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Morphology of the first instar larva in the tribe Clytrini, with two new descriptions in the subtribe Megalostomina (Coleoptera: Chrysomelidae: Cryptocephalinae)

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Abstract

Original descriptions and illustrations of the first instar larva of *Megalostomis (Heterostomis) lacordairei* Lacordaire and of *Coscinoptera argentina* Burmeister (Clytrini: Megalostomina) are provided. Based on the available information on first instar larvae, the tribe Clytrini is diagnosed. Unique of the larvae of clytrini is the antennal sensorium dome-like. Characters in common between Clytrini, Cryptocephalini, and Chlamisini (Cryptocephalinae) are highlighted, like the body J-shaped (in association with case-bearer habits); frons, clypeus, and labrum fused; spiracles with reticulate peritreme; egg-bursters present on meso- and metathorax, each situated anterior to a very long seta and a short seta ventral to these.

Key words. Larvae, morphology, Cryptocephalinae, Clytrini, *Megalostomis*, *Coscinoptera*

Introduction

The chrysomelid subfamilies Cryptocephalinae and Lamprosomatinae are collectively known as the “Camptosomata” or “case-bearers”, for the peculiar habit of their eggs, larvae and pupae, living in a portable protective case (Erber 1988; Brown & Funk 2005; Chaboo *et al*. 2008 and references therein). In a worldwide compilation of the fossil chrysomelid literature, Santiago-Blay (1994) reported a species assigned to *Clytra* Laichairting and two species of *Cryptocephalus* Geoffroy from the Jurassic. However, as Santiago-Blay noted in that paper, many late Paleozoic/early Mesozoic records of fossil chrysomelids are questionable and the actual specimens need to be reexamined. Besides uncertainties about the earliest records of Cryptocephalinae, their distinctive larval habit of carrying a case made principally of feces has been conserved for millions of years. Fossils of cryptocephaline larvae in their cases are amazingly well preserved in Miocene amber (Grimaldi & Engel 2005: Fig. 10.65).

Adults of case-bearing chrysomelids feed on foliage of a variety of eudicots (Erber 1988), but their larvae often show departures from strict phytophagy. Besides those with true herbivore larvae, that feed on green plant parts and complete development on the host plant, the larvae of most species live on the ground, in leaf-litter, and feed on dry vegetable material and detritus (Erber 1988; Brown & Funk 2005 and references therein). The larvae of some clytrine species live in ant nests (see Erber 1988: Table 2; Brothers *et al*. 2000 and references therein), but besides these mirmecophiles, many other clytrine larvae live in leaf litter and some few others on plants (Erber 1988; Jolivet 1988). The larval feeding habits and habitats in the subtribe Megalostomina are very little known, and larval association with ants is reported only for some Nearctic species in the genus *Coscinoptera* Lacordaire: *C. dominicana* (Fabricius) (Riley 1874; Jolivet 1952), *C. vittigera* LeConte (although its identification is doubtful, probably *C. dominicana*, see Erber 1988), and *C.* sp.

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indet. (Wasmann 1894; Jolivet 1952), and in the genus *Megalostomis* Chevrolat: *M. (Pygidiocarina) dimiata* (Klug) (Moldenke 1970; Rojas 1989). There is still much more to explore, particularly on Neotropical Clytrini.

The clytrine subtribe Megalostomina is defined on the basis of adult characters, being particularly important the claws simple and the prosternum evident between procoxae. For the aproximatelly 141 species in the Megalostomina (Moldenke 1970) almost nothing is known on their larvae, except for some general descriptions and drawings published for *Megalostomis* (*Minturnia) dimiata* Lacordaire (Dugès 1876), *Megalostomis (Scaphigenia) gazella* Lacordaire (Monrós 1953), and *Coscinoptera dominicana* Fabricius (Riley 1874; Medvedev 1998). In the tribe Clytrini, published information on the first instar larva is available for six genera: *Lachnaia* Chevrolat (Fiori 1948), *Smaragdina* Chevrolat (Medvedev 1962), *Clytra* Laicharting (Lee & Morimoto 1991), *Anomoea* Agassiz (LeSage & Stiefel 1996), *Coptocephala* Lacordaire (Pietrykowska 2000), and *Labidostomis* Germar (Wąsowska 2007).

