Bulletin of Insectology ***73*** *(1): 11-27, 2020*
ISSN 1721-8861 eISSN 2283-0332

First insight into detailed morphology of monotomids, with comments on chaetotaxy and life history based on myrmecophilous *Monotoma angusticollis*

Grzegorz K. Wagner[1], **Bernard Staniec**[1], **Mirosław Zagaja**[2], **Ewa Pietrykowska-Tudruj**[1]
[1]*Department of Zoology, Maria-Curie Skłodowska University, Lublin, Poland*
[2]*Isobolographic Analysis Laboratory, Institute of Rural Health, Lublin, Poland*

Abstract

This paper is the first morphological description of the developmental stages of a representative species of Monotomidae family. The paper describes the external structures of the early (L_1) and last (L_3) larval instars of the Euro-Siberian myrmecophilous monotomid beetle *Monotoma angusticollis* (Gyllenhall) (Coleoptera Monotomidae), associated with the *Formica rufa* species group. This is also the first complete, detailed and richly illustrated description of larval morphology and its chaetotaxy for any member of Monotomidae. A description of the pupa of *M. angusticollis* is also provided; this is the only one to date of a pupa morphological description from this coleopteran family. For the imago, several morphological details are given. According to the head measurements, this species passes through three larval instars (L_1-L_3). The morphological differences between L_1 and L_3 relate to the antennal and leg structures, the shape of the labrum and the body surface microsculpture. Diagnostic characters for larvae of Monotomidae and members of *Monotoma* have been established. The larva of *M. angusticollis* is distinguished from other known monotomid larvae by its exceptionally asymmetrical mandibles and the short, clavate setae. The morphological and behavioural characters enabling the larvae and imagines of this species to live among ants have also been established, although integration with the host is not as far advanced as in the case of some other myrmecophiles.

Key words: root-eating beetles, monotomid, ants, developmental stages, larva, chaetotaxy, immature, adult, pupa, morphology, biology, symbiont.

Introduction

Beetles (Coleoptera) are the largest order of insects (nearly 400,000 species described) with the largest number of myrmecophilous species (Wasmann, 1894; Kistner, 1979; 1982; Hölldobler and Wilson, 1990). The taxonomic diversity of myrmecophilous beetles is imposing: as early as 1894, Wasmann's catalogue listed 993 coleopteran species among 1177 arthropods associated with social insects. At present we can assume that the number of species with this lifestyle has doubled at the very least (Parker, 2016).

The diversity of beetles means that it is easier to find species that are relatively better adapted to co-occurrence with ants than other insects. Both adults and larvae of the great majority of Coleoptera and Formicidae have microhabitats in common, e.g. leaf litter or dead wood. Like ants, beetles mainly move around using their legs, unlike dipterans or lepidopterans, which prefer to fly, and among which it is mainly the pre-imaginal stages that may be myrmecophilous, e.g. *Microdon* sp., *Phengaris* sp. (Scarparo *et al.*, 2017; Witek *et al.*, 2011). This means of locomotion enable beetles to explore more easily the same ecological niches as ants. Hence, beetles may initially be better adapted to the temporary habitation of ant colonies, for example, in order to forage or seek shelter, after which they may remain in the ant nest, completing their life cycle in this specific environment (Parker, 2016). In addition, the transformation of the forewings into hard elytra, characteristic of the whole coleopteran order, equips myrmecophilous beetles with a protective shield against the aggressive attentions of their hosts. The elytra protect the dorsal surface of the abdomen and hindwing pair in adult beetles from predators or harsh environmental conditions (Wilts *et al.*, 2012, Linz *et al.*, 2016, Goczał *et al.*, 2018).

These features - both morphological (strongly sclerotized body) and behavioural-ecological (inhabiting a similar environment, thanatosis) - are possessed by members of the family Monotomidae, in particular the genus *Monotoma* Herbst, to which the studied species belongs.

The family Monotomidae Laporte belongs to the Cucujoidea superfamily in the Cucujiformia series. In early classifications, this family used to be treated as a subfamily Cucujidae but is now considered as an independent unit in the rank of family. According to the latest data (Robertson *et al.*, 2015), 36 genera and 258 species belong to Monotomidae and are classified into two subfamilies: Rhizophaginae and Monotominae. The latter includes the genus *Monotoma*, containing 40 species with a cosmopolitan distribution. Ten of these have been recorded in Poland (Burakowski *et al.*, 1986a).

Most species of the genus *Monotoma* (root eating-beetles) inhabit a variety of often anthropogenic forms of decomposing, dead organic matter, for example, compost prisms (Peacock, 1977). Some species are known as synanthropic nidicoles, e.g. *Monotoma picipes* Herbst, which occur in hen houses. Others, classified in the subgenus *Gyrocecis* Thomson, including *Monotoma* (*Gyrocecis*) *angusticollis* Chevrolat, or the frequently co-occurring *Monotoma* (*Gyrocecis*) *conicicollis* Chevrolat, belong to the myrmecophilous fauna associated with *Formica* ants (Ślipiński, 1981).

Monotoma angusticollis (Gyllenhall) is a Euro-Siberian species. Its range in Europe extends northwards far beyond the Arctic Circle, southwards to France and northern Italy, and eastwards to Romania and Ukraine. In Poland, this beetle is rarely come across, probably because of the specific habitat it occupies, i.e. the ant nests of *Formica rufa* L. and related species like *Formica pratensis* Retzius, *Formica aquilonia* Yarrow, *Formica polyctena* Foerster, *Formica lugubris* Zetterstedt and *Formica exsecta* Nylander (Burakowski *et al.*, 1986a; Koch, 1989; Päivinen *et al.*, 2002; 2003; Härkönen and Sorvari, 2014; Parmentier *et al.*, 2014). The adults of *M. angusticollis* are tiny (3 mm in length), slow-moving beetles. Although rarely attacked by their hosts, if such an event does take place, they tuck their legs under their bodies to prevent them being caught by the ants (Parmentier *et al.*, 2014; own observations).

Even though myrmecophilous beetles are very interesting objects of research and have fascinating morphological, ecological and behavioural adaptations to life among ants (Hölldobler and Wilson, 1990), the literature is scarce of descriptions of the morphology of the pre-imaginal stages of these insects. To date, descriptions of the external structure of early developmental stages have mostly been limited to the family Staphylinidae (Staniec, 2004; Staniec *et al.*, 2009; 2017; 2018; Zagaja *et al.*, 2014) and to members of the subfamily Paussini belonging to Carabidae (Di Giulio *et al.*, 2003; 2011; Moore *et al.*, 2011). Papers on the larval morphology of species from other families appear only occasionally in the literature and describe particular species, e.g. *Sphaerocetum arboreum* Fikacek, Maruyama, Komatsu, von Beeren, Vondracek et Short from Hydrophilidae (Fikáček *et al.*, 2015) or *Cremastocheilus wheeleri* LeConte from Scarabaeidae (Ratcliffe, 1977). Detailed morphological data of immature forms, especially larvae, may be particularly useful for acquiring an understanding of the specific adaptations of these species to life within anthills, as well as of their relationships with the ants themselves.

The principal aim of this paper was to describe in detail the hitherto unknown external morphology, including chaetotaxy and ultrastructure, of the larva and pupa of *M. angusticollis*, a myrmecophile associated with the nests of ants from the *F. rufa* species group. New details of the morphology of the adult form of this species are added to the existing description (Ślipiński, 1981) and some details of its biology are given.

Materials and methods

Material examined

Larval instars were obtained by rearing 59 adults of *M. angusticollis.* Specimens were collected at Lake Długie (51°27'04.0"N 23°09'39.9"E) on 21 April 2017 and at Lake Moszne (51°26'57.4"N 23°07'34.0"E) on 5 May 2017; both sites are situated in the Polesie National Park near Lublin (SE Poland). The insects were sifted from nest material of *F. rufa*. Live beetles of *M. angusticollis* were placed in transparent plastic containers (diameter 10 cm, height 4 cm) filled with nest substrate and observed in the laboratory at room temperature (22-25 °C) from 28 April to 21 June. Adults and larvae of various species of ants, including *F. rufa,* crushed larvae of *Tenebrio molitor* L. and small springtails, were supplied as a source of adult food.

