Larval morphology of the Neotropical genus *Epispasta* (Coleoptera, Meloidae)

Andrea Di Giulio

Dipartimento di Biologia, Università degli Studi "Roma Tre", Viale Marconi 446, 00146 Roma, Italy

John D. Pinto

Department of Entomology, University of California at Riverside, Riverside, California 92521, United States of America

Marco A. Bologna[1]

Dipartimento di Biologia, Università degli Studi "Roma Tre", Viale Marconi 446, 00146 Roma, Italy

Abstract—The first-instar (triungulin), second-instar, and third-instar larvae of the South American monotypic genus *Epispasta* Selander, 1960 are described and figured. The triungulin of *E. abbreviata* (Klug, 1825) is highly adapted for phoresy on bees and resembles the triungulins of several other phoretic genera in the subfamily Meloinae. The second- and third-instar larvae of *Epispasta* are unique in that they retain the campodeiform phenotype of the first instar. These instars in other meloid genera are scarabaeiform. A discussion is provided on the similarity of the triungulin of *Epispasta* to that of other phoretic meloines. We argue that this similarity is a result of morphological convergence correlated with phoretic behavior and is not evidence of a relationship. The position of *Epispasta* in Meloinae remains questionable, as none of its larval or adult features ally it to any other genus.

Résumé—Dans ce travail sont décrits et figurés le premier, deuxième et troisième étages larvaires du genre monotypique *Epispasta* Selander, 1960, endémisme de l'Amérique du Sud. La larve primaire, ou triungulin, de *E. abbreviata* (Klug, 1825) c'est très modifié et adapté à la phorésie sur les abeilles sauvages. Le phénomène de convergence morphologique parmi les triungulins phorétiques de la sous-famille Meloinae est aussi discuté. Le deuxième et troisième étages larvaires sont très particulières car elles, case unique parmi les Méloides, gardent le phenotype campodeiforme du triungulin tandis que une phenotype scarabeiforme. Les similitudes entre le triungulin de *Epispasta* et ceux d'autres Méloines phorétiques sont discutées et indiquent qu'il s'agit de convergence évolutive, corrélée à la phorèsie, plutôt que des relations phylogénétiques. La position du genre *Epispasta* dans la sous-famille Meloinae n'est pas clarifié par les caractères larvaires. Aussi les caractères des adultes n'aident pas à clarifier des relations étroites avec d'autres genres de ce group taxonomique.

Introduction

Epispasta Selander, 1960 (Coleoptera, Meloidae) (Fig. 1) is a poorly known monotypic genus endemic to the "chaco-parana" area of the Neotropical Region. Its phylogenetic position has been controversial. Denier (1935*a*) compared the type species of the genus, *Lytta abbreviata* Klug, 1825, to other members of *Lytta* Fabr., 1775 and despite finding differences, temporarily maintained the species in *Lytta*. When Selander (1960) transferred *L. abbreviata* to the new genus *Epispasta*, he initially maintained the genus in Lyttini. Upon discovery that its first-instar larva was adapted for phoresy, Selander (1991) transferred the genus to the tribe Meloini, in which he included all other Meloinae that he believed to be phoretic, namely the genera *Cyaneolytta* Péringuey, 1909, *Lydomorphus* Fairmaire, 1882 (as *Cylindrothorax* Escherich, 1896), *Lyttomeloe* Denier, 1920, *Meloe* L., 1758, *Spastomeloe* Selander, 1985, and *Spastonyx* Selander, 1954. Pinto and Bologna (1999) followed this tribal arrangement in their review of the New World meloid genera.

Received 23 November 2004. Accepted 4 September 2005.

[1]Corresponding author (e-mail: bologna@uniroma3.it).

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

Fig. 1. *Epispasta abbreviata*, adult male (Brazil, Santarém).



In a recent phylogenetic analysis, Bologna and Pinto (2001) showed that phoresy almost certainly evolved several times in the Meloinae and that the phoretic genera included in Meloini by Selander (1991) are not closely related. They restricted the tribe to *Meloe* and *Physomeloe* Reitter, 1911, a monotypic and probably non-phoretic Iberian genus earlier placed in Lyttini (Bologna and Aloisi 1994). Regarding the other genera formerly placed in Meloini by Selander, all analyses showed them to be considerably dispersed from one another. *Lydomorphus* was shown to have non-phoretic larvae (Bologna and Aloisi 1992; Bologna and Pinto 2001; M.A. Bologna *et al.*, unpublished data), and its placement in the subfamily was unresolved. *Lyttomeloe* and *Spastonyx* clustered together but well apart from other phoretic groups. *Cyaneolytta* (for a review, see Di Giulio *et al.* 2003) was allied with the non-phoretic tribe Epicautini, and *Spastomeloe* showed greatest affinity to South American *Acrolytta*, a genus also lacking phoretic features. *Epispasta* was not convincingly allied to any other genus. Bologna and Pinto (2001) suggested it as a possible sister taxon to the redefined Meloini, but the character evidence is minimal and its placement in the subfamily remains unresolved.

Although Selander (1991) considered the morphological features of the *Epispasta* triungulin in his classification, he did not describe the triungulin and provided no details of larval structure. In 1988, upon examining material in the Natural History Museum (London), we found a single triungulin from Brazil attached to a carpenter bee (*Xylocopa virginica* (L., 1771)). Similar to larvae of *Meloe* (*Meloe*), it showed several modifications associated with phoresy. Because *Meloe* does not occur in Brazil, we were unable to place the triungulin to genus. Upon studying the Lorraine F. and Richard B. Selander Collection of Meloidae in the Florida State Collection of Arthropods in Gainesville in 1995, we found a rich store of adults and associated larvae of *Epispasta abbreviata* (Klug, 1825), material that Selander considered for his 1991 classification. Bologna and Pinto (2001) utilized the first-instar larvae from this collection but also did not include a formal larval description. The aims of this study of *E. abbreviata* are to (*i*) describe its egg and first three larval instars, (*ii*) study the striking phoretic adaptations of its first-instar larva, stressing those features that are convergent in other phoretic Meloinae, and (*iii*) summarize its distribution and add new records and information on natural history. This paper is dedicated to the memory of Richard B. Selander, on whose material and research our study is largely based.

Material and methods

As indicated, this study of *E. abbreviata* is based largely on material in the Selander Collection in the Florida State Collection of Arthropods, Gainesville, Florida (FSCA) (RBS Notes 25–88). Included are preserved eggs,

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

first-instar larvae hatching from a portion of these eggs, and second- and third-instar larvae (FG2 and FG3, respectively) resulting from a partial laboratory rearing on an unspecified host (RBS rearing 2–88). Eggs were oviposited in the laboratory by adults collected in Villa Olivari, Ituzaingo, Argentina (30.xii.1987, 1.i.1988) by A. Martinez and R.B. Selander. Two egg masses were deposited. Mass No. 1 (120 eggs) did not develop; the egg description is based primarily on this mass. Mass No. 2 (number of eggs unknown; laid 2.i.1988, hatched 4–5.ii.1988) produced numerous first instars; rearings of several of these resulted in approximately 30 FG2 larvae and 3 FG3 larvae. All were available for study. Exemplar first-instar larvae are deposited in the Marco A. Bologna Collection, Università degli Studi "Roma Tre", Rome, Italy, (hereafter, CB) and the University of California Riverside Collection (UCRC). Also examined was a single slide of a triungulin in the Natural History Museum, London, (BMNH) labelled as follows: "*Xylocopa carbonaria* Smith, Utumarí, Santarem, Parà, Brazil, IX.15.1955, M.G. Silva, coll.".

Eggs, larvae, and associated exuviae were kept in 70% ethanol. A number of triungulins and FG2 larvae were mounted on slides in Canada balsam and examined with Olympus SZX12 and Leitz Laborlux S microscopes. Several eggs, triungulins, and FG2 larvae, mounted on stubs after critical-point dehydration and gold sputtering, were analysed and photographed using a Philips XL-30 scanning electron microscope (Interdepartmental Laboratory of Electron Microscopy (L.I.M.E.), Università degli Studi "Roma Tre").