The present study contributes original descriptions of the first instar of two species in two genera: *Megalostomis (Heterostomis) lacordairei* Lacordaire and *Coscinoptera argentina* Burmeister (Clytrini: Megalostomina). A larval definition of the tribe Clytrini is elaborated, and phylogenetic notes on Cryptocephalinae are provided. Although the existence of a "Camptosomata" clade, comprising cryptocephalines, clytrines, chlamisines, and lamprosomatines, is still an open question, the present study contributes evidence from larval morphology for the broad concept of Cryptocephalinae that includes Clytrini, Cryptocephalini and Chlamisini.

Materials and methods

First instar larvae were obtained from eggs laid by adults collected on their host plants in the field (Collection data are provided under "Material examined" in the descriptions). The localities of collection belong in Chaco and Monte biogeographic provinces (Morrone 2006). Adults of both sexes were kept in vials in the laboratory and fed with leaves of the host plant "Algarrobo" or *Prosopis* sp. (Fabaceae: Mimosoideae), until oviposition occurred. Eggs were placed on tissue paper in plastic cap vials, kept moist with water, and daily checked until the little larvae hatched. They were then removed, killed with hot water and preserved in 70 – 80 % ethanol. Voucher adults (38 specimens) are also deposited in the entomological collection of IADIZA ("Instituto Argentino de Investigaciones de las Zonas Áridas", Mendoza, Argentina).

Techniques for dissection and slide-mounting of the larvae follow May (1979, 1993), which basically consist in separation of head, mouth-parts and cuticle, clearing in KOH, washing in distilled water with a drop of acetic acid, transfer into pure ethanol, and mounting in Euparal™. The terms used in the descriptions follow conventions for beetle larvae (Lawrence 1991), and are mostly in agreement with works on chrysomelids (*e.g.*, LeSage 1982, 1984a; Lee & Morimoto 1991a, 1991b) and on weevils (*e.g.*, May 1993; Marvaldi 1997, 1999).

Descriptions are based on the first instar larva, which carries egg bursters, which are lost after first molt (Cox 1988), and shows primary chaetotaxy, which in later instars may be difficult to homologize due to the addition of secondary setae (e.g., see LeSage 1984a). Numbers correspond to one side of bilateral body structures, and thus should be considered as "pair/s of" in the descriptions. Cox (1988) is followed for describing the egg bursters, also called hatching spines in some publications (e.g., LeSage 1984a). These structures are considered homologous across Cryptocephalinae, based on their position on the body segments, and their location on particular tubercles (see Cox 1988 for a review). The term egg-case is used for the first case, of maternal origin, formed by a mixture of fecal material with secretions from particular glands opening into a specialized region of the rectum, with sclerites and muscles (also called "rectal apparatus") (Karren 1972; Hinton 1981; Erber 1988; Brown & Funk 2005).

Photographs were obtained with a digital camera mounted on a stereomicroscope (Leica MZ 16F). Auto-Montage software was used to combine source images taken at different focus into a single one showing all features in focus. Drawings of slide-mounted anatomical structures were made with a camera lucida attached to a compound microscope (Leica Leitz Laborlux S). Scale bars in mm are indicated on each figure.

