Entomologia 2014; volume 2:164

SYSTEMATICS AND PHYLOGENY

Morphology of a new blister beetle (Coleoptera, Meloidae) larval type challenges the evolutionary trends of phoresy-related characters in the genus *Meloe*

A. Di Giulio,[1] M. Carosi,[1] R. Khodaparast,[2] M.A. Bologna[1]

[1]Department of Sciences, Roma Tre University, Rome, Italy; [2]Young Researcher Club, Kazerun Branch, Islamic Azad University, Kazerun, Iran

Abstract

The discovery of some specimens of a new first instar larval type in blister beetles, collected in Iran on *Anthophora* bees, confirms the existence of repetitive and parallel trends in morphological specialization to phoresy in distinct lineages of Meloidae and in particular in the subfamily Meloinae. The new Iranian larva, herein described and illustrated, shows several characters and a peculiar phoretic strategy that closely parallel that of the *Meloe* subgenus *Lampromeloe*, with similar modifications of the fronto-clypeal setae into strong lanceolate spines used to pierce the intersegmental membranes of the bees. Both parallel and shared derived evolution of these characters seem possible. The coexistence in this larva of characters in both primitive and derived state is of particular interest in order to analyse the different rates and trends of evolution of phoretic adaptations. A morphological comparison (SEM) of this new meloine larva (*incertae sedis*), tentatively assignable to *Meloe*, with the *M. (Lampromeloe)* larvae is carried out in order to discuss the evolutionary implications of its placement in *Lampromeloe*, and the relative characters that would support it, *vs* other possible alternative scenarios.

Correspondence: Marco Alberto Bologna Department of Sciences, Roma Tre University, Viale G. Marconi 446, 00146 Rome, Italy.
Tel. + 39.06.573.36327 - Fax: +39.06.573.36321.
E-mail: marcoalberto.bologna@uniroma3.it

Key words: Meloinae, *Meloe*, *Lampromeloe*, triungulin, phoresy, SEM, Iran.

Acknowledgements: this work was partially supported by grants from University Roma Tre. We thank the curators of the following Museums for their help in the examination of *Lampromeloe* types: Bernd Jaeger and Manfred Uhlig (Museum für Naturkunde, Entomologie, Berlin), who sent us the photos of *Meloe stellatus* paratypes; Petra Kranebitter (Museo di Storia naturale di Bolzano), who helped us in the search for the type of *Meloe specularis* in the Gredler entomological collection (Ginnasio dei Francescani, Bolzano); Luca Picciau (previously at the Museo regionale di Scienze naturali, Turin) for the photo of type of *Meloe variegatus* var. *cupreus*. We are particularly grateful to two anonymous referees for their comments and suggestions that greatly improved an earlier version of the manuscript.

Contributions: the authors contributed equally.

Received for publication: 27 September 2013.
Revision received: 12 May 2014.
Accepted for publication: 12 May 2014.

Licensee PAGEPress, Italy
Entomologia 2014; 2:164
doi:10.4081/entomologia.2014.164

Introduction

The Meloidae, or blister beetles, are a beetle family with about 120 genera and 3000 species, mostly tropical or subtropical and related to open habitats, almost cosmopolitan (absent only from New Zealand, Antarctica and most Polynesian islands; Bologna *et al.*, 2013). Members of this family are morphologically very heterogeneous, but adults are well characterized by the head clearly separated from the pronotum by a *neck* and by bilobed claws. Adults are mostly diurnal and phytophagous, feeding on flowers and/or leaves of several plant families, while larvae are predaceous, feeding on the provisions and immature stages of various aculeate Hymenoptera (mostly Apoidea) or on Acridoidea egg pods.

Blister beetles are largely known in the biological literature because of their importance for applied science (biological control of grasshoppers, pharmacology, veterinary and agricultural problems) as well as their distinctive biology (hypermetamorphic development, parasitoid larval habits, defensive attributes, and diverse courtship behavior). The most recent extensive review of meloid systematics, bionomics and biogeography was published by Bologna (1991), but other syntheses were recently published by Bologna *et al.* (2010) and, specifically considering larval morphology and biology, by Bologna & Di Giulio (2011). The systematics of the family is well studied: two phylogenetic studies, based on morphology (adult and larva) and behavior (Bologna & Pinto, 2001), and on molecular evidence (Bologna *et al.*, 2008), respectively, differ in considering four (Eleticinae; Nemognathinae; Tetraonycinae; Meloinae) or only three subfamilies (Eleticinae; Nemognathinae; Meloinae, including Tetraonycini). We adopted here the classification of Bologna *et al.* (2008).

The rich literature of the last century on larval morphology and biology of this family was reviewed by Bologna & Di Giulio (2011) who synthesized critically the information on the diversified radiation in both morphology and biology, proposing a new scenario which amended several previous hypotheses. In particular, based on the discovery of primitive, non-parasitic larvae in the subfamily Eleticinae (Pinto *et al.*, 1996; Bologna *et al.*, 2001), hypermetaboly must be considered a derived condition of Nemognathinae and Meloinae rather than a synapomorphy of the whole family. The evolution of parasitism and hypermetaboly supported a great adaptive radiation in larval morphology and biology. At least in some meloid lineages such radiation seems connected to phoresy, a strategy typically related to dispersion of scarcely movable life stages or to specialized parasitic behaviors. The phoretic strategy of the meloid first instar larvae on bees represents a passive transport from flowers, where eggs are laid (some Nemognathinae) or where triungulins climb after their hatching from the ground (some Meloinae) to the host nest. It is now acknowledged that in Meloidae, phoresy evolved several times (Bologna & Pinto, 2001; Bologna *et al.*, 2008), as a derived condition, in both Nemognathinae and Meloinae. A gradient of specialization to phoretic habits and specialized parasitic biology is clearly recognizable in triungulins of the nemognathine tribes (Di Giulio *et al.*, 2010): Palaestrini, Horiini and Nemognathini, especially concerning the morphology of legs, mouthparts and abdominal spiracles. The subfamily Meloinae shows a similar, though independent, gradient of specialization to phoresy, with repeated and complex events of trophic and dispersal adaptations (Bologna & Pinto, 2001). Starting from a typical campodeiform larva actively searching the host bee nest, the adaptation to phoresy apparently evolved separately at least five times in this subfamily, as well as trophic specialization to feed on termite eggs (Di Giulio *et al.*, 2003), but also on Masaridae and Vespidae nests (Bologna, 2003), or on Acridoidea egg batches in the tribes Mylabrini and Epicautini (for a synthesis see Bologna, 1991).

Focusing on the tribe Meloini, the Old World genus *Meloe* Linnaeus, 1758, represents a paradigmatic study case of the radiation in larval morphology. The genus includes ca. 155 species in 16 subgenera (Bologna, 1991; Bologna & Pinto, 1998; Di Giulio *et al.*, 2002). All subgenera are represented in the Old World, the region harboring the vast majority of species (ca. 130). In the New World only the nominate subgenus, *Treiodous* Dugès, 1869, and, on the Aleutian Islands, *Eurymeloe* Reitter, 1911, occur.

The first instar larvae of 12 out of the 16 subgenera have been described: information on subgenera and references are reported in Table 1 (Di Giulio *et al.*, 2002; 2013). The only subgenera for which larvae remain unknown include *Alveomeloe* Prispinova, 1987, *Chiromeloe* Reitter, 1911, *Desertimeloe* Kaszab, 1964, and *Meloenellus* Reitter, 1911, all from Central Asia.

Both the different degree of morphological specialization related to phoresy and the presence of progressive trends of complexity in morphological traits adapted to phoresy have been partially analyzed in the nominate subgenus and in *Treiodus* (Pinto & Bologna, 1993; Bologna & Pinto, 2001; Bologna & Di Giulio, 2011). Larval morphology and taxonomy of the subgenus *Lampromeloe* Reitter, 1911 have never been revised, even though the first instar larvae of two species have been described (namely *M. cavensis* Petagna, 1819 and *M. variegatus* Donovan, 1793; see Table 1 and Results). The main larval apomorphy of this subgenus is the modification of the anterior fronto-clypeal setae into nine strong lanceolate spines, four of which elongate, directed forward and inserted medially at the anterior apex of the head (Figure 1d-f). These spines form an anterior spear used to pierce the thin intersegmental abdominal membranes of the bees and act in combination with the modified trident-shaped claws and strongly curved mandibles to remain steadily attached to the host. As far as known, this is a unique phoretic strategy not only for Meloidae, that use only their modified mandibles to seize one or a few hairs of the host (Bologna, 1991; Bologna & Pinto, 2001), but also considering other phoretic insects.