Study techniques

Larvae (40 specimens) and pupae (6 specimens) were killed in boiling water and preserved in 75% ethanol.

To prepare temporary microscope slides, 10 larvae (L) were macerated in cold 10% KOH for two (L_1 instar) or three hours (L_3 instar), immersed in cold lactic acid for subsequent preparation and mounting of antennae, mouthparts, sensory structures, chaetotaxy of body, legs and urogomphi. They were then traced from photographs taken with an Olympus DP72 or Olympus DP21 digital camera mounted on a binocular Olympus SZX16 or Olympus BX63 compound microscope (figures 1-3, 13, 15-16, 19-24, 29, 32-33, 41-42, 49-51, 52-54, 69). The final image adjustments were made using CorelDraw Graphics Suite X6 and Corel PhotoPaint.

Habitus illustrations of larvae, pupae and imago, structure of setae, chaetotaxy of head, functional position of mouthparts, structural details of antennae, microsculpture, spiracles and various details of their external structure were recorded using SEM, model VEGA3 TESCAN (figures 4-12, 14, 17-18, 25-27, 28, 30-31, 34-40, 43-48, 55-68, 70-76). For the SEM work, 5 larval specimens taken from alcohol were dried at a critical point of CO_2 using Critical Point Dryer, model Emitech K850 and coated with layer of gold using Vacuum Sputter Coated, model Emitech K550X. Finally, samples were placed directly in the SEM chamber for observation.

Measurements and their abbreviations

Measurements of the larvae, pupae and imagines (table 1), made on freshly killed specimens using the Olympus BX63 compound microscope in cellSens Dimension v1.9 software, are given in millimetres, as explained in detail in Pietrykowska-Tudruj and Staniec (2012). Because of the small number of available materials in the literature relating to Monotomidae, the terminology of the morphological structures, chaetotaxy (selected aspects only) and their abbreviations are generally based (with some modifications) on works containing morphological descriptions of beetles from other families (e.g. Staniec *et al.*, 2016; 2018; Wagner and Gosik, 2016). The material examined for the measurements includes all larval instars (L_1-L_3) and it is specified in table 1. The voucher specimens are deposited in the collections of the Department of Zoology, Maria Curie Skłodowska University, Lublin.

Results

Generic diagnosis of the late larval instar of genus *Monotoma*

A series of shared morphological characters have been established for the larval instars of genus *Monotoma* basing on descriptions of members of Monotomidae available in the literature and own observations

Table 1. Some measurements of larval instars of *M. angusticollis.* Abbreviations: A - average, L_{1-3}/X - larval instar/number of specimens examined, R - range, SV - standard variation. Measurements expressed in millimetres.

Measurement	L_1/4			L_2/4			L_3/32		
	R	A	SV	R	A	SV	R	A	SV
Body length	1.06-1.63	1.41	0.34	1.83-2.57	2.20	0.27	2.21-3.95	3.06	0.40
Thorax length	0.33-0.58	0.45	0.09	0.55-0.69	0.61	0.05	0.56-1.02	0.84	0.13
Head length	0.19-0.21	0.20	0.01	0.22-0.26	0.24	0.02	0.21-0.36	0.29	0.04
Head width	0.27-0.31	0.30	0.01	0.38-0.39	0.39	0.01	0.46-0.53	0.50	0.02

(Bousquet, 2001; 2010; Sen Gupta, 1988; Lawrence 1991; this paper): (1) body extended, cylindrical or flattened dorso-ventrally; (2) body covered with characteristic tuberose processes; (3) setae long and straight, or clavate; (4) head narrower than thoracic segments; (5) frontal suture absent; (6) antennae 3-jointed; (7) mandibles symmetrical, rarely asymmetrical, with a smooth or toothed incisor, and an additional tooth below the apex, dorsally or ventrally, and a straight or toothed prostheca; (8) 3-jointed maxillary palp; (9) falcate maxillary galea; (10) 1- or 2-jointed labial palp; (11) abdomen of 10 segments with urogomphi on segment IX; (12) anal hooks absent.

Description

Mature larva of *M. angusticollis*

Body (figures 1-3) - length: 2.21-3.95 mm (mean 3.06 mm); cylindrical, quite stocky, only slightly flattened dorso-ventrally, head somewhat narrower than prothorax, thoracic segments gradually widening to metathorax; abdominal segments I-IV of uniform width (mean 0.72 mm), segments V-X tapering. Colour: head poorly sclerotized, slightly brownish, not very different from the rest of the body; mouthparts darker, more strongly sclerotized. Thorax and abdominal segments yellowish, with tergites slightly darker than sternites. Setae yellow, single, mace-shaped dorsally (figure 4), some sharply tipped ventrally, straight (figure 5). Very distinct microsculpture on all of the body, more prominent dorsally (figure 6) than ventrally (figure 7).

Head (figures 8-11) - length: 0.21-0.36 mm (mean 0.29 mm), width 0.46-0.53 mm (mean 0.50 mm), about 1.7 as wide as long, widest at level of setae Em2, lateral margins rounded in frontal, protruding tips in the posterior part of head; single oval brownish stemma (St) on each side. Chaetotaxy: frontal region with 12 setae [2(Fd1-2, Fl1-2, Fm1-2)], epicranial region with 14 [2(Ed1-4, El1-3)] and lateral region with 10 setae [2(Em1-3, T1-2)]. Ventral side with 6 setae [2(Vl1-3)]. Position of antennae (At), labrum (Lr), epipharynx (Ep), mandibles (Md), maxillae (Mx), hypopharynx (Hp) and labium (Lb) as in figures 10-11.

Antenna (At) (figures 12-14) - short, thickset, three-articled, length ratio of articles I-III: 3:1:2, respectively. Article I about 0.5 × as long as wide; article II 0.3 × as long as wide, with 3 sensilla (IISe) and one stocky sensory appendage (Sa); article III 1.5 × as long as wide, with 6 sensilla apically (IIIS 1-6), of which IIIS1 and 2 are visibly longer than the others.

Labrum (Lr) (figures 15-18) - trapezoida, distinctly rounded anteriorly, with a marked protuberance in posterodorsal part; 12 setae on dorsal side [2(Ld1-2, Ll1-3, Lm1)]; adoral side of labrum (epipharynx, Ep) membranous with 2 setae [2(Lv1)] and numerous sensory cuticular processes of different length and thickness directed to pharynx (figure 15).

Mandibles (Md) (figures 19-23) - asymmetrical, strongly sclerotized, basal part significantly expanded with 2 setae laterally and 4-5 pores; left Md (figures 20, 22) with well-developed dorsal tooth (Td) and 6 subapical teeths (T1-6) along incisor edge (figure 20), prostheca (Pst) bifid with one additional small tooth preapically (figure 22); right Md (figure 21) with well-developed ventral tooth (Tv) (figure 21a) and 5 subapical teeth (T1-5) along incisor edge (figure 21), prostheca (Pst) single (figure 23).

Maxilla (Mx) (figures 24-27) - consisting of triangular cardo (Cd) divided by sclerotized ridge into two unequal parts, elongated stipes (Stp) of almost uniform width mala and three articled maxillary palp (Pm); cardo with 1 ventral seta; stipes with 5 setae (3 ventral and 2 lateral) and 1 pore; mala (Ma) without clear border from stipes, with 3 protuberant teeth and 5 spine-shaped setae on the apical area (figures 25, 26); adoral margin with 7 spine-like setae; inner margin of stipes with about 30-40 spinose cuticular processes; maxillary palp (Pm), length ratio of articles I-III: 1.4:1:2.1, respectively; article I wider than second, about 1.5 × as wide as long with 1 seta and 1 pore; article II smaller, with similar ratio of width to length as article I, with 2 setae and 1 pore; article III narrower than I and II, about 1.9 × as long as wide, with 2 setae and 1 pore; apical area with 10 tiny sensilla and 3 sensory appendages (figure 27).

Hypopharynx (Hp) (figure 32) - membranous, distinctly pubescent, with surface with sensory cuticular processes of different lengths.

