Larval morphology of the genus *Cerocoma* (Coleoptera: Meloidae) and phylogenetic implications

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The Palaearctic blister beetle genus *Cerocoma* Geoffroy, 1762 includes species with great morphological differences in the adults, emphasised in the four subgenera. First instar larvae of three species, belonging to two different subgenera — *C*. (*Cerocoma*) *schaefferi* (Linnaeus, 1758), *C*. (*Metacerocoma*) *prevezaensis* Dvorak, 1993, *C*. (*Metacerocoma*) *schreberi* Fabricius, 1781 — are described and compared to that of the single other species previously known in literature, *C*. (*Cerocomina*) *vahli* Fabricius, 1787. First instar larvae of *Cerocoma* have typical features of the subfamily Meloinae, without derived characters. No relevant differences were found by a SEM morphological study, and the species can be distinguished only by morphometric characters. Consequently, subgeneric divisions, based on the adult morphology, are not supported by larval characters.

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1. Introduction

The tribe Cerocomini includes five Old World genera of Meloinae with very distinctive epigamic modifications of the male head (mostly antennae and maxillary palpi) and fore legs (Bologna 1991, Turco *et al*. 2002). The tribe is typically Palaearctic in distribution, with only one species of the genus *Anisarthrocera* Semenov, 1895 being distributed in Northern Somalia (Bologna & Pinto 2002). Some larval characters of *Cerocoma schreberi* Fabricius, 1781 were used for a phylogenetic analysis of the family (Bologna & Pinto 2001), but the first instar larva of this species has remained undescribed. This recent cladistic study, based on larval, adult and biological characters, supports the recognition of the tribe Cerocomini (*sensu* Bologna 1991, *nec* Selander 1991) as a monophyletic group.

Adults of the genus *Cerocoma* Geoffroy, 1762 are characterised by metallic aposematic colours (green, copper or blue), are associated with defensive behaviour linked to toxic cantharidin production and spend most of their time feeding, with modified mouthparts, on pollen and nectar of herbaceous plants, such as Asteraceae and Apiaceae (Bologna 1991) or performing complex sexual behaviours (Turco *et al*. 2002). Eggs are laid in holes dug by the female in the soil (Beauregard 1884, 1890, Fabre 1886, Cros 1919, 1924, Molitor 1931, Bologna 1991). First instar larvae are not phoretic, but actively reach the host nest where they de-

velop to the adult stage. As far as we know, larvae are parasitoids of Hymenoptera: Apoidea (Colletidae and Megachilidae, *C. schreberi* and *C. vahli*) and Sphecoidea (Sphecidae, *C. schaefferi*), feeding respectively on larvae and honey of the host, or on eggs and food stored by the host. Parasitism on Sphecidae by Meloidae is uncommon (see Bologna 1983, 1991 for a review) and must be confirmed.

In the whole tribe Cerocomini, preimaginal stages of only three species of the genus *Cerocoma* were known. The first instar larva (or triungulin, as well as other instar larvae and pupa) was described only for *C. vahli* Fabricius, 1787, a North African species belonging to the subgenus *Cerocomina* Kaszab, 1951 (Cros 1924). The II–VII stages and the pupa of *C. schaefferi* (Linnaeus, 1758), belonging to the nominate subgenus, were described by Fabre (1886). The V–VII stages and the pupa of *C. schreberi*, belonging to the subgenus *Metacerocoma* Kaszab, 1951, were described by Beauregard (1884, 1890).

The aim of this paper is to describe the first instar larvae of *C.* (*Metacerocoma*) *schreberi* and *C.* (*M.*) *prevezaensis* Dvorak, 1993 and that of *C.* (*Cerocoma*) *schaefferi*. Larval morphology of these species is compared with that of *C.* (*Cerocomina*) *vahli* described in the literature (Cros 1924), and phylogenetic relationships of the tribe Cerocomini among the subfamily Meloinae are briefly discussed. Larvae of the subgenera *Mesocerocoma* Kaszab, 1951 still remain unknown, as well as those of the species of the nominate subgenus, referred by Dvorak (1990) to a distinct subgenus (*Meloides* Piller & Mitterpacher, 1783).

