the consistency of larval features previously proposed to be synapomorphic for the tribe Belonopterygini, and it discusses the evolution of belonopterygine myrmecophily within the context of the newly available data on *Abachrysa* and recently published phylogenetic studies of chrysopid genera (Garzón-Orduña *et al*. 2019, Winterton *et al*. 2019).

Materials and methods

Specimens. Adult specimens were collected between 15 August and 17 October 2015 at two localities in College Station, Brazos County, Texas, U.S.A. (30.58849°N, 96.25366°W and 30.53145°N, 96.28170°W ± 120m [WGS 84]). Collections were primarily made at sheets lit with black lights or mercury vapor bulbs, and by searching the surrounding area during the evening and early the following morning. Adults were held in plastic vials containing a paper strip as an oviposition site. After oviposition, eggs and first instars were held in vials and offered food under laboratory conditions. Some of these larvae were preserved for the morphological study here. Other larvae were randomly selected for feeding trials and offered a variety of prey as food; none of the first instars fed sufficiently to molt to the next instar.

First instars selected for morphological study were boiled in water for about one minute and then placed in 80% EtOH. Two days later, some (n=19) were transferred to 10% KOH for clearing. After another two days, ten of these larvae were transferred to chlorazol black for staining. After being dehydrated through increasing concentrations of EtOH, all 19 larvae were slide mounted in Canada balsam under coverslips. Additional first instars (n = 48) were point mounted, as were unhatched eggs (n = 8) and eclosed chorions (n = 30); their stalks were included when possible. All of these specimens, as well as the field-collected adults, were deposited in the Texas A&M University Insect Collection (TAMUIC) under Voucher Number 712. Several larval specimens (n = 4 on slides, 4 point mounted) were retained in the Tauber research collection in Davis, CA, for future study. MacLeod's original drawing, photos, and notes are also held in the TAMUIC.

Descriptive procedures and measurements. The description of the first instar was made from both cleared and dried specimens. Slide-mounted specimens (n = 3–4 per structure) were used to estimate the length of the body and to measure the head; because of possible compression, the head measurements (length and width) may be slightly larger than actual size. Thus, caution should be used when comparisons are made with previously published measurements by the first author (e.g., Tauber *et al*. 2006) and others who measured specimens without a coverslip.

Measurements included the following: cranial width—across the widest part of the head, between the exterior margins of the eyes; cranial length—along the midline between the anterior and posterior margins of the head; mandibular length—along the midline of the curved dorsal surface of the mandibles. All measurements were made with Image J public domain software (ver. 1.46r, National Institutes of Health, USA; http://imagej.nih.gov/ij).

The description of the third instar is based on MacLeod's photographs and drawing and is compared with descriptions of *I. italica* by Principi (1943, 1944) and *I. insignis* by Tauber & Winterton (2014). Nomenclature for larval morphology and setation follows Rousset (1966) for the head, and Stehr (1987), Tauber & de Léon (2001), and Tauber *et al*. (2006) for the thorax and abdomen. Primary cephalic setae are designated with an "S" followed by a number; setae on the thoracic and abdominal lateral tubercles are designated as LS and LDS respectively, and submedian setae on the dorsum of the thorax and abdomen as SMS.

For some taxa or specimens, the taxonomically important thoracic sclerites are easily identified; they are both tanned (light or dark brown, or black) and obviously sclerotized (rigid, smooth, reflective in liquid medium). However, in *A. eureka* first instars, the entire notum of each thoracic segment (most notably, the pronotum) appeared lightly sclerotized, and we were not able to identify specific thoracic sclerites. Finally, in previous larval descriptions by CAT, the integument is described as with or without "spinules", a term that is only vaguely defined [e.g., Torre-Bueno (1989): spinule, "a small spine (T-B); see microtrichia"], but well illustrated (Stehr 1987: 296). The definition of "microtrichia" stands in contrast to "macrotrichia", which include hairlike projections that are articulated in cuticular sockets. The "spinules" reported for chrysopid larvae appear to be sessile, acute, scalelike, unarticulated, and without sockets; thus, they are "microtrichia". Here we use this term in lieu of "spinules".

To facilitate morphological comparisons, an error in a previous article (Tauber *et al*. 2006: 222, Fig. 1, as *Berchmansus*) is noted here: in this article the basal antennal "segment" labeled as the scape ("sc") is actually a pedicellate extension of the cranium beneath the antenna, not a segment of the antenna. Thus, the true scape was misidentified as the pedicel, and the true pedicel was misidentified as an enlarged flagellum. The true scape is a simple, unmodified segment; it can be partially withdrawn into the pedicellate cranial extension. The true pedicel is elongate, swollen, and annulated throughout; it has a very small seta about 1/3 the distance from its tip (not shown in the original figure). The true flagellum, which extends from the tip of the true pedicel, is slender, tapered, and also annulated; it bears a large basal spur (perhaps a modified seta) that extends distally beyond the tip of the flagellum; the tip of the flagellum bears a pair of slender, elongate terminal setae. These corrections are illustrated in Fig. 14B.

Descriptions of the Immature Stages of *Abachrysa eureka* (Banks)

Egg (Fig. 1)

Length 3.0 mm, width 1.1 mm (n = 1); fusiform, with apical pole bearing micropyle; laid singly on an erect, smooth, shiny stalk. Stalk 9.2 mm long (n = 1); sticky, but without fluid droplets. Catanach (2007) provided additional measurements (see Table 1).

Catanach (2007) stated that eggs were pale blue-gray if fertile, but light green if infertile. Subsequent work has shown that eggs are light green when laid; if fertile and healthy, they assume a pale bluish-gray color as the embryo becomes visible beneath the chorion.

First instar (Figs 2–9)

Body. Small, compact, slightly thickened dorsoventrally through mesothorax, metathorax, and anterior abdominal segments, but dorsal surface probably not abruptly elevated; length of shriveled, unfed specimens slightly greater than 1.5 mm. Integument smooth, without microtrichia, bearing four types of setae: (i) moderately long to medium length, stout, slightly denticulate, with acute tip (primary cephalic setae); (ii) long, robust, lightly denticulate to smooth, straight-to-curved basally, curved-to-bent distally, with acute apex (most setae on the lateral and laterodorsal tubercles of the thorax and abdomen; LS, LDS); (iii) very long, slender, smooth, curved submedian setae (SMS) on dorsum of mesothorax, metathorax, and first to sixth abdominal segments; (iv) short to medium length, straight, smooth, with acute tip (some primary setae on the cranium, pronotum, seventh and eighth abdominal segments). The SMS are extremely tapered and thin distally; it is difficult to determine if the tips of these setae are acute or minutely hooked.

FIGURE 1. *Abachrysa eureka* (Banks), egg (with stalk), lateral. Photo: E. G. MacLeod.

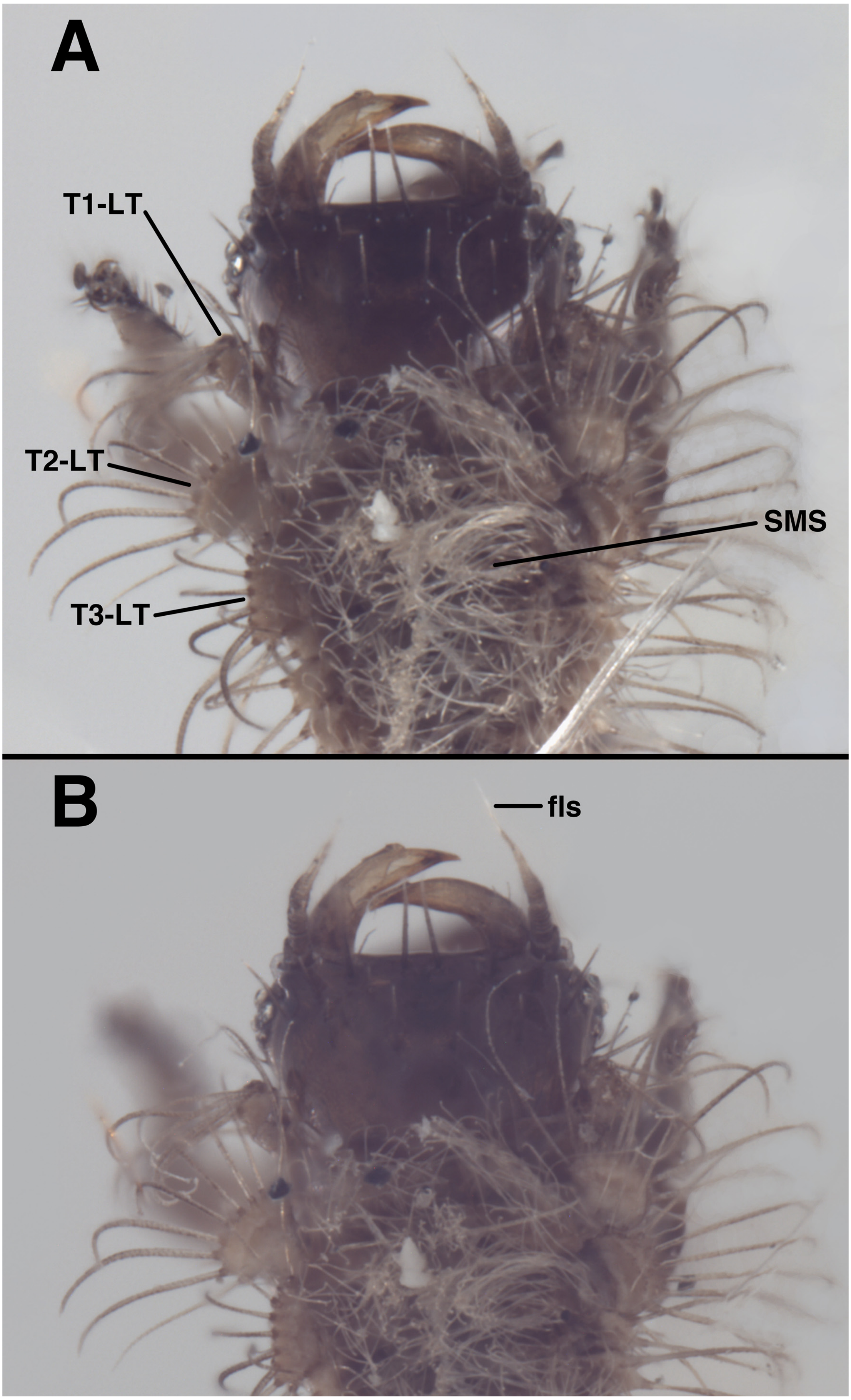

FIGURE 2. *Abachrysa eureka* (Banks)*,* first instar, head and thorax, dorsal (specimen point mounted). A. Dorsal cephalic setae visible. B. Flagellar setae visible. fls flagellar setae; SMS, submedian setae of thorax; T1-LT, T2-LT, T3-LT, lateral tubercles of prothorax, mesothorax, and metathorax.