Labium (figure 29) - ligula (Lg) broad and flattened; labial palps (Pl) slightly longer than ligula with 2 setae and some cuticular processes in basal parts, apex area with 8 elongated and 3 shortened sensilla; prementum (Pmnt) triangular, transverse, well-sclerotized with 2 setae and 2 pores in central area and 2 micro-setae posteriorly; mentum (Mnt) tapering in posterior part with 2 long and 2 short setae lateroposteriorly; submentum (Smnt) with 2 setae lateroposteriorly.

Thorax - foreleg (figure 33) strong and stocky, consistsing of massive coxa (Cx) with 15 setae (Ad1-4, Al1- 4, Av1-2, D1-2, Pv1-2), large trochanter (Tr) with

4 setae (Av1, Pv1–2, Pd1) and 8 pores (C1-8), femur (Fe) 1.4 × as long as wide with 7 setae (Ad1-2, Al1, Av1, Pv1-2, D1) and 2 pores (C1-2), tapered tibia (Tb) with 9 setae (Al1, Av1, D1-2, Pl1, Pd1-2, Pv1) and slightly inward-curving tarsungulus (Tg) with 2 setae; length ratio of pronotum (Pnt), mesonotum (Msn) and metanotum (Mtn): 1.7:1.1:1 (figure 35), respectively. Pronounced microsculpture with tubercular processes of different size (figures 36-37). Pnt with 34 setae [2(A1-4, Da1. Db1, Dc1-2, L1-5, P1-4)] (figures 35, 42); Msn with 20 setae [2(A1-4, L1-2, P1-4)] (figure 35); chaetotaxy of metanotum identical to that of mesonotum; all setae of Pnt, Msn and Mnt on tubercles arranged in distinct rows; between Pnt and Msn with 1 pair of spiracles (Sp); prosternum (Prs) with 2 setae [2(Eu1)], mesosterum (Mss) and metasterum (Mts) with 1 pair of setae [2(St1)] on each of them (figure 35a).

Abdomen (figures 41-51) - chaetotaxy of tergites: I-VIII with 14 setae [2(A1-3, P1-2, L1-2)]; IX with 6 setae [2(A1-2, P1)] and urogomphus (Ug) with 7 setae; microsculpture with numerous tubercular processes and tubercles in basal parts of setae (figure 47). Abdominal segments I-VIII each with a pair of paratergites (with 1 setae) and parasternites (without setae) laterally; segment X shortened (figures 46, 48); abdominal sternites I-IX each with 6 setae and numerous microsetae, segment X with 12 setae; clavate setae on tergites.

First larval instar (figures 18, 42, 50)

Differences between L_1 and L_3 larval instar of *M. angusticollis* involve: (1) structure of antenna - length ratio of articles I-III: 1.5:1:2.1 in L_1; length to width ratio of articles I-III: 1:1:3.5 in L_3; (2) shape of anterior edge of labrum - tapering and more pointed than in the last larval instar; (3) structure of legs - length to width ratio of femur and tibia: 1:1.2 and 1.2:1 in L_1, 1.8:1 and 1.5:1 in L_3; foreleg more massive and relatively shorter than in the last larval instar; (4) the whole body surface with a more delicate microsculpture than in L_3 and a smaller number of tuberose processes characteristic of the mature larva (figures 41-42, 50-51).

Table 1 lists some measurements of all the larval instars bred.

Morphology of pupa (figures 52-68)

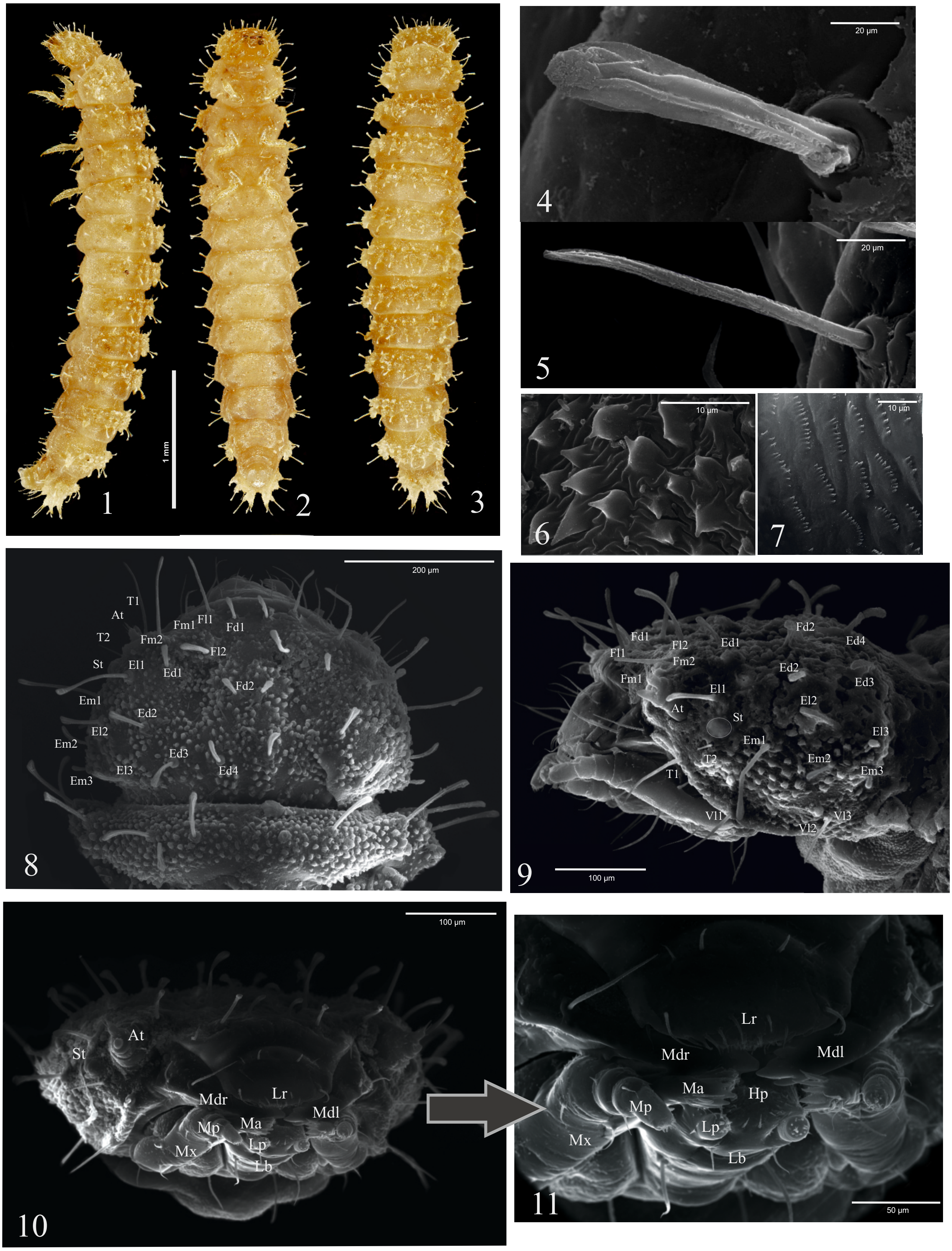
Mean body length 2.15 mm, mean width (measured at the level of the second pair of legs) 1.02 mm, moderately elongated, slightly curved, oblate dorso-ventrally, abdominal segments tapering gradually, chaetotaxy well-developed on the whole body, setae hair-like, straight or slightly curved, relatively long; colour: yellowish to greyish, in advanced and late pupal stages some structures (eyes, mouthparts, elytra) darker, brownish; head (figures 57-58) bent under prothorax, narrow, slightly triangular, eyes well-visible, brownish; with 22 setae [2(C1-2, 1-9)] and 2 campaniform sensilla (2Cs); pronotum (figures 60, 62) transversely wrinkled, lateral and posterior margins folded; armed with 34 setae [2(A1-4, Da1-2, Db1-2, Dc1-2, Dd1, De1-2, Df1-2, P1-2)], straight, of various length; mesonotum with 4 setae, almost half as long as metanotum, with 2 visible short setae; elytra with microsculpture as on figure 59, similar to microsculpture of pronotum (figure 60); femora with several setae (figure 65); abdominal segments I-VI each with a pair of paratergites and parasternites, tergites I-VI slightly wrinkled transversally, with 4 setae on each, paratergites each with 2 setae and II-IV each with 1 functional spiracle (figure 66), atrophied spiracles on segments I and V (figure 67), the rest of segments without spiracles; sternites each with a pair of setae, but not visible on sternites I-VII; gonotheca of male (figure 63) undivided, inconspicuous, that of female (figure 64) divided, elongated.