2. Material and methods

The description of triungulins is based on the following specimens, preserved in 70% ethanol and deposited in the M. Bologna collection at the Department of Biology of the Roma Tre University (Rome, Italy). Measurements represent the average of at least three specimens for each species, and were taken by using both light and scanning electron microscopes.

— *Cerocoma schreberi*, vial 378 (more than 30 larvae); slide M308; stub 54: adults from Italy, Lazio, Maccarese (Rome Province), about 40 m a.s.l., 29.VII.1995, M. Mei leg., on *Mentha* sp. (Lamiaceae); deposition 1/2.VIII.1995, hatch 14/15.VIII.1995.

— *C. schreberi*, vials 323, 324 and 325 (more than 120 larvae): adults from France, Puget sur Argens (Var Province), about 100 m a.s.l., 26.VII.1995, M. Bologna leg., on *Daucus* sp. (Apiaceae); deposition 26/27.VII.1995, hatch 20/26.VIII.1995.

— *C. prevezaensis*, vial 417 (more than 50 larvae); stub 53: adults from Greece, 9 Km W Patra Airport on the E55 road, 38°05´N 21°25´E (Ahaia Province), at sea level, 04.VI.1999, M. Bologna, P. De Salvo, F. Turco and M. Zapparoli leg., on *Achillea* sp. (Asteraceae); deposition 05.VI.1999, hatch 23.VI.1999.

— *C. schaefferi*, vials 454, 455 and 456 (more than 200); adults from Italy, Calabria, Sila Massif, Montescuro Pass (Cosenza Province), 39°20´N–16°20´E, 1350 m a.s.l., 3.VII.2001, A. Di Giulio, S. Fattorini and F. Turco leg. on *Achillea* sp. (Asteraceae); deposition 5.VII.2001, hatch 14–15.VII.2001.

Adults and eggs were held at 24–25 °C in a thermostatic cell with photoperiod control. Morphological analyses utilised a light microscope for material mounted on slides in Canada balsam, and a scanning electron microscope for material mounted on stubs, after critical point dehydration and gold sputtering. Measurements reported in the descriptions are mainly based on cleared, slide-mounted larvae. For terminology of larval structures, we refer to MacSwain (1956), Lawrence (1991) and Bologna and Pinto (2001). As regards some characters of larval chaetotaxy we adopted notational conventions suggested by Selander (1990) and Bologna and Di Giulio (2002).

3. Egg and larval morphology

3.1. Egg morphology

Eggs of *C. schreberi, C. prevezaensis* and *C. schaefferi* were studied. They are very similar: pale yellow, elongate, round at both ends, a little wider at one apex. Egg length/maximal width: *C. schreberi*, 1/0.25 mm; *C. prevezaensis*, ca. 0.9/0.22 mm; *C. schaefferi*, ca 0.9/0.25 mm.

3.2. Description of first instar larvae

As previously discussed, certain larval characters of *Cerocoma schreberi* were used for a phylogenetic analysis of the family (Bologna & Pinto 2001), but the first instar larvae of this genus have remained undescribed. Scarce differences were found in the larval morphology of species currently referred to the different subgenera of *Cerocoma*. In the following, we describe the

triungulin of one species in detail (*schreberi*) and report the distinctive characters of the other two species (*prevezaensis*, *schaefferi*) only for comparison. The main differences among the species are summarised in Table 1.