Terminology of larval structures follows Parker and Böving (1924), MacSwain (1956), Lawrence (1991), and Bologna and Pinto (2001). For certain characters of larval chaetotaxy we have adopted the notational conventions of Selander (1990) and Bologna and Di Giulio (2002).

Measurements of first-instar larvae reported in the description represent ranges from 10 slide-mounted larvae and 4 dehydrated stub-mounted specimens and were taken using light and scanning electron microscopes, respectively. We also examined 44 adult specimens from BMNH, CB, and FSCA.

Bionomics of *Epispasta abbreviata*

The distribution and biology of *E. abbreviata* are virtually unknown. The species was described from Brazil, "Parà", and cited from "S Brazil, Paraguay, N Argentina" by Pinto and Bologna (1999), without details. Actually, this species is distributed from northern Brazil to northeastern Argentina. The following is the complete list of localities known from collections and literature.

BRAZIL. Brazil (Denier 1935*b*); southern Brazil (Pinto and Bologna 1999). **Pará:** Pará (Klug 1825, type locality; Fischer 1827; Denier 1940); Santarém (Denier 1940; CB; FSCA, specimen compared with type); Utumarí, Santarém (BMNH). **Mato Grosso:** Presidente Murtinho, Vazle Algore (Denier 1940).

ARGENTINA. Corrientes: Villa Olivari (CB, FSCA, UCRC).

No information is available on the habitat preference of this species. According to the literature and museum records, adults were collected in Santarém in March, May, July, and November, and in Corrientes in December. The single larva from Utumarí was collected in September. The Argentinean specimens oviposited in January and eggs hatched in February, after 32–33 days.

The triungulin from Utumarí, Brazil, was collected on *Xylocopa carbonaria* (Apidae), which could represent the bee host of larvae of *E. abbreviata*. *Xylocopa* is known as a host of the nemognathine tribe Horiini (for a review, see Bologna 1983) and as an occasional vector of a few other meloid species.

Results

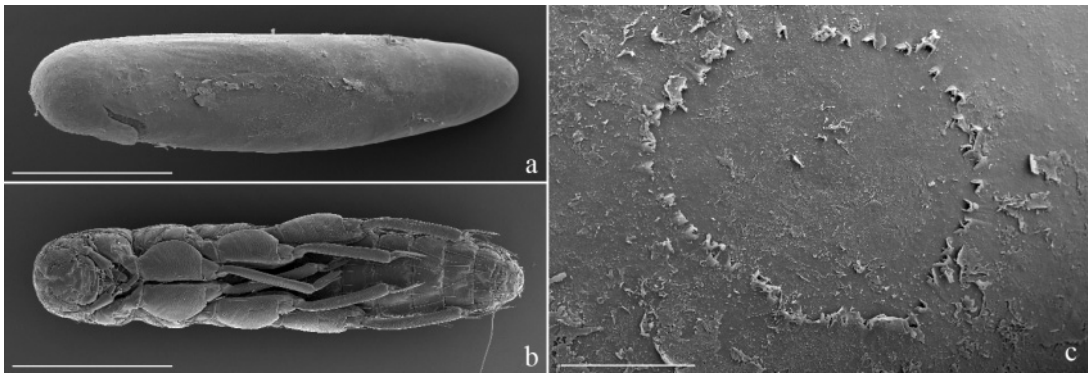
Taxonomic remarks

Adults from northeastern Argentina (Villa Olivari) differ from those close to the type locality of the species in northeastern Brazil (Santarém) in that the integument is more lustrous, punctures of the body are less dense, the pronotum is narrower, and the antennal segments are more moniliform. Triungulins from Villa Olivari also differ from the Utumarí specimen mostly in morphometric characters (see below). An evaluation of differences between these populations requires further study.

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

Fig. 2. *Epispasta abbreviata*: *a*, egg, lateral view; *b*, mature embryo extracted from egg; *c*, egg, anterior apical view showing micropylar area. Scale bars = 1 mm (*a*, *b*) and 50 µm (*c*).



Descriptions of egg and first-, second-, and third-instar larvae of *Epispasta abbreviata*

Egg

Shaped as in other Meloidae (Figs. 2*a*, 2*c*) (see Church *et al.* 1970; Bologna and Di Giulio 2002, 2003; Di Giulio *et al.* 2002). Length = 2.8–3.0 mm. Pale yellow, elongate, cylindrical, rounded at both ends, enlarged anteroapically. A micropylar area (Fig. 2*c*) is present at the anterior pole, consisting of about 40 small, subcircularly arranged micropyles; each micropyle consists of a sloping U- or V-shaped chorionic flap overhanging a central cavity.

First-instar larva

Habitus and microsculpture. Triungulin campodeiform with peculiar adaptations to phoresy at level of head (*e.g.*, shape and orientation of mandibles) and legs (very long and with distinctly swollen femora); body elongate, subparallel-sided (Figs. 3*a*, 3*b*), covered by long, thick setae. Tergites and sternites of thorax and abdomen well sclerotized and entire. Light brown; mandibles and claws strongly sclerotized, reddish brown; bulged genal areas dark brown. Cuticle of sclerotized areas of body reticulate with polygonal cells of various shapes and sizes (Figs. 3*f*, 4*a*, 4*b*), cells extremely elongate on tibiae (Fig. 3*d*), wider and enlarged on bulged genal areas (Fig. 5*f*).

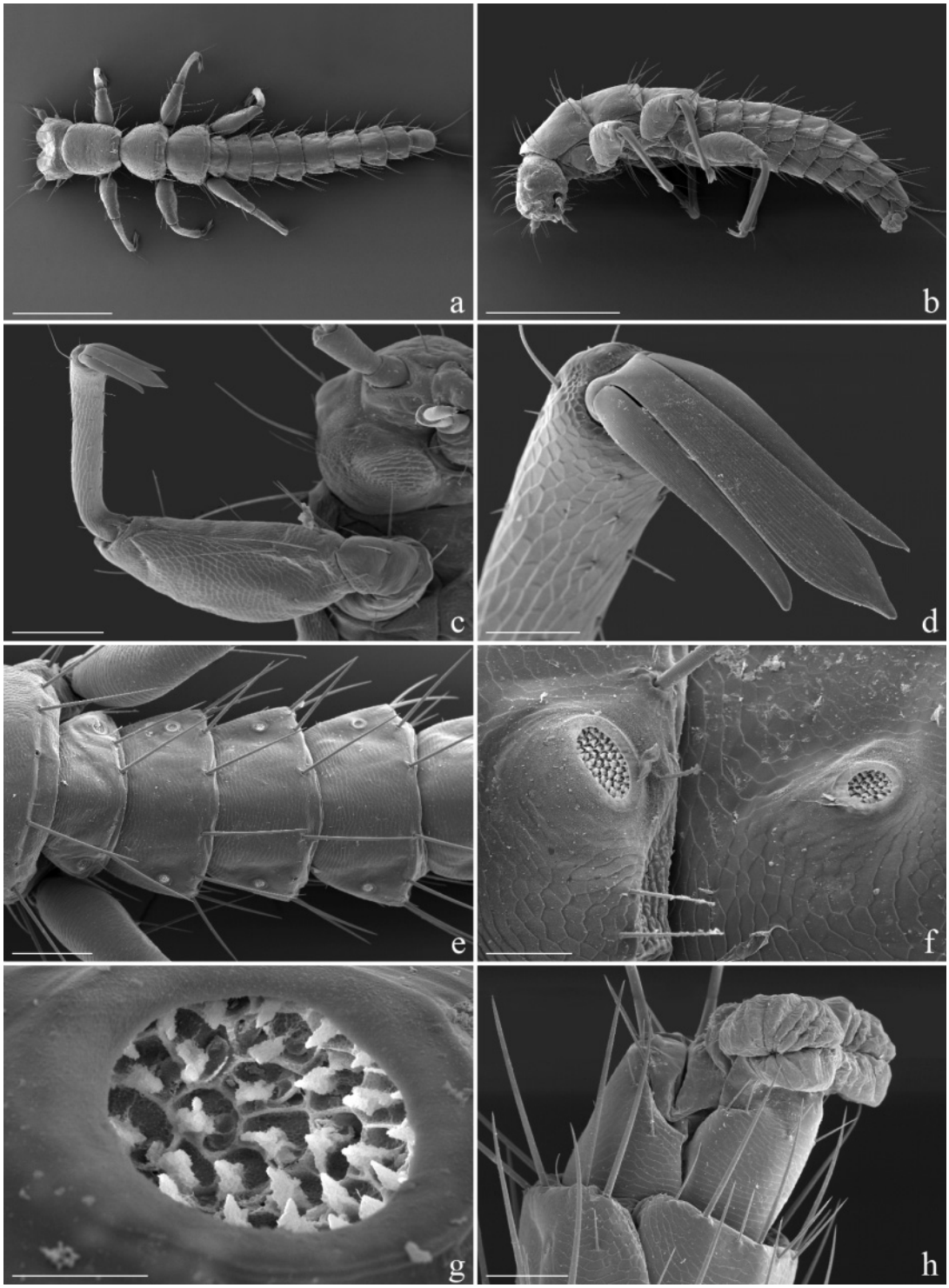
Measurements (specimens from Argentina mounted on slides and single specimen from Brazil (in brackets)). Body length 4.2–5.1 [3.5] mm (from abdominal apex to clypeolabral suture); head length 0.51–0.56 [0.48] mm (from occipital foramen to clypeolabral suture), maximum width 0.68–0.76 [0.58] mm; diameter of stemmata 90–100 [80] µm; epicranial stem 0.16–0.17 [0.16] mm; antennal length 0.28–0.30 [0.26] mm, terminal antennal seta length 0.33–0.36 mm; length of prothorax 0.53–0.56 [0.48] mm, maximum width 0.74–0.88 [0.64] mm; length of abdomen 2.2–3.0 [2.0] mm, maximum width (at level of segments III–IV) 0.27–0.31 [0.25] mm, length of caudal setae 1.1–1.2 mm [0.72]; diameter of spiracles (external diameter including peritreme): mesothoracic 50–60 [52] µm, abdominal I 74–86 [68] µm, abdominal II–VIII from 54–58 µm to 30–34 µm [46 to 26 µm].