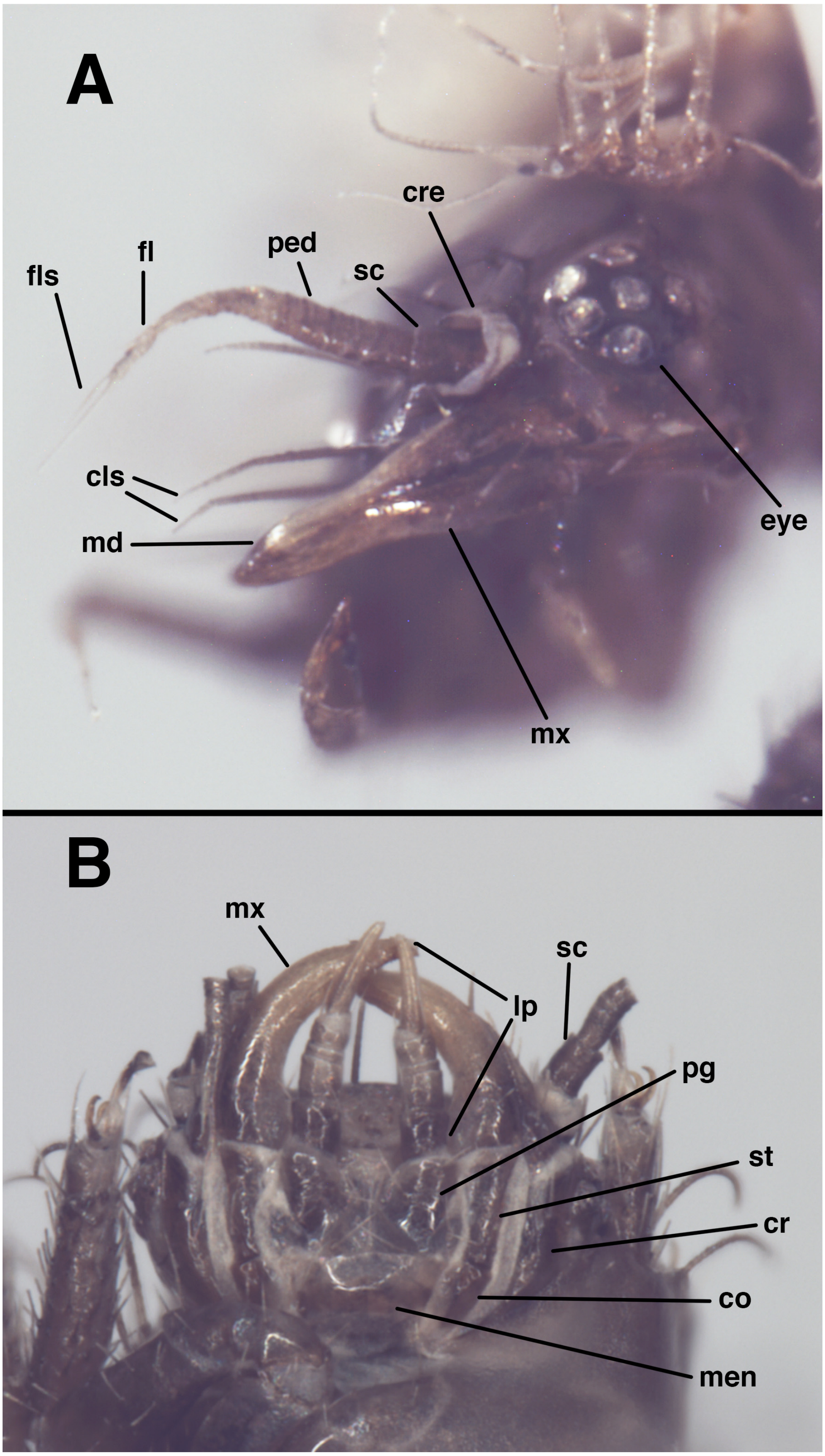

FIGURE 3. *Abachrysa eureka* (Banks), first instar, head (specimen point mounted). A. Lateral view. B. Ventral view. cls, clypeal setae; co, cardo; cr, cranium; cre, pedicellate cranial extension; eye, eye including six stemmata; fl, flagellum; fls, flagellar setae; lp, labial palpus; md, mandible; men, mentum; mx, maxilla; ped, pedicel; pg, palpiger; sc, scape; st, stipes.

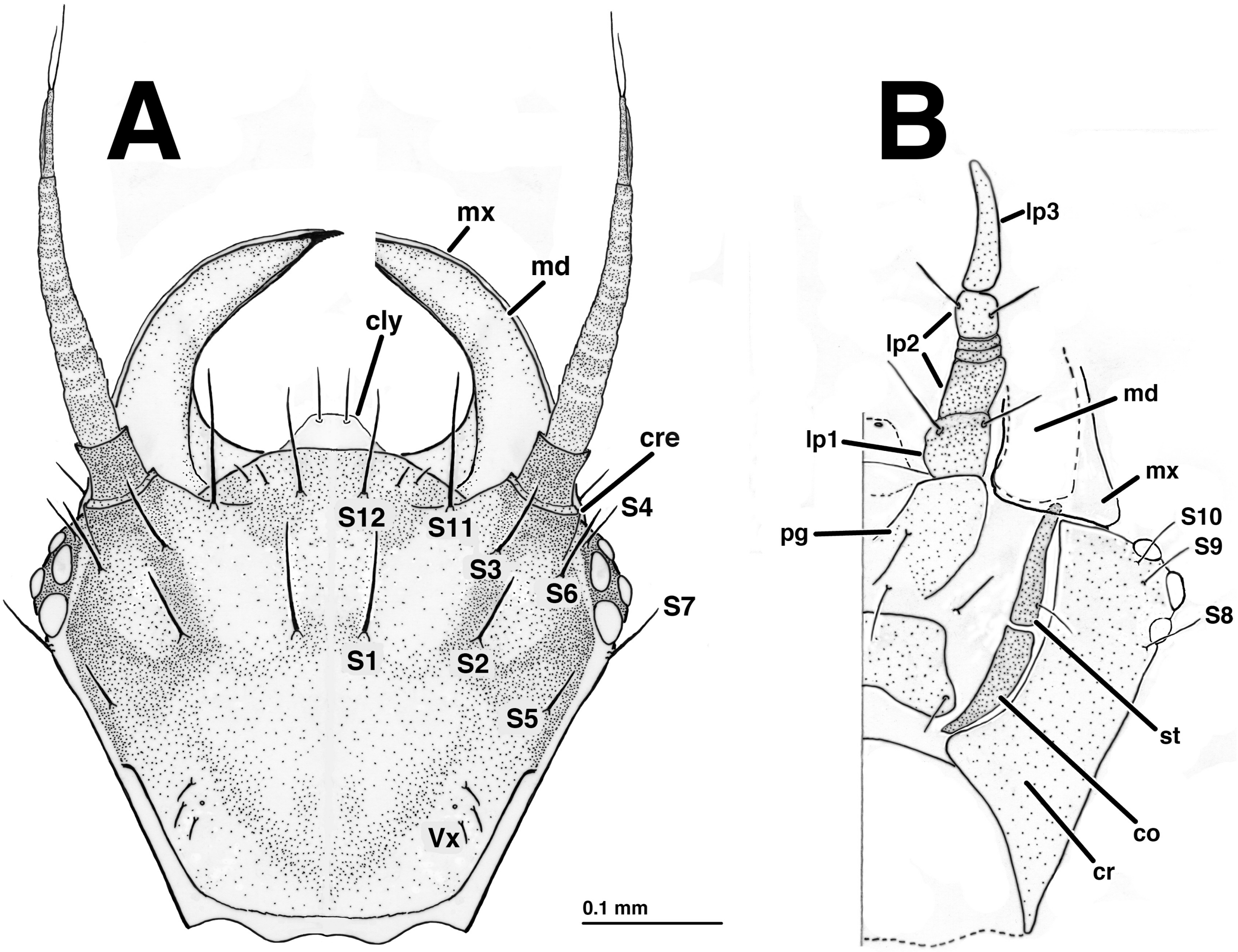

FIGURE 4. *Abachrysa eureka* (Banks)*,* first instar, head. A. Dorsal view (tip of right mandible and labial palps excluded). B. Ventral view (antenna, mandible excluded). cly, clypeus; co, cardo; cr, cranium; cre, pedicellate cranial extension; lp1, lp2, lp3, basal, middle, and distal subsegments of labial palpus; md, mandible; mx, maxilla; pg, palpiger; st, stipes; S1–S12, primary cephalic setae; Vx, three short posterior setae surrounding a pore.

Cranium (Figs 2–5). Width 0.54–0.55 mm; length ~0.46–0.47 mm. Dorsum smooth, well sclerotized; posterior margin quadrate, partially withdrawn into cervix (larva at rest); anterior region beneath base of antenna forming pedicellate extension, capable of receiving retracted base of scape. Six stemmata, all well separated, relatively small. All primary cephalic setae (S1–S12) present, with acute tips (Figs 4, 5). Dorsal setae (S1–S7, S11, S12) with surface slightly denticulate; S11, S12 robust, long, directed anteriorly; S1, S2, S3, S6 medium length, robust, but slightly more slender than S11, S12; S5 relatively small; Vx with three short setae, pore detected on some specimens; anterior region of cranium (anterior to S11) with two pairs of small, smooth, acute setae (possibly S14-cl, S15-cl of *V. elegans*); anterior tip of clypeus with pair of large, lightly denticulate, acute setae projecting anteriorly (possibly S13-cl of *V. elegans*). Venter with cardo and stipes narrow, elongate, rectangular; primary setae (S8–S10) smooth, short to medium length; S8 posterior to eye (sometimes near cardo); S9, S10 near each other, medial to eye. Ventral midregion with ~three pairs of setae on or near mentum; base of palpiger with single seta.

Cephalic appendages (Figs 4–6). Clypeus large, extending laterally toward base of mandibles; anterior margin extending forward as truncated process. Mandible short, stout, heavily sclerotized, especially at tip and along lateral margin of distal half; 0.35–0.39 mm long; 0.11–0.13 mm wide, at base; with sharply acute tip, ~7–8 acute teeth in saw-like row along inner edge just below apex. Maxilla broad basally, with two short basolateral setae; lateral margin with two acute teeth (spurs) near terminus, basal one small, pointed basally, distal one larger, near terminus, pointed apically; tip rounded, heavily sclerotized, with small patch of microsetae. Labial palp extending to tip of mandible or slightly beyond; second segment broad (~0.05 mm wide at widest point; ~0.10–0.12 mm long), with

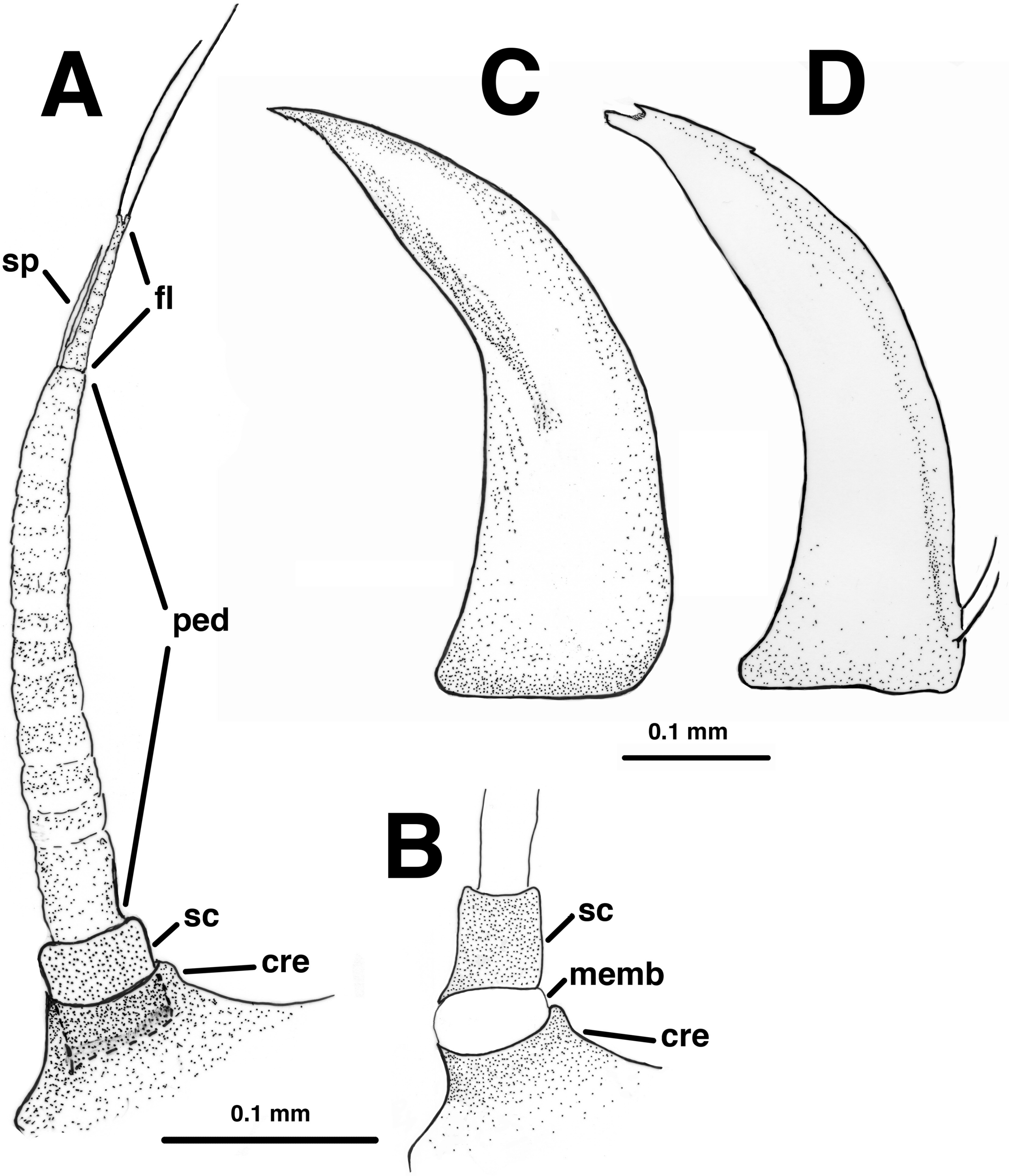

FIGURE 5. *Abachrysa eureka* (Banks), first instar, cephalic appendages. A. Antenna, dorsal (scape partially withdrawn into pedicellate cranial extension). B. Base of antenna, lateral (scape exerted). C. Mandible, dorsal. D. Maxilla, ventral. cre, pedicellate cranial extension; fl, flagellum; memb, membrane between scape and cranium; ped, pedicel; sc, scape; sp, flagellar spur. Scale bars: upper (C, D), lower (A, B).