3.2.1. Cerocoma schreberi (Figs. 1b, 2b–h)

Triungulin campodeiform; body elongate, subcylindrical, subfusiform. Body length 1.52 mm (from abdominal apex to labrum); head length 0.2 mm (from occipital foramen to clypeolabral suture), maximum width 0.26 mm; diameter of stemmata 18 mm; basal stem of epicranial suture 0.06 mm; antennal length 0.1 mm, terminal seta length 0.14 mm; prothorax length 0.18 mm, maximum width 0.3 mm; abdominal length 0.9 mm, terminal setae length 0.46 mm; diameter of spiracles: mesothoracic about 22 mm, abdominal I about 24 mm, abdominal II–VIII respectively from 10 to 8 mm. Colour light brown; abdominal sternites gradually more sclerotisized from segment I to IX; thoracic sterna not sclerotisized. Cuticle reticulate, with transverse polygonal meshes.

Head slightly transverse with subparallel sides; basal elevation absent; anterior margin of head slightly rounded. Epicranial suture Y-shaped; frontal sutures complete to antennal fossae, sinuate, widely diverging at base, curved at medial third, and markedly curved laterally at distal third. One stemma present on each side of the head capsule, dorsal in position; stemmata convex, round, slightly smaller than the mesothoracic spiracle. Setae disposed as in Fig. 2a–c. Frontoclypeal region with a total of 14 setae; frontoclypeal suture obliterate, boundary area between clypeus and frons with one transverse row (frontoclypeal row, FCR) of 3 pairs of setae; one sensory pit between FCR_2 and FCR_3; 4 pairs of setae

Table 1. Differences among larvae of *Cerocoma*.

	C. schreberi	*C. prevezaensis*	*C. schaefferi*	*C. vahli*
Shape of the head	slightly transverse with subparallel sides, posteriorly slightly narrowed	transverse, with posteriorly distinctly narrowed sides	squared, with parallel sides, posteriorly slightly narrowed	slightly rounded sides transverse, with sub-parallel sides
Medial part of frontal sutures	curved	subparallel	curved	curved
Stemmata	slightly smaller than mesothoracic spiracle	slightly smaller than mesothoracic spiracle	slightly larger than mesothoracic spiracle	?
Cutting edge of mandibles	serrate with distinct teeth	with extremely short teeth	with extremely short teeth	serrate with distinct teeth
Segment II of maxillary palpi	longer than segment I and asymmetric	longer than segment I and asymmetric	subequal to segment I and only slightly asymmetric	subequal to segment I and asymmetric
Segment III of maxillary palpi	about 3 times as long as I	about 3 times as long as I	about 2 times as long as I	about 2 times as long as I
Antennal segment I length	1/3 of segment II	1/2 of segment II	1/2 of segment II	1/3 of segment II
Apical antennal seta	less than 1.5 as long as the antenna	1.5 as long as the antenna	more than 1.5 as long as the antenna	1.5 as long as the antenna
Abdominal spiracle I	distinctly wider than others	distinctly wider than others	slightly wider than others	slightly wider than others

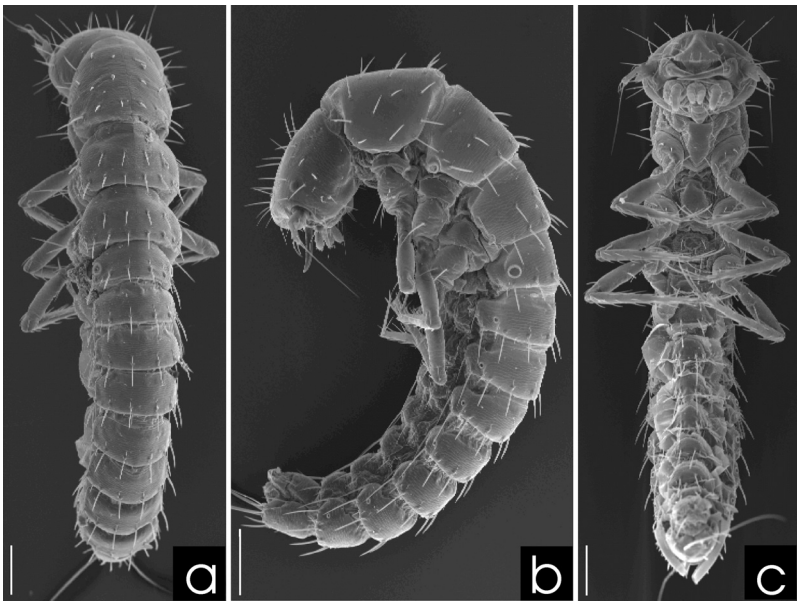

Fig. 1. Habitus of first instar larvae — a. *Cerocoma prevezaensis* (Greece, Patra airport), dorsal view. — b. *C. schreberi* (Italy, Maccarese), left lateral view. — c. *C. prevezaensis*, ventral view. Scale bar = 100 μm.