Head (Figs. 4*a*–4*d*, 6). Cephalic capsule (Fig. 6) prognathous (width/length ratio = 1.3), transversely subhexagonal, widest at level of posterior margin of stemmata; dorsal surface biconvex, characterized by two bulging lateral protuberances that intersect anteriorly along a short medial line and posteriorly along stem of epicranial suture; each main protuberance transversely subdivided; depressed medial frontal area present between the two main protuberances. Anterior margin of head truncate at level of clypeolabral suture, posterior margin almost straight, lateral margins distinctly protruding at level of stemmata; basal elevation absent. Epicranial suture incomplete, consisting of long basal stem alone or accompanied by vestigial frontal arms. Epicranial plates each with suboval protuberance ventrally (Fig. 4*d*), which occupies almost entire anterior third of plate surface on underside of head, laterally with 3 moderately long setae (2 anterior, 1 posterior). Occipital foramen (Fig. 4*d*) wide and posteroventral, resulting in shortening of ventral head length. Stemma (Figs. 4*a*, 4*b*) dorsolateral, hemispherical, about as large as abdominal

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

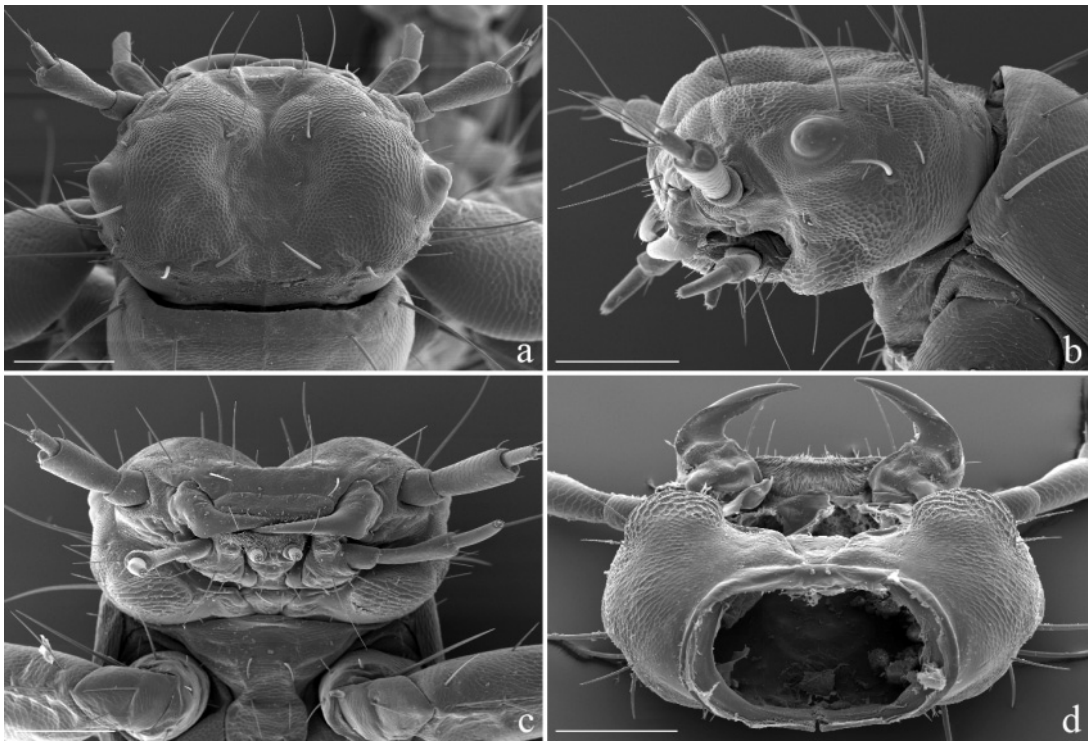
Fig. 3. *Epispasta abbreviata*, first-instar larva: *a*, dorsal view; *b*, lateral view; *c*, right foreleg, posteroventral view; *d*, foreclaw; *e*, abdominal segments I–IV, dorsal view; *f*, abdominal spiracles I–II, lateral view; *g*, abdominal spiracle IV; *h*, apex of abdomen, lateral view. Scale bars = 1 mm (*a*, *b*), 200 µm (*c*, *e*), 50 µm (*d*, *f*), 10 µm (*g*), and 100 µm (*h*).



© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

Fig. 4. *Epispasta abbreviata*, first-instar larva, head: *a*, dorsal view; *b*, left lateral view; *c*, frontal view; *d*, posteroventral view. Scale bars = 200 μm.