The recent discovery of an unidentified Meloinae first instar larva from Iran, with phoretic adaptations very similar to those of *Lampromeloe*, provides the opportunity to explore deeply the conflicting

Table 1. *Meloe* subgenera with described larvae (left column), alphabetically ordered; *Meloe* species, divided per subgenera, with described larvae (middle column); main bibliographic references for larval taxonomy for each subgenus of *Meloe* (right column).

Meloe subgenus	*Meloe* species	Main references
Afromeloe Schmidt, 1913	*caffer* Péringuey, 1886	Bologna & Pinto (1998)
Coelomeloe Reitter, 1911	*tuccius* Rossi, 1792	Cros (1929); Di Giulio *et al.* (2013)
Eurymeloe Reitter, 1911	*affinis* Lucas, 1832; *apenninicus* Bologna, 1989; *apivorus* Reitter, 1895; *brevicollis* Panzer, 1773; *corvinus* Marseul, 1876; *flavicomus* Wollaston, 1854; *ganglbaueri* Apfelbeck,1905; *glazunovi* Pliginskji, 1910; *mediterraneus* G. Müller, 1925; *rugosus* Marsham, 1802; *scabriusculus* Brandt and Erichson, 1832	Bologna *et al.* (1989); Di Giulio *et al.* (2013)
Lampromeloe Reitter, 1911	*cavensis* Petagna, 1819; *variegatus* Donovan, 1793	Cros (1927); present paper
Lasiomeloe Reitter, 1911	*olivieri* Chevrolat, 1833	Bologna & Pinto (1995)
Listromeloe Reitter, 1911	*hungarus* Schrank, 1776	Cros (1930); Bologna & Pinto (2001)
Meloe Linnaeus, 1758	*americanus* Leach, 1815; *angusticollis* Say, 1824; *auriculatus* ? Marseul, 1877; *campanicollis* Pinto & Selander, 1970; *coarctatus* Motschulsky, 1858; *dianella* Pinto & Selander, 1970; *dugesi* Champion, 1891 or *nebulosus* Pinto & Selander, 1970; *hottentotus* Péringuey, 1886; *impressus* Kirby, 1837; *menoko* Kono, 1936; *niger* Kirby, 1837; *occultus* Pinto & Selander, 1970; *proscarabaeus* Linnaeus, 1757; *rhodesianus* Péringuey, 1904; *strigulosus* Mannerheim, 1852; *violaceus* Marsham, 1802	MacSwain (1956); Pinto & Selander (1970); Kifune *et al.* (1973); Bologna & Pinto (1998)
Meloegonius Reitter, 1911	*cicatricosus* Leach, 1815; *rufiventris* Germar, 1832	Selander (1989); Lückmann & Scharf (2004)
Mesomeloe Reitter, 1911	*coelatus* Reiche, 1857	Di Giulio *et al.* (2002)
Micromeloe Reitter, 1911	*decorus* Brandt and Erichson, 1832	Bologna & Pinto (1995), Lückmann & Scharf (2004)
Taphromeloe Reitter, 1911	*erythrocnemus* Pallas 1782	Bologna & Pinto (1992)
Treiodous Dugès, 1869	*afer* Bland, 1864; *autumnalis* A.G. Olivier, 1797; *barbarus* LeConte, 1861; *laevis* Leach, 1815	Pinto & Selander (1970); Pinto & Bologna (1993)

character evolution (phylogenetic traits and convergence related to phoresy) in Meloidae.

Aims of this paper are: i) to describe and illustrate a new Meloinae sp. (*incertae sedis)* first instar larval type and its peculiar phoretic strategy; ii) to comparatively analyze by SEM the morphological characters of the new meloine larva from Iran and those of the *Meloe (Lampromeloe)* larva; iii) to discuss the evolutionary implications of its placement in the genus *Meloe*, inside or outside the subgenus *Lampromeloe*, *versus* other possible alternative scenarios; iv) to discuss the general problem of convergent adaptation and trends of progressive derived condition in several morphological features of phoretic blister beetles, especially in the genus *Meloe*.

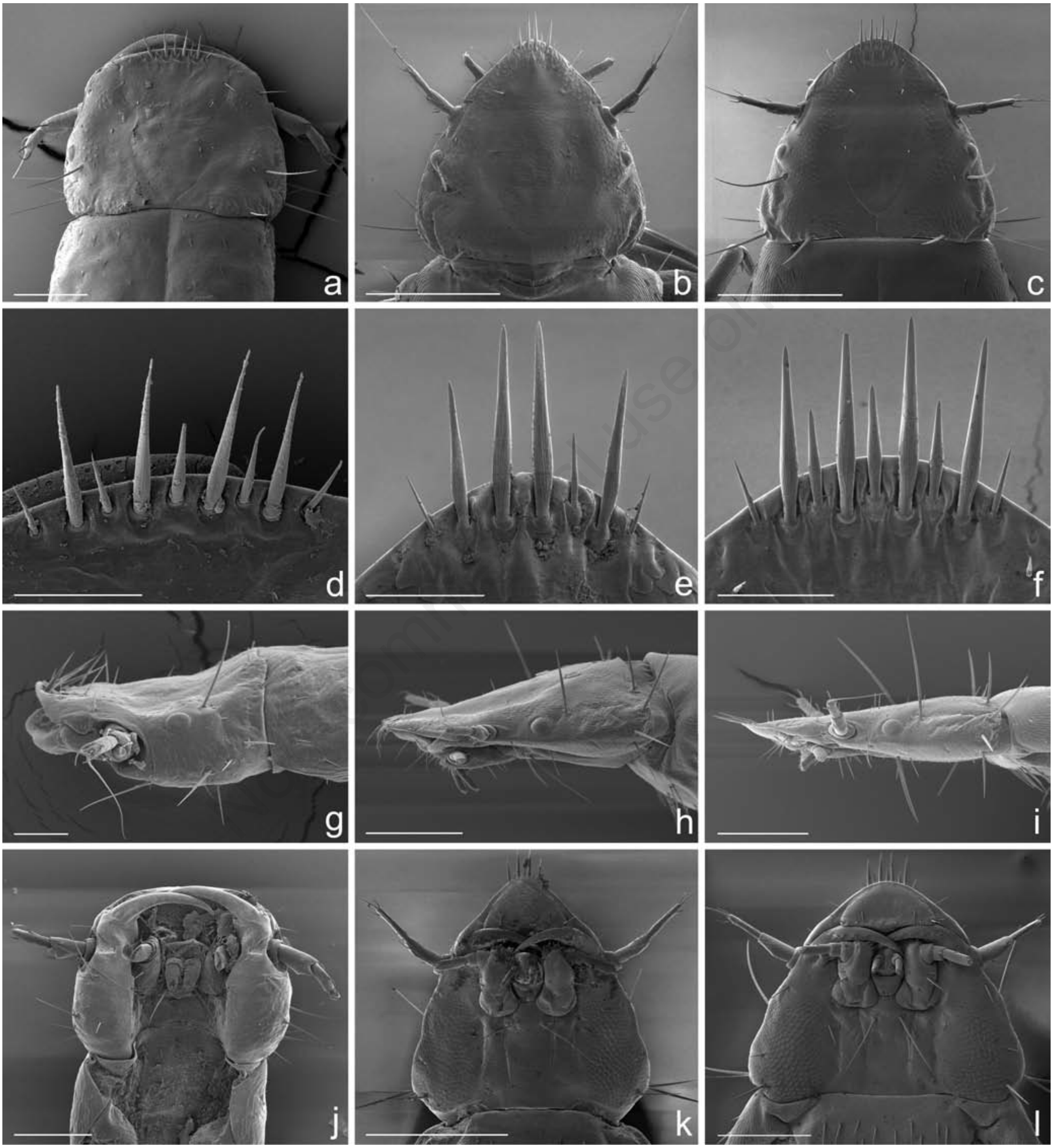

Figure 1. First instar larvae of Meloinae sp. (*incertae sedis*) and *Meloe* (*Lampromeloe*). Meloinae sp. (*incertae sedis*) (Iran): head capsule in dorsal (a), left lateral (g) and ventral (j) views; detail of clypeo-labral spines (d). *M.* (*Lampromeloe*) *cavensis*: head capsule in dorsal (b), left lateral (h) and ventral (k) views; detail of clypeo-labral spines (e). *M.* (*Lampromeloe*) *variegatus*: head capsule in dorsal (c), left lateral (i) and ventral (l) views; detail of clypeo-labral spines (f). Scale bars: a, j=100 µm; b, c, k=300 µm; d=40 µm; e, f, g=50 µm; h, i, l=200 µm.

Materials and Methods

The description of first instar larvae is based on the following material preserved in 70% ethanol and/or mounted on slides or on stubs. If not indicated otherwise, larvae and adults are kept at Roma Tre University, Rome, Italy, in the M.A. Bologna collection. Sampled localities are ordered by country, from north to south and from west to east.