posterior to FCR, following a curved line paralleling the arms of the epicranial suture (from posterior to anterior setae 1–4); 1 sensory pit present between setae 1 and 2. Each epicranial half dorsally with a basal group of 4 very small setae and 1 pit near occipital foramen; 4 pairs of setae lined at the level of the base of frontal arms of epicranial suture (codified as setae 1–4, from internal to external); 1 sensory pit just anterior seta 1; seta 2 smaller and slightly displaced in front of others; 3 setae around the stemma: 1 anterior, just behind antennal fossa, the second posterolateral, external to the stemma, the third (the ocular seta) inserted at the same level of stemma, longer than the adjacent, posterior to ocular sensory pit. Gulamentum weakly sclerotised with 2 anterior setae. Antennae (Fig. 2d) moderately long, anteriorly directed; segment I short, ring-like with 1 dorsal sensory pit; segment II almost three times as long as I, with 4 anterior setae near sensory appendix (1 long dorsal, 1 long lateral on the outer side, 1 short lateral on the inner side, 1 small lateral on the outer side) and 1 dorsolateral pit; sensory appendix on segment II ventral, conical, acute at apex, about as long as segment I; segment III slender, cylindrical, slightly longer than II, with a long apical seta (slightly longer than the entire antenna), 3 long subapical setae, 2 dorsolateral and 1 ventral in position; 1 small seta near the base of apical seta, and 1 lateral pit on outer side of the segment. Labrum (Fig. 2c) narrow, transverse, with rounded sides, with 8 dorsal setae different in size, approximately lined along the margin; some additional very small setae and pits present anteroventrally. Epipharynx with the aspect of a coarsely granular plate. Mandibles (Fig. 2h) falcate, dorsoventrally flattened, acute at apex, enlarged at base, without mola; cutting edge serrate with 12 distinct small teeth decreasing in size from base to apex, ventrally longitudinally keeled near the incisor apex; outer margin of mandible with 2 setae and 1 sensory pit between them; 1 pit mesodorsally. Maxillae with broad and subsquared stipes with two rows of setae: the anterior one with 3 setae, 1 long, more external, 1 extremely long (as long as the entire maxillary palpus), more internal, and 1 short and inner in position; the posterior row with 3 short setae and 1 pit basally; mala simple, lobiform, slightly protruding, with 7–8 spiniform setae; segment I of maxillary palpi short, ring-like, with 1 ventral pit; segment II asymmetric, straight at inner side, longer and enlarged on the outer side, with 2 lateral setae, 1 longer (external side) and 1 shorter (inner side); segment III subcylindrical, about 3 times the length of I, swollen at apex, with 1 small dorsolateral seta (inner side) and 1 apical, stick-like sensory appendix, inserted in a prominent base