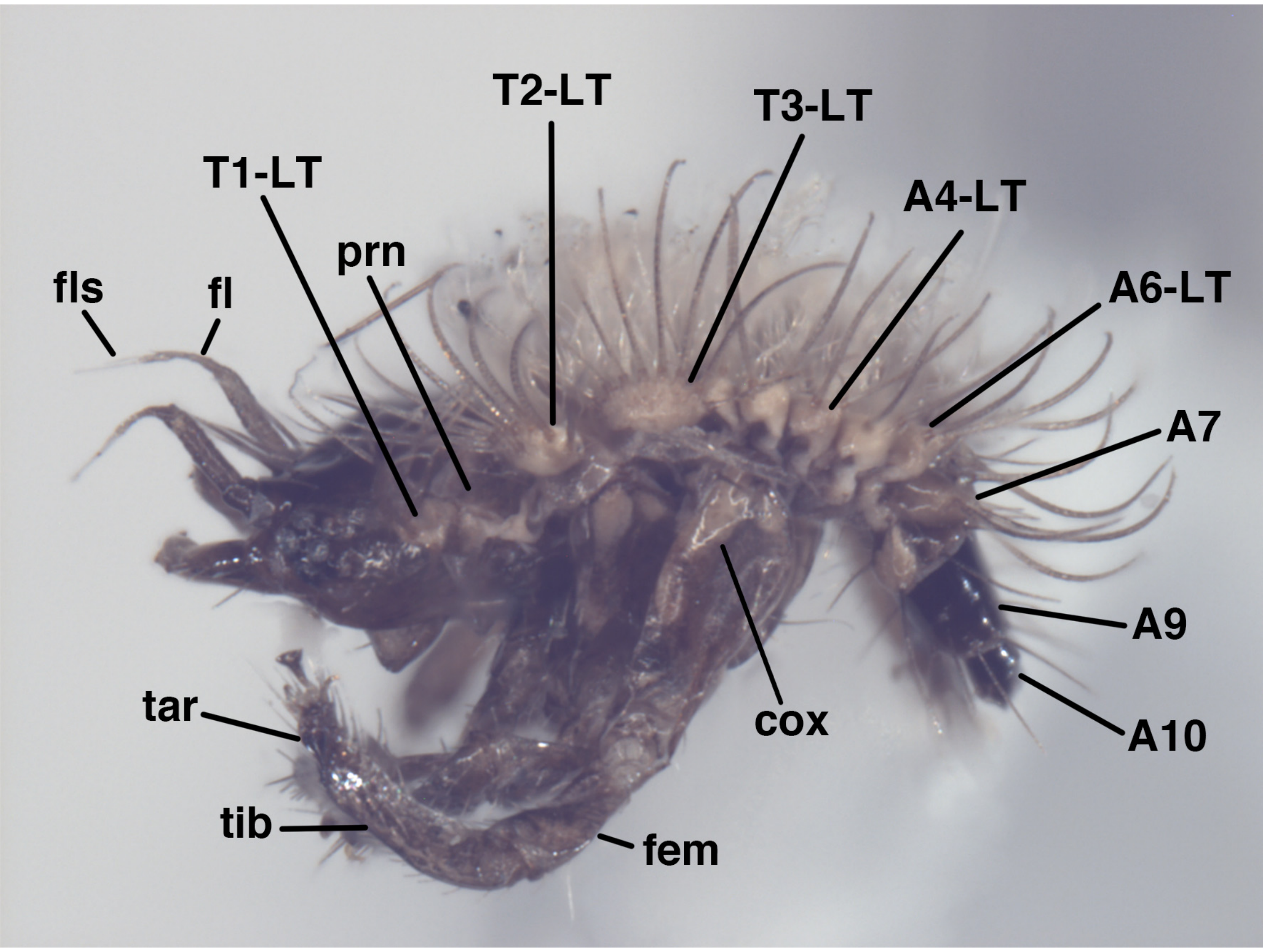

FIGURE 6. *Abachrysa eureka* (Banks)*,* first instar, habitus, lateral (specimen point mounted). cox, coxa; fem, femur; fl, flagellum; fls, two flagellar setae; prn, pronotum; tar, tarsus; tib, tibia; A7, A9, A10, seventh, ninth, and tenth abdominal segments; A4-LT, A6-LT, lateral tubercles of fourth and sixth abdominal segments; T1-LT, T2-LT, T3-LT, lateral tubercles of prothorax, mesothorax and metathorax

three to four annulations; terminal (third) segment rounded, tapering distally, terminus with small, pale, round projection bearing ventral pore and several microsetae apically; maximum width of terminal segment approximately one-half maximum width of second segment. Basal (first) palpal segment with two pairs of long distal setae, one lateral, one mesal; terminal annulation of middle segment with two long setae near apex, one lateral, one mesal. Antenna 0.35–0.38 mm long; scape set within pedicellate cranial extension, heavily sclerotized, rounded, tubular, straight sided, with sharp projection on lateral base; pedicel elongate, tapering, with ~five or six rounded annulations on basal half, with irregular annulations on distal half. Flagellum round in cross section, narrow, tapering to slender, bifurcated terminus; base with lateral spur; spur sheath-like, slender, elongate, wrapped partially around flagellum, extending distally almost to terminus of flagellum, closely pressed against lateral margin of flagellum (often difficult to see); terminus with two elongate (length up to 0.1 mm), very fine terminal setae extending anteriorly, then curving toward each other, with mesal seta usually longer than lateral one.

Cephalic coloration (Figs 2, 3, 6). Anterodorsal surface of cranium entirely dark brown, becoming pale near posterior margin (normally concealed within cervical membrane), no specific cephalic markings distinguished; integument around and between stemmata dark brown; pedicellate cranial extension dark brown dorsally, pale ventrally. Venter with cranial margin, sclerites dark brown; intersegmental membrane pale. Antenna with scape, base of pedicel dark brown; pedicel with annulations brown basally, lighter brown distally; flagellum light brown to amber. Mandible and maxilla brown basally, light brown to amber distally. Labial palp with basal segment dark brown; annulations of second segment brown, membrane between annulations pale; distal segment brown basally, becoming lighter brown to amber distally.

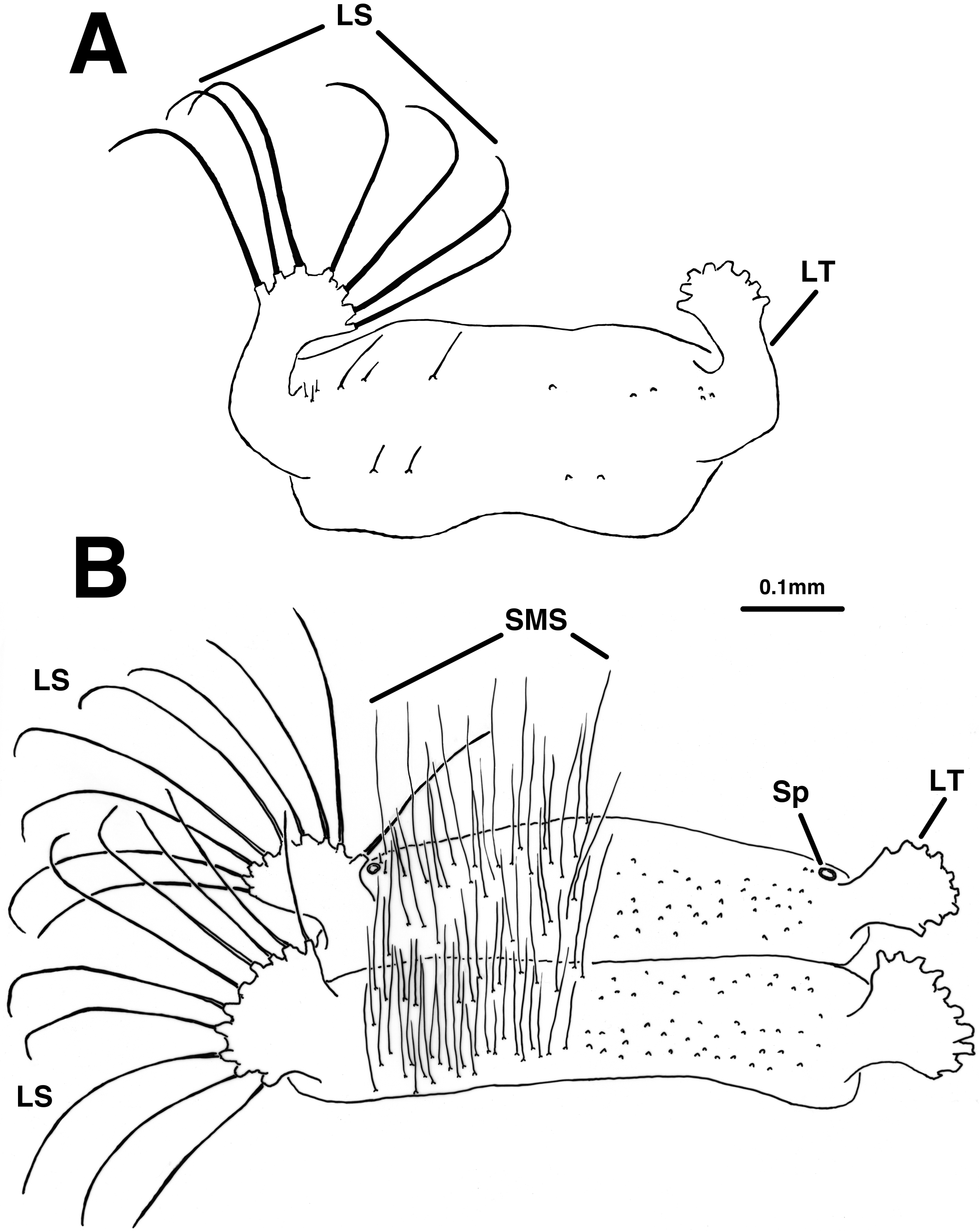

FIGURE 7. *Abachrysa eureka* (Banks), first instar, thorax, dorsal. A. Prothorax. B. Mesothorax and metathorax (SMS more numerous than shown). LS, setae on lateral tubercle; LT, lateral tubercle; SMS, submedian setae; Sp, spiracle. Scale applies to A and B.

Thorax (Figs 6, 7). Each segment with pair of broad, thick, palmate, lateral tubercles (LTs); distal margin of each LT with robust chalazae bearing prominent setae (LS); LS long, robust, denticulate, with distal region usually bent at 90° angle, with tip stout, straight, unhooked; sclerites not distinguished. Prothorax with dorsal surface dark brown, smooth, probably well sclerotized throughout, having sparse setae, no microsetae; each LT with seven to eight LS, anterior LS extending above head well beyond posterior margin of eyes; pronotal setae medium length (not extending beyond segmental margin), smooth, straight, with acute (unhooked) tips, arising from small chalazae: three short setae mesal to each LT, two medium-length setae anteromesal to base of each LT, one pair of shorter setae between them, two pairs of short setae posteriorly. Mesothorax, metathorax with dorsal surface having dense covering of submedian setae (SMS), no microsetae; LTs similar to those on prothorax, each bearing eight to ten long LS; laterodorsal tubercles (LDTs) absent; SMS arranged in two broad bands across surface of each segment; SMS very long, slender, smooth, extending anteriorly from small chalazae. Mesothoracic spiracle very small, oblong, sessile, located near anteromesal base of LT; spiracular seta (SSp) not identified.

Leg (Figs 6, 8). Brownish distally, pale basally; setae smooth, with acute tips. Coxa elongate, trochanter triangular, both with few setae; femur with moderately dense setae; tibia with numerous setae, separate from tarsus; tarsus short, with two setae at tip, above claws; tarsal claws slender, deeply cleft; empodia long, with stiff, elongate bristle beneath.

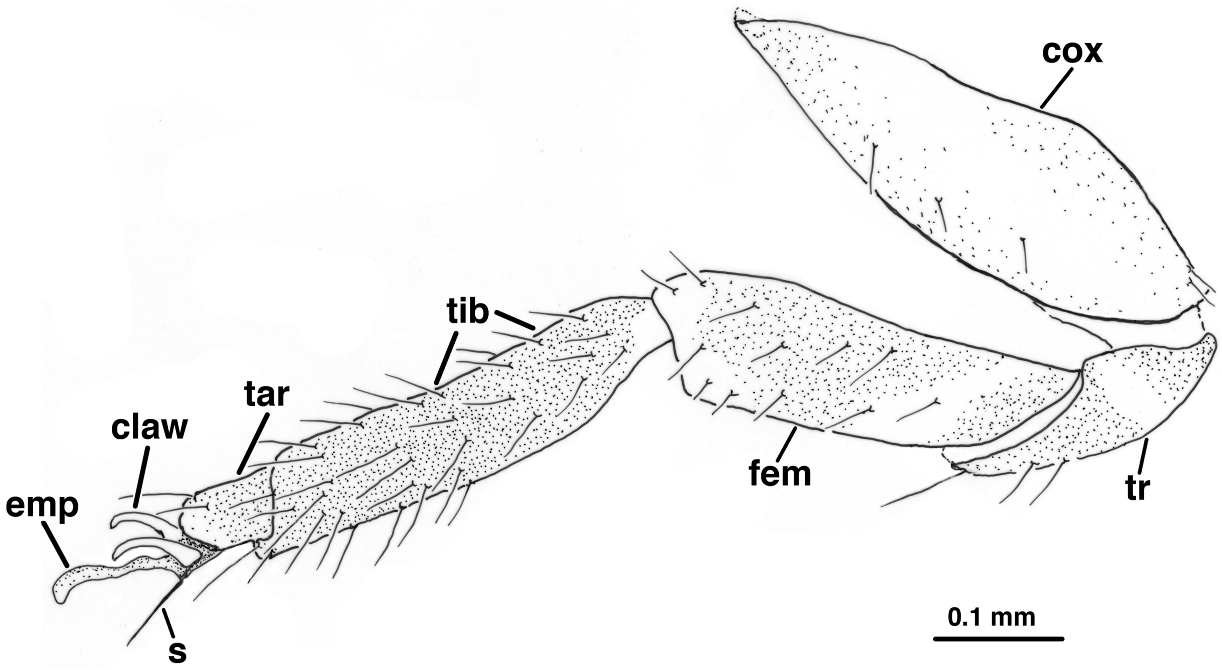

FIGURE 8. *Abachrysa eureka* (Banks)*,* first instar, metathoracic leg, lateral. claw, pretarsal claw; cox, coxa; emp, empodium; fem, femur; s, stiff apical seta; tar, tarsus; tib, tibia; tr, trochanter.