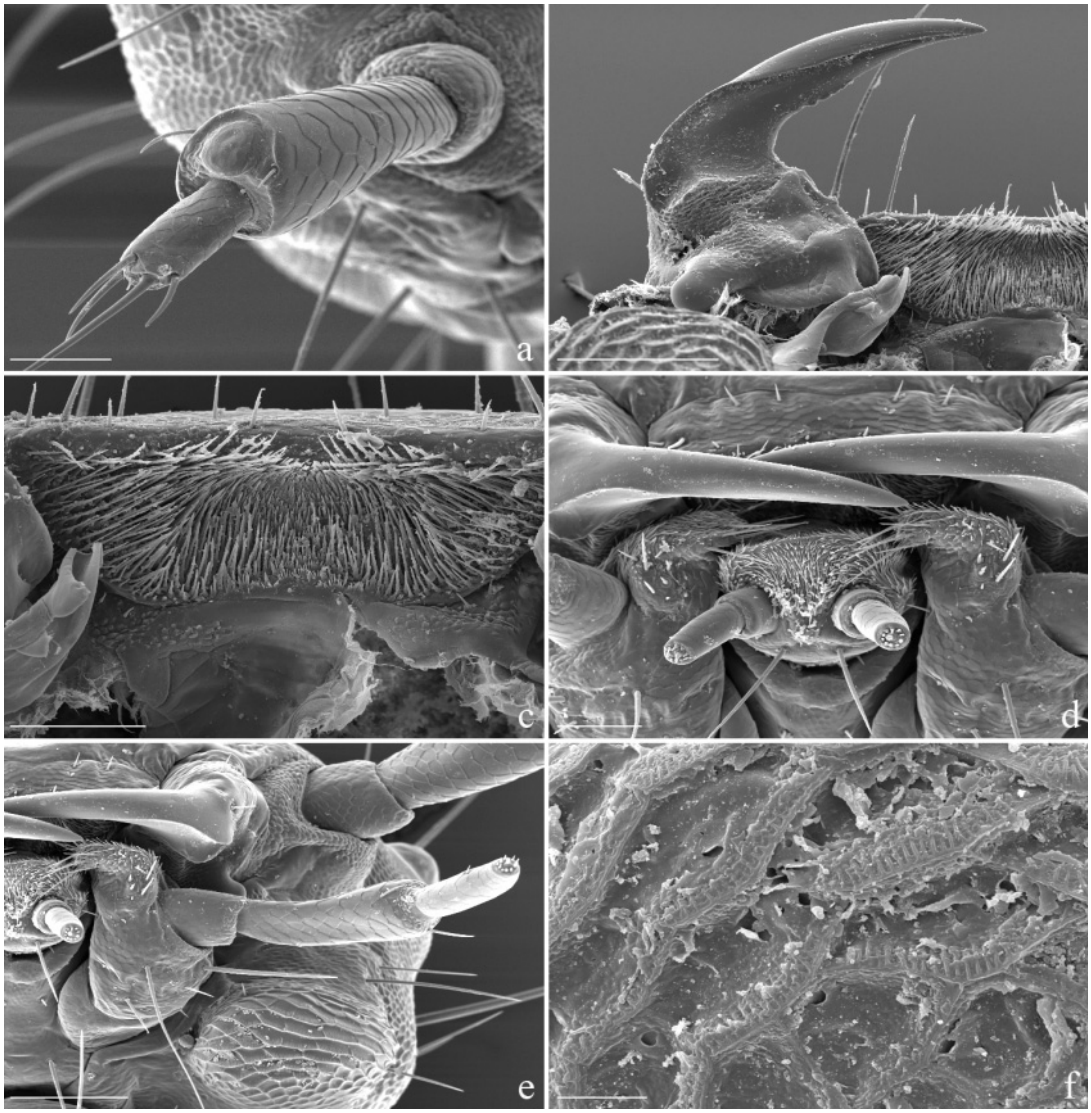


spiracle I. Frontoclypeus (Figs. 4*a*, 4*b*) greatly sloping, with one transverse row (frontoclypeal row, FCR) (Fig. 6) of 3 pairs of setae decreasing in size from external (FCR3) to internal (FCR1) pair; FCR3 very long; 1 sensory pit between FCR2 and FCR3. Four pairs of frontal setae posterior to FCR: 1 long, slightly anterior to antennal insertion; 1 long, medial; 1 very short, slightly internal and posterior to the latter; and 1 short and more basal. One large pair of pits present between long medial setae of frons. Each epicranial plate dorsally with 2 setae adjacent to each stemma (Figs. 4*b*, 6), 1 short, anterior, between stemma and antennal fossa, and 1 (the ocular seta) very long, placed behind posterior margin of stemma, distinctly posterior to ocular sensory pit; ocular sensory pit medial to stemma; 1 very long and thick lateral seta positioned posteriorly to stemma; 3 pairs of setae along occipital cranial margin, the 2 internal pairs very long and thick, the external pair short and lateral; 1 sensory pit anterior to the more internal pair; 1 additional pair of setae and 1 small sensory pit slightly displaced in front of the external pair; 4 minute, spinelike setae and 1 small pit obliquely lined basally near occipital foramen. Labrum strongly transverse, lateral margins rounded (Fig. 4*c*), frontally positioned, with 8–10 short setae transversely arranged along its base (the 2 lateral ones thick and longer than the others); some additional minute setae and pits present anteroventrally; epipharynx covered by a fine pubescence, pubescence shorter medially, anteromedially directed; basal epipharyngeal margin open, without thickened border. Hypopharyngeal rods present. Antennae (Figs. 4*a*, 5*a*, 7*a*) moderately long, anterolaterally directed; segment I short, cylindrical, slightly asymmetrical, with 1 dorsal sensory pit; segment II subcylindrical, enlarged from base to apex, more than twice as long as segment I, with 3 short apical setae (2 dorsolateral, 1 ventral) and 1 dorsal pit; additionally, 2 minute setae (1 spinelike above and 1 extremely small below) near sensory appendix; sensory appendix reduced to a lateroventral (lateral side), slightly convex disk; segment III slender, half length of segment II, cylindrical, with an apical seta (antennal seta) slightly longer than entire antenna, and 3 subapical setae, 1 dorsal, 1 ventral, and 1 lateral; 1 minute seta and 1 lateral pit

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

Fig. 5. *Epispasta abbreviata*, first-instar larva: *a*, left antenna, apical view; *b*, right mandible, ventral view; *c*, epipharynx; *d*, labium, frontal view; *e*, left maxilla, frontal view; *f*, bulged genal area, showing pores on meshes of microsculpture. Scale bars = 50 μm (*a*, *c*, *d*), 100 μm (*b*, *e*), and 10 μm (*f*).