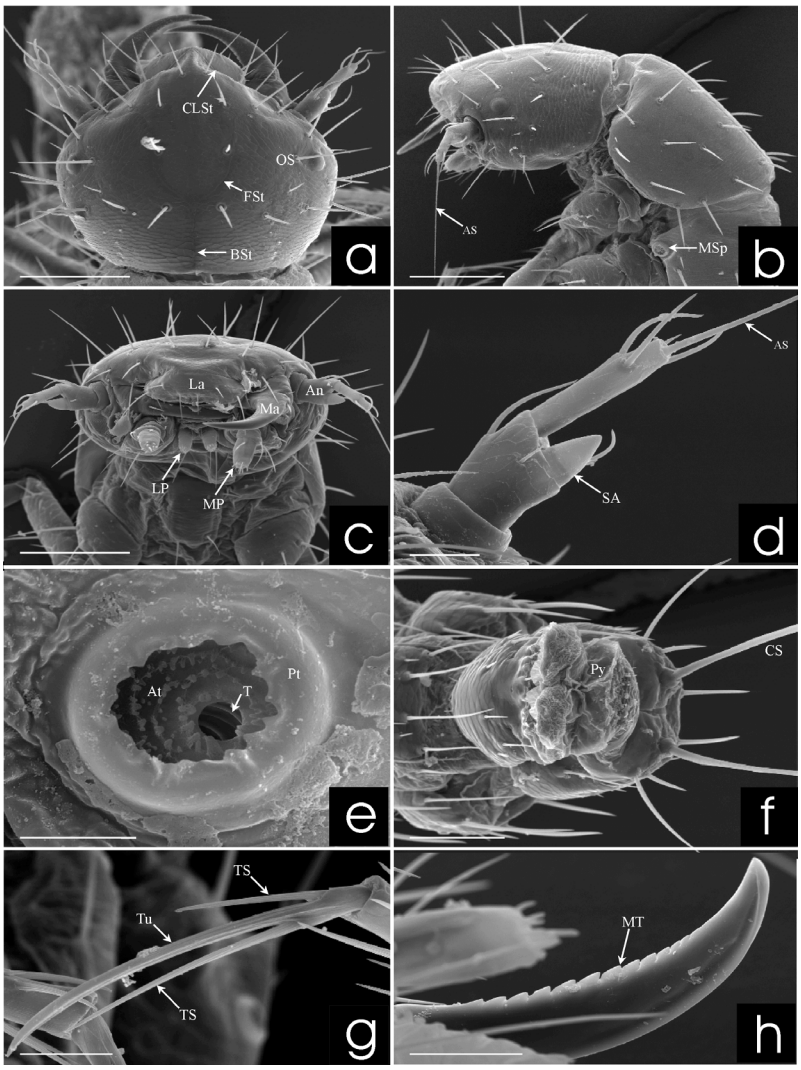

Fig. 2. — a. *Cerocoma prevezaensis* (Greece, Patra airport), head of first instar larva, dorsal view (clypeolabral suture: CLSt; ocular seta: OS; frontal suture: FSt; basal suture: BSt). b–h. First instar larva of *C. schreberi* (Italy, Maccarese). — b. Head, left lateral view (mesothoracic spiracle: MSp) — c. Frontal view (Labrum: La; Mandible: Ma; antenna: An; labial palpus: LP; maxillary palpus: MP) — d. Left antenna, lateral view (sensory appendix: SA; antennal seta: AS) — e. Mesothoracic spiracle (atrium: At; taenidia: T; peritreme: Pt) — f. Pygidium (Py), ventral view (caudal seta: CS) — g. Metathoracic claw (tarsungulus: Tu; tarsal seta: TS) — h. Left mandible, ventral view (mandibular teeth: MT). Scale bars: 100 μm (Fig. 2a–c); 50 μm (Fig. 2f); 20 μm (Fig. 2d, g–h); 10 μm (Fig. 2e).

and surrounded by 7–8 shorter papillae; outer side with 1 slender digitiform sensillum, flattened and enlarged at tip, appressed to the surface of a shallow sulcus longitudinally extending from base to near the apex of segment; cardo transverse, subrectangular, with 1 very short seta. Prementum with 1 pair of medial setae and 1 pair of posterior sensory pits, and 2 very short setae near the insertions of palpi; mentum with 1 pair of small setae and 1 pair of posterior sensory pits; labial palpi with segment I short and broad; segment II cylindrical, long twice than segment I, swollen at apex, with 1 stout, subconical, apical sensory appendix, inserted in a prominent base and surrounded by a crown of 8 shorter subconical papillae, and 1 sensory pit laterally at base.