Abdomen (Figs 6, 9). First segment (A1) short, narrow, with no spiracle, LT, or LDT; dorsum with transverse band of dense SMS arising from small chalazae. Segments A2–A5 more robust (longer, broader) than A1, each bearing pair of bulbous LTs, round spiracular opening near dorsomesal margin of LT, no laterodorsal tubercles (LDTs). LTs white to cream dorsally, with brown marking on ventrolateral base, visible laterally; each LT with two denticulate LS, no microsetae. Spiracular opening large, round, with well sclerotized ring around margin, with bulbous atrium beneath. Dorsum of each segment with transverse band of dense SMS similar to those on A1. Segments A6–A7 each with LTs, LS, and spiracles similar to those on A2–A5, pair of laterodorsal tubercles (LDTs) near anteromesal margin of LT base. LDTs each bearing two (A6) or three (A7) robust, denticulate, acute, laterodorsal setae (LDS), one long, others short to medium length; segments without microsetae. Dorsal surface of A6 with transverse band of SMS between LTs; posterior section without setae. Dorsum of A7 dark brown, well sclerotized, without elongate, slender SMS as on A1–A6, with shorter, smooth, acute setae as follows: one pair of setae (SSp) associated with spiracles, two pairs of anterior setae between spiracles, two pairs of longer, more robust setae between LTs, single pair of setae near posterior margin. Segment A8 dark brown, well sclerotized dorsally; LT short, bulbous laterally,

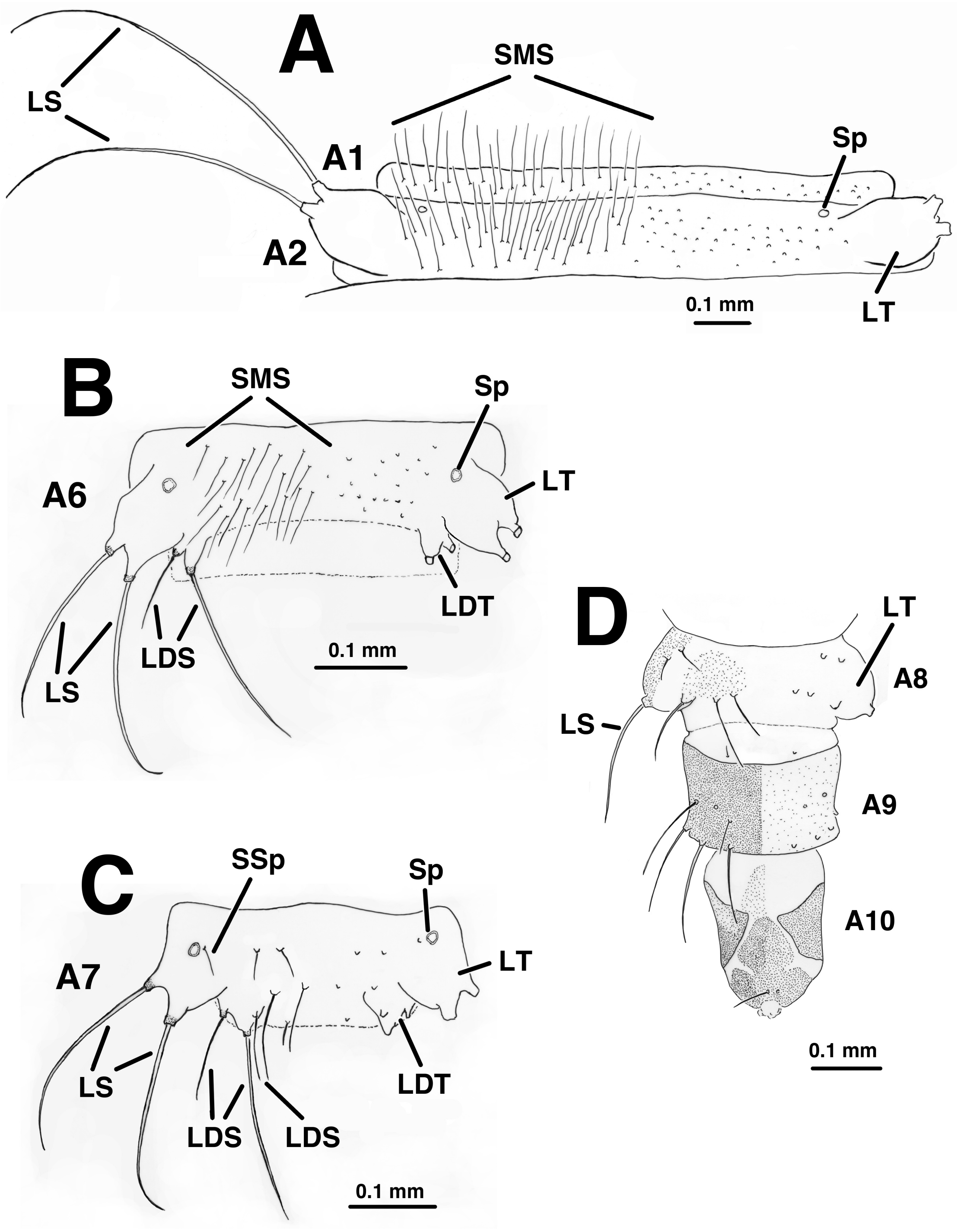

FIGURE 9. *Abachrysa eureka* (Banks)*,* first instar, abdomen, dorsal. A. First and second segments (SMS more numerous than shown). B. Sixth segment. C. Seventh segment. D. Eighth, ninth, and tenth segments. A1–A10, abdominal segments; LDS, setae on laterodorsal tubercle; LDT, laterodorsal tubercle; LS, setae on lateral tubercle; LT, lateral tubercle; SMS, submedian setae; Sp, spiracle; SSp, spiracular seta.

with robust, denticulate LS—one longer than other; dorsum with two pairs of robust, denticulate setae in midsection between LTs, two pairs of short, smooth, acute setae anterolaterally. Segment A9 tubular, dark brown to black, heavily sclerotized posteriorly; anterior (lighter) section with pair of very small setae; midsection with single pair of long, robust, denticulate setae laterally, pair of white spots (pores) mesal to setae; posterior section with three pairs of long, robust, denticulate setae near posterolateral margin. Segment 10 with large, dark brown to black sclerites; dorsum without setae except for single pair of smooth, acute setae near terminus.

Third instar (Figs 10–12)

Body. Stocky, globose dorsally, flat ventrally; thoracic, abdominal nota wide, extending fully over sides of body, with LTs extending laterally from ventral margins of nota. Integument of thorax and abdomen with dark transverse (possibly sclerotized) bands, separated by pale bands and intersegmental membrane. Four types of setae: (i) smooth, hooked, as described for *I. insignis* (covering almost entire exposed dorsal surface of body); (ii) stout, short, straight, with acute tip, possibly with rough surface (on upper surface of head, distal margins of trochanters); (iii) stout, with blunt to acute tip, possibly with rough surface, some curved, others with distal one-third to one-fourth bent almost perpendicularly, as described for *I. insignis* (on distal margins of LTs of T1–T3, A2–A7); (iv) simple, small, straight, with acute tip (at base of LTs on A7; on dorsum of A8, A9; on venter of A3–A7; on femora, tibiae).

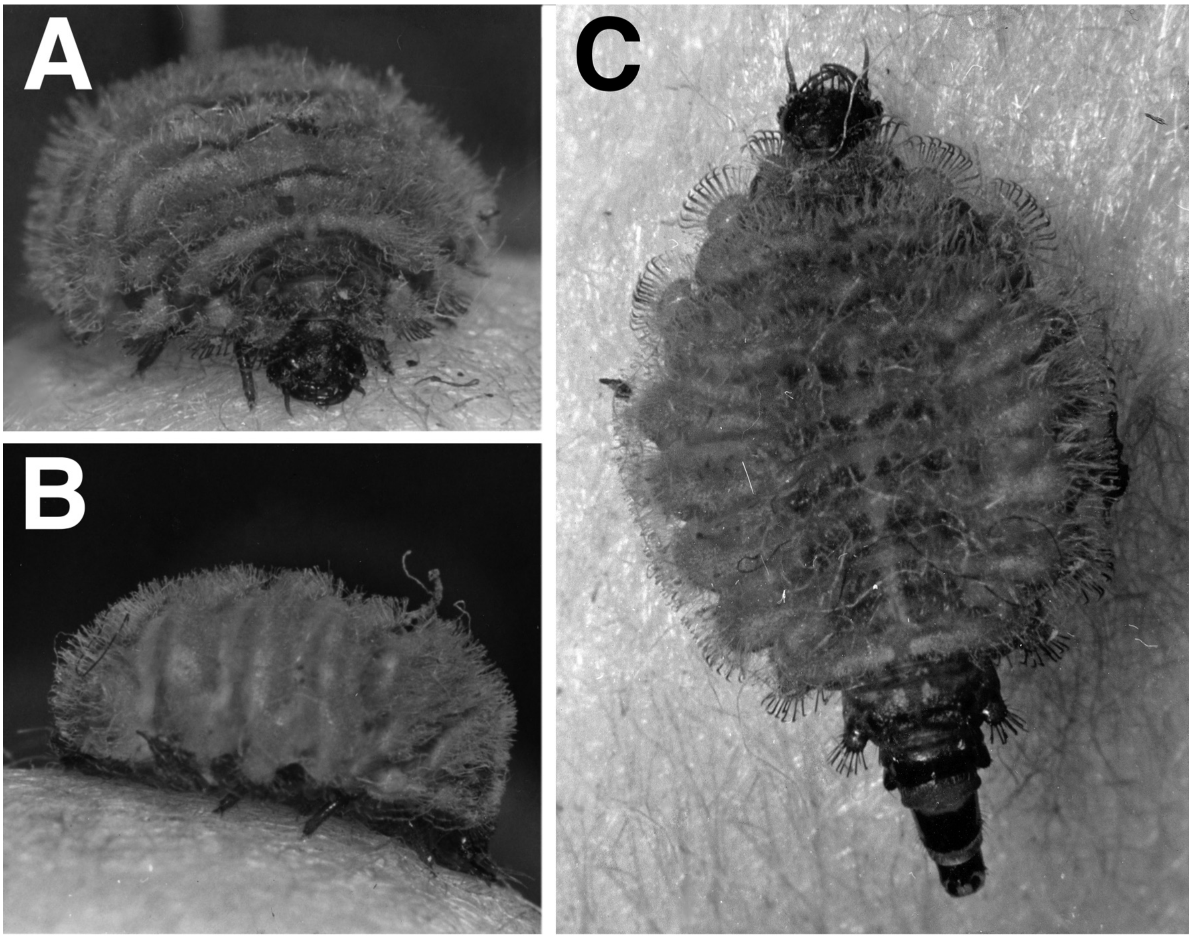

FIGURE 10. *Abachrysa eureka* (Banks), third instar. A. Head and thorax, anterior. B. Habitus, lateral (head and apical abdominal segments withdrawn). C. Habitus, dorsal (head and apical abdominal segments extended). Photos: E. G. MacLeod.

Cranium. Appearing quadrate, but perhaps not as much as in *I. insignis*; anterior margin slightly convex; without noticeable markings; dorsal setae dark.

Cephalic appendages. Mandibles short, stout, with acute tip. Antenna filiform, tapering, extending beyond end of mandibles; scape located within sclerotized cranial extension, with stout setae on distolateral margin; pedicel annulated; flagellum tapered, apparently with elongate terminal seta(e), as illustrated by Principi (1944) for *I. italica* (and broken off of Tauber and Winterton's specimen of *I. insignis*). Cervix dark, probably well sclerotized, at least laterally.