Descriptions

Tribe Clytrini Lacordaire

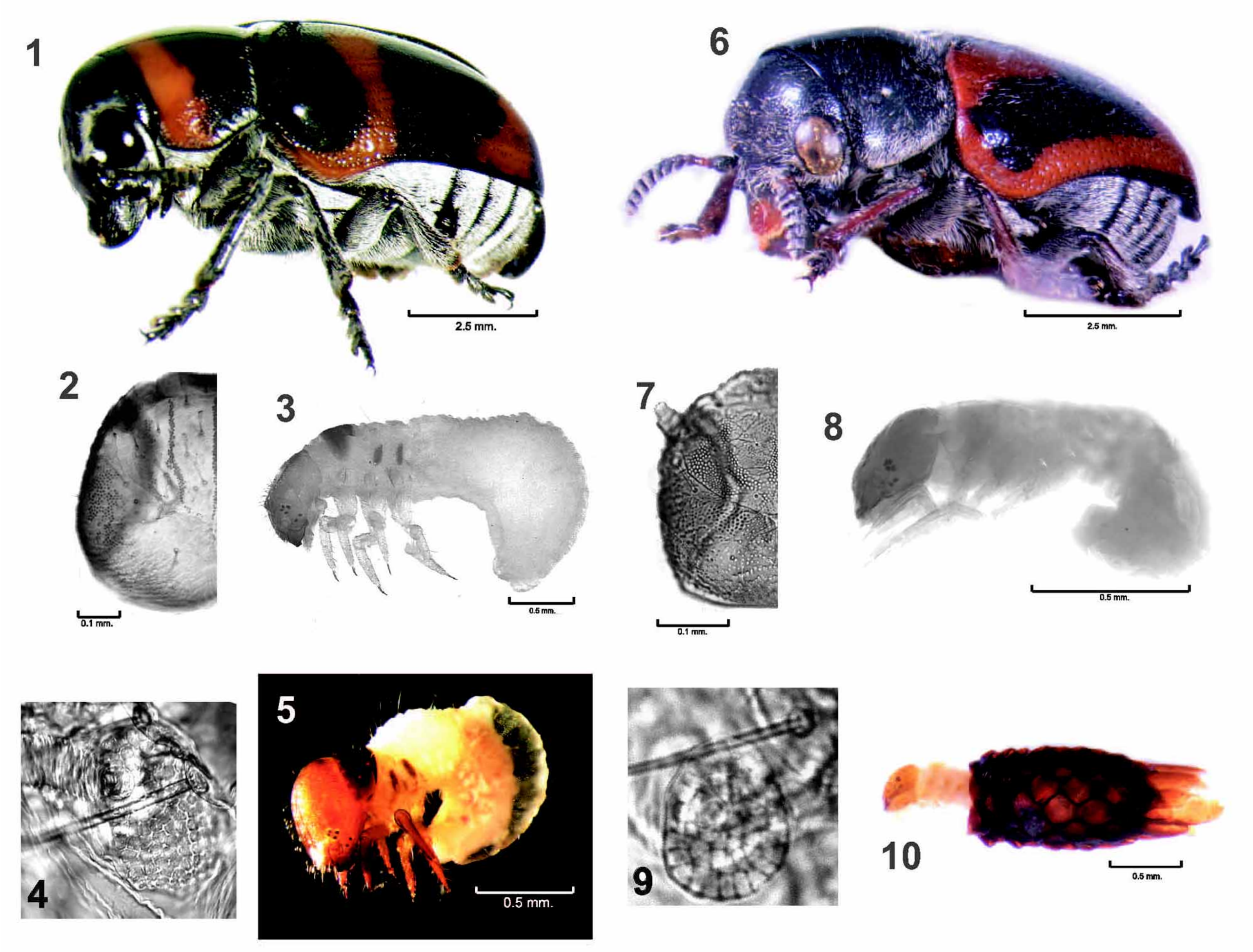
The following tribal description is based on the first instar larvae of two species in the genera *Megalostomis* and *Coscinoptera* described herein, and on published information of ten species in six genera: *Lachnaia* (Fiori 1948), *Smaragdina* (Medvedev 1962), *Clytra* (Lee & Morimoto 1991a), *Anomoea* (LeSage & Stiefel 1996), *Coptocephala* (Pietrykowska 2000), and *Labidostomis* (Wąsowska 2007).

General body aspect (see Figs. 3, 8). Body J-shaped; head hypognathous, legs long and well developed.