Thorax with segments transverse and subrectangular, slightly broader than head, decreasing in size from prothorax to metathorax, with anterior and posterior margins weakly rounded (the anterior one only slightly rounded on prothorax); meso- and metanotum rounded. Ecdysial line well marked, complete on pro- and mesonotum, and restricted to anterior half on metanotum. Pronotum subrectangular, 1.7 times wider than long; 13 setae (12 long and 1 small) and 5 pits symmetrically disposed on each lateral half, approximately disposed on 3 transverse, sub-

parallel rows; anterior row (AR) with 4 long and 1 additional, small (on the angle) setae and 2 pits; medial row (MR) with 4 setae (third seta from ecdisial line slightly anteriorly displaced); posterior row (PR) with 4 setae and 2 pits; prosternum with 3 pairs of medial setae of different length: anterior pair extremely short, medial pair elongate, posterior pair two times as long as medial pair. Mesonotum slightly narrower and shorter than pronotum; AR with 4 setae and 1 pit extremely small compared to the omologous of pronotum, and irregularly lined on each lateral half; MR with 3 long setae and 2 shorter setae near the stigma; PR with 4 long setae and 2 pits; 3 pairs of medial setae on mesosternum increasing in length from anterior to posterior. Setae of metathorax similar in number, position and relative dimensions to those of mesothorax.

Legs slender, coxa short and broad, with 4 elongate setae at base, gradually decreasing in size, and 3 pits disposed longitudinally at middle; trochanter with 3 setae and 4 pits; femur with 6 setae and 1 pit, the major ventral femoral seta, much shorter than femur; tibiae and tarsunguli slightly decreasing in length from meta- to prothorax, strongly tapered at apex; tibiae with 4 longitudinal rows of 5–6 thick setae; tarsungulus (Fig. 2g) thin, acute and slightly curved at apex, with 2 subbasal setae different in length, the distal one longer than proximal; surface of tarsungulus longitudinally corrugated.

Mesothoracic (Fig. 2e) and first abdominal spiracles round, internally papillate; marginal ring slightly protruding; mesothoracic spiracle anterolateral in position, placed on pleural membrane; abdominal spiracle I similar in size to the mesothoracic one but distinctly larger than the others, dorsolateral in position on laterotergite; abdominal spiracles II–VIII small, laterally positioned, placed on laterotergites, decreasing in size from II to VIII.

Abdomen slightly fusiform, with transverse, rectangular tergites well sclerotised; maximum width at segment IV; ecdysial line absent; tergites almost completely fused with pleurites, forming laterotergites (pleural setae are here described as laterotergal); sternites poorly sclerotised, sclerotisation increasing from segment I to IX. Laterotergites with 3 transversal rows of setae; 2 small setae (4 on laterotergite I) and 1 pit on AR; 3–4 small setae on MR; 4–5 long setae (3 on laterotergite I), 2 short setae (4 on laterotergite I) and 3 pits on PR; laterotergite IX with 2 pairs of setae of PR (codified as setae 2 and 3 from midline) elongate, seta 2 as long as the last five abdominal segments (caudal setae). AR and MR of sternite each with 1 short seta, and PR with 4 setae different in length. Sternite IX with 1 small seta on AR; 3 setae on MR; 2 small setae and 2 pits lined and alternate on PR. Abdominal apex (segment X or pygopod; Fig. 2f) membranous, transversally divided in two parts: dorsal part semicircular with 6 extremely small setae transversally lined, ventral part longitudinally divided in 2 lobs, moderately produced.

3.2.2. Cerocoma prevezaensis (Figs. 1a–c, 2a)

Body length 1.62 mm (from pygidium to labrum); head length 0.2 mm (from occipital foramen to clypeolabral suture), maximum width 0.28 mm; diameter of stemmata 22 mm; basal stem of epicranial suture 0.06 mm; antennal length 0.1 mm, terminal seta length 0.15 mm; prothorax length 0.18 mm, maximum width 0.31 mm; abdominal length 0.92 mm, terminal setae length 0.52 mm; diameter of spiracles: mesothoracic about 29 mm, abdominal I about 30 mm, abdominal II–VIII respectively from 18 to 14 mm.