Morphology of imago (figures 69-76)

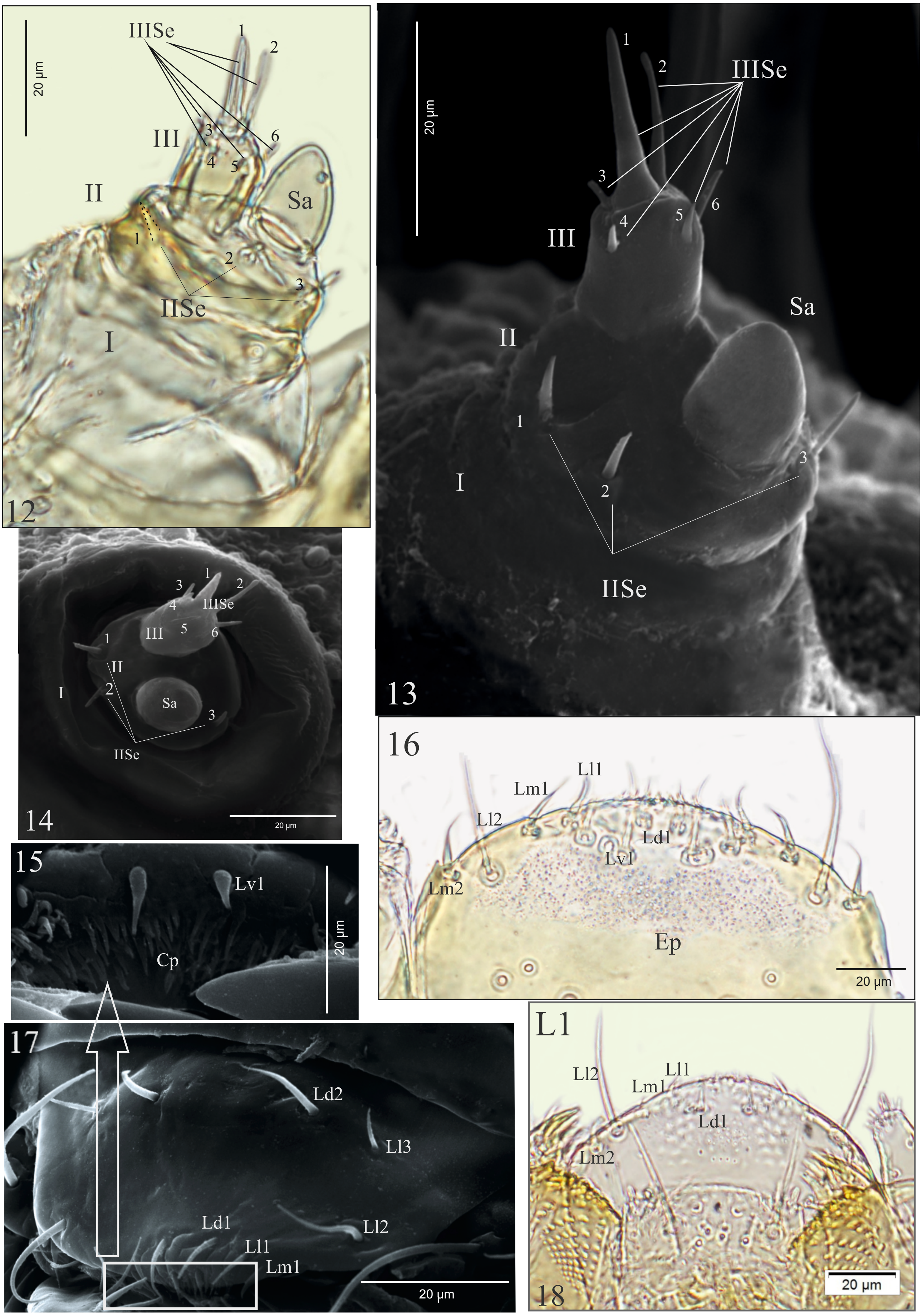
Mean body length 2.80 mm, elongated and slightly flattened dorso-ventrally, head prognathous, narrower than pronotum, elongated and tapering anteriad; all covered by short setae, which are of a similar type all over the body (figure 73a); eyes lateral, protuberant; antenna (figure 72) ten articled with distinct one articled club; short labrum concealed beneath clypeus (figure 73); mandible (figure 74) short and broad, about 1:1 × as long as wide, slightly curved toward apex, with rows of setae on external area, incisor edge simple, not dentate, covered with rows of sensilla (figure 75), molar area well-developed (figure 74a); maxilla (figure 76) with pronounced galea and lacinia; galea elongated, finger-like, with some sensilla apically, lacinia covered with numerous setae on internal edge, maxillary palp four articled, with numerous sensory appendages apically (figure 76a); hypopharynx with rows of cuticular processes; labial palps three articled; pronotum slightly elongated, tapering slightly anteriad, with the bumps on the anteriolateral corners, serrated laterally, covered by short, mace-shaped setae; scutellum exposed; elytra moderately elongated, about 1.6 as long as wide, from mid-length converging posteriad, punctate with setae arranged in regular rows; legs rather short, tarsus five articled, of which I very short and V as long as the others jointly; prosternum convex, with small process reaching half-length of coxa of first pair of legs; anterior part of mesosternum extended into wide process, metasternum as long as pro- and mesosternum jointly; pygidium uncovered; colour: body dark brown, antenna and legs reddish, setae yellow.

Biological observations

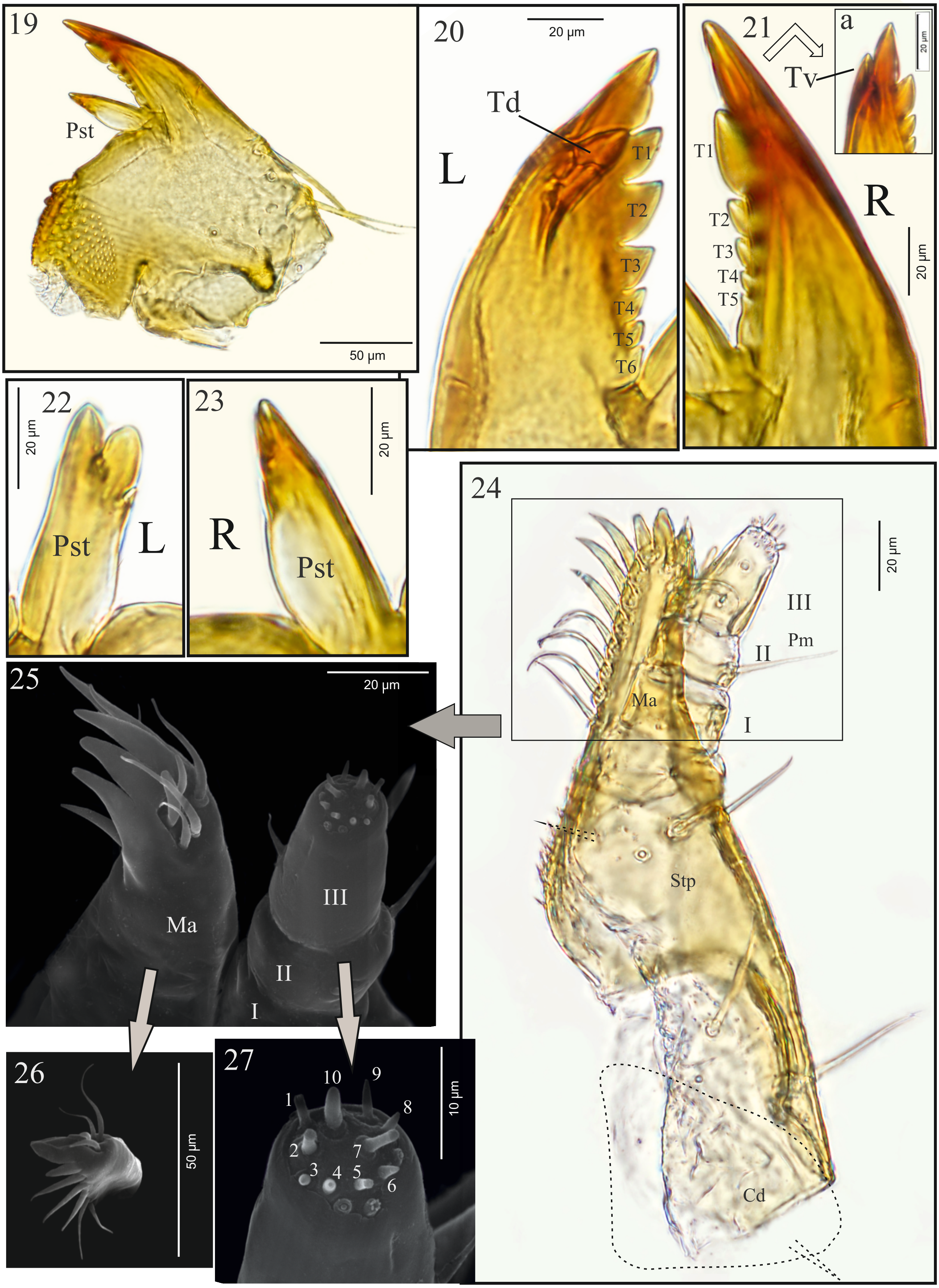
Based on the breeding carried out here, it is difficult to determine the duration of the different developmental stages because of the species' very secretive behaviour. Breeding started on 28 April, and on that first day the copulations of imagines were observed. The first larval instars were seen on 12 May, over 2 weeks after breeding began. Mature larvae appeared around 28 May, so about 16 days elapsed between L_1 and L_3. Observations showed that the most frequently consumed food (crushed larvae of *T. molitor* and ants) was partially decomposed, a few days old.