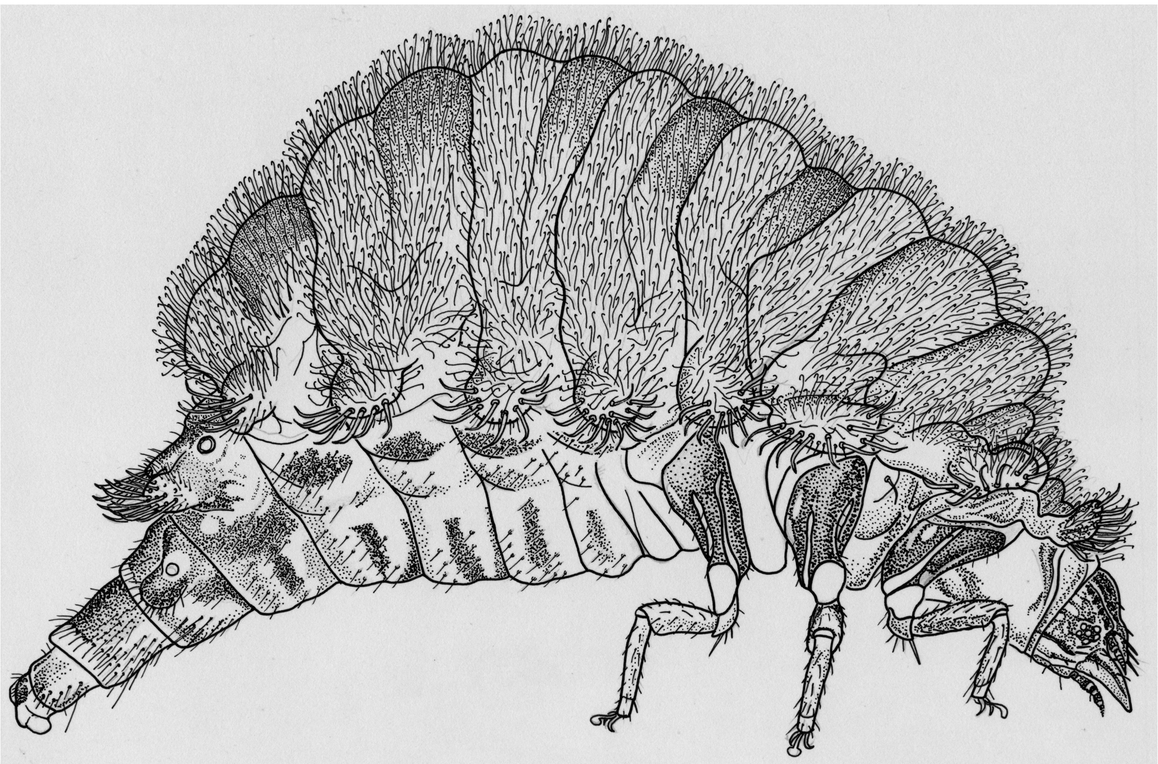

FIGURE 11. *Abachrysa eureka* (Banks), third instar, habitus (walking), lateral. Drawing: E. G. MacLeod.

Thorax. Segments broad, dorsoventrally thickened, each with pair of LTs; LTs robust, palmate, rounded distally, with distal margin bearing stiff, robust, bent LS, with dorsal surface bearing sparse, smaller, apparently acute setae; prothorax appearing to have two subsegments, mesothorax with three subsegments, metathorax apparently with one. Legs short, stocky, dark; coxae elongate dorsoventrally, appearing well sclerotized and dark; tarsi particularly short.

Abdomen. Segments A1–A6 broad, thick; together with thorax forming large, densely setose, dorsal arch of body; A1 with only one visible subsegment, without LTs, dorsally about as long and wide as metathoracic posterior subsegment, excluding LTs. Segments A2–A6 each with two subsegments dorsally, subsegments merging above LTs; LTs round, spherical distally, with short base, bearing robust, curved, or bent LS distally, smaller, hooked setae dorsally. Segments A7–A10 with subsegmentation not apparent; each segment narrower than, and probably partially retractable within preceding segment; surfaces with sparse, short, acute setae. A7 with LTs about as long as those on A5 or A6, but much narrower, their apices with dense covering of robust, acute LS extending posteriorly; spiracles near anterior margin of segment. A8 with small lateral LTs bearing short, slender, acute setae; spiracles at base of segment. A9, A10 conical (LTs absent), with short slender, acute setae.

Biology

Little is known about the biology of *A. eureka*. However, based on our experiences and MacLeod's notes, we can provide some new information.

Egg stage. Five field-collected females laid 57 eggs, 49 (86%) of which hatched. The eggs were laid between September 19 and October 14, 2015 and hatched in 10 to 14 days (under laboratory conditions).

Larval development. MacLeod's rearing started with a female specimen that Joseph Sheldon collected on Boot Key, FL (July 25, 1968) and sent to him at the University of Illinois. The specimen laid nine eggs en route by July 30; two were used for chromosome preparations, and four hatched on August 8 and 9. Three additional eggs were laid during the first week of August. MacLeod's notes do not indicate a hatching date for either the three remaining eggs that were laid before arrival or the three that were laid after arrival. Presumably, they did not hatch.

MacLeod recorded rearing notes for four *Abachrysa* larvae held in shell vials (25°C, L:D 14:10, 80% relative humidity); all instars fed on the larvae and pupae of the ants that he provided (species not specified), but none accepted aphids, disabled termites, or ether-killed *Drosophila*. He recorded the following developmental times for the various stages—L1: 15 days (n = 2); L2: 8 and 11 days (n = 2); L3: 28 days (n = 1), mature L3 within cocoon: 10 days (n = 1); pupa within cocoon: 15 days (n = 1, a male that emerged on October 23). One second instar and one third instar were preserved. Unfortunately, the specimens are missing; however, MacLeod made an excellent drawing and took photos of the third instar.

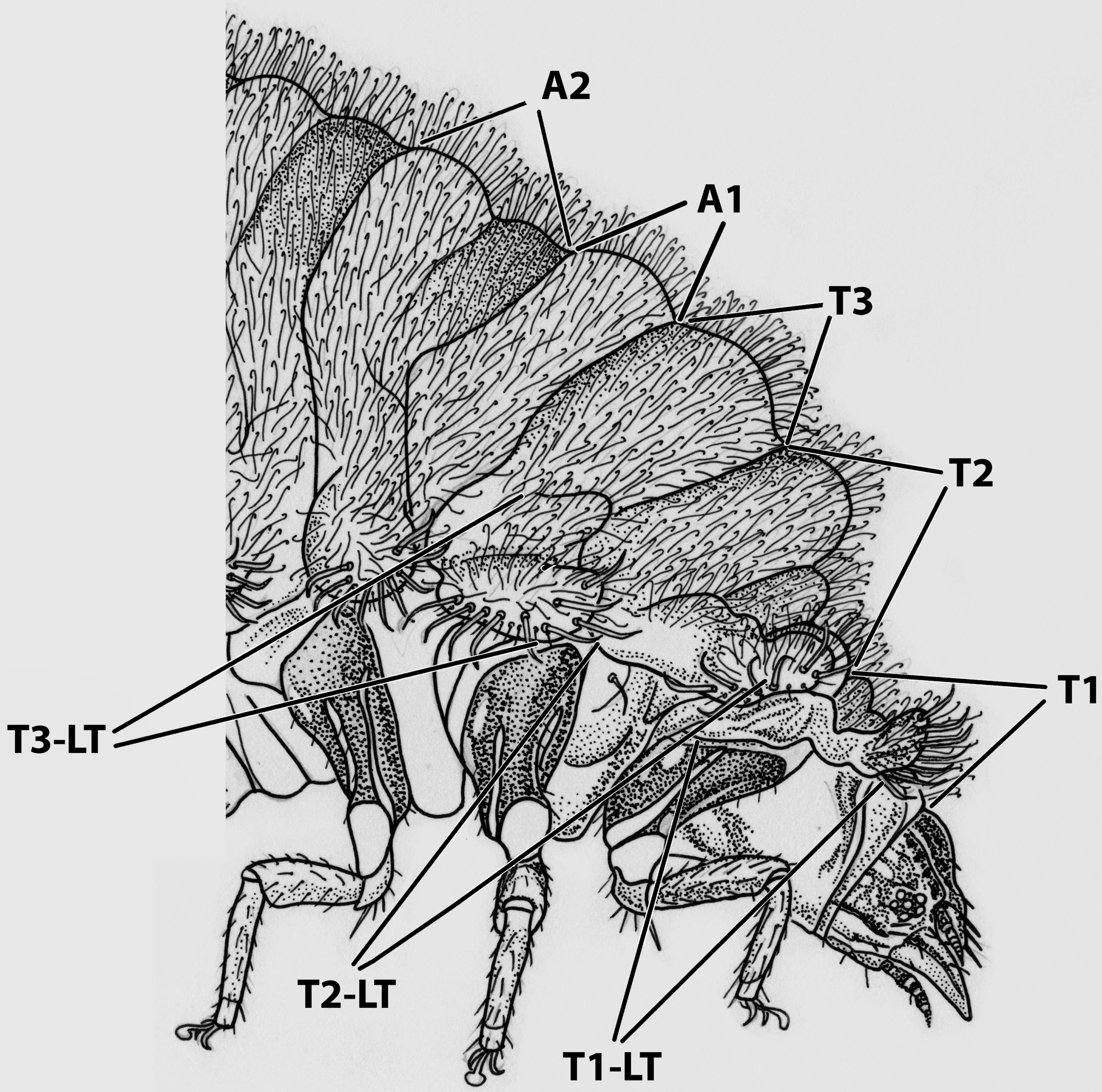

FIGURE 12. *Abachrysa eureka* (Banks), third instar, head and thorax, lateral. A1, A2, first and second abdominal segments; T1–T3, first to third thoracic segments; T1-LT, T2-LT, T3-LT, prothoracic, mesothoracic, and metathoracic lateral tubercles. Drawing: E. G. MacLeod.

Larval behavior. MacLeod's notes do not mention that the larvae engaged in "loading behavior", i.e., the series of movements that debris-carrying chrysopid larvae typically exhibit in order to apply debris to their dorsa.

Adult behavior. MacLeod indicated that adults emit a defensive odor similar to that of many species of green lacewings; he referred to it as a "moderate", "usual" odor (see Blum *et al*. 1973). Also, his notes include a photo of a pinned adult *A. eureka* that he examined at the Museum of Comparative Zoology, Harvard University, Cambridge, MA. This specimen carries a worker ant (*Pheidole* sp.) firmly attached to a metathoracic leg (Fig. 13), perhaps indicative of an ant association.

FIGURE 13. Ant worker (*Pheidole* sp.) attached by its mandibles to the metatibia of a female *A. eureka* specimen in the Museum of Comparative Zoology (MCZ). Photo: E. G. MacLeod.

Seasonal emergence. Based on collection records from numerous museums, Catanach (2007) concluded that *A. eureka* has two peaks of adult emergence, one in the spring and another in the fall. The second emergence appears to be smaller in the southeastern states than in Texas, where it can be substantial.

Systematics of Belonopterygini—Larval Characters

Tribal features

A number of larval features have been proposed as possible synapomorphies for the tribe Belonopterygini (Tauber *et al*. 2006, 2014; Monserrat & Díaz-Aranda 2012). The most recent and comprehensive list was based on published information from species in three genera: *Calochrysa* (L1, one species)*, Italochrysa* (L1, two species; L3, one species), and *Vieira* (as *Berchmansus,* L1, one species) (Tauber *et al*. 2014). Here, with the addition of data from *Abachrysa* (L1, L3) and *Nacarina* (L3) which was not considered in earlier work, we re-examine and refine the list of possible larval belonopterygine synapomorphies. We caution readers that the taxon sampling for our conclusions here is small, both in terms of the number of genera and the number of species within each genus for which larval descriptions or biological data are available. It is also noteworthy that the Old World belonopterygine genera are closely related to each other; indeed, at least two of them branch phylogenetically from within *Italochrysa* and may be synonymous with the genus (Winterton *et al*. 2019). Their larvae are unknown.

For our discussion in the paragraphs below, characters marked with an asterisk [*] are proposed as synapomorphic for Belonopterygini, because they are present in all described larvae within the tribe and are absent from outgroup taxa in Leucochrysini (sister to Belonopterygini), Nothochrysinae, and Apochrysinae (all sensu Winterton *et al*. 2019). Morphological data for outgroup taxa were derived from the following sources: Nothochrysinae—

Pimachrysa, Nothochrysa: Monserrat & Díaz-Aranda (2012), Tauber & Faulkner (2015); Apochrysinae—*Apochrysa*: Tsukaguchi (1995), Tauber (2014); Leucochrysini—*Berchmansus*: Tauber & Tauber (2013);—*Gonzaga*: Tauber *et al*. (2008a);—*Leucochrysa* (*Nodita*): Mantoanelli *et al*. (2011);—*L. (Leucochrysa*): Mantoanelli *et al*. (2006), Tauber *et al*. (2011, 2013);—*Santocellus*: Tauber *et al*. (2008b); and Chrysopini—*Ceraeochrysa*: Tauber & de León (2001);—*Chrysopodes*: Silva *et al*. (2013).