Head (see Figs. 11–17, 21–27). Fully exposed, subcircular, well sclerotized, surface of frons and epicranial halves with tuberculate sculpture pattern. Epicranial line (coronal suture) well developed, about 1/3 the length of head, frontal lines broadly divergent and weakly bisinuate. Endocarina absent. Stemmata well developed, 6 in number, in two groups: 4 behind antenna and visible in dorsal view, and 2 below antenna and visible in ventral view. Antennae mounted on ventral surface and partially hidden in dorsal view by frontal projection, 2-segmented, basal segment with 2 sensilla, apical segment with several sensilla and minute setae plus one long seta close to the sensorium, the latter dome-like. Epicranium with 4 minute posterior epicranial setae accompanied by 1 sensillum; 5 dorsal epicranial setae, spatulate and papillate, with 3 dorsal sensilla; 3 lateral epicranial seta and 3 stemmatal setae; frons usually with 6 spatulate and papillate setae (more than 6 setae, 13-14, in *Megalostomis lacordairei* and *Coptocephala rubicunda* (Laicharting)). Frons, clypeus and labrum fused, without distinct frontoclypeal or clypeolabral sutures. Clypeus-labrum transverse, on each side with 4-5 setae and 2 sensilla: 1 seta and sensillum apparently of clypeus and 3-4 labral setae, 1 on disc and near labral sensillum and 2-3 along antero-lateral margin. Labrum incised on anterior margin, usually sinuate. Epipharynx with 5-7 pairs of setae on anterior margin. Head in ventral view, with tentorial bridge narrow, with a pair of anterior tentorial arms. Mandibles robust, symmetrical, 4-toothed: two apical teeth and 2 blunt projections on incisor section; without mola, penicillus and retinaculum; 2 mandibular setae, longitudinally placed on outer margin, 2 sensilla, one near base of innermost tooth and the other between setae. Maxilla: cardo with 1 seta; stipes more than 2 X longer than wide, with 2 large setae and 1 sensillum on outer margin and 1 minute inner apical seta; palpiger sclerotized and with 2 setae and 1 sensillum; maxillary palp 3-segmented, basal segment with 2 sensilla, middle segment with 2 setae and 1 sensillum, apical segment with 1 seta and 1 sensillum plus elongate "accessory process"; lacinia fused with stipes, forming inconspicuous lobe at base of galea, bearing 2 stout setae on inner side; galea with 5 ventral setae and 1 sensillum, and a row of 4-5 dorsal setae plus 2 other setae at base. Labium with prementum and postmentum not fused. Postmentum connected ventrally with thoracic sternum and laterally directly with maxillae, without articulatory area or lobe; 3 postmental setae *(pms)*, basal pair (*pms1*) distantly separated from *pms2* and *pms3*, 1 sensillum between *pms2* and *pms3*; prementum with 1 minute seta (at base) and 1 long seta and 1 sensillum; ligula membranous, with 3 setae and 2 sensilla; labial palp 2-segmented, basal segment with 1 sensillum, apical segment with 1 sensillum and sensory papilla at apex.

Thorax (Figs. 18–20, 28–30). Pronotum sclerotized, pigmented (brown), pale median line separating both halves, each with 14 pronotal setae and 7 sensillae (5 of these on anterior margin). Meso- and metathorax pigmented laterally, only weakly sclerotized. Egg bursters present on meso- and metathorax, on weakly sclerotized dorso-lateral postero-interior (DLpi) tubercles, each consisting of a small subtriangular "spine" situated anterior to base of very long seta and near short seta ventral to these. Meso-thoracic spiracle, uniforous, peritreme broad and reticulate, subcircular to oval. **Legs,** well developed, similar sized, similar shaped, and sclerotized; with coxa, trochanter, femur, tibiae and tarsungulus; first four bearing setae and sensilla, the tarsungulus slightly curved (claw like), with 1 seta at base.

Abdomen (Figs. 3, 8, 18, 28). Abdominal segments not sclerotized, widest at middle part (abdominal segments V and VI), distal end (segments V- X) bent downwards and recurved ventrally (body J-shaped). Spiracles on abdominal segments I to VIII, lateral, similar to thoracic spiracle, with reticulate peritreme, but smaller.