Adults of *Meloe (Lampromeloe)* were reared at 24-25°C in a thermostatic chamber with photoperiod control (LD 12:12 h); females oviposited in sand provided as a substrate in rearing boxes, where their eggs were kept till hatching.

Meloe (*Lampromeloe*) *cavensis* Petagna, 1819

- Vials 469-470 (ca. 400 triungulins). Adult: Italy, Sardinia, Oristano province, Cabras, Torregrande Sa Mardini, 8.xi.2002, leg. A. De Lucia; oviposition 30.xi.2002, hatch 12-13.xii.2002.
- Vials 169/175, 204, 220 (ca. 800 triungulins and some eggs), slides M190/M192 (6 triungulins), stub 102 with 7 specimens. Adults: Italy, Calabria, Crotone province, Rocca di Neto, Vitravo river, 31.i.1993, leg. M.A. Bologna; oviposition 11/12.ii.1993, hatch 7/15.iii.1993.
- Vial 601 (1 triungulin). Triungulin on the underside of *Pygopleurus orientalis* (Artovitz, 1952) (Coleoptera, Glaphyridae), Palestine, Netanya city south, 17.iii.2006, leg. G. Witzes.

The first instar larva of *M. cavensis* was described by Zanon (1919, 1922); Cros (1919, 1927, 1941) from Libya and Algeria. The specimens we examined from Italy and Palestine do not differ from these descriptions.

Meloe (*Lampromeloe*) *variegatus* Donovan, 1793

- Slide M40 (2 triungulins). Triungulin: Algeria, Teniet El Had env., 1000 m a.s.l., 19.v.1984, leg. M.A. Bologna, netting on *Genista* Linnaeus flowers (Fabaceae).
- Vial 66 (1 triungulin). Triungulin: Turkey, 10 km E of Simav, 800 m a.s.l., 6.vi.1986, leg. M.A. Bologna, netting on *Anthemis* Linnaeus flowers (Asteraceae).
- Vial 127 (1 triungulin). Triungulin: Turkey, Karaman province, 10 km S of Karaman, 1190 m a.s.l., 7.v.1991, leg. M.A. Bologna, netting on Lamiaceae indet.
- Vial 65 and 109 (11 triungulins). Triungulins: Turkey, Adana province, Ha ara env., 15 km S of Tufanbeyli, 1500 m a.s.l., 10.vi.1986, leg. M.A. Bologna, on anthophorid bees of the genus *Anthophora* Latreille, and netting on *Centaurea* Linnaeus flowers (Asteraceae).
- Vial 179 (ca. 50 triungulins), slides M 193/195 (6 triungulins), stub 103 (7 triungulins). Adult (female ovipositing): Turkey, Malatya province, 10 km S of Balaban, 1800 m a.s.l., 6.v.1993, leg. M.A. Bologna and M. Zapparoli; oviposition 6.v.1993, hatch 25/28.v.1993.

The first instar larva of *M. variegatus* was described by Brandt & Ratzenburg (1833), Assmus (1865), Cros (1929, 1941), Hachfeld (1931), Blair (1943), van Emden (1943), Krzyzanska (2000), Topolska *et al.* (2001), and Lückmann & Scharf (2004) from United Kingdom, Germany, Slovakia, Poland, and Algeria. Our specimens from Turkey and Algeria do not differ from these descriptions. We are able to confirm what Cros (1941) noted about the Maghrebian triungulins differing from the Euro-Anatolian ones because of a greater sclerotization of the body, and the head being wider on temples and less narrowed in front.

Meloinae sp. (*incertae sedis*)

- Slide M464 (2 triungulins), vial 609 (3 triungulins), stubs 148 and 149 (1+1 triungulins). Triungulins: Iran, Fars province, Shiraz, Zangench, 2128 m a.s.l., 25/31.iii.2012, leg. R. Khodaparast, on 59 females (100% parasitized) of the anthophorid bee *Anthophora* (*Pyganthophora*) *atroalba* Lepeletier, collecting honey on *Matthiola* Aiton (Brassicaceae).

Morphological analysis was performed by an Olympus BX51 light microscope equipped with a Colorview II camera (SIS) and Cell*D image 285 analysis software (SIS) to examine and photograph the cleared specimens mounted on slides in Canada balsam, and a FEI dualbeam FIB/SEM Helios Nanolab for material mounted on stubs after critical point dehydration and gold sputtering.

Terminology of larval structures follows MacSwain (1956), Lawrence (1991), and Bologna & Pinto (2001). For some traits of larval chaetotaxy we followed notational conventions as suggested by Selander (1990).

Results

Description of Meloinae sp. (*incertae sedis*) first instar larva of from Iran

Habitus and measures

Triungulin campodeiform (Figure 2a,d,g), distinctly tapered at the base of the abdomen, with maximum width on pronotum, characterized by large, oval head (Figure 1a,j), antennae posterolaterally directed (Figure 1a,j), long and stout legs (Figure 2a, d, g), fusiform abdomen (Figure 2a,g), elongate medial caudal setae (Figure 2a). Color pale yellow, weakly sclerotized.

Measures (in mm, based on two slide-mounted specimens, the first measure reported in the following always refers to the same specimen). Body length: 1.63-1.82; Head length: 0.25-0.26; head width: 0.34-0.37; Diameter of stemmata: 0.020-0.19; Epicranial stem length: 0.03; Length of antennomeres, I: 0.023-0.027, II: 0.058-0.062, III: 0.054-0.058; length of apical antennal seta: 0.19-0.20; Prothorax length: 0.23-0.25; prothorax width: 0.39-0.42; Mesothoracic spiracle maximum width: 0.036-0.045; abdominal spiracle I maximum width: 0.051-0.053; Length of abdomen: 0.9-1. Length of caudal setae: 0.31-0.36.

Head

Cephalic capsule (Figure 1a,g,j) transverse, 1.5 times wider than long, ovoid, widest behind stemmata; anterior margin broadly rounded. Stemmata latero-dorsal, small, slightly prominent, set at middle level of head. Transverse ridge at base of vertex present, partially covering the anterior margin of pronotum. Epicranial suture (Figure 1a) Y-shaped, with very short stem, dividing into arms at the level of transverse ridge, near base of head; arms basally V-shaped, clearly diverging from base, slightly sinuate at the level of stemmata, diverging towards the edge of frontoclypeus and ending just beyond the base of antennae. Frontoclypeus (Figure 1a,g) slightly concave between arms of epicranial suture. Frontoclypeal region (Figure 1a) with 19 setae: frontoclypeal row (FCR) with 5 pairs of setae and one impair seta in the middle: FCR1 short, normally trichoid, the others strong, spiniform, lanceolate, sharp at tip, antero-dorsally directed, forming a typical 9-spined anterior spear (Figure 1d); spines of the anterior spear alternated in size, short/long (4 long and 5 short, the impair short); sensory pit anterior to FCR1; frontal region with 4 pairs of setae paralleling the arms of epicranial suture; sensory pit between first and second pair. Two pairs of setae (the internal shorter than the external and with a sensory pit just anteriorly positioned) on either side of epicranial stem, transversally lined along basal transverse ridge; 4 grouped minute setae and one pit on each side, basal to the transverse ridge; ocular sensory pit anterior, and long ocular seta posterior to each stemma (Figure 1a); two pairs of long setae on lateral margin of head; parietalia ventrally each with 5 setae, the anterolateral ones longer than the others, and 1 medial pit. Antennae (Figures 1a,j and 3j) postero-laterally directed; segment I short and transverse, slightly asymmetrical with 1 dorsal sensory pit; segment II approximately 3 times longer than I, subclavate, with 3 long apical setae (1 dorsal, 1 lateral, 1 ventral), 1 minute seta (outer side) near sensory appendix and 1 dorsolateral pit; sensory appendix on segment II well developed, conical, lateroventral (outer side); segment III slender, slightly shorter than II, 2.5 times longer than I; III with a long apical seta (approximately 1.3 times longer than entire antenna), 3 long subapical setae, 2 lateral (1 on outer and 1 on inner side) and 1 dorsal in position, 1 minute seta near the base of apical seta, 1 lateral and 1 sub-basal pit. Mandibles (Figure 3g) elongate, directed forward, moderately curved, narrowed toward apex, with broad and prominent base; outer margin of mandible with 2 setae, 1 sensory pit between them and 1 pit dorsolaterally; inner and outer surfaces smooth, ventral surface medially with 10-12 teeth that represent the apices of rounded notches. Maxillae (Figures 1j and 3g) with mala simple, lobiform, slightly protruding, with about 10 spiniform setae; cardo transverse, small, with 1 minute seta; maxillary palpi with joints as follows: I extremely short, with 1 ventral pit; II slightly longer than I, with 2 ventrolateral subequal setae, 1 on the external and 1 on the internal side; III about twice as long as segment I and II together, asymmetrical (lateral side longer than medial side), with 1 dorsolateral seta (inner side); apex of segment III obliquely truncate, with a large, sensorial area composed of 1 apical, elongate, spiniform sensillum surrounded by several shorter papillae; outer side with 1 slender digitiform sensillum. Gulamentum (Figure 1j) weakly sclerotised with 2 very long anterior setae. Prementum (Figure 1j) and mentum fused, with 1 pair of basal setae lined with 1 pair of external sensory pits; 1 pair of ligular setae present dorsally between insertion of palpi and one pair ventrally; labial palpi well developed, with segment II longer than I, with 1 distinct cylindrical, bluntly tipped, apical sensillum inserted in a prominent base and surrounded by shorter subapical papillae. Labrum (Figure 1j) narrow, fusiform, transverse, with angulated sides, not visible dorsally and distinctly separated from frontoclypeus, with 18 setae: 10 setae and 2 pits along the anterior edge and 8 setae and 4 pits in middle of labrum.