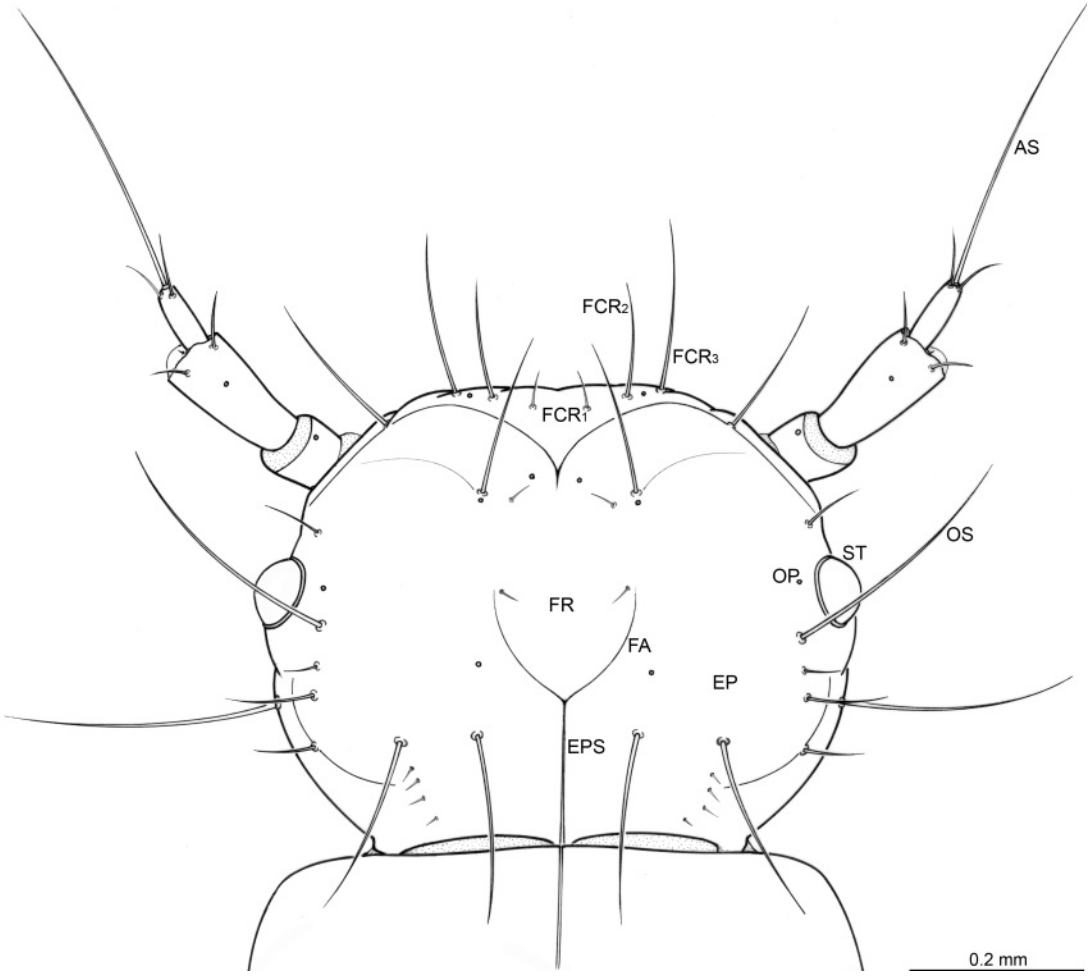


near base of apical seta. Mandibles (Figs. 4*c*, 4*d*, 5*b*) moving in oblique plane; base of mandibles broad, suboval, with large ventral condyle; apical half deeply excavated ventrally, strongly curved inwards, evenly narrowing toward acute apex; ental surface microcrenulate; lateral margin with 2 minute setae, 1 sensory pit between these setae, and another pit mesodorsally positioned. Maxillae (Figs. 5*e*, 7*b*) with stipes short, with 2 rows of setae: anterior (or apical) row with 2 setae, the medial seta distinctly longer than the lateral one, also with 1 pit on the ental side; posterior row with 2 shorter setae, the external one slightly smaller and displaced anteriorly; additionally 1 lateral pit present basally; cardo small, transverse, with 1 very small lateral seta; mala simple, lobiform, elongate and curved towards buccal cavity, with 7–8 subbasal setae and a tuft of 10–12 elongate spiniform apical setae; surface of mala pubescent; maxillary articulating area present; maxillary palpi extremely long; segment I cylindrical, slightly asymmetrical (anterior surface slightly longer), about half as long as segment II, with 1 ventral pit; segment II slightly narrowed and curved at middle, 1.5

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

Fig. 6. *Epispasta abbreviata*, first-instar larva, head, dorsal view. AS, antennal seta; EP, epicranial plate; EPS, epicranial stem; FR, frontal area; FA, frontal arm; FCR_1–FCR_3, setae of frontoclypeal row; OP, ocular sensory pit; OS, ocular seta; and ST, stemma.



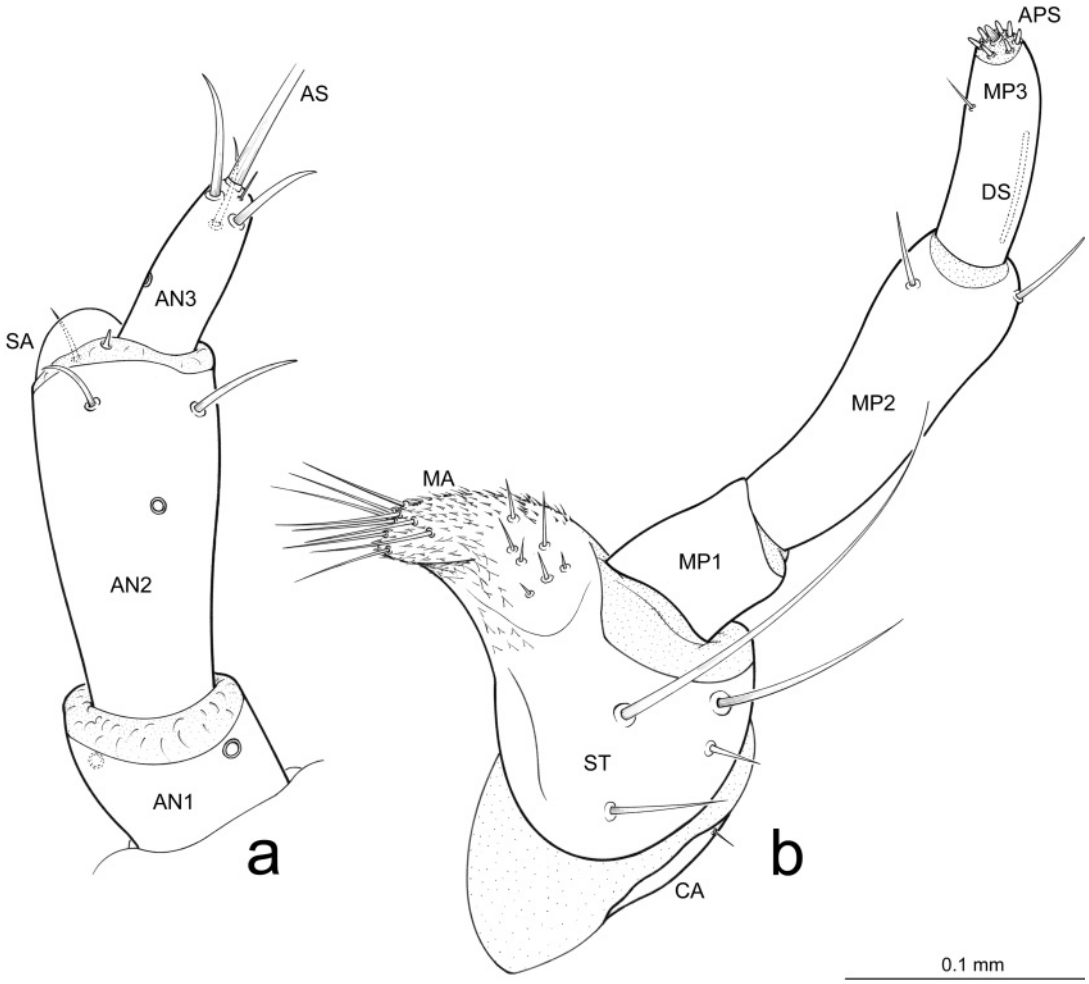
times longer than segment III, with 2 ventrolateral subequal setae (1 lateral and 1 medial); segment III digitiform, curved and narrowed at apex, with 1 dorsolateral seta (medial side); apex of segment III obliquely truncate, with 1 slender, lateral, digitiform sensillum in basal half and a sensory area composed of 7–10 short papillae surrounding one medial, slightly larger appendix. Gulamentum (fused submentum and gula) short, subtriangular, weakly sclerotized, with 2 very long setae anteriorly; basal part of mentum with 1 pair of minute setae and 1 pair of anterior sensory pits; prementum with 1 pair of minute basal setae and 1 pair of moderately long anterior setae; surface of prementum and hypopharynx covered by short pubescence; 1 pair of setae present between insertion of palpi; labial palpi (Fig. 5*d*) with segment I short, cylindrical, segment II about twice as long as segment I, slightly narrowed distally, with 1 small apical sensory appendix surrounded by 6–8 smaller papillae.

Thorax (Figs. 3*a*, 3*b*). Segments transverse, slightly narrower than head; pronotum and mesonotum subrectangular with slightly rounded sides; metanotum subtrapezoidal; ecdysial line very thin, complete on pronotum, absent at base of mesonotum, and absent or vestigial at basal third of metanotum. Pronotum 1.3 times wider than long, each half of pronotum with 13 setae and 7 pits almost symmetrically placed along three transverse, subparallel rows; anterior row (AR) with 4 setae and 3 pits (from medial to lateral: 2 pits, 1

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

Fig. 7. *Epispasta abbreviata*, first-instar larva: *a*, left antenna, dorsal view; *b*, left maxilla, ventral view. AN1–AN3, antennomeres; AS, antennal seta; APS, apical sensilla of MP3; CA, cardo; DS, digitiform sensillum; MA, mala; MP1–MP3, maxillary palpomeres; ST, stipes; and SA, antennal sensory appendix.



long seta, 1 pit, 1 minute seta, 1 long seta, 1 small seta); middle row (MR) with 3 small setae (2 medial and 1 external); 1 small seta and 1 pit lateral, between AR and MR; posterior row (PR) with 5 setae and 2 pits (from medial to lateral: 1 moderately short seta, 1 pit, 1 long seta, 1 small seta, 1 long seta, 1 pit, 1 long seta); prosternum with 5 pairs of setae: 2 pairs of minute setae present anteriorly, 3 pairs on the sclerotized sternal plate, the posterior pair extremely long. Mesonotum slightly shorter than pronotum; AR with 5 small setae (2 medial, 2 lateral, and 1 anterior to the spiracle) and 1 medial pit; MR with 4 small setae (1 medial, 2 at the level of or slightly posterior to the spiracle, 1 well posterior of spiracle); PR as in pronotum; 3 pairs of medial setae on mesosternum increasing in length from anterior to posterior, the anterior one minute and in the membranous area, second and third on the sclerotized plate, the posterior one extremely elongate. Setae of metathorax similar in number, position, and relative dimensions to those of mesothorax.