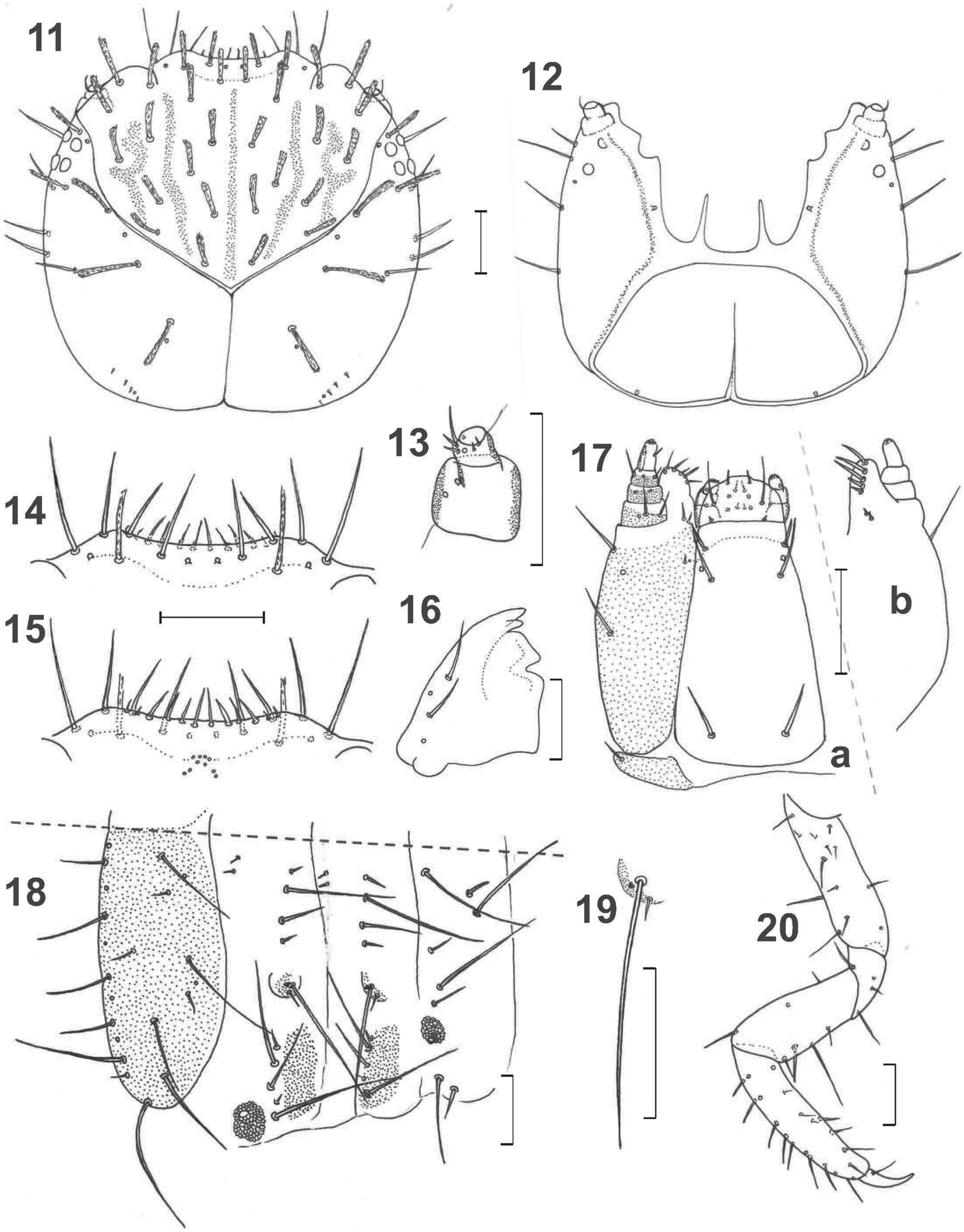


FIGURES 1–10. (1–5) ***Megalostomis (H.) lacordairei*** **Lacordaire**. 1. Adult female habitus, anterolateral; 2 – 5. First instar larva, 2. Head capsule, one half dorsal, showing cuticle sculpture pattern of frons and epicranium; 3. habitus, lateral; 4. Detail of thoracic spiracle; 5. Larva in its case.
(6–10) ***Coscinoptera argentina*** **Burmeister**, 6. Adult female, habitus, anterolateral; 7 – 10. First instar larva, 7. Head capsule, one half dorsal, showing cuticle sculpture pattern of frons and epicranium; 8. Habitus, lateral; 9. Detail of thoracic spiracle; 10. Larva in its case.