Thorax

Segments transverse and subrectangular (Figures 2a and 4a): prothorax broader than head, meso- and metathorax about as wide as head; margins of pronotum almost straight and subparallel, meso- and metanotum campaniform, with margins slightly rounded. Ecdysial line (Figure 2a) well marked, complete on pro- and mesonotum, vestigial or absent on metanotum. Pronotum about 2 times wider than long; each half of pronotum with 13 small setae and 5 pits symmetrically placed along 3 transverse, subparallel rows; anterior row (AR) with 5 setae and 2 pits; medial row (MR) with 3 setae; posterior row (PR) with 5 setae and 2-3 pits; prosternum with 3 pairs of medial setae, the two anterior pairs similar in length, posterior pair longer than others. Mesonotum slightly shorter than pronotum; AR with 2 setae grouped with one pit mesodorsally, 2 setae laterally, anterior to the spiracle. MR with 5 setae (1 shorter near the spiracle); PR with 5 setae and 2 pits; 3 pairs of medial setae on mesosternum, the anterior pair extremely short. Setae of metathorax similar in number, position and relative dimensions to those of mesothorax. Legs elongate and stout (Figure 2a,d,g): coxa short and broad, with 4 elongate setae, transversally arranged, 4-5 minute basal setae and 1 pit; trochanter with 2 moderately long setae and 4-6 pits; femur not swollen,

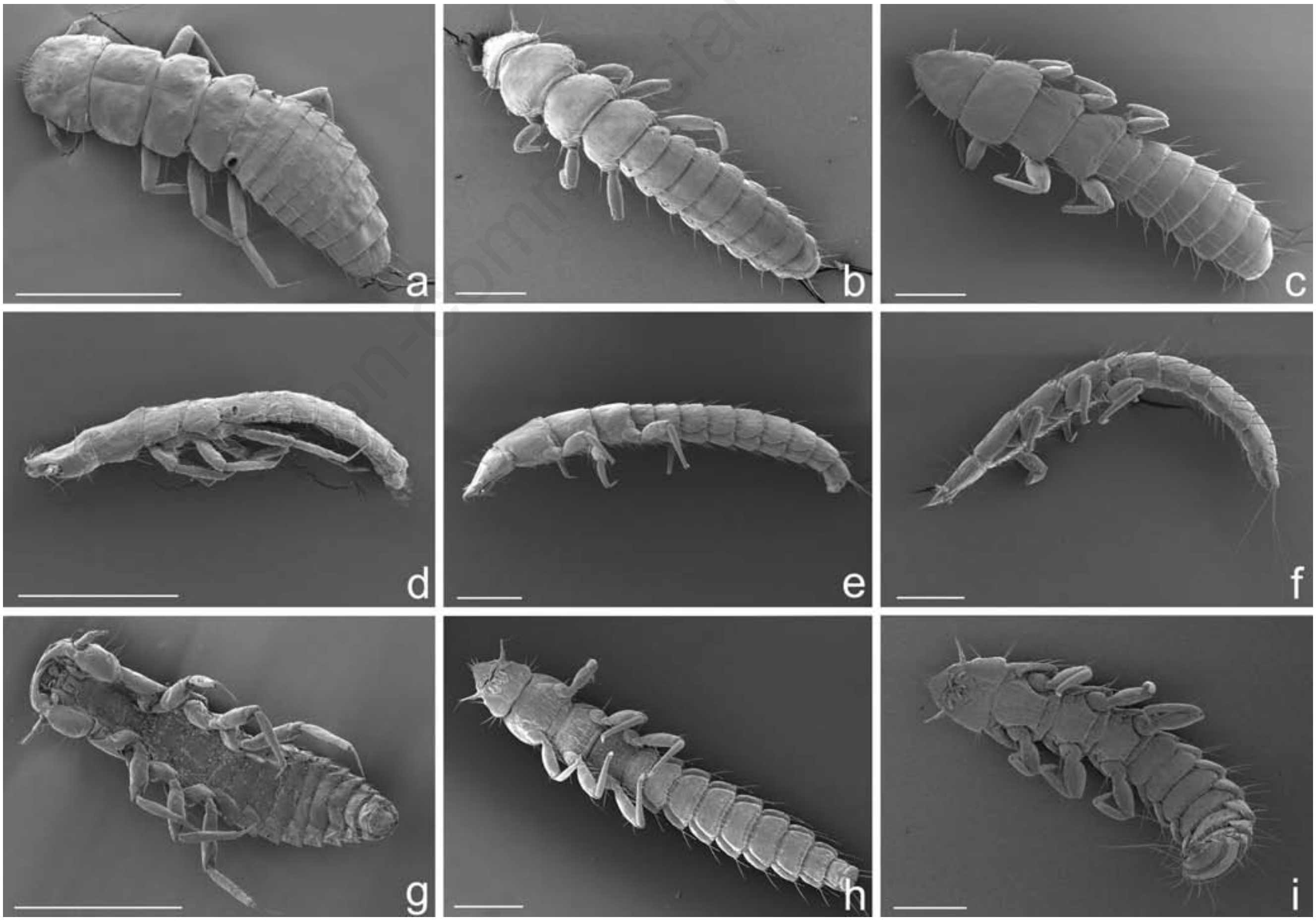

Figure 2. Comparative habitus (in dorsal, lateral and ventral view, from top to bottom) of first instar larvae of Meloinae sp. (*incertae sedis*) (Iran) (a, d, g), *Meloe* (*Lampromeloe*) *cavensis* (b, e, h), and *Meloe* (*Lampromeloe*) *variegatus* (c, f, i). Scale bar=500 μm.