1. *Mandible considerably shorter than sagittal length of cranium (L1, L3). The *A. eureka* mandibles range from 0.76–0.82x the sagittal length of the cranium, similar to measurements of other belonopterygine genera with known larvae. All other known chrysopid larvae have mandibles that are at least the length of the cranium. Thus, with the addition of data from *A. eureka*, this feature remains synapomorphic for the tribe Belonopterygini.
2. Antenna with base of scape at least partially retractable into a prominent expansion of the cranium (here referred to as "sclerotized cranial expansion") (L1, L3). We have confirmed this feature in *A. eureka* first instars, and from MacLeod's photos it appears to occur in third instars. A prominent cranial expansion is reported from the *I. insignis* third instar, and moderately enlarged ones from *V. elegans* and *I. stigmatica* first instars. A weakly developed, antenna-bearing, cranial protuberance is present in some Leucochrysini (e.g., *Berchmansus*) and some Chrysopini (e.g., *Ceraeochrysa, Chrysopodes*), but in all of these cases, the protuberance is smaller, and it does not appear that the scape can be retracted. Such cranial expansions are not reported from other outgroup larvae.
3. *Mandibles stout, with width ~one-third length (L1, L3). The *A. eureka* mandibles are short and stout (W : L = ~0.33), similar to those of the other three belonopterygine genera. Larvae from all of the outgroups have mandibles that are considerably more slender (W : L < 0.20).
4. Labial palpus with second segment short, stout, less than length of first and third segments combined (L1, L3). The *A. eureka* larvae share this feature with the other three belonopterygine genera, and they differ from the outgroup larvae, which tend to have slender palps in which the second segment is longer, often considerably longer than the first and third segments combined.
5. Flagellum with two apical setae (L1). In *Abachrysa* the flagellum terminates with two elongate, filamentous setae that extend and curve toward each other distally. The first instar *Vieira* has two filamentous terminal setae; they are of differing lengths. In *Calochrysa*, the flagellum terminates in an elongate, slender seta and a short, more robust seta. Also, in *Italochrysa* there appears to be a single moderately long filamentous seta and a small, spike-like seta beside it. Thus, unlike the outgroup larvae—which have only one terminal flagellar seta—all four belonopterygine species have two terminal setae. However, the variation in the size and structure of the second seta is considerable, and the character needs further comparative study.
6. Pronotal sclerites apparently absent or very small (L1). We did not discern thoracic sclerites on *A. eureka* first instars. However, on our cleared specimens we noted that the entire pronotum may be at least lightly sclerotized. It is smooth and without microtrichia, and the texture appears similar to sclerotized regions on other cleared chrysopid larvae. We suggest that the pronotal sclerites may have coalesced into a contiguous pronotal covering, as is the case in the *L. insignis* first instar [photos by R. A. Pantaleoni and C. F. Cesaroni, published in Tauber & Winterton (2014)] and the *I. insignis* third instar (Tauber & Winterton 2014). This tentative belonopterygine pattern remains consistent for belonopterygine larvae and differs markedly from that described for leucochrysine larvae, which have discrete, well developed pronotal sclerites.
7. Setae associated with lateral tubercles (thoracic and abdominal LS) robust, with rough texture (L1). All of the belonopterygine first instars studied thus far share this feature, but some larvae in other tribes may express it as well. Thus, the character may not be synapomorphic for Belonopterygini, but it remains worthy of further investigation.

Significant generic features

The following features show considerable variation among the belonopterygine genera for which first instars have been studied. In most cases, if not all, the pattern of variation affiliates *Abachrysa* with *Calochrysa* and *Italochrysa,* but separates it from *Vieira*. See details and images of *Italochrysa* by New (1983) and Monserrat & Díaz-Aranda (2012); *Calochrysa* by New (1986); and *Vieira* by Tauber *et al*. (2006).

1. Cranial shape. First instars of *Abachrysa*, *Calochrysa, and Italochrysa* share a quadrate posterodorsal margin to the cranium. The *Vieira* first instar*,* with its basally rounded posterodorsal margin, is the unique outlier (Fig. 14).
2. Pedicel shape. *Abachrysa*, *Calochrysa,* and *Italochrysa* all have a slender pedicel that tapers gradually throughout its length, and the diameters of the pedicel and flagellum are similar at their articulation. *Vieira* is distinct in possessing a mesally swollen pedicel, and at their junction the flagellum and pedicel have dissimilar diameters (Fig. 14).

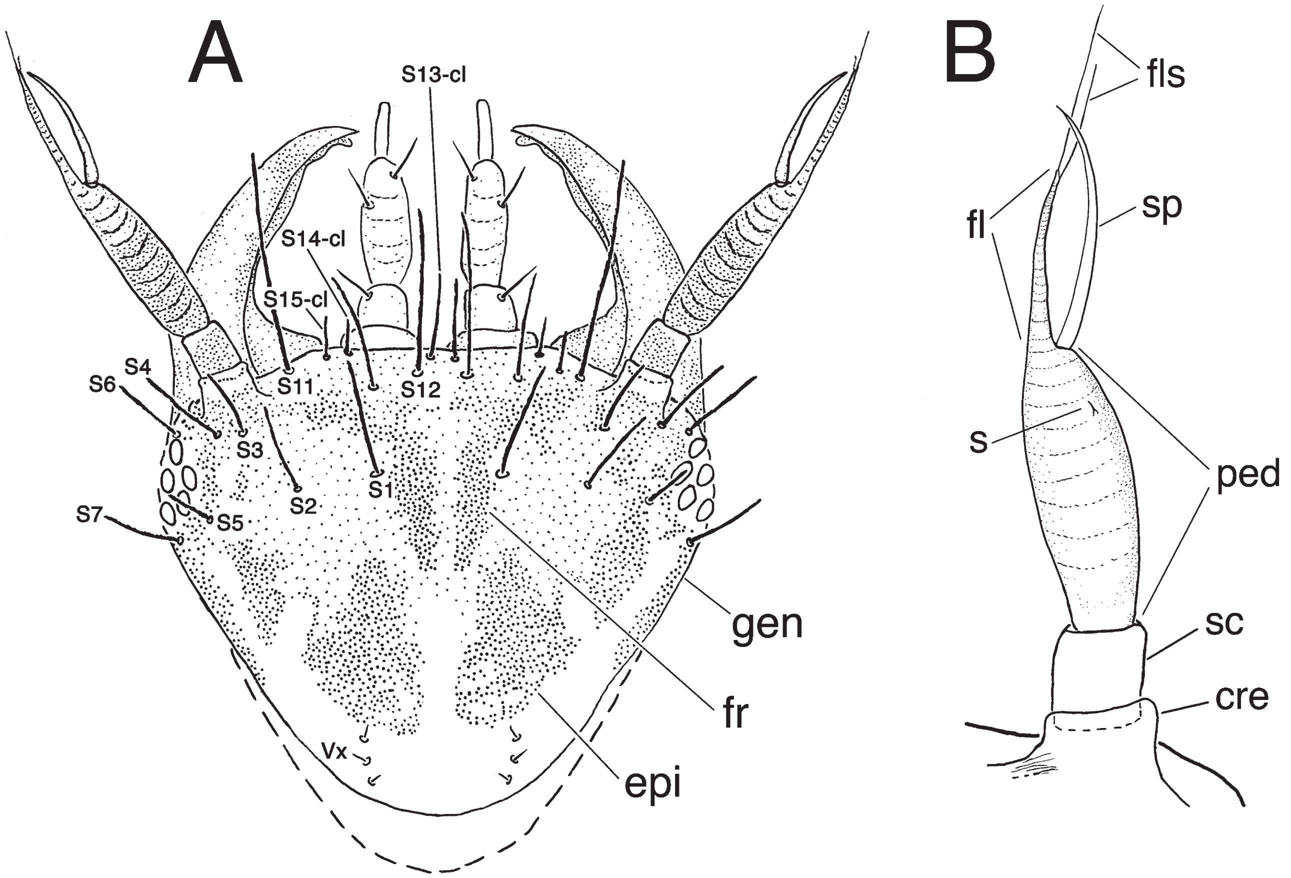

FIGURE 14. *Vieira elegans* (Guérin-Méneville), first instar, correction of Figures 1 (left) and 5 (right) from Tauber *et al.* (2006). A. Head, dorsal. B. Antenna, lateral. cre, pedicellate cranial extension; epi, epicranial marking; fl, flagellum; fls, flagellar setae; fr, frontal marking; gen, genal marking; s, seta; sc, scape; sp, flagellar spur; S1–S7, S11–S12, primary cranial setae; S13-cl, S14-cl, S15-cl, clypeal setae; Vx, three short posterior setae.

3. Antennal ornamentation. In *Abachrysa,* a rounded sheath-like structure extends distally from the base of the flagellum or tip of the pedicel. It is long, thin, acute, and closely appressed to the distal part of the flagellum. In *Italochrysa* no modification is reported at the base of the flagellum, and in *Calochrysa* the only modification near the base of the flagellum is a stout, acute seta. By contrast, in *Vieira* a very large articulated spur arises mesally from the base of the flagellum or tip of the pedicel; the spur is slightly longer than the flagellum. Whether any of the modifications are homologous is unknown, but they are intriguing and worthy of further investigation.
4. Thoracic lateral tubercles (LTs). First instars of *Abachrysa, Calochrysa,* and *Italochrysa* have thoracic LTs that are broadly palmate distally; each LT bears at least six long LS distally. The plesiomorphic condition is a 2-3-3 pattern of pro-/meso-/metathoracic LS. This character state is typical of first instars of all other studied chrysopids, including the first instar of the belonopterygine *V. elegans*.
5. Mesothoracic and metathoracic laterodorsal tubercles (LDTs). *Abachrysa*, *Calochrysa,* and *Italochrysa* all lack LDTs (and therefore also LDS). *Vieira elegans* possesses both meso- and metathoracic LDTs that each bear ~12–14 long, hooked LDS.
6. Pronotal setae. *Abachrysa* and *Italochrysa* have relatively few (~10) pronotal setae; most are small to medium sized and simple. The character state for *Calochrysa* is unknown; New (1986) described the *Calochrysa* thorax

as having a "dense vestiture of long slender filaments, some of them hooked", but he did not illustrate them. *Vieira* differs from *Abachrysa* and *Italochrysa* in that it possesses a prominent row of ~14 long, robust, hooked setae along the anterior margin of the pronotum and a shorter second row of ~6 long, hooked, chalazate setae along the posterior margin.

7. Mesonotal and metanotal submedian setae (SMS). The first instars of *Abachrysa*, *Calochrysa*, and *Italochrysa* possess numerous meso- and metanotal SMS that are densely packed in irregular transverse rows or are arranged in a dense dorsal patch that lacks distinct rows. In all three genera the SMS are filamentous; in *Abachrysa* they are extremely fine. In contrast, the robust, hooked meso- and metanotal SMS of *Vieira* have distinct chalazae and are arranged in two discrete transverse rows.
8. Abdominal laterodorsal tubercles (LDTs). *Abachrysa, Calochrysa,* and *Italochrysa* lack LDTs A1–A5; LDTs are present on A6 and A7 in *Abachrysa* and *Calochrysa*, and only on A7 in *Italochrysa*; each of these LDTs bears two or three LDS. *Vieira* possesses LDTs on A1–A7; the LDTs on A1–A5 bear ~10–14 long, hooked LDS; the LDTs on A6–A7 each bear three LDS.
9. Dorsal setation of proximal abdominal segments (A1–A6). In *Abachrysa, Calochrysa,* and *Italochrysa*, the dorsal setae of A1–A6 occur in a dense patch or are arranged in tightly packed transverse rows of filamentous SMS arising from small chalazae. By contrast, segments A1–A6 of *Vieira* each have two somewhat irregular, transverse rows of SMS between the LDTs. The SMS are more elongate and stout than those of the other genera, and they arise from large chalazae.
10. Pattern of setation. With slight modification of the earlier description of setal type (i) from only "blunt" to "blunt or acute", larvae of all three genera, *Abachrysa, Calochrysa,* and *Italochrysa*, express a shared pattern of setation (setal type and position), as follows: (i) ornamented, robust, blunt or acute setae (primary setae on dorsal cranium); (ii) elongate, robust, denticulate, acute or hooked setae that are strongly curved or perpendicularly bent distally (lateral setae, LS, on tips of thoracic and abdominal lateral tubercles); (iii) long, slender, hooked or sometimes straight, submedian setae, SMS (dorsal integument of T2, T3, A1–A6, and dorsal surfaces of thoracic and abdominal LTs); (iv) short, straight, acute setae (e.g., primary setae on ventral cranium; some setae on dorsum of T1, T2, A7–A10; setae on venter of thorax and abdomen). The above pattern of setation, as well as setal type (ii) itself, appear to be unique among the Chrysopidae; to our knowledge, they have not been reported from larvae other than the three belonopterygine genera *Abachrysa, Calochrysa,* and *Italochrysa*. In the fourth belonopterygine genus, *Vieira*, first instars are similar to those of the other studied belonopterygine genera in both the form and placement of setal types (i) and (iv). However, they lack types (ii) and (iii) of the other genera. Their thoracic and abdominal LS are elongate, smoothly curved, and hooked terminally, and their SMS setae are stout, hooked terminally, and extending from enlarged chalazae.
11. Egg size. Egg size now has been reported for six benolopterygine species in four genera (Table 1). While their egg sizes differ, the *Abachrysa, Calochrysa,* and *Italochrysa* species all have eggs that are substantially larger than those of *V. elegans*.