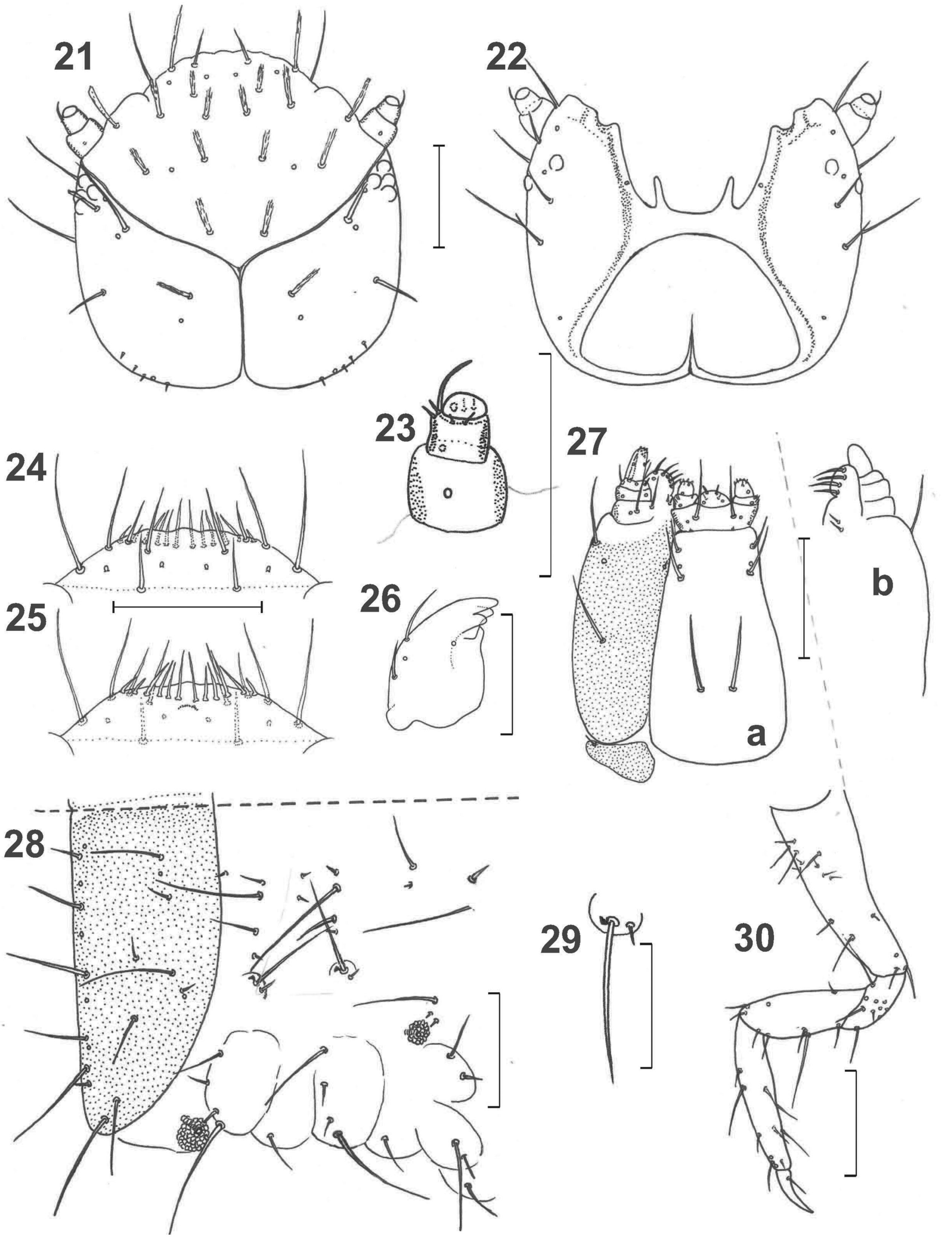
Megalostomis (Heterostomis) lacordairei **Lacordaire**
(Figs. 1–5, 11–20).

First instar larva (characters defining the tribe are not repeated here) (Figs. 2–5, 11–20).

Maximum dimensions: Body length 3.46 mm; head width 0.63 mm. Body of typical shape; coloration pale yellow when alive (body coloration turning white after preservation in ethanol). Head with a characteristic sculpture pattern, of round tubercles grouped in stripes between setae, on frons and epicranial halves (Fig. 2). Frons with 13 setae, spatulate papillate in shape. Labrum incised on anterior margin, without distinct lobes. Epipharyngeal sensilla in clusters of 3 (anterior) and 2 (posterior). Maxillary galea with row of 5 dorsal setae plus 2 setae at base.