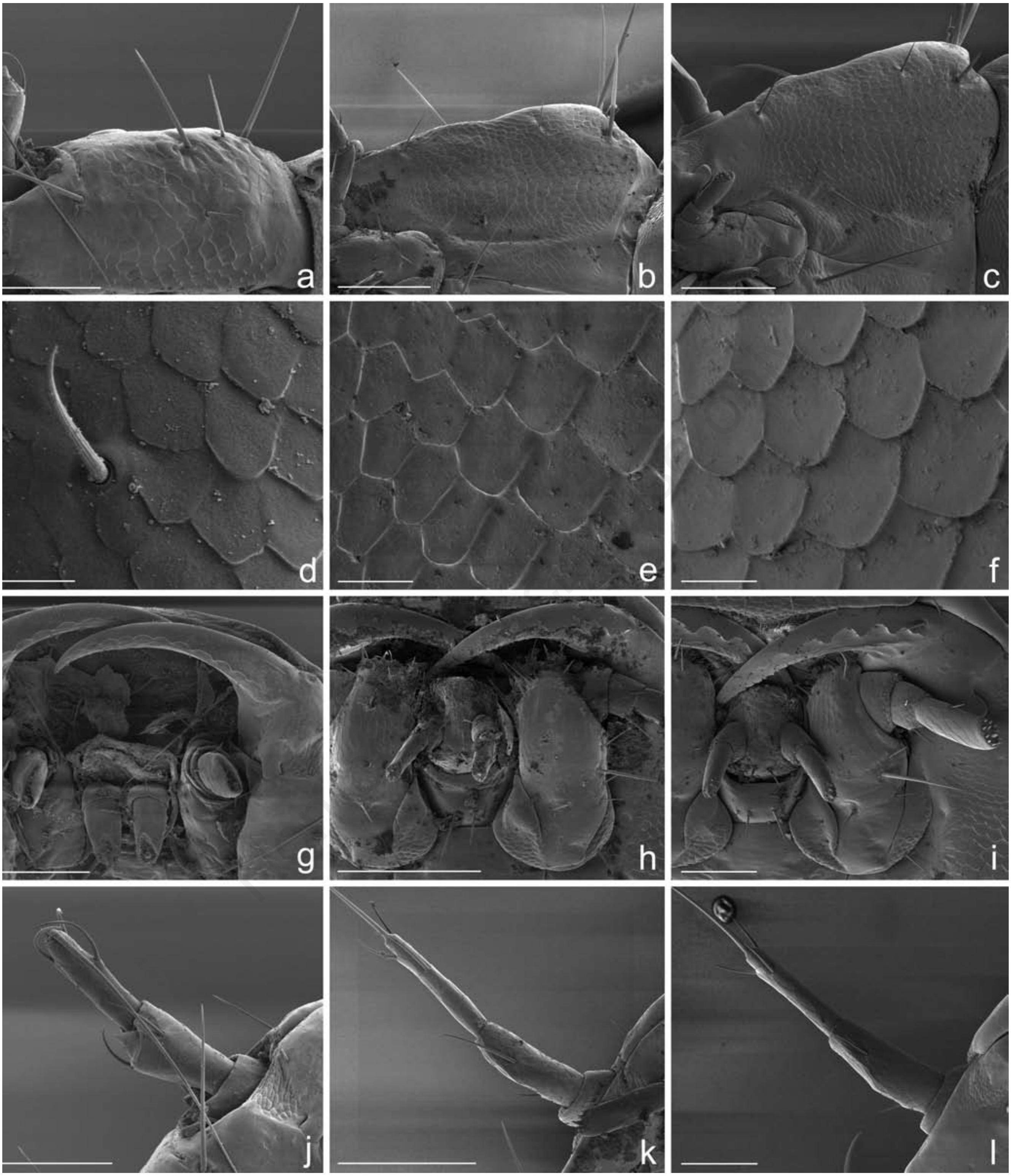

Figure 3. First instar larvae of Meloinae sp. (*incertae sedis*) and *Meloe* (*Lampromeloe*). Meloinae sp. (*incertae sedis*) (Iran): left ventral parietale of head capsule (a), with detail of microsculpture (d); mouthparts in ventral view (g); right antenna in ventral view (j). *M.* (*Lampromeloe*) *cavensis*: left ventral parietale of head capsule (b), with detail of microsculpture (e); mouthparts in ventral view (h); right antenna in ventral view (k). *M.* (*Lampromeloe*) *variegatus*: left ventral parietale of head capsule (c), with detail of microsculpture (f); mouthparts in ventral view (i); right antenna in ventral view (l). Scale bars: a, g, i, j, l=50 µm; b, c, h, k=100 µm; d, e, f=10 µm.

with 7 setae and 1 pit, the longest ventral femoral seta much shorter than femur; tibiae and claws slightly increasing in length from pro- to metathorax; tibiae tapered at apex and with 4 longitudinal rows of 5-6 moderately long setae; claw (Figure 4g) thin and elongate, curved basally inward, somewhat spathulate, acute at apex, flanked by 2 long and spiniform setae, forming a slender trident.

Abdomen

Abdomen is fusiform with transverse, rectangular tergites (Figure 2a,g); maximum width at segment III-IV; sternites entire. Mediotergites with 3 transverse rows of setae; their arrangement on each half of tergites as follows: AR with 2 minute setae (4 on tergite I, 2 medial and 2 lateral) and 1 pit, MR (at the level of spiracles) with 2 small setae, PR with 8 setae and 1 pit, the 4 lateral (including 2 on laterotergites) setae distinctly elongate on abdominal segments II-VIII; tergite IX with 1extremely elongate pair of setae on PR (medial caudal setae), which are shorter than the last four abdominal segments combined. AR of each sternite with 2 pairs of minute setae, MR absent and PR with 8 elongate setae, each slightly different in length. Sternite IX with 1 small seta on AR; 6 long setae on PR. Abdominal apex (segment X or pygopod) apically membranous, transversally divided in two parts: dorsal part semicircular with 6 extremely small setae transversally arranged, ventral part longitudinally divided in 2 lobes, moderately produced, with two pairs of setae along the posterior margin.

Spiracles

Marginal ring (peritreme) of mesothoracic and abdominal spiracles I distinctly protruding (Figure 4j). Mesothoracic spiracle elliptical, obliquely placed on laterotergite. Abdominal spiracle I (Figure 4j) dorsally placed on laterotergite, transversely elliptical; abdominal spiracles II-VIII small, round, subequal and slightly protruding, laterally positioned, placed on laterotergites, decreasing in size from II to VIII.

Morphological comparison of the new larva with *Meloe* (*Lampromeloe*) first instar larvae

The new Iranian first instar larva differs from the triungulins of all other Meloidae, except for those of the subgenus *Lampromeloe,* in having 9 modified frontoclypeal setae (5 short and 4 long, alternate, Figure 1d-f), lanceolate, strong and pointed, forming an anterior spear, combined with the presence of mandibles ventrally denticulate, with teeth representing the apices of longitudinally serial, rounded indentations, and in the integument of parietalia having imbricate squamiform microsculpture (Figure 3d-f). The first instar larvae of *M. cavensis* and *M. variegatus* are very similar in most characters; however, triungulins of *M. cavensis* differ from those of *M. variegatus* in smaller size (length: ca. 3 mm; width: 0.4 mm; length of long caudal setae: 0.7 mm; Bologna, 1991), the presence of only two elongate and two short medial caudal setae, and a more triangular and pointed head.

The new larva from Iran differs from first instar larvae of both species of *Lampromeloe* [*Meloe cavensis* (Figures 1b,e,h,k; 2b,e,h; 3b,e,h,k and 4b,e,h,k) and *M. variegatus*, (Figures 1c,f,i,l; 2c,f,i; 3c,f,i,l; 4c,f,i,l)] by its smaller size (body length (BL) 1.73 mm *vs* BL *M. cavensis* and *M. variegatus*: 4 mm); scarce sclerotization (*vs* strong sclerotization, especially of the head); subrectangular head (*vs* triangular); frontal arms sinuate (*vs* straight and parallel); antennomere II clavate with conical sensorium (*vs* cylindrical, without sensorium); mandibles long and moderately curved, directed forward with smooth cutting edge (*vs* short and abruptly curved, ventrally directed with microserrate cutting edge); maxillary palpomere III wide and flattened (*vs* cylindrical); thoracic sterna without (*vs* with many elongate and spiniform) additional setae; femora only slightly swollen (*vs* distinctly swollen); tibiae robust, regularly tapering to apex (*vs* thin, cylindrical, stick-like); mesothoracic and abdominal spiracle I large and distinctly protruding (*vs* small and slightly protruding); claws very slender and slightly spathulated (*vs* wide and distinctly spathulated).

Table 2. Characteristics of some features related to phoresy in the triungulin of 12 *Meloe* subgenera.

	Eurymeloe	*Coelomeloe*	*Micromeloe*	*Mesomeloe*	*Lasiomeloe*	*Afromeloe*	*Taphromeloe*	*Meloegonius*	*Listromeloe*	*Treiodus*	*Meloe*	*Lampromeloe*
Antennal sensory appendix: position and shape	Apical, conical long	Apical, conical short	Apical, conical short	Apical, conical short	Apical, conical long	Apical disk-like	Apical disk-like	Apical semispheric	Apical, semispheric	On ventro-apical platform, flat	Apical, disk-like or semispheric	Apical, conical or on ventro-apical platform, flat
Setae of labrum	Regular	Regular	Regular	Regular	Regular	Regular	Regular	Regular	Regular	Regular	Regular	Lanceolate spiniform
Mandible: position and inner margin	Suboblique; smooth	Suboblique; smooth	Suboblique; smooth	Suboblique; smooth	Suboblique; smooth but minutely serrate apically	Suboblique; smooth	Suboblique; smooth	Suboblique; smooth	Directed forward; greatly dentate	Oblique; smooth	Oblique; smooth or microdentate at apex	Forward or obliquely; directed falcate smooth or crenulate
Femours	Not swollen	Not swollen	Not swollen	Not swollen	Not swollen	Not swollen	Not swollen (only prefemur moderately)	Moderately swollen	Greatly swollen	Swollen or moderately swollen	Swollen or greatly swollen	Moderately swollen or greatly swollen
Claw and lateral setae	Conicofalcate, setiform	Conicofalcate, setiform	Conicofalcate, setiform	Conicofalcate, setiform	Conicofalcate, setiform	Narrowly spathulated, setiform	Both narrowly spathulate	Spathulate	Slightly spathulate with setae setiform (?)	Spathulate	Both spathulate, or both greatly spathulate	Both spathulate, or both greatly spathulate