Legs (Fig. 3*c*) extremely long. Coxae short and broad, cylindrical, with 5 setae (2 very long) and 2 pits distally, and 8–10 minute setae and 1 pit proximally; trochanters ventrally divided by a transverse, thin, medial, unsclerotized area around the whole trochanter with a row of 4–6 pits and 3 setae (1 ventral moderately long, 2 short); basal part of trochanters without setae, distal part with 2 moderately long setae; femora highly modified, swollen, slightly compressed laterally, ventral margin

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

almost straight, dorsal surface extremely swollen; metafemora slightly longer than the others; femora each with 10 setae (a subapical row of 4 moderately long setae, 3 long ventral setae, 2 moderately long medial setae, and 1 small basal seta dorsally projecting near articulation with trochanter) and 1 pit, the longest ventral femoral seta much shorter than femur; tibiae cylindrical, not tapered, subequal on pro-, meso-, and meta-thoraces, about as long or slightly longer than femora, basally curved and slightly enlarged apically; tibiae with four longitudinal rows (two dorsal and two ventral) of 7–10 minute setae gradually increasing in length from base to apex; apical seta more than 2 times as long as diameter of tibia. Claws (Fig. 3*d*) increasing slightly in length from prothorax to metathorax, spatulate, basally curved, longitudinally corrugated, with basal setae also spatulate and combining with claws to form a trident-like structure.

Spiracles (Figs. 3*d,* 3*e*) slightly ovoid, internally reticulate and papillate (Fig. 3*g*). Mesothoracic spiracle anterolateral in position. Abdominal spiracle I (Fig. 3*f*) much larger than the others (about twice as long as mesothoracic spiracle), dorsolaterally placed in slightly elevated position along posterior margin of tergite I; abdominal spiracles II–VIII slightly more dorsally placed relative to I, gradually decreasing in size from II to VIII.

Abdomen (Figs. 3*a*, 3*b*, 3*e*) elongate, subparallel, only slightly fusiform, tergites transverse, rectangular with posterior margin entire; maximum width at segments III–IV; laterotergites completely fused with tergites (sutures not visible) into single tergum. Lateral half of each tergum on segments I–IX with three transverse rows of setae as follows (Fig. 3*e*): AR with 2 small setae (4 on tergum I) and 1 pit, MR with 1 medial pit and 3 minute setae, PR of segments I–VIII with 4 long setae, 2 medial and 2 lateral to the spiracle (the lateral pair shorter on segment I), the first 3 alternated with 2 short setae, 1 pit behind the spiracle; tergum IX with 1 extremely elongate pair of setae on PR (caudal setae), slightly shorter than the last four abdominal segments combined; additionally, PR of tergum IX with 1 moderately long pair of setae medial to caudal pair, and 5 pairs of setae lateral. Sterna well sclerotized, entire, subrectangular; AR and MR of each sternum with 1 pair of minute setae, PR with 5 pairs of setae (from medial to lateral: 1 moderately long, 1 long, 1 moderately long, 1 long, 1 moderately long); sternum IX with 3 pairs of short setae on PR. Pygopod membranous (Fig. 3*h*), transversely divided into two parts: dorsal part semicircular with 2 pairs of small setae and 2 pairs of pits; ventral part longitudinally divided into 2 lobes, distinctly produced.

Second-instar larva

Habitus and microsculpture. Body retaining campodeiform phenotype, largely membranous and microspinulate; head, tergites, and legs smooth. Yellowish white. Setation extremely reduced throughout body, mouthparts, and legs (mainly due to miniaturization and loss of sensilla chaetica and trichodea). Abdomen fusiform (Figs. 8*a*, 8*b*), dorsally flat, and ventrally very convex, with 10 distinct abdominal segments, maximum width at segment III.

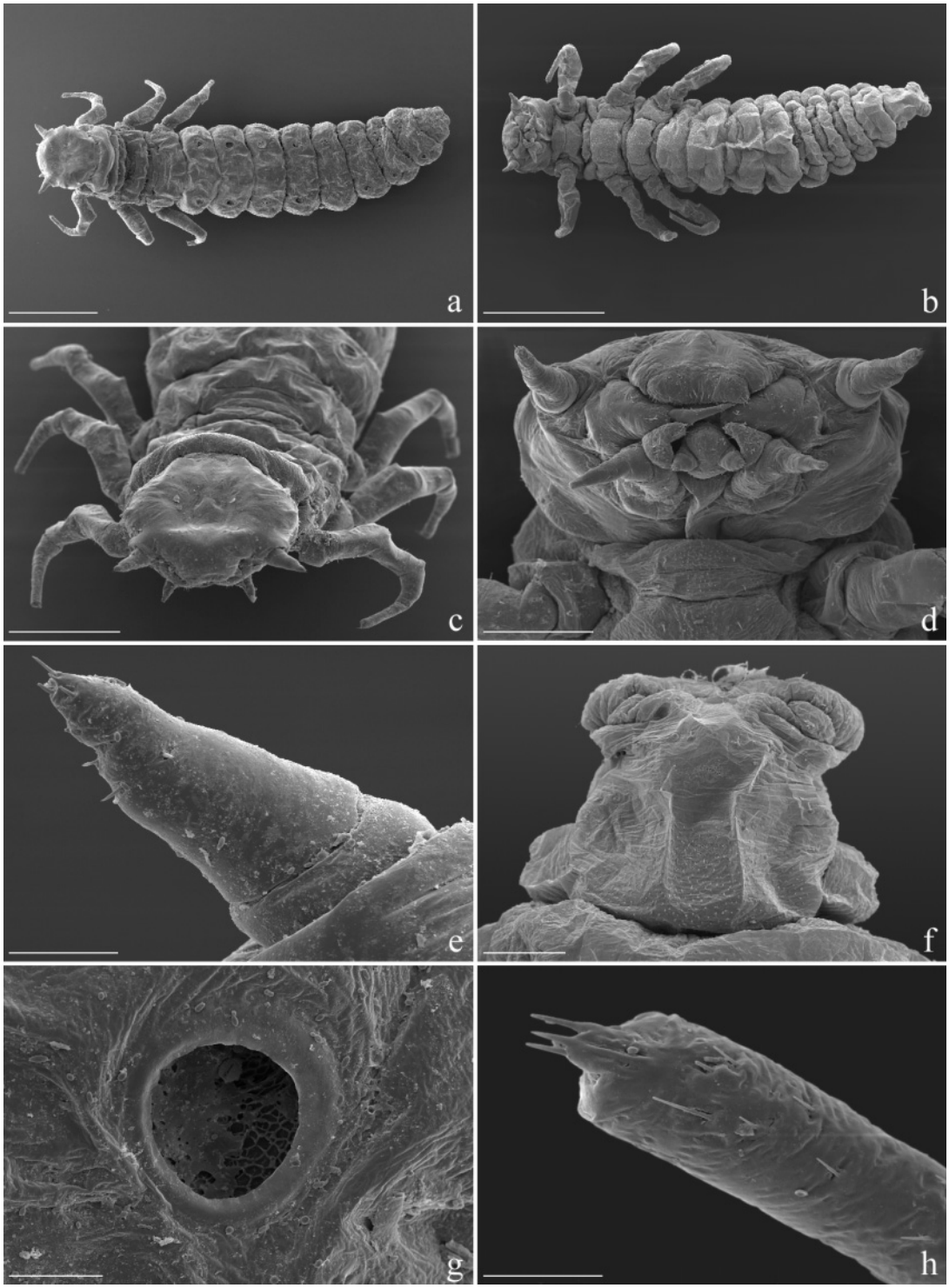
Measurements (specimens mounted on slides). Body length immediately after first moult, 6 mm, before second moult, 7 mm; head length 0.58 mm, maximum width 0.75 mm; antennal length 0.2 mm; length of abdomen 3 mm; diameter of spiracles: mesothoracic 130 μm, abdominal I 160 μm, abdominal II–VIII from 140 μm to 86 μm.