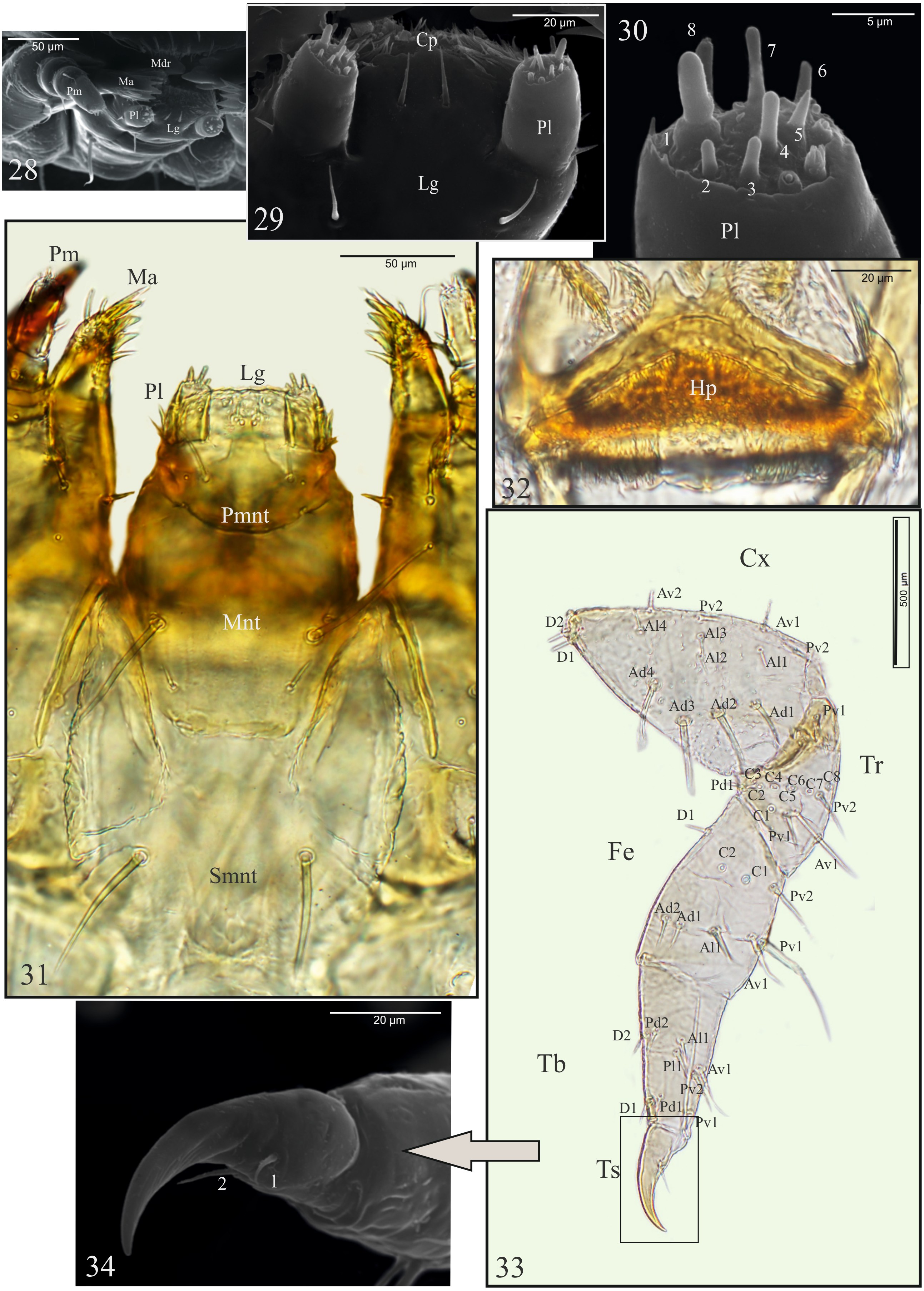
Figures 1-11. *M. angusticollis*, mature larva. **1-3**, entire lateral **(1)**, ventral **(2)** and dorsal **(3)** aspect; **4**, mace-shaped single seta of dorsal part of head; **5**, sharp-ended single seta of ventral part of head; **6-7**, microsculpture of the body, dorsal part **(6)** and ventral part **(7)**; **8-11**, head in dorsal **(8)**, lateral **(9)** and frontal **(10**, **11)** aspect. Abbreviations: At, antenna; Ed, epicranial dorsal setae; El, epicranial lateral setae; Em, epicranial marginal setae; Fd, frontal dorsal setae; Fl, frontal lateral setae; Fm, frontal marginal setae; Hp, hypopharynx; Lb, labium; Lr, labrum; Lp, labial palp; Ma, mala; Mdr, right-hand mandible; Mdl, left-hand mandible; Mx, maxilla; Mp, maxillary palp; St, stemma; T, temporal setae; Vl, ventral lateral setae.