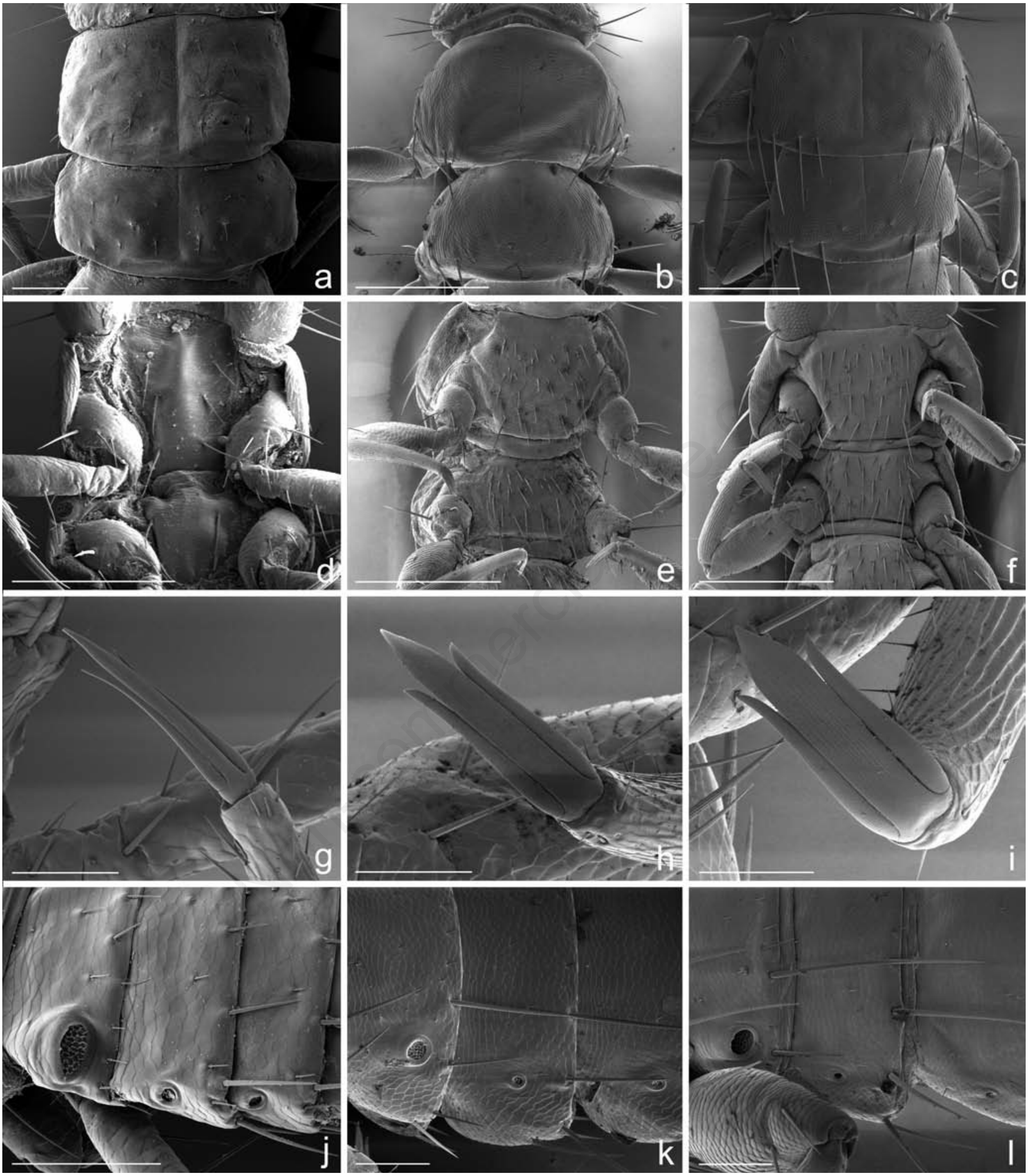

Figure 4. First instar larvae of Meloinae sp. (*incertae sedis*) and *Meloe* (*Lampromeloe*). Meloinae sp. (*incertae sedis*) (Iran): pro- and mesonotum in dorsal (a) and ventral (d) view; left mesothoracic claw, dorsal view (g); left half of abdominal segments I-III, dorsolateral view (j). *M.* (*Lampromeloe*) *cavensis*: pro- and mesonotum in dorsal (b) and ventral (e) view; left mesothoracic claw, dorsal view (h); left half of abdominal segments I-III, dorsolateral view (k). *M.* (*Lampromeloe*) *variegatus*: pro- and mesonotum in dorsal (c) and ventral (f) view; left mesothoracic claw, dorsal view (i); left half of abdominal segments I-III, dorsolateral view (l). Scale bars: a, j, k, l=100 µm; b, e, f=400 µm; c=300 µm; d=200 µm; g=40 µm; h, i=50 µm.

Larval behavioral notes

The new Iranian triungulins have been collected in number (Materials and Methods) on *Anthophora* (*Pyganthophora*) *atroalba* Lepeletier (Figure 5a) on flowers, attached by the modified frontal setae, to the intersegmental abdominal membranes of the bee (Figure 5b).

This phoretic strategy is exactly the same of that of first instar larvae of *Lampromeloe* (*M. cavensis* and *M. variegatus*), a derived behavior, unique among blister beetles and phoretic insects in general. After piercing the host abdomen, some bee individuals are damaged and have neurologic problems (Bologna, 1991). Host bees of *M. cavensis* and *M. variegatus* are *Anthophora nigrocincta* Lepeletier, *A. pennata* (Lepeletier), and *A. femorata* (Olivier) respectively. Rare cases of parasitism on honey bee (*Apis mellifera* Linnaeus) were also described in both species. Other Apoidea are reported as vectors but they are not confirmed hosts (Bologna, 1991).

Discussion and Conclusions

The body shape and most other characters of the new larva are typical of the subfamily Meloinae, and strongly differ from those of the other two subfamilies, Eleticinae and Nemognathinae (Bologna & Pinto, 2001; Bologna *et al.*, 2008). For this reason, its assignment to a phoretic lineage of the Meloinae seems to be obvious. It has been demonstrated, however, that, in this subfamily, phoresy has evolved independently at least five times (Bologna *et al.*, 2008), with convergent, phoresy-related adaptive characters. Twenty Meloinae genera are distributed in Iran, only 16 in Fars and in western Iran, while four are spread only in the extreme desert coastal area or in the north east semi-desert regions. The first instar larva of 13 out of 16 genera is well known, and the triungulins of only three Lyttini genera (*Calydus* Reitter, 1896; *Eolydus* Denier, 1913; *Syriolytta* Kaszab, 1962) remain unknown.

Based on current knowledge (Bologna & Pinto, 2001), the dorsal position of the first abdominal spiracle on the tergite would refer the new larva to the tribe Meloini, genus *Meloe*. Although the occurrence of this character in other Meloinae (*e.g. Cabalia*, Bologna & Di Giulio, unpublished data) challenges its general validity, and its association with multiple phoretic adaptations (mouthparts, antennae, legs, claws, etc.) could also potentially characterize other Meloini genera, in our opinion the assignment of the Iranian larva to the genus *Meloe* is the most likely and parsimonious solution at the moment, waiting for more records from the same locality.

Within *Meloe*, we found that the new larva shares at least three strong similarities with the greatly specialized subgenus *Lampromeloe*: i) presence of nine homologous spiniform and directed forward frontoclypeal setae on medial anterior part of the head; ii) mandibles ventrally denticulate, with teeth representing the apices of longitudinally serial, rounded indentations; iii) parietalia with unique imbricate, squamiform microsculpture. Concerning the first, it is worth stressing that the presence of this anterior setal spear underlies an highly specialized phoretic strategy of piercing the abdominal intersegmental membranes of the bee, strengthening the action of legs and mandibles to remain more strongly attached to the host. This phoretic strategy, as well as the anterior spines, the indentations on the ventral side of the mandibles and the head pattern of microsculpture are found, until now, only in *Lampromeloe*. Although these derived characters seem to be potential synapomorphies of the new Iranian larva and *Lampromeloe*, several other characters of the new larva are in a plesiomorphic, or in a completely different derived condition, and would suggest to have followed a different evolutionary pathway from that of *Lampromeloe*, as well as from other *Meloe* subgenera.