Features unique to *A. eureka*

Two features appear to distinguish first instar *A. eureka* from first instars of other belonopterygines.

1. Cranium entirely dark brown, without distinguishable pale marks. *Italochrysa insignis* has large, paired, brown epicranial marks and small, paired frontal marks; *I. stigmatica* has small, indistinct, brownish cephalic spots. *Calochrysa extranae* has small epicranial and frontal marks; and in *Vieira elegans* the cranium generally is light brown, with distinguishable, darker brown, paired epicranial and frontal markings. No postfrontal markings have been reported for belonopterygine larvae. The entirely dark cranium also appears to be characteristic of the third instar *Abachrysa*; both *I. italica* and *I. insignis* L3 differ in having distinct brownish markings on a lighter cranial background.
2. Denticulate type (i) cephalic setae (S1–S7, S11, S12) acute. In the other belonopterygine genera, including *Vieira*, these cephalic setae are blunt.

Phylogeny and the evolution of myrmecophily in belonopterygine larvae

Two recent phylogenetic studies of Chrysopidae—one based on a molecular supermatrix approach (Garzón-Orduña *et al*. 2019) and another based on an anchored phylogenomics approach (Winterton *et al*. 2019)—tested exemplars from three of the four New World belonopterygine genera—*Vieira, Nacarina*, and *Abachrysa*—and seven of the eleven Old World genera, including the two with known larvae, *Italochrysa* and *Calochrysa.* Both of these studies recovered a monophyletic tribe Belonopterygini in which the New World genera resolve as basal, and the Old World genera form a distal clade. The authors interpreted their recovered branching patterns as the result of a single divergence of Old World belonopterygines from a New World ancestor during the Paleogene.

TABLE 1. Egg size in four genera of Belonopterygini.

Species	Egg length (mm)	Egg width (mm)	Volume[1] (mm^3)	Stalk length (mm)
[2]*Abachrysa eureka* (n=48–50)	1.5–2.7	0.4–0.8	0.57	5.5–11.7
[3]*Abachrysa eureka* (n=1)	3.0	1.1	1.90	9.2
[4]*Calochrysa extranea* (n=1)	1.5	0.7	0.38	5.7
[5]*Italochrysa italica* (n=1)	2.7	0.9	1.14	10.0
[6]*Italochrysa insignis* (n=5)	1.6	0.6	0.30	8.3
[7]*Italochrysa stigmatica* (n=1)	2.5	0.8	0.84	10–15
[8]*Italochrysa japonica* (n=1)	1.5	-	-	-
[9]*Vieira elegans* (n=1)	0.8	0.4	0.07	6.6

[1] Volume of prolate ellipsoid = $\frac{\pi}{6}(minor\ \ axis)^2(major\ \ axis)$ In this case the major axis is egg length, and the minor axis is egg width; see Tauber *et al.* (1991).
[2] Catanach (2007); volume calculated from means of egg length and egg width
[3] Egg photographed, with scale, by SKK (TAMUIC, Lot 712)
[4] New (1986)
[5] Principi (1944)
[6] New (1983)
[7] Monserrat & Díaz-Aranda (2012); width estimated from their Fig. 1
[8] Tsukaguchi (1995)
[9] Tauber *et al*. (2006)

The results from our morphological study are consistent with the interpretation based on the two molecular studies, and they provide additional insights that we discuss here (summarized in Fig. 15). Most significant is our finding that the highly derived larval morphology of the New World *Abachrysa* clearly aligns the genus with those in the Old World. Thus, it appears that the major developmental and morphological modifications that typify the known larvae in the Old World lineage first appeared in the New World and persisted after the introduction and diversification of an *Abachrysa*-like ancestor into the Old World (e.g., as exemplified by the genera *Calochrysa* and *Italochrysa*). We refer to the New and Old World belonopterygines that express this pattern of highly modified larval morphology as the "*Abachrysa-Italochrysa* clade".

This congruence of findings provides a framework for exploring several questions concerning the evolution of larval morphology in relation to lifestyle, specifically myrmecophily and debris carrying as expressed in the Belonopterygini.

Question 1. What evidence supports the proposal of a myrmecophilic lifestyle for the tribe Belonopterygini?

The term myrmecophily ("ant-loving") is used in a variety of different ways depending on the author and the taxon of interest (e.g., Allaby 1985, Parker 2016), but all involve the derivation of some essential benefit (food or protection) from living in or near ant colonies, and usually some form of morphological and/or behavioral adaptations for avoiding harm from the host ants. Here we use this simple definition in our discussion of myrmecophily in the tribe Belonopterygini.

The tribe Belonpterygini is the only chrysopid clade currently known to contain any myrmecophilic species, in this case, predaceous larvae associated with ant colonies (externally or internally) and using ant brood as prey. Also, no species in the tribe are known to feed on prey other than ant brood (e.g., Brooks & Barnard 1990). Biological information on the various belonopterygine taxa is relatively sparse, and ant associations are confirmed from field observations and/or rearing from only three genera. Of these, two occur in the derived *Abachrysa-Italochrysa* clade and one in a basal New World genus, *Nacarina*.

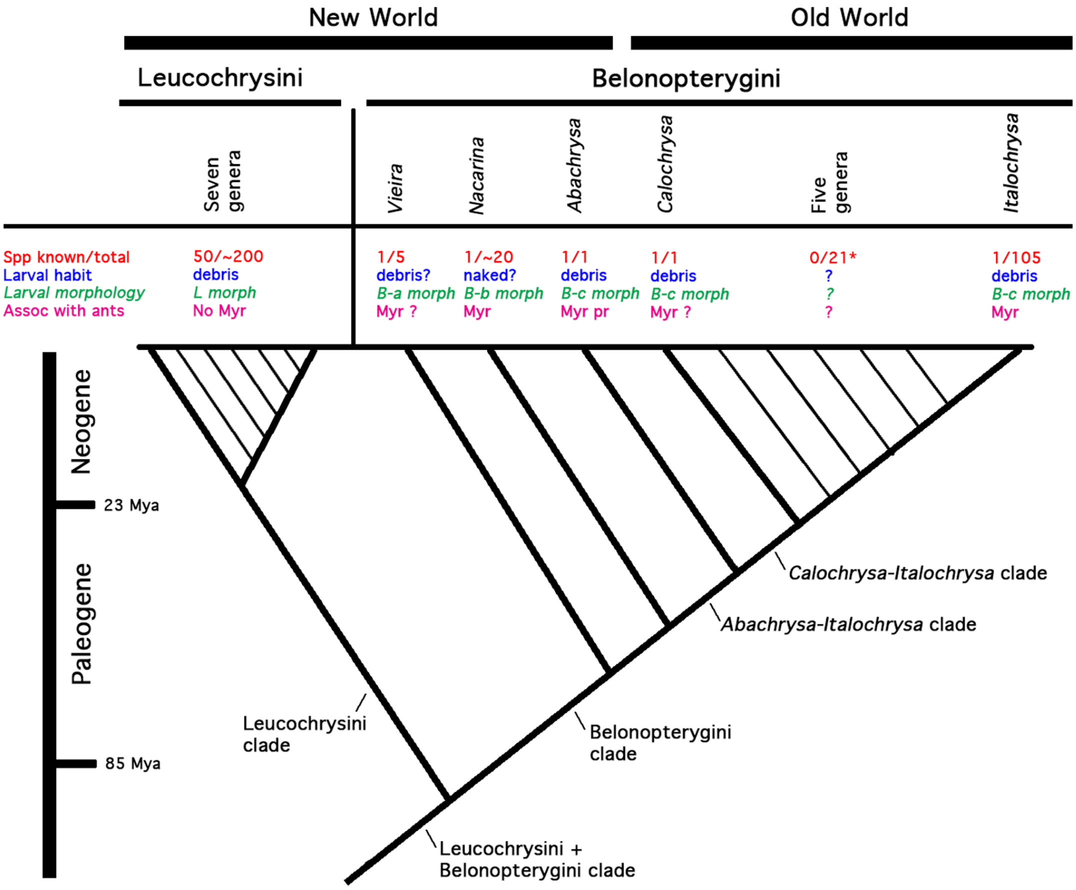

FIGURE 15. Schematic framework for evaluating the evolution of myrmecophily in Belonopterygini (Chrysopidae: Chrysopinae). The phylogeny is roughly illustrated based on congruent trees by Winterton *et al.* (2019) and Garzón-Orduña *et al.* (2019). *Currently, there are 15 described genera in Belonopterygini, but the number of genera in the *Calochrysa-Italochrysa* clade is open to question (Winterton *et al.* 2019). Of these, three of four from the New World and seven of eleven from the Old World were tested in at least one of the two phylogenetic studies. Data on the larval habits or morphology are available for one species from each of the five genera named on the figure. No such data are available from any of the five other Old World genera that the phylogenetic studies included. The outgroup (Leucochrysini) currently comprises eight genera (assuming that *Leucochrysa* and *Nodita* are considered distinct genera). Of these eight, four were included in the phylogenetic study, and data on the larval morphology and habits of species from five genera are known. Based on available data, the tribe is considered monophyletic and the larvae are classified as debris carriers. The generic level phylogeny is not depicted here.

Spp known/total. Number of species for which data on larval morphology and/or larval habits are available / total number of species in the taxon.

Larval habit. "debris": debris carrying confirmed by field observations; "debris?": debris carrying suspected on the basis of larval morphology, but not confirmed; "naked?": on the basis of an anecdotal field report (Weber, 1942), larvae suspected to be without debris.

Larval morphology. "*L morph*": leucochrysine morphotype [L1 with plesiomorphic pattern of 2, 3, 3 primary lateral setae (LS) on thoracic tubercles (LTs); LS elongate, slender; other notal setae not exceptionally elongate; L2, L3 with digitiform LTs bearing elongate, slender LS throughout]. "*B-a morph*": belonopterygine morphotype 'a' [L1 with plesiomorphic pattern of 2, 3, 3 primary LS on thoracic LTs; LS elongate, slender; numerous elongate, slender pronotal, mesonotal setae; L2, L3 unknown]. "*B-b morph*": belonopterygine morphotype 'b' [based on a sketch and notes by Weber (1942); L3 somewhat scarabaeiform; thoracic LTs reduced]. "*B-c morph*": belonopterygine morphotype 'c' [L1 with apomorphic pattern of 7–8, 8–10, 8–10 primary LS on thoracic LTs; notal setae numerous, short to elongate, slender; L1, L3 with palmate thoracic LTs; L3 with dorsal, lateral surfaces of thorax and abdomen densely covered with rigid, hooked setae].

Association with ants. "No Myr": myrmycophily not reported, probably absent; "Myr ?": myrmycophily suspected on the basis of larval morphology, but not confirmed by rearing or field observations; "Myr pr": myrmecophily probable on the basis of rearing and larval morphology; "Myr": myrmecophily confirmed from one or more field observations.

The observations by Principi (1943, 1944) of *I. italica* larvae in association with ants (*Crematogaster scutellaris* Oliv.) in the field are classic in their detail and scope. They indicate that females of this species oviposit in the vicinity of the host ant nest; newly hatched and older larvae are protected from ant attack in the region of the nest by hiding beneath their dorsal debris packets. Larvae acquire their debris packets by affixing pieces of bark to the dorsal thoracic and abdominal setae (using their mandibles and peristaltic movement). Occasionally, the larvae feed on brood that workers carry outside of the nest, and they were observed to grab, extensively "squeeze", and then release ant workers (perhaps to obtain a colony pheromone). Although Principi apparently did not open the ant nest, she concluded that the larvae most likely entered the nest and fed on ant prey therein (personal communication between M. M. Principi and R. A. Pantaleoni, transmitted to us by RAP).

Winterton's collection of *I. insignis* third instars in association with an ant colony in the field (*Technomyrmex jocusus* Forel.) is strong evidence in support of myrmecophily and myrmecophagy in *I. insignis* (see Tauber & Winterton 2014). And, MacLeod's successful rearing of *A. eureka* on ant prey (in conjunction with numerous unsuccessful, anecdotal attempts by him and others to rear *Abachrysa* on other prey) provides strong support as well. These two genera constitute the most basal (*Abachrysa*) and the most highly derived (*Italochrysa*) arms of the *Abachrysa-Italochrysa* clade (Fig. 15).

For the other New World genera, no field observations or rearings of *Vieira* larvae have been reported, except for a failed attempt to rear larvae on prey other than ant brood (Tauber *et al*. 2006). However, a detailed and illustrated article reported *Nacarina* (as *Nadiva*) larvae living without interference in a nest of *Camponotus* (*Myrmothrix*) *abdominalis* (Fabr.) (Weber 1942). When Weber discovered the *Nacarina* larvae in the field, he collected and reared some using ant brood as food. One spun a cocoon and yielded an adult. He sent this specimen to Nathan Banks, who identified it as *Nadiva valida* (Erichson) [= *Nacarina valida* (*Erichson*)]. Despite the fact that neither the adult specimen nor any of Weber's larval specimens can be found today, his published report and his interaction with Banks provide credible (albeit unvouchered) support that *Nacarina* larvae are associated with ants. Finally, neither published observations nor larval specimens are known for the fourth New World belonopterygine genus *Belonopteryx* or from the remaining nine Old World genera.