FIGURES 11–20. ***Megalostomis (H.) lacordairei*****, first instar larva**. 11, 12. Head, dorsal and ventral; 13. Detail of (left) antenna; 14. Clypeus-labrum; 15. Epipharynx; 16. Mandible; 17. Maxilla and labium (a, ventral; b, dorsal maxilla); 18. Thorax and 1st abdominal segment, dorsolateral (one side); 19. Detail of tubercle bearing egg burster and setae; 20. Pro- leg, lateral. Scales = 0.1 mm.



FIGURES 21–30. ***Coscinoptera argentina*, first instar larva**. 21, 22. Head, dorsal and ventral; 23. Detail of (left) antenna; 24. Clypeus-labrum; 25. Epipharynx; 26. Mandible; 27. Maxilla and labium (a, ventral; b, dorsal maxilla); 28. Thorax and 1st abdominal segment, dorsolateral (one side); 29. Detail of tubercle bearing egg burster and setae; 30. Proleg, lateral. Scales = 0.1 mm.

Egg and first larval case (Fig. 5) ovoid, yellow, without fecal plates, covered with a bright, transparent, secretion.

Material examined. Three first instar larvae (two slide-mounted) from eggs deposited by adults collected in ARGENTINA: Catamarca Province, between Esquiú and Ramblones (Lat. - 29.288054; Long. - 65.367721), 3 March 2006, feeding on leaves of *Prosopis* sp., F. A. Agrain, S. Roig and T. Erwin coll. (IADIZA). A total of 34 adults (both sexes) were collected by hand, from host plant foliage; some females laid eggs, together producing seven eggs soon after capture, and although eggs were later contaminated by fungi, three first instar larvae successfully hatched after six days.

Remarks. The lack of egg fecal coating by the female of *Megalostomis (Heterostomis) lacordairei* cannot be due to inadequate nourishment, as has been suggested for *Clytra quadripunctata* by Rosenbauer 1852, since oviposition occurred within a few minutes after females were captured, and thus they were naturally fed (there were abundant fresh leaves available in the collecting site, and plant material was found in the digestive system of dissected females).

Coscinoptera argentina Burmeister
(Figs. 6–10, 21–30)

First instar larva (characters defining the tribe are not repeated here) (Figs. 7–10, 21–30).

Maximum dimensions. Body length 1.56 mm; Head width 0.33 mm.

Head with a characteristic sculpture pattern, of round tubercles evenly distributed between setae, on frons and epicranial halves (Fig. 7). Frons with 6 setae, spatulate papillate in shape. Labrum sinuate on anterior margin, without 3 distinct lobes. Epipharyngeal sensilla clustered anteriorly in a row. Maxillary galea with row of 4 dorsal setae plus 2 setae at base. Sides of prementum protrudent and with microtrichae.

Egg and first larval case (Fig. 10) brown, fecal plates forming a regular sculptured pattern of subhexagonal shapes, ending posteriorly in elongated plates.

Material examined. Three first instar larvae (two slide-mounted) from eggs deposited by adults collected in ARGENTINA: Mendoza Province, Cdad. Mendoza, Parque Gral. San Martín (Lat. -32.893142; Long. - 68.890388), December 2002, feeding on leaves of *Prosopis chilensis*, A. E. Marvaldi coll. (IADIZA). A total of four adults were collected by hand, from the host plant foliage.

Remarks. The egg-case of *C. argentina* is similar in aspect to that of *C. dominicana*, documented by Riley (1874) and reproduced by Erber (1988: Fig. 16.5), but the latter has an egg stalk or pedunculus.

Discussion

The first instar larvae of *Megalostomis (Heterostomis) lacordairei* and of *Coscinoptera argentina* (Clytrini: Megalostomina) are different in a number of characters. The microsculpture of the head and the number of frontal setae are among the most obvious. Many characters in common between them and with the previously known larvae in other clytrine genera, allow a tribal definition. However, a larval characterization of the "subtribe Megalostomina" is not possible based on the species herein studied, since no obvious character in common differentiates them from the remaining Clytrini.