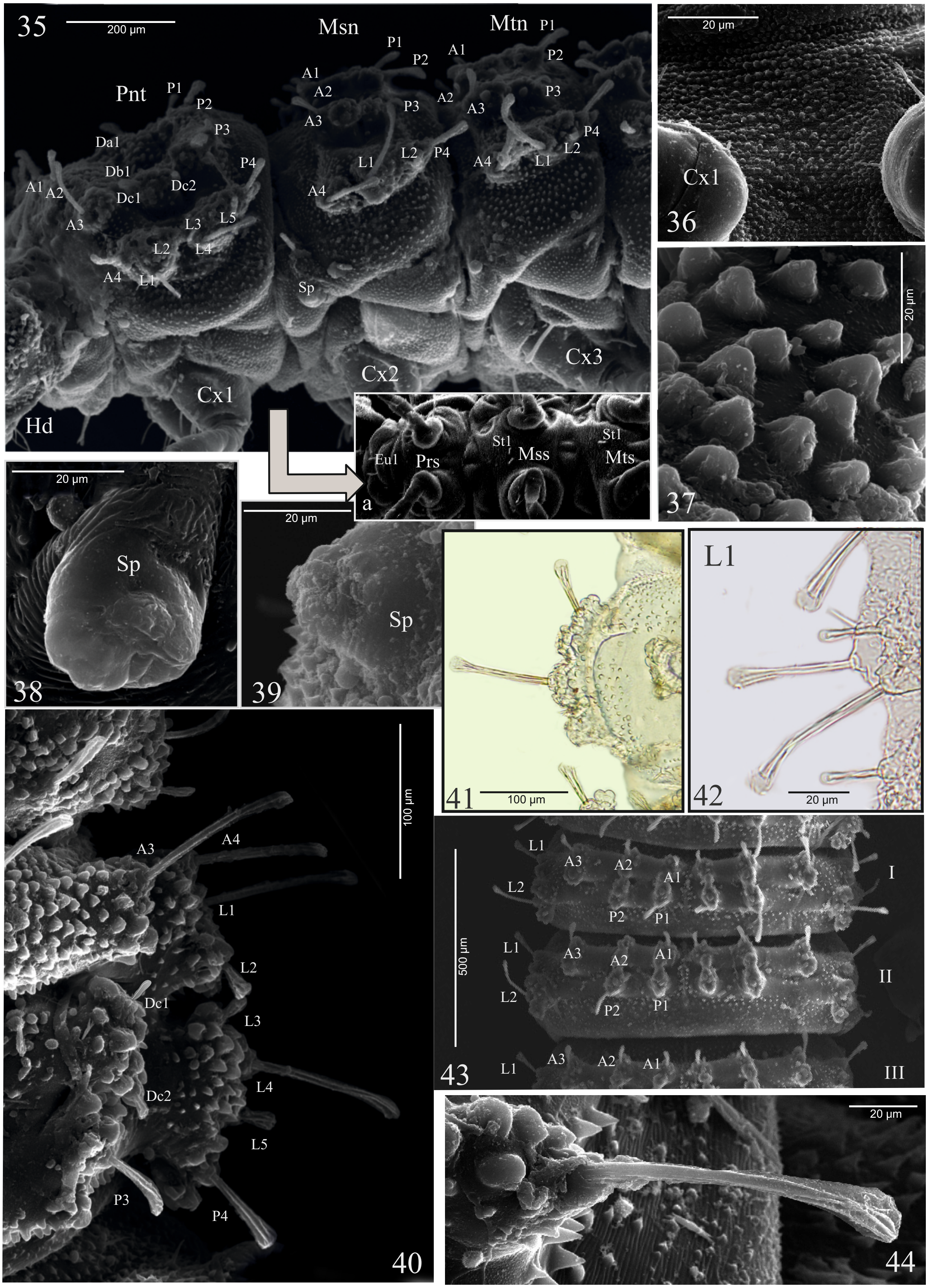
Figures 12-18. *M. angusticollis*, larva; first larval instar **(18)**, last (third) larval instar **(12-17)**. **12-14**, right-hand antenna in lateral **(12, 13)** and frontal **(14)** aspect; **15-18**, labrum of first **(18)** and last larval instars **(15-17)**. Abbreviations: I-III, antennal articles; IISe1-3, sensilla of antennal article II; IIISe1-6, sensilla of antennal article III; Cp, cuticular processes; Ep, epipharynx; Ld, labral dorsal setae; Ll, labral lateral setae; Lm, labral marginal setae; Lv, labral ventral setae; Sa, sensory appendage.



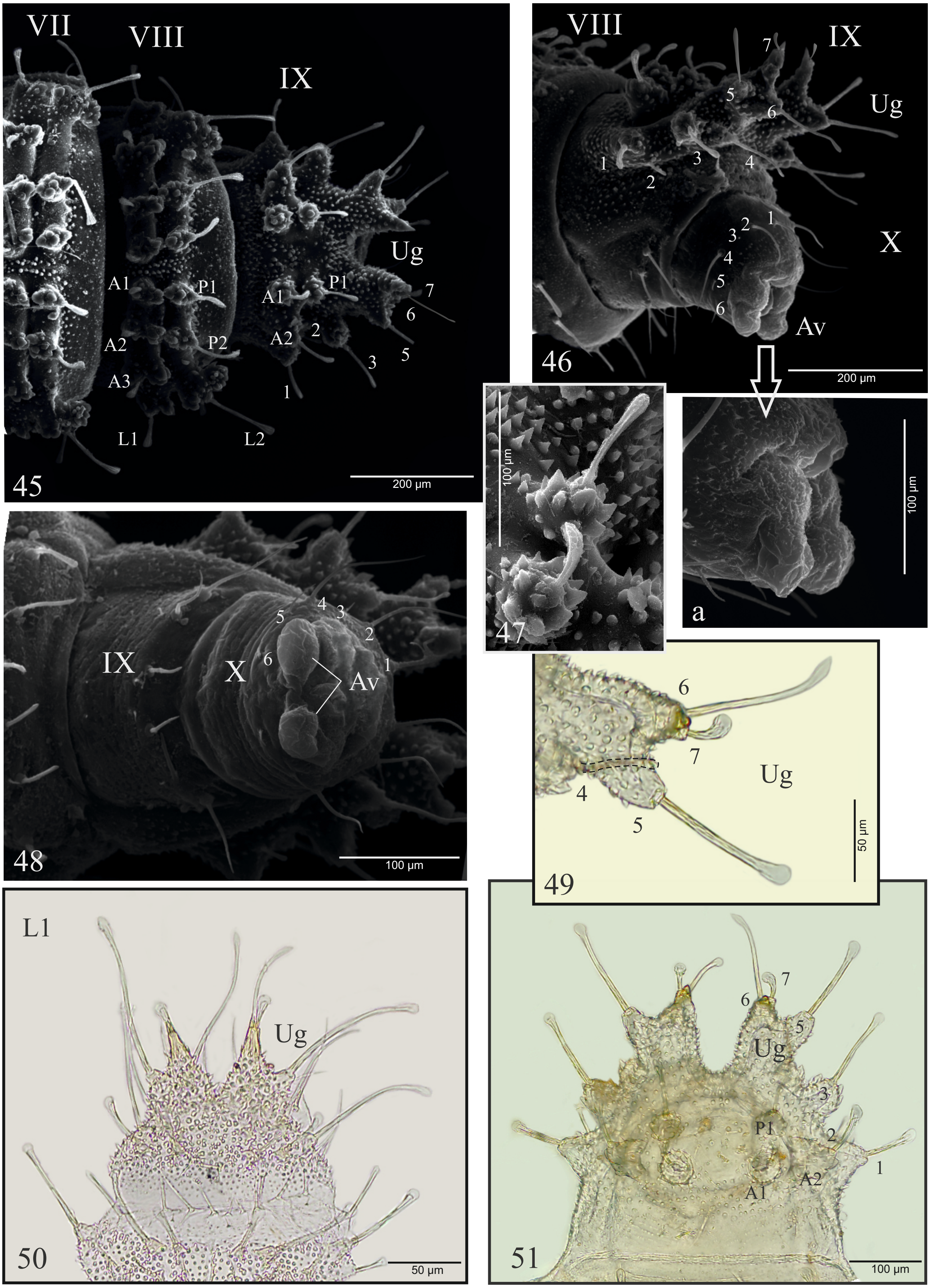
Figures 19-27. *M. angusticollis*, mature larva. **19-23**, mandibles; right-hand mandible: in dorsal aspect **(19**, **21)**, apical part in ventral aspect **(21a)**, prostheca **(23)**; left-hand mandible in dorsal aspect **(20)**, prostheca **(22)**; **24-27**, right-hand maxilla in dorsal aspect **(24)**, mala and maxillary palp in anterodorsal aspect **(25)**, apical portion of mala **(26)** and article III of maxillary palp **(27)** in anterior aspect. Abbreviations: I-III, articles of maxillary palp; Cd, cardo; Ma, mala; Pm, maxillary palp; Pst, prostheca; Stp, stipes; T, subapical teeth of mandible on incisor edge; Td, subapical tooth of left-hand mandible in dorsal portion; Tv, subapical tooth of right-hand mandible in ventral portion.