In summary, despite significant gaps, firm observational evidence currently supports the conclusion of a general myrmecophilic lifestyle for the Belonopterygini. While the taxon sample is small, it is also phylogenetically diverse and includes taxa from the near basal New World belonopterygine genus *Nacarina,* and the most basal and most derived genera in the morphologically specialized *Abachrysa*-*Italochrysa* clade.

Question 2. What is the origin of belonopterygine myrmecophily?

As stated earlier, myrmecophily has not been reported for any chrysopids other than those in Belonopterygini. Although we (CAT) have an anecdotal report of several dead adult ant exoskeletons along with other material within the debris packet of a *Leucochrysa* larva (a possible example of myrmecophagy), a sustained association with ants has not been reported for Leucochrysini (sister tribe of Belonopterygini). So, on the basis of current observational information and phylogenetic data (Garzón-Orduña *et al*. 2019, Winterton *et al*. 2019), we suggest that chrysopid myrmecophily first appeared in the New World during the Paleogene in a basal or near-basal belonopterygine. Because *Vieira*'s association with ants is unknown, the position of the origin of myrmecophily within Belonopterygini remains somewhat ambiguous.

Question 3. What is the pattern of larval variation within the Belonopterygini in relation to its sister clade Leucochrysini?

From our descriptive study here and previous descriptions of belonopterygine and leucochrysine larvae, some systematically relevant features are apparent (Fig. 15).

(i) *Abachrysa-Italochrysa* clade: The three genera in this clade with known larvae (first and/or third instars)—*Abachrysa*, *Italochrysa*, and *Calochrysa*—share a unique suite of larval morphological modifications including: dense, stout setae; enlarged, palmate, very setose lateral tubercles on the thorax and abdomen; and withdrawn, quadrate heads with short cranial appendages (*B-c morph* on Fig. 15). In comparison with other debris-carrying chrysopid larvae, these features appear highly modified for debris carrying and defense against natural enemies. Indeed, elaborate packets of debris (soil, pieces of wood, other dried plant materials) are reported from the field-collected larvae of both *I. italica* and *I. insignis* (Principi 1944, Tauber & Winterton 2014).

Most intriguing among the modifications shared by these three belonopterygine genera is their unusual first instar setation. Except for Belonopterygini, in all chrysopid taxa with known larvae, including Leucochrysini, the first instars have a highly conserved pattern of (i) thoracic segments T1–T3 each bearing a pair of lateral tubercles (LTs) with 2, 3, and 3 setae (LS), respectively, and (ii) abdominal segments A2–A5 each bearing a pair of LTs with two LS. Also, in the leucochrysine clade, larvae typically have abdominal segments A1–A5 bearing a pair of LDTs with one to three LDS. However, in *Abachrysa–Italochrysa* first instars: (i) thoracic segments T1–T3 each bear a pair of lateral tubercles (LTs) with six to eight large LS, and (ii) LDTs are absent from A2–A5. Interestingly, the plesiomorphic condition of two LS on the LTs of A2–A7 and also a pair of LDTs on A6 and A7 is retained. [For specifics from other chrysopid taxa, see Monserrat & Díaz-Aranda (2012), Silva *et al*. (2013), Tauber & de León (2001), Tauber *et al*. (2008a, 2008b, 2011, 2013, 2014).] This unusual setal pattern in a first instar is similar to that of the plesiomorphic second instar; it appears to represent accelerated development of the embryo so that the first instar expresses characteristics typically seen only in later instars.

In addition to the derived form of first instar setation and accelerated development, the *Abachrysa-Italochrysa* clade also exhibits a pattern of unusually large eggs. Four species in three genera of the *Abachrysa-Italochrysa* clade (*Abachrysa*, *Calochrysa*, and *Italochrysa*) have egg volumes ranging from 0.30 to 1.90 mm^3 (Table 1). In contrast, the *V. elegans* egg has a volume of only ~0.06 mm^3 (Tauber *et al*. 2006), which is similar to that found in many other chrysopid species (e.g., 0.06 to 0.12 mm^3 reported by Tauber *et al*. 1991). Large egg size, as observed in the *Abachrysa-Italochrysa* clade, appears to be correlated with and perhaps facilitates accelerated embryonic development. The small egg size of *Vieira*, which has the common (plesiomorphic) 2, 3, 3 thoracic setal pattern, is consistent with this proposal.

Our emphasis here on physical features of the *Abachrysa-Italochrysa* clade is not meant to imply that chemical, vibrational, or other forms of defense did not also evolve as part of the suite of defensive traits in the *Abachrysa-Italochrysa* lineage. Indeed, from currently available data, it is reasonable to conclude that the behavioral components of debris carrying are integral in the larval physical defense against ants. In addition, Principi (1944) observed larval behavior that she suggested was involved in *I. italica* larvae acquiring a chemical pheromone that protects them from their host ants.

(ii) *Vieira*: The first instar of *V. elegans* expresses a number of morphological features that resemble those of first instars in the *Abachrysa-Italochrysa* clade (*B-a morph* on Fig. 15). These include foreshortened cranial appendages; antenna with modified pedicel; lateral tubercles of the thorax and abdomen with stout, robust setae; forward location and enlargement of prothoracic setae; and a somewhat enlarged cranial expansion below the antennae, into which the scapes may be at least partially withdrawn (Fig. 14). Moreover, the dorsal setae on the thoracic segments and A1–A5 are more numerous and larger than those of other chrysopid first instars. However, compared with the larval morphology of the *Abachrysa-Italochrysa* clade, these features appear less extreme in their modification. In addition, and perhaps most importantly, the *Vieira* first instar retains a number of plesiomorphic features. Most notable are its retention of the 2-3-3 condition in the setal pattern of the thoracic tubercles and the elongate structure of the thoracic tubercles. Hence, *Vieira* expresses a mixture of plesiomorphic and derived larval features that make its unknown prey association and lifestyle especially intriguing.

(iii) *Nacarina*: In his short article, Weber (1942) reported his *N. valida* larvae as having blue coloration and a high rate of activity, and that the *Camponotus* workers treated them as brood. Given that he could discern the color of the larvae but did not mention debris carrying, and also given that his sketch of a larva did not show any debris or morphological modifications typically associated with debris carrying, we conclude that his *Nacarina* larvae were naked or did not carry a pronounced packet of debris. His simple sketch of a fully developed larva (perhaps prepupa) shows a scarabaeiform body (*B-b morph* on Fig. 15), with a small, withdrawn head; plump, C-shaped thorax and abdomen; and slender legs that appear undersized relative to the body. Although spiracles are apparent on the sketch, no setae or tubercles are shown. Thus, it does not appear that the larva expressed morphological modifications that are typical of chrysopid debris carriers.

(iv) Leucochrysini (sister group of Belonopterygini): Of the eight genera/subgenera that comprise the tribe Leucochrysini, larvae are currently reported from five: *Berchmansus, Gonzaga, Leucochrysa* (*Leucochrysa*),

Leucochrysa (*Nodita*), *Santocellus* (Tauber *et al*. 2014). Field observations and laboratory rearings confirm that larvae from all of these genera are debris carriers. Leucochrysine larvae are typically found with well-integrated, cohesive dorsal packets of debris. Moreover, larval descriptions indicate that these genera share a diagnostic suite of morphological modifications for debris carrying (*L morph* on Fig. 15). The most distinctive of these are digitiform thoracic LTs; prothoracic LTs extending at least to the middle of the cranium; thoracic LS slender, elongate; and A2–A5 with seta-bearing LDTs (Tauber *et al*. 2014). These traits differ markedly from those of larvae in the *Abachrysa-Italochrysa* lineage, but some are found in debris-carrying chrysopine taxa and in *Vieira*.

Question 4. When viewed within a phylogenetic context, how does the pattern of larval variation inform our knowledge of the evolution of myrmecophily in the Belonopterygini?

Based on the larval morphology of *Vieira* and field observations of *Nacarina* (Weber 1942, Tauber *et al*. 2006), it appears that these two basal belonopterygine genera express forms of larval defense that do not rely primarily on debris carrying (*B-a morph* and *B-b morph* on Fig. 15). Although no specific defense mechanisms have been reported in these taxa, we speculate that their protection from ant attacks depends primarily on some combination of non-physical mechanisms, e.g., chemical or vibrational cues such as those found in some other myrmecophilic insects (Holldobler & Wilson 1990, Lenoir *et al*. 2001, Nash *et al*. 2008, Sala *et al*. 2014). Noteworthy in this regard is the report of larvae in the related neuropteran family Myrmeleontidae (antlions) that detect vibratory signals deep in sand (Devetak *et al*. 2018). Thus, as a working hypothesis based on the current phylogenies of Garzón-Orduña *et al*. (2019) and Winterton *et al*. (2019), we propose that originally several modes of belonopterygine myrmecophily appeared near contemporaneously in different lineages. Comparative first instar morphology indicates that these early modifications involved certain physical features (e.g., reduced head size, altered setal structure) and the acquisition of non-morphological (e.g., chemical and/or vibrational) defense mechanisms for repelling attacks by ants. We suspect that the initial morphological changes yielded body structure and function similar to those in *Vieira* larvae today. Subsequently, as the *Nacarina* lineage diverged, debris carrying was reduced and lost, in conjunction with the intensification of chemical and/or other forms of defense that deceive ants into recognizing and treating the predaceous larvae as brood.

In contrast to the lack of morphological defenses expressed by *Nacarina*, the *Abachrysa-Italochrysa* clade evolved protective mechanisms that favored the elaboration of physical defenses against ants. This process included at least three, probably mutually dependent, changes: (i) the acquisition of enlarged eggs, (ii) the evolution of a unique pattern of accelerated embryonic development allowing morphological structures that are normally seen in second and third instars to be expressed in the first instar, and (iii) the elaboration of morphological and behavioral features that subserve debris carrying in all instars (*B-c morph* on Fig. 15). Apparent precursors of some, but not all, of the modified morphological features are found in the *Vieira* first instar—notably the forward movement, increased number, and enlargement of prothoracic setae; modifications to the antenna and labial palpus; and reduction in the sizes of the head and cephalic appendages.

Thus, it appears that myrmecophily involving the elaborate morphological (and presumably behavioral) modifications for debris carrying expressed by the *Abachrysa-Italochrysa* clade first appeared in the New World during the Paleocene, when the *Abachrysa* lineage diverged from its more basal *Vieira-Nacarina* stem. The first and third instars of the two genera from disparate ends of the *Abachrysa-Italochrysa* clade appear to express strikingly similar morphological modifications for myrmecophily based on debris carrying. In addition, they also share the pattern of enlarged eggs and accelerated embryonic development. The most parsimonious explanation for this extensive pattern of shared features among the basal and derived *Abachrysa-Italochrysa* genera is that the features initially evolved in the common ancestor of the clade as an integrated suite of developmental and morphological modifications, and that this integrated suite was retained, without major change, as the clade diversified.

In this respect, it is noteworthy that the diversity of Belonopterygini in the New World largely resides in the 21 currently recognized species of *Nacarina* (see Oswald 2019), which presumably have naked larvae that are chemically and/or vibrationally defended. The New World *Abachrysa*, with its highly modified debris-carrying larvae, has only one described species. In contrast, the diversity of Old World belonopterygines is concentrated in *Italochrysa*, with ~115 species (Oswald 2019), all of which are likely to have highly modified debris-carrying larvae.

Given the above information, it is interesting that (i) in the most speciose genus of New World belonopterygines—*Nacarina*—larval defense against ants appears to be centered on modifications other than morphological structures related to debris carrying, presumably chemical and/or vibrational mechanisms, while (ii) larvae in the speciose *Calochrysa-Italochrysa* clade (Fig 15) of Old World belonopterygines are presumed to be primarily physically defended. Neither the New World nor the Old World belonopterygine faunae appear to contain both a substantial lineage that is primarily chemically/vibrationally defended and an independent lineage that is primarily physically defended. Presumably, the Old World belonopterygine lineage began with the introduction of a morphologically well protected *Abachrysa*-like ancestor; thus, it is possible that this lineage never co-existed in the Old World with a primarily chemically/vibrationally defended lineage. However, it is tempting to speculate whether there might be significant competitive interactions among lineages in the New World that display different kinds of myrmecophilic defensive strategies, and if so, whether such interactions might help account for the lack of species diversity in the morphologically defended New World *Abachrysa* and the almost completely allopatric distributions of *Abachrysa* and *Nacarina* in the New World (Penny *et al*. 1997). Complex interspecific interactions that suggest such a possibility have been reported for the *Maculinea-Myrmica* parasitoid-host system (Thomas & Elmes 1998; Assis *et al*. 2018). Currently, relevant comparative data from Belonopterygini are absent, and we await further information on the host ranges and ant-larval interactions of belonopterygine species in both the New World and the Old World.

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