Larvae of Clytrini share the following features in common with larvae in the tribes Cryptocephalini and Chlamisini (e.g., LeSage 1982, 1984a,b, 1985, 1986; Lee & Morimoto 1991a; Bienkowski 1999), and thus characterize the subfamily Cryptocephalinae in broad sense (i. e., including Clytrini, Cryptocephalini and Chlamisini). Among them, the following are probably synapomorphies of cryptocephalines, by outgroup comparison with other chrysomeloids and weevils (e. g., Lee 1993 and references therein; Cox & Windsor 1999; Kuschel & May, 1990; Napp 1994; May 1993): Body J-shaped (see Figs. 3, 8); Frons, clypeus, and labrum fused (see Figs. 11, 21); 6 stemmata, clustered 4 + 2 (see Figs. 3, 8); Spiracles uniforous with reticulate peritreme (see Figs. 4, 9, 18, 28); Egg bursters on TII and TIII and associated with a long and a short seta (see Figs. 18, 19, 28, 29).

The following larval character seems to be unique (probably synapomorphic) of Clytrini: antennal sensorium dome-like in shape, apically flat (see Figs. 13, 23). The (plesiomorphic) condition of sensorium conical in shape, is observed in larvae of Cryptocephalini, Chlamisini, and other chrysomelids.

The other group of case-bearers, the Lamprosomatinae, show a number of larval features in common with the cryptocephalines (Lee & Morimoto 1991b), being the body J-shaped among the most obvious (and related with their habit of carrying a case), as well as the fusion of frons, clypeus and labrum. The latter feature is also observed in the Megascelini (Cox & Windsor 1999), the Palophaginae (Kuschel & May 1990), some cerambycids (Napp 1994) and in basal weevils (May 1993). Unlike the cryptocephaline larvae, those of Lamprosomatinae have bicameral spiracles with peritreme simple, and five stemmata grouped 2 + 3. The maxillary palp 3-segmented plus the palpiger, as present in both groups, is almost likely a plesiomorphy, and although both subfamilies have egg-bursters confined to meso- and metathorax, those in Lamprosomatinae lack the short ventral seta (Cox 1988). The existence of a “Camptosomata” clade (i. e., Cryptocephalinae plus Lamprosomatinae) is still an open question, and the coding of some larval characters, as in Lee (1993) and Reid (1995, 2000), requires re-evaluation in future analyses. Moreover, recent molecular phylogenetic studies (Gomez Zurita *et al*. 2007; Marvaldi *et al*. 2009) suggest the Cryptocephalinae are closer to the Cassidinae and belonging to an “Eumolpinae” clade.

The egg-case is considered of importance in providing protection against desiccation and predators (Erber 1988). There is experimental evidence for the fecal cover being effective to prevent predation (Müller & Hilker 2004), and also for its function as a chemical signal to attract ants in myrmecophilous taxa (Erber 1969). Thus the absence of egg fecal coating in *M. (H.) lacordairei*, coupled with the observation that the newly hatched larva later did not keep the empty egg corion, is suggestive of a different life strategy. It is hard to imagine that eggs and larvae can survive on the detritus without fecal protection, and this lead to speculate about they probably being attracted to ants that carry them to their nest, where larval development and pupation may occur. It is worth mentioning that eggs produced by females of *Urodera vau* Lacordaire (Clytrini: Babiina), collected on the same trip, were similar to those of *Megalostomis*, except for their spherical shape, but also lacking fecal covering (Agrain, pers. obs.). This suggests that naked eggs may be more common than previously thought among clytrines. Because the females studied of *M. (H.) lacordarei*, *Urodera vau*, and *Coscinoptera argentina*, all have well developed rectal sclerites, their presence even in those species not showing egg fecal coating, suggest that the rectal apparatus may have importance in other functions, other than molding the fecal plates, like in water retention (as proposed by Schöeller 1995). Also, additional observations on oviposition, preferably in natural conditions, should be made to confirm the absence of egg stalk in *C. argentina*. This may be informative of ecological variation within Megalostomina, since the presence *versus* absence of egg stalks are thought to be associated with host plant fidelity of strict phytophages *versus* detritivory or myrmecophily, respectively (Chaboo *et al*. 2008).

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