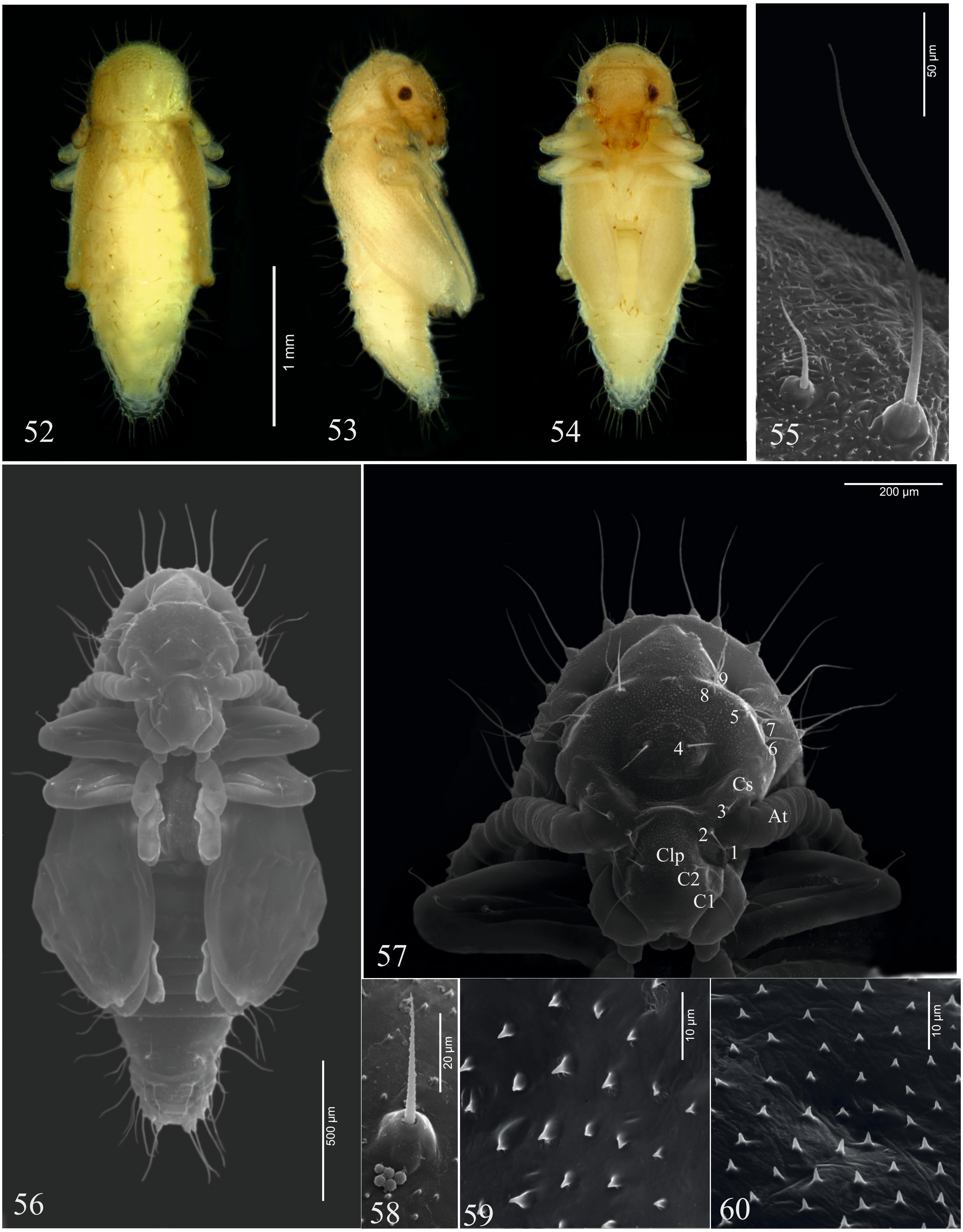
Figures 28-34. *M. angusticollis*, mature larva. **28**, **31**, labium in frontal (**28**) and ventral (**31**) aspect; **29**, ligula and labial palps in anteroventral aspect; **30**, apical portion of labial palp; **32**, hypopharynx; **33**, foreleg in anterior aspect; **34**, tarsungulus. Abbreviations: 1-2, setae of tarsungulus; 1-8, apical sensilla of labial palp; Ad, anterodorsal setae; Al, anterolateral setae; Av, anteroventral setae; C, campaniform sensilla; Cp, cuticular processes; Cx, coxa; Fe, femur; D, dorsal setae; Fe, femur; Hp, hypopharynx; Lg, ligula; Ma, mala; Mdr, right-hand mandible; Mnt, mentum; Pd, posterodorsal setae; Pmnt, prementum; Pl, labial palp; Pl1, posterolateral seta; Pm, maxillary palp; Pv, posteroventral setae; S1-8, apical sensilla of labial palp; Smnt, submentum; Tb, tibia; Tr, trochanter; Ts, tarsungulus.



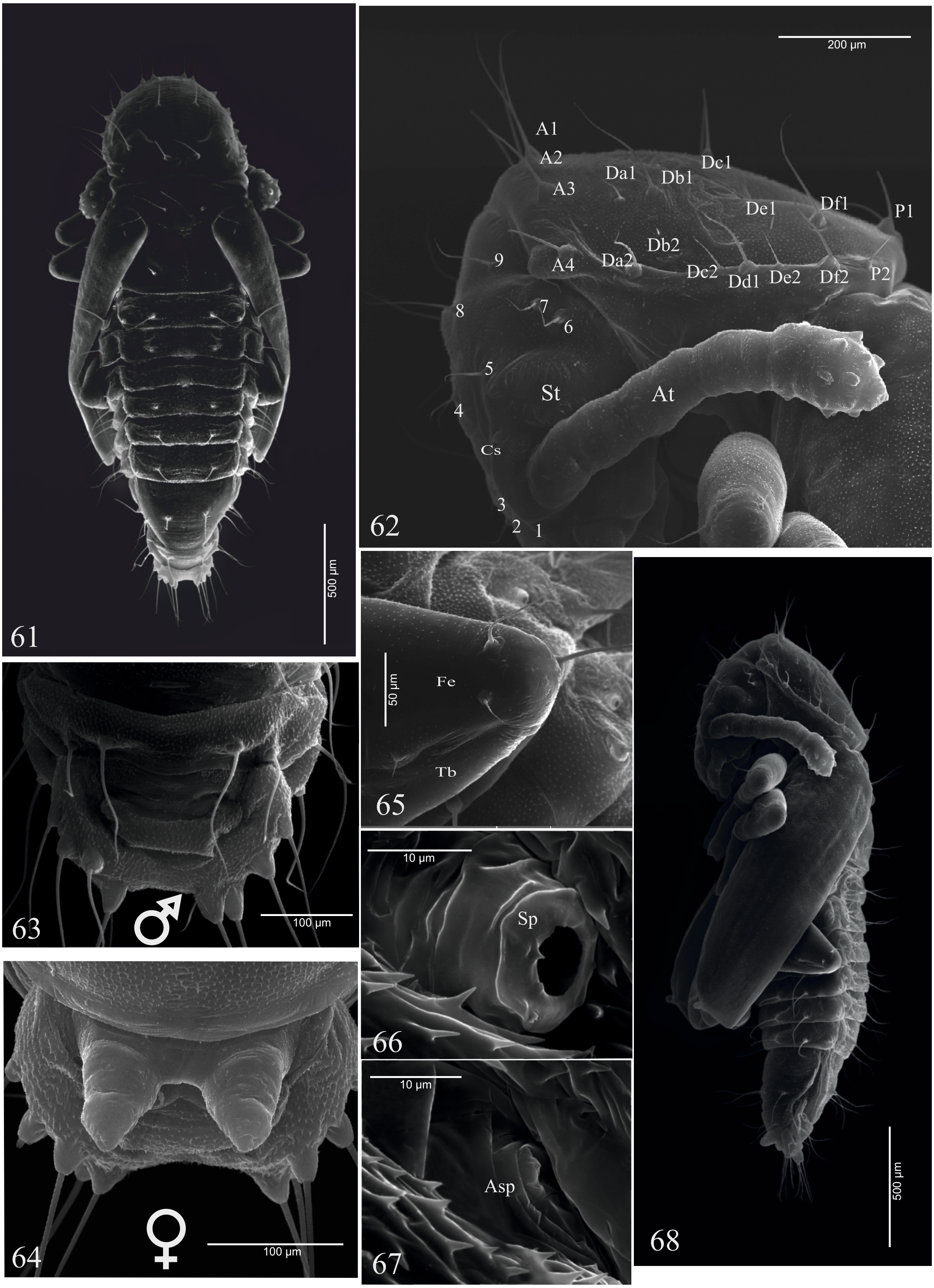
Figures 35-44. *M. angusticollis*, larva; first larval instar **(42)** and last larval instar **(35-41**, **43-44)**. **35**, thorax in lateral and ventral aspects **(35a)**; **36-37**, microsculpture of presternum **(36)** and pronotum **(37)**; **38-39**, spiracle of abdominal segment VII **(38)** and mesonotum **(39)**; **40**, lateral margin of pronotum; **41-42**, lateral margin of abdominal segment I in last **(41)** and first **(42)** larval instar; **43**, abdominal segments I-III in dorsal aspect; **44**, lateral seta (L) of dorsolateral part of abdominal segment. Abbreviations: I-III, abdominal segments; A, anterior setae; Cx, coxa; D, discal setae; Eu, eusternal setae; Hd, head; L, lateral setae; Msn, mesonotum; Mss, mesosternum; Mtn, metanotum; Mts, metasternum; P, posterior setae; Pnt, pronotum; Prs, presternum; Ps, presternal setae; Sp, spiracle; St, sternal setae.