Bologna & Pinto (2001) pointed out that phoresy of triungulins is a strategy evolved independently and repeatedly, at least 6 times in the Meloidae family in both Nemognathinae and Meloinae. In the first subfamily, the tribe Stenoderini is probably not phoretic, while the three remaining tribes (Palaestrini, Horiini, Nemognathini) are phoretic, showing a progressive trend of morphological specialization (Di Giulio *et al.*, 2010). Within Meloinae, larval phoresy evolved independently in some genera of Lyttini, Mylabrini and Meloini. In this last tribe, the genus *Physomeloe* Reitter, 1911, is not phoretic (Bologna & Aloisi, 1994; Bologna & Pinto, 2001; Bologna *et al.*, 2008), while the genus *Meloe*

Figure 5. ***Anthophora*** **(*Pyganthophora*)** ***atroalba*** **Lepeletier, habitus in lateral view (a), parasitized by triungulins of Meloinae sp. (*incertae sedis*) and *Meloe* (*Lampromeloe*) sp., attached by the modified frontal setae (b, arrows) into the ventrolateral intersegmental abdominal membranes of the bee.**

includes only phoretic species in 12 examined out of 16 subgenera.

As pointed out in the previous literature on larval morphology of *Meloe* (Di Giulio *et al.*, 2002), the coexistence of characters in both plesiomorphic and apomorphic conditions, most of them clearly related to phoresy, is of particular interest. This puzzle of character conditions is summarized in Table 2.

Compared to non-phoretic genera of Meloinae, plesiomorphic/ancestral conditions include: body short and broad with abdomen being navicular; weak sclerotization; mandibles smooth; sensory appendix on antennomere II conical, positioned on apex; legs elongate with femora not swollen; claws conicofalcate with setae setiform; abdominal spiracle I oval and transverse; lateral pair of caudal setae short, medial pair elongate. Apomorphic conditions include: body elongate, subparallel-sided; great sclerotization; mandibles denticulate; sensory appendix on antennomere II apical but disk-like or on a ventro-apical platform and flattened; legs shortened with femora more or less swollen; claws and lateral setae more or less spathulate; abdominal spiracle I rounded; both pairs of caudal setae similar in length (short or elongate).

The presence of trends of parallel apomorphic conditions in different *Meloe* lineages supports the hypothesis of an evolutionary radiation related to phoresy in *Meloe*, rather than a unique progressive evolution. The ancestral condition is that of some subgenera (*Eurymeloe, Coelomeloe, Micromeloe, Mesomeloe, Lasiomeloe*), which have all characters plesiomorphic; three (*Afromeloe, Meloegonius, Taphromeloe*) have some of these characters moderately derived; others (*Listromeloe*, *Treiodous, Meloe*) have all characters derived, or both states (*Lampromeloe*). In the subgenus *Meloe*, Pinto & Bologna (1993) pointed out a modest progressive reduction of the antennal sensory appendix, but the derived state of this character is not present in the subgenus.

The new Iranian larva, is the first case of *Meloe* with a mosaic of both plesiomorphic and apomorphic characters. The three characters discussed above (frontoclypeal spines, mandibles ventrally denticulated and squamiform microsculpture on parietalia), similar to those of *M. (Lampromeloe)*, represent clearly synapomorphic or independently apomorphic characters. However, comparing this larva with those known in other *Meloe* subgenera, and in other phoretic Meloini lineages, a peculiar *cocktail* of conflicting phoresy-related characters can be recognized: i) body short and broad with abdomen navicular, very small dimensions and integument weakly sclerotized (plesiomorphic condition); ii) distinctive subrectangular head capsule with anterior margin broadly curved, and not triangular and pointed like in the derived head capsules of triungulins of *Lampromeloe* and other *Meloe* subgenera (Di Giulio *et al.*, 2013); iii) mandibles long and wide, directed forward (derived). Similar mandibles seem to be unusual for the genus *Meloe.* The only *Meloe* subgenus known with mandibles similar in shape (but smooth and without ventral indentations), is the monotypic *Listromeloe* (*M. hungarus* Schrank, 1776), which lacks modified setae on fronto-clypeus and shows a distinct head (greatly rounded laterally), pronotum (greatly transverse and wider than mesonotum), and tarsungulus less modified (claw spathulate but lateral setae almost setiform) (Cros, 1930; Di Giulio *et al.*, 2002). iv) Labial and maxillary apical palpomeres stout and flattened (plesiomorphic); v) antennomere II with conical and well developed sensorium apically positioned (plesiomorphic); vi) regular pattern of three main couples of setae on thoracic sterna (plesiomorphic); vii) legs long and robust, with femora not swollen (plesiomorphic); viii) tibiae robust regularly tapering to apex (plesiomorphic); ix) claw and lateral setae only slightly spathulate (apomorphic); x) abdominal spiracle I large, suboval (plesiomorphic); xi) medial caudal setae elongate (plesiomorphic).

Given its tentative assignment to the genus *Meloe*, we can basically depict three different scenarios: i) this larva is actually a *Lampromeloe*; ii) it belongs to a different subgenus, sister to *Lampromeloe*; iii) it belongs to a different subgenus not related to *Lampromeloe*. In the following we explore these possibilities, discussing the related evolutionary implication.

Meloe (*Lampromeloe*) is a Palaearctic element, which includes with certainty two species: *M. cavensis* and the polytypic *M. variegatus*. Two other species were referred to this subgenus: *M. specularis* Gredler, 1877, from Gondokoro in southern tropical Sudan and *M. stellatus* Pliginsky, 1923, from Lorestan in western Iran. *M. specularis* is a mysterious species; we tried locating the type in the Gredler's collection without success (Natural History collection of Franciscans in Bolzano, Italy). It was possibly collected during a missionary expedition by father Comboni in Equatoria, but the occurrence of the genus *Meloe* in that part of central Africa is doubtful (Bologna & Pinto, 1998). We suspect that the specimen was collected in the subdesert area near Khartoum, in Sudan, where the catholic mission was established. According to its description, *M. specularis* is very similar to *M. cavensis*, which is distributed also in Egypt. *M. stellatus* was never studied after its description. We examined the photos of 14 syntypes of this species (Museum für Naturkunde, Berlin), which seems extremely similar to *M. cavensis,* but the synonymy cannot be defined without direct examination of types in the framework of a revision of the subgenus.

In Iran 22 (and 2 uncertain) species of the genus *Meloe* have been recorded, belonging to 11 subgenera (Bologna, 2008; Fekrat & Modaress Awal, 2012); representative larvae of all these subgenera are known. Adults of *Lampromeloe* are easily recognizable because of the entirely metallic (blue-green and cupreous) body coloration, male head with a longitudinal depression behind the eye, and elytra with flat areolas (Bologna, 1991). Both *M. variegatus* and *M. cavensis* are distributed in Iran, and *M. stellatus*, previously considered as possible synonym of *M. cavensis* by Bologna (1991, 2008), seems to be endemic to this country. We could infer that the new larva here described actually refers to *M. stellatus* or to a new unknown *Lampromeloe* species. However, there are no records of adult *Lampromeloe* specimens from the site where larvae have been collected by one of us (RK), neither during recent field researches, nor in historical entomological collections.

Alternatively the new triungulin from Iran could represent a sister taxon of the *Lampromeloe* lineage, distinct from the former by the characters listed in Results (second paragraph) and discussed above. In this case, we could hypothesize that this larva presumably shows the plesiomorphic condition of the characters shown by the more specialized *Lampromeloe* larvae; in particular the modification of the spiniform frontal setae and the strategy of piercing the intersegmental membranes of the abdomen of the bees would have evolved in this lineage before the modification of other phoresy-related characters like those of the legs (swollen femora, slender tibiae and flattened, wide, trident shaped claws) or the reduction of the sensorium.

The less parsimonious hypothesis is that this larva belongs to another lineage of *Meloe* completely unrelated to *Lampromeloe*. In this scenario, the strikingly convergent characters of the anterior spear, the ventral mandibular indentations and the head microsculpture would have been acquired independently by the two lineages, which developed a similar phoretic strategy in parallel. In this case the polarization of the characters of the larva from Iran relative to a *Lampromeloe* larva would not be possible.

In synthesis, the present new finding strongly supports the previous hypothesis of a non-parsimonious multiple evolution to phoresy in the genus, with several parallelisms. We hypothesize that the parasitic behavior on bees of most Meloidae, could have played an important role for the repeated evolution in several lineages of similar more or less complex specializations to phoresy.

References

ASSMUS E., 1865 - Die Parasiten der Honigbiene und die durch dieselben bedingten Krankheiten dieses Insects. Nach eigenen

Erfahrungen und dem neuesten Standpunkt der Wissenschaft. - Schotte & Co., Berlin.

BLAIR K.G., 1943 - The first-stage larva of *Meloe violaceus* Marsh. (Col. Meloidae). - Ent. Month. Mag. 78: 112-116.

BOLOGNA M.A., 1991 - Coleoptera Meloidae. Fauna d'Italia. XXVIII. - Calderini, Bologna.

BOLOGNA M.A., 2003 - *Australytta*, a new blister beetle genus from Southern Africa (Coleoptera: Meloidae). - Ann. Soc. Ent. France 39: 139-152.