Head transverse with rounded sides distinctly narrowed posteriorly (Fig. 2a). Cutting edge of mandibles with extremely short teeth. Medial part of frontal sutures subparallel. Antennal segment I as long as half of II.

3.2.3. Cerocoma schaefferi

Body length 1.5 mm (from pygidium to labrum); head length 0.22 mm (from occipital foramen to clypeolabral suture), maximum width 0.26 mm; diameter of stemmata 22 mm; basal stem of epicranial suture 0.07 mm; antennal length 0.11 mm, terminal seta length 0.18 mm; prothorax length 0.18 mm, maximum width 0.3 mm; abdominal length 0.86 mm, terminal setae length 0.5 mm; diameter of spiracles: mesothoracic about 18 mm, abdominal I about 16 mm, abdominal II–VIII respectively from 15 to 9 mm.

Head with parallel sides slightly narrowed

posteriorly; stemmata slightly larger than mesothoracic spiracle. The cutting edges of mandibles with extremely short teeth. Segment II of maxillary palpi subequal to segment I and only slightly asymmetric; segment III about 2 times the length of I. Antennae with apical seta more than 1.5 as long as the entire antenna. Antennal segment I as long as half of II. Abdominal spiracle I slightly wider than the others.

4. Discussion

Possible relationships among the five genera of the tribe Cerocomini were proposed only on the basis of adult characters (Bologna 1991, Bologna & Pinto 2002) because of the complete lack of information on larval morphology of species in genera other than *Cerocoma*. Despite this scarcity of knowledge, a recent phylogenetic analysis carried out on a large selection of adult, larval, behavioural and biological features considered the genus *Cerocoma* as a representative of the entire tribe (Bologna & Pinto 2001). In this way, Cerocomini is characterised by larval features not specialised to phoresy, and by several plesiomorphic characters, with an unresolved position among the subfamily Meloinae. The few differences found in the larval morphology of the two additional species studied in the present contribution do not include generic characters considered in the matrix, and phylogenetic results remain unmodified. Preliminary results of a molecular phylogenetic analysis (Wirz *et al*. 2000, Bologna unpubl.) do not resolve this ambiguous position of the tribe.

Concerning the relationships among the genus *Cerocoma*, the present study offers a possibility of a comparison of larval characters among three of the four recognised subgenera of *Cerocoma*. The description of the triungulin of *C.* (*Cerocomina*) *vahli* (Cros 1919, 1924) is extensive and permits a comparison with that of the two subgenera (*Metacerocoma* and *Cerocoma*) studied in the present research. The few larval differences found at the species level are summarised in Table 1. No larval apomorphies were found to distinguish the recognised *Cerocoma* subgenera, which are however well distinguished by adult male characters, particularly those of the frons and antennae, and partially also those of the fore tibiae and pygidium. Triungulins of the species of the subgenus *Metacerocoma* have only some morphometric characters in common, slightly different among the species and difficult to evaluate: (a) the size of stemmata, slightly smaller than mesothoracic spiracle (wider in *Cerocoma* and *Cerocomina*), (b) the palpal segments more elongate (shorter in *Cerocoma* and *Cerocomina*), (c) the abdominal spiracle I wider than others (subequal in *Cerocoma* and *Cerocomina*). Other characters are more ambiguous and mixed in the subgenera: e.g. the shape of mandibles (serrate in *schreberi* and *vahli*, but almost smooth in *prevezaensis* and *schaefferi*) or that of the head (posteriorly narrowed only in *prevezaensis*). This result was unexpected because clear larval differences were found at the subgeneric level in other Meloinae genera (e.g. *Lytta*, *Meloe*, *Mylabris*) (for a review see MacSwain 1956, Bologna & Pinto 2001). According to the present study, the use of larval morphology to resolve taxonomic and phylogenetic problems in the genus *Cerocoma* seems to have great limits.

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