Head (Figs. 8*c*, 8*d*) prognathous and transverse (width/length ratio = 1.3), anteriorly rounded, laterally enlarged behind stemmata and narrowed from middle to base. Epicranial area at antennal insertion widely produced into anterolateral cylindrical expansions. Dorsal surface of head capsule deeply depressed in middle at level of posterior frontal area. Epicranial suture almost completely obliterated: basal stem absent and frontal arms scarcely recognizable. Occipital foramen wide, broadly oval, and posteroventral. Stemmata dorsolateral, round, and slightly convex. Frontoclypeal region anteriorly extended and separated from labrum by fine suture. Postgenae with remnants (Fig. 8*d*) of hemispheric protuberances of triungulin. Gular region subtriangular, diverging posteriorly, about twice as long as wide. Labrum (Fig. 8*d*) small, subrectangular, not visible in dorsal view, partially covering mandibles. Epipharyngeal surface with dense pubescence. Antenna (Fig. 8*e*) three-segmented, thick and conical, apically pointed, about one fourth length of head; basal joint cylindrical, about one fourth as long as wide, the remaining two joints with suture obsolescent; sensory appendix on second joint not clearly distinguishable; antennal seta extremely reduced on third joint; a few small sensilla present apically and subapically.

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

Fig. 8. *Epispasta abbreviata*, second-instar larva: *a*, dorsal view; *b*, ventral view; *c*, head and thorax, anterodorsal view; *d*, head, frontal view; *e*, left antenna, dorsal view; *f*, apex of abdomen, ventral view; *g*, abdominal spiracle II; *h*, apex of tibia and claw, dorsal view. Scale bars = 1 mm (*a*, *b*), 500 µm (*c*), 200 µm (*d*), 50 µm (*e*, *g*), 100 µm (*f*), and 40 µm (*h*).



© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

Mandible (Fig. 8*d*) triangular, rather soft, apical third strongly sclerotized, slightly upcurved and acute at apex, with medial margin minutely serrate basally (8–9 teeth) and smooth apically; base of mandible broad and bulged. Maxilla (Fig. 8*d*) fleshy, with stipes wide at base and narrower apically; cardo absent or fused with basal part of stipes; mala wide, digitiform, fleshy, incurved, with several short, spinelike setae; palpi thick and conical with partially fused joints, subequal in length. Labium (Fig. 8*d*) bulged, highly swollen dorsally; labial palpi consisting of two fused segments, the first much wider than the second. Apex of maxillary and labial palpi with papillate, basiconic sensilla. Hypopharynx fleshy, soft, and with densely microspinulate microsculpture.

Thorax. Segments scarcely sclerotized, subequal in length, increasing in width from prothorax to metathorax (Fig. 8*a*). Pronotum shield-like, suboval, about as wide as head, anterior margin straight, posterior and lateral margins rounded. Mesothorax and metathorax subrectangular, mesothorax wider than prothorax and metathorax with spiracles anterolaterally.

Legs (Figs. 8*c*, 8*h*) elongate, with segments partially fused. Coxae about as long as trochanters; femora longer than tibiae, strongly angulated in the middle, with basal part wider, cylindrical, and apical part subconical; tibiae cylindrical, slightly curved basally, and truncate at apex; claws spinelike, very short, about as long as spinelike tarsal setae.

Spiracles (Fig. 8*g*) dorsally placed on terga, annular, round, with prominent peritremes, internally reticulate with irregular polygonal meshes. Mesothoracic spiracle anterolateral in position, similar in size to abdominal spiracle II. Abdominal spiracle I transverse and wider than the following; spiracles circular, gradually decreasing in size from I to VIII.

Abdomen (Figs. 8*a*, 8*b*) fusiform with maximum width at segment III; relative width increasing considerably from early to late FG2 larvae; segments subequal in length, extremely transverse, rounded at sides. Terga and sterna with setae reduced to very small, spinelike sensilla. Pygidium (Fig. 8*f*) transversely bilobate.

Third-instar larva

Habitus, microsculpture, and measurements. Retaining campodeiform phenotype. Soft, thick, straight, subovate, very similar to that of second instar in shape, colour, setation, and microsculpture but a little more fusiform than the mature second instar. Length of larva immediately after second moult about 4 mm, before third moult about 7 mm. Width after second moult about 1 mm, before third moult about 2 mm.

Head. Head capsule slightly sclerotized. Stemmata flat, represented by round, dark, pigmented area. Antenna wider at base than in second instar. Mandible and maxilla as in second instar.

Thorax. Length about one fourth or less than that of entire body; mesothorax and metathorax wider than prothorax. Legs similar in shape to those of second instar, but comparatively smaller in proportion to rest of body. Abdomen composed of 10 segments; segment IV widest. Spiracles dorsal in position, annular, very large, as long as half their segment length or more, decreasing slightly in size from I to VIII. Mesothoracic spiracle similar in size to abdominal spiracle I; shape as in FG2.

Discussion

The remarkable first-instar larva of *E. abbreviata* is characterized by unique features as well as characteristics common to phoretic Meloidae in general, although some of these are exaggerated in this species. Characteristics apparently unique to *E. abbreviata* larvae are all associated with the head. Included are the strongly depressed frontal area, the obsolescent epicranial suture, the enormously bulged genal areas, the extremely elongate second maxillary palpal segment, and the highly setose maxillary mala.

Several features of *E. abbreviata* larvae are obviously correlated with their phoretic behavior and are shared with other phoretic members of the Meloinae or, in some cases, with the almost universally phoretic Nemognathinae. Features common to *E. abbreviata* larvae and all other phoretic Meloinae include the structure of the cephalic region in particular. In these taxa the labrum shows varying degrees of fusion with the clypeus and its orientation is either almost completely ventral or perpendicular to the frontal plane of the head. Correlated with this we find that the mandibles are relatively slender, sickle-shaped, and directed ventrally, and that their movement conforms to an oblique dorsoventral plane. It is assumed that these modifications of the head aid all phoretic larvae in grasping and holding the setae of the carrier

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

host (Selander 1985). Another larval *E. abbreviata* trait common to phoretic Meloinae triungulins is the fine pubescence on the epipharynx. It also occurs in several *Meloe* spp. as well as the genera *Spastonyx*, *Lyttomeloe*, and *Cyaneolytta*. The function of this pubescence is not clear but may be analogous to the dense tuft of thick cuticular structures occurring in nemognathines (see Bologna and Pinto 2001). Although the degree of bulging of the genal areas on the ventral surface of the epicranial plates in *E. abbreviata* is distinctive, some swelling in this area of the head also occurs in certain species of *Meloe* (*e.g.*, *M. dianella* Pinto *et* Selander, *M. occultus* Pinto *et* Selander, *M. autumnalis* Olivier, and *M. laevis* Leach). The cuticular surface in these areas is uniquely sculptured and set with numerous pores in *E. abbreviata* (Fig. 5*f*), suggesting outlets for glandular secretions. The function of this modification, unique to these phoretic taxa, is unknown.

Other larval *E. abbreviata* characteristics are common to most or all phoretic Meloidae larvae, including those of the clearly unrelated subfamily Nemognathinae. In all phoretic Meloidae the stemmata are lateral in position, not dorsal, the antennal sensory appendix is reduced (disk-like in *Epispasta* and many other phoretic groups), and the apex of the abdomen bears a bilobed pygopod. Larval *E. abbreviata* features shared with several but not all phoretic taxa include the enlarged femora and the trident-shaped claw structure. These two traits occur not only in several other phoretic meloines (*e.g.*, nominate *Meloe*, *Spastonyx*, and *Lyttomeloe* species) but also in the distantly related nemognathine genus *Stenoria* Mulsant, 1857 and in at least one species of *Nemognatha* Illiger, 1807 (Blochtein and Wittman 1988; Bologna and Pinto 2001). The pygopod presumably is an adaptation facilitating movement on smooth plant surfaces where larval encounters with carrier hosts occur, and the leg modifications are probably related to attaching behavior. The trident-like claw has been associated with grasping of the hairs of carrier bees in *Meloe* spp. (Pinto and Selander 1970), and femoral enlargement presumably also enhances grasping behavior, possibly by housing powerful adductor muscles of the claw.