BOLOGNA M.A., 2008 - New nomenclatorial and taxonomic acts, and comments, Meloidae; family Meloidae Gyllenhal, 1810. In: LÖBL I., SMETANA A., (eds). Catalogue of Palaearctic Coleoptera. Vol. 5. Apollo Books, Stenstrup, pp 45-49, 370-412.

BOLOGNA M.A., ALOISI G., 1994 - Systematics and bionomics of *Physomeloe* Reitter, with description of the first instar larva (Coleoptera Meloidae). - EOS, Rev. Esp. Ent. 69: 45-56.

BOLOGNA M.A., DI GIULIO A., 2011 - Biological and morphological adaptations in the pre-imaginal phases of the beetle family Meloidae. - Atti Accad. Naz. Ital. Ent. 59: 141-152.

BOLOGNA M.A., PINTO J.D., 1992 - A review of *Meloe (Taphromeloe)*, including a description of the first instar larva of *M. (T.) erythrocnemus* and comments on the classification of the tribe Meloini (Coleoptera: Meloidae). - Proc. Ent. Soc. Wash. 94: 299-308.

BOLOGNA M.A., PINTO J.D., 1995 - The triungulin of two Palaearctic *Meloe* subgenera: *Lasiomeloe* Reitter and *Micromeloe* Reitter (Coleoptera, Meloidae), with bionomic and taxonomic notes. - Boll. Zool. 62: 383-393.

BOLOGNA M.A., PINTO J.D., 1998 - A review of the Afrotropical species of *Meloe* (Coleoptera, Meloidae) with description of first instar larvae, a key to species and an annotated catalogue. - Trop. Zool. 11: 19-59.

BOLOGNA M.A., PINTO J.D., 2001 - Phylogenetic studies of the Meloidae (Coleoptera), with emphasis on the evolution of phoresy. - Syst. Ent. 26: 33-72.

BOLOGNA M.A., ALOISI G., MARANGONI C., 1989 - Nuove osservazioni su *Eurymeloe* Reitter e descrizione di larve di I stadio (Coleoptera, Meloidae). - Bull. Ann. Soc. R. Belge Ent. 125: 67-75.

BOLOGNA M.A., FATTORINI S., PINTO J.D., 2001 - Review of the primitive blister beetle genus *Iselma* with description of the first instar larva (Coleoptera: Tenebrionoidea: Meloidae). - Afr. Ent. 9: 105-129.

BOLOGNA M.A., OLIVERIO M., PITZALIS M., MARIOTTINI P., 2008 - Phylogeny and evolutionary history of the blister beetles (Coleoptera, Meloidae). - Mol. Phyl. Evol. 48: 679-693.

BOLOGNA M.A., TURCO F., PINTO J.D., 2010 - Meloidae Gyllenhal 1810, 11.19. In: LESCHEN R.A.B., BEUTEL R.G., LAWRENCE J.F., LIPI SKI, A. (eds). Handbook of Zoology. Coleoptera, Beetles, Vol. 2: Morphology and Systematics (Elateroidea, Bostrichiformia, Cucujiformia partim). De Gruyter, Berlin/New York, pp 681-693.

BOLOGNA M.A., TURCO F., PINTO J.D. 2013 - The Meloidae (Coleoptera) of Australasia: a generic review, descriptions of new taxa, and a challenge to the current definition of subfamilies posed by exceptional variation in male genitalia. - Invert. Syst. 27: 391-427.

BRANDT J.F., RATZENBURG J.T.C., 1833 - Medizinische Zoologie, oder getreue Darstellung und Beschreibung der Thiere die in der Arzneimittellehre in Betracht kommen, in systematischer Folge herausgegeben. Hirschwald, Berlin, 1 (1827-1829); 2 (1830-1833).

CROS A., 1919 - Notes sur les larves primaires des Meloidae avec indication de larves nouvelles. - Ann. Soc. Ent. France 88: 261-279.

CROS A., 1927 - Le *Meloe cavensis* Petagna. Étude biologique. - Ann. Sci. Nat. Zool. 10: 347-391.

CROS A., 1929 - Observations nouvelles sur le Meloés. - Ann. Sci. Nat. Zool. 12: 137-191.

CROS A., 1930 - Description de la larve d'un Coléoptère inconnu de la famille des Meloidae. - Bull. Soc. Sci. Natur. Maroc. 10: 57-61.

CROS A., 1941 - Le *Meloe variegatus* Donovan. Sa presence dans le Nord de l'Afrique. Sa biologie. - EOS Rev. Esp. Ent. 17: 313-334.

DI GIULIO A., ABERLENC H.P., VIGNA TAGLIANTI A., BOLOGNA M.A., 2003 - Definition and description of larval types of *Cyaneolytta* (Coleoptera Meloidae) and new records on their phoretic association with Carabidae (Coleoptera). - Trop. Zool. 16: 165-187.

DI GIULIO A., BOLOGNA M.A., 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). - Ital. J. Zool. 69: 339-344.

DI GIULIO A., PINTO J.D., BOLOGNA M.A., 2010 - First instar larva of *Palaestra rufipennis* (Westwood, 1841) and other Australian blister beetles (Coleoptera, Meloidae, Nemognathinae). - Austr. J. Ent. 49: 332-340.

DI GIULIO A., SCIOTTI A., BOLOGNA M.A., 2013 - Revision of first instar larvae of *Meloe*, subgenera *Eurymeloe* and *Coelomeloe*, with new descriptions and a key to the species (Coleoptera: Meloidae). - Ital. J. Zool. 80: 242-254.

FEKRAT L., MODARESS AWAL M., 2012 - A contribution to the knowledge of Meloidae (Insecta: Coleoptera) fauna of Northeastern Iran. - J. Crop Protect. 1: 303-311.

HACHFELD G., 1931 - Über die Primärlarve der *Meloë brevicollis* Panz. und über die bis jetzt bekannten Primärlarven deutscher Meloiden. - Z. Wiss. Insectenbiol. 26: 42-47.

KIFUNE T., MAETA Y., SATO T., 1973 - Biological notes on some Japanese species of the genus Meloe with description of their first instar larvae (Coleoptera: Meloidae). (Studies on Meloidae. II). - Mushi 47: 47-65.

KRZYZANSKA K., 2000 - An incident of an apiary invaded by larvae of *Meloe variegatus*. - Bee World 81: 142-143.

LAWRENCE J.F., 1991 - Order Coleoptera. In: STEHR F.W., (ed). Immature Insects, Vol. 2. Kendall/Hunt, Dubuque, pp 144-298.

LÜCKMANN J., SCHARF S., 2004 - Description of the first instar larvae of three species of *Meloe* with a key to the triungulins of Central European species of this genus (Coleoptera: Meloidae). - Eur. J. Ent. 101: 313-322.

MACSWAIN J.W., 1956 - A classification of the first instar larvae of the Meloidae (Coleoptera). - Univ. Calif. Publ. Ent. 12: 1-182.

PINTO J.D., BOLOGNA M.A., 1993 - The first instar larvae of *Meloe afer* and *M. occultus*, with a clarification of antennal structure in larval *Meloe* (Coleoptera: Meloidae). - Col. Bull. 47: 340-348.

PINTO J.D., SELANDER R.B., 1970 - The bionomics of blister beetles of the genus *Meloe* and a classification of the New World species. - Illin. Biol. Monogr. 42: 1-222.

PINTO J.D., BOLOGNA M.A., BOUSEMAN J.K., 1996 - First-instar larvae, courtship and oviposition in *Eletica*: amending the definition of the Meloidae (Coleoptera: Tenebrionoidea). - Syst. Ent. 21: 63-74.

SELANDER R.B., 1989 - The triungulin of *Meloe cicatricosus* Leach (Col., Meloidae). - Deutsche Ent. Z. (N.F.) 36: 401-407.

SELANDER R.B., 1990 - Blister beetles of the genus *Pseudopyrota* (Coleoptera: Meloidae). - J. Kansas Ent. Soc. 63: 46-79.

TOPOLSKA G., HARTWIG A., KRZYZANSKA K., 2001 - Triungulin larvae of *Meloe variegatus* Donov. (Coleoptera: Meloidae); morphology, biology and an incident of apiary infestation. - Wiad. Parazyt. 47: 115-117.

VAN EMDEN F.I., 1943 - Larvae of British beetles. Various small families. - Ent. Month. Mag. 78-79: 209-223.

ZANON V., 1919 - L'apicoltura a Bengasi. - Apicolt. Mod., Torino, pp 7-9, 33-36, 48-49, 61-63, 79-81, 113-115, 125-128, 143-146.

ZANON V., 1922 - La larva triungulina di *Meloe cavensis* (Petagna) dannosa alle api in Cirenaica. - Agric. Colon. 16: 345-354.