The phenetic similarity of all phoretic first-instar larvae of Meloinae is considerable, and it is not surprising that Selander (1991) felt this to be compelling evidence for placing the taxa they represent in the same tribe, the Meloini. The similarity is especially striking among the larvae of *Epispasta*, *Spastonyx*, *Lyttomeloe*, and the nominate subgenus of *Meloe*. As indicated previously, however, phylogenetic support of a close relationship among these genera is lacking (Bologna and Pinto 2001). None of the numerous analyses performed utilizing 126 adult and larval characters and 85 meloid taxa retrieved a monophyletic all-phoretic Meloinae as proposed by Selander (1991). Analysis constrained for such a taxon was clearly less parsimonious than alternative hypotheses proposing the independent origin of phoresy and phoretic traits several times in the subfamily. With the exception of *Lyttomeloe* and *Spastonyx*, all phoretic meloine genera were divorced from one another and grouped with non-phoretic taxa (Bologna and Pinto 2001).

All of the distinctive traits of *Epispasta* larvae discussed thus far are either autapomorphic or homoplastic; none provide guidance as to the placement of this genus in the subfamily. Bologna and Pinto (2001) proposed a possible sister-group relationship between *Epispasta* and their redefined Meloini (= non-phoretic *Physomeloe* + *Meloe*), but the single synapomorphy supporting this, the presence of hypopharyngeal rods, is considerably homoplastic in the family and does not provide strong evidence of a relationship. Consequently, the placement of *Epispasta* remains an open question.

Finally, mention should be made of the general campodeiform phenotype of the second- and third-instar larvae of *Epispasta*, which retain overall similarity with the first instar. This apparently is a unique feature of this genus. Although larvae other than the first instar are known for relatively few genera of Meloidae, all post-triungulin instars of groups that have been studied, including those of the phoretic genus *Meloe*, are scarabaeiform with a cylindrical body and hypognathous mouthparts (*e.g.*, Selander and Mathieu 1964; Pinto and Selander 1970).

Acknowledgements

This paper is dedicated to the late R.B. Selander, who contributed enormously to our knowledge of blister beetles during a long career studying this insect group (1952–1993). In particular, this study of *Epispasta* would not have been possible without access to his reared larval material. We thank G. Platner (UCRC)

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

for technical assistance with some of the larval preparations, and L. Vignoli for the picture of the adult of *Epispasta*. The scanning electron microscopy analyses were carried out at L.I.M.E. (Laboratorio Interdipartimentale di Microscopia Elettronica), Università degli Studi "Roma Tre", Rome. Many thanks also to P.E. Skelley and M.C. Thomas (FSCA) for their kind assistance and for providing us with material in the Lorraine F. and Richard B. Selander Collection, and to M. Brendell for making accessible the larval collection of BMNH.

References

Blochtein, B., and Wittmann, D. 1988. Mating site specificity, reproduction and vector selection in *Nemognatha nigrotarsata* (Col., Meloidae), a nest parasite of leaf-cutter bees and other pollinator of crops in Rio Grande do Sul. Journal of Applied Entomology, **105**: 414–419.

Bologna, M.A. 1983. Utilizzazione dei dati biologici nella sistematica dei Meloidae (Coleoptera). Atti XII Congresso Nazionale Italiano di Entomologia Roma (1980), **2**: 21–36.

Bologna, M.A., and Aloisi, G. 1992. Systematics of *Lydomorphus* Fairmaire 1882, with description of the first instar larva of *L. dusaulti* (Dufour 1821) (Coleoptera Meloidae). Tropical Zoology, **5**: 55–71.

Bologna, M.A., and Aloisi, G. 1994. Systematics and bionomics of *Physomeloe* Reitter, with description of the first instar larva (Coleoptera Meloidae). EOS-Revista Espanola de Entomologia, **69**: 45–56.

Bologna, M.A., and Di Giulio, A. 2002. Review of the Southern African genus *Prolytta* Kaszab, with a description of the first instar larva, and bionomic and taxonomic remarks (Coleoptera, Meloidae). Invertebrate Systematics, **16**: 177–194.

Bologna, M.A., and Di Giulio, A. 2003. First instar larval morphology of *Prionotolytta binotata* (Péringuey, 1888), an endemic southern African species (Coleoptera, Meloidae). African Entomology, **11**: 213–219.

Bologna, M.A., and Pinto, J.D. 2001. Phylogenetic studies of Meloidae (Coleoptera), with emphasis on the evolution of phoresy. Systematic Entomology, **26**: 33–72.

Church, N.S., Salkeld, E.H., and Rempel, J.G. 1970. The structure of the micropyles of *Lytta nuttalli* Say and *L. viridana* LeConte (Coleoptera: Meloidae). Canadian Journal of Zoology, **48**: 894–895 + 1 plate.

Denier, P.C.L. 1935*a*. Estudios sobre Meloidos Americanos. Apuntes criticos de sistematica y de nomenclatura. Revista Argentina de Entomologia, **1**: 15–28.

Denier, P.C.L. 1935*b*. Coleopterorum Americanorum familiae Meloidarum enumeratio synonymica. Revista de la Sociedad Entomologica Argentina, **6**: 139–176.

Denier, P.C.L. 1940. Description de *Lytta neivai*, n. sp. du Brésil et notes sur quelques *Lytta* F. de l'Amérique du Sud (Col., Meloidae). Revista de Entomologia (Rio de Janiero), **11**: 799–802.

Di Giulio, A., Bologna, M.A., and Pinto, J.D. 2002. Larval morphology of *Meloe* the subgenus *Mesomeloe*: inferences on its phylogenetic position and a first instar larval key to the *Meloe* subgenera (Coleoptera: Meloidae). Italian Journal of Zoology, **69**: 339–344.

Di Giulio, A., Aberlenc, H.P., Vigna Taglianti, A., and Bologna, M.A. 2003. Definition and description of larval types of *Cyaneolytta* (Coleoptera Meloidae) and new records on their phoretic association with Carabidae (Coleoptera). Tropical Zoology, **16**: 165–187.

Fischer, J.B. 1827. Tentamen Conspectus Cantharidiarum. Dissertatio inauguralis, quam pro summis in Medicina et Chirurgia honoribus legitime obtinendis eruditorum examini subjicit Johannes Baptista Fischer, monacensis, bavarus. Lindauer, Monachii.

Klug, J.C.F. 1825. Entomologiae Brasilianae specimen alterum, sistens insectorum coleopterorum nondum descriptorum centuriam. Nova Acta Academiae Caesareae Leopoldino Carolinae Germanicae Naturae Curiosorum, **12**: 419–476.

Lawrence, J.F. 1991. Order Coleoptera. Immature insects. Vol. 2. *Edited by* F.W. Stehr. Kendal/Hunt, Dubuque, Iowa. pp. 144–298.

MacSwain, J.W. 1956. A classification of the first instar larvae of the Meloidae (Coleoptera). University of California Publications in Entomology, **12**: 1–182.

Parker, J.B., and Böving, A.G. 1924. Blister beetle *Tricrania sanguinipennis* — biology, descriptions of different stages, and systematic relationship. Proceedings of the United States National Museum, **64**(23): 1–40.

Pinto, J.D., and Bologna, M.A. 1999. The New World genera of Meloidae (Coleoptera): a key and synopsis. Journal of Natural History, **33**: 569–619.

Pinto, J.D., and Selander, R.B. 1970. The bionomics of blister beetles of the genus *Meloe* and a classification of the New World species. Illinois Biological Monographs, **42**: 1–222.

Selander, R.B. 1960. Restriction of the genus *Lytta* Fabricius (Meloidae). The Coleopterists Bulletin, **14**: 80–86.

Selander, R.B. 1985. *Spastomeloe,* a new genus of Meloini from Peru (Coleoptera: Meloidae). Journal of the Kansas Entomological Society, **58**: 668–685.

Selander, R.B. 1990. Blister beetles of the genus *Pseudopyrota* (Coleoptera: Meloidae). Journal of the Kansas Entomological Society, **63**: 46–79.

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press

Selander, R.B. 1991. On the nomenclature and classification of the Meloidae (Coleoptera). Insecta Mundi, **5**: 65–94.

Selander, R.B., and Mathieu, J.M. 1964. The ontogeny of blister beetles (Coleoptera, Meloidae). I. A study of three species of the genus *Pyrota*. Annals of the Entomological Society of America, **57**: 711–732.

© 2005 Entomological Society of Canada

https://doi.org/10.4039/n04-105 Published online by Cambridge University Press