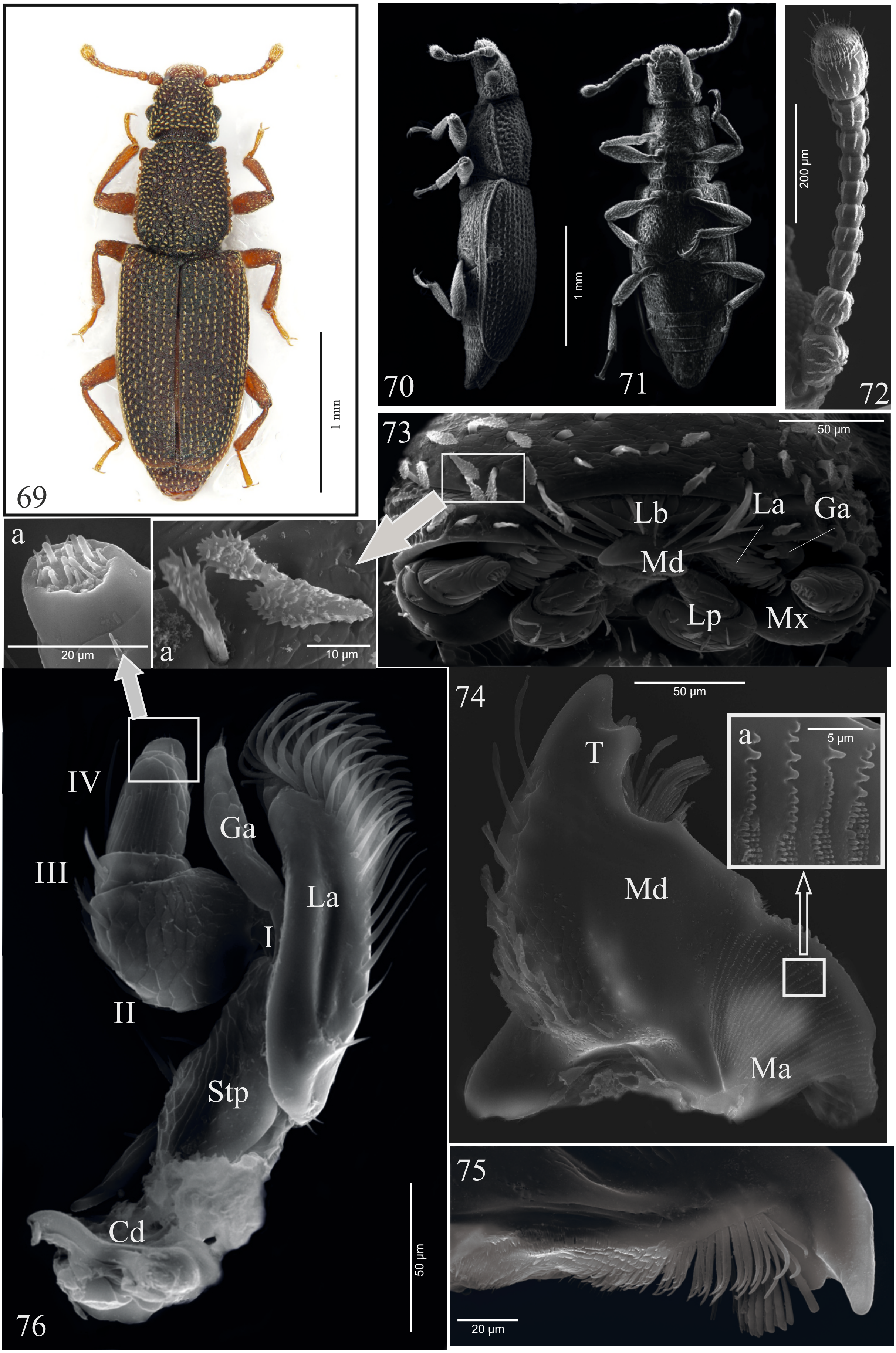
Figures 45-51. *M. angusticollis*, larva; first larval instar **(50)** and last larval instar **(45-49**, **51)**. **45**, terminal abdominal segments with urogomphi in dorsal aspect; **46**, abdominal segments VIII-X with urogomphi and anal vesicles **(46a)** in lateral aspect; **47**, setae of dorsal area of abdominal segment XI; **48**, abdominal segments IX and X in ventral aspect; **49-51**, urogomphi of first larval instar **(50)** and mature larva **(49**, **51)**. Abbreviations: 1-6, setae of abdominal segment X; 1-7, setae of urogomphus; VIII-X, abdominal segments; A, anterior setae; Av, anal vesicle; L, lateral setae; P, posterior setae; Ug, urogomphus.



Figures 52-60. *M. angusticollis*, pupa. **52-54**, entire dorsal **(52)**, lateral **(53)** and ventral **(54)** aspect; **55**, setae of pronotum; **56**, pupa in ventral aspect; **57**, frontal section of head; **58**, seta of head; **59**, microsculpture of elytra; **60**, microstructure of pronotum. Abbreviations: 1-9, setae of head; At, antenna; C1-2, setae of clypeus; Clp, clypeus; Cs, campaniform sensilla.



Figures 61-68. *M. angusticollis*, pupa. **61**, pupa in dorsal aspect; **62**, pronotum and part of head in lateral aspect; **63-64**, gonotheca of male **(63)** and female **(64)**; **65**, knee of leg pair III; **66**, spiracle of abdominal segment II; **67**, atrophied spiracle of abdominal segment I; **68**, pupa in lateral aspect. Abbreviations: 1-9, setae of head; A, anterior setae; Asp, atrophied spiracle; At, antenna; D, discal setae; Fe, femur; St, stemma; P, posterior setae; Sp, spiracle; Tb, tibia.



Figures 69-76. *M. angusticollis*, imago. **69-71**, entire dorsal **(69)**, lateral **(70)** and ventral **(71)** aspect; **72**, right-hand antenna in dorsal aspect; **73**, mouthparts in frontal aspect; **73a**, setae of head; **74-75**, mandible in ventral aspect **(74)**, molar area **(74a)** and incisor edge **(75)**; **76**, left-hand maxilla in dorsal aspect with apical portion of maxillary palp **(76a)**. Abbreviations: I-IV, articles of maxillary palp; Cd, cardo; Ga, galea; La, lacinia; Lb, labium; Lp, labial palp; Ma, molar area; Md, mandible; Mx, maxilla; Stp, stipes; T, subapical tooth.

Discussion and conclusions

This article contains a detailed description of the external structure of the hitherto unknown developmental stages of *M. angusticollis*, a myrmecophilous species of beetle associated with the *F. rufa* species group. It provides the first description of the larva and pupa of this species and at the same time the first complete, detailed work on the developmental stages of Monotomidae. Likewise for the first time, the larval chaetotaxy, often crucial in phylogenetic studies of Coleoptera, has been analysed (Ashe and Watrous, 1984; Ashe, 1986). The chaetotaxy is described in accordance with the terminology used in papers dealing with Staphylinidae (Ashe and Watrous, 1984, Staniec *et al*., 2018).

Based on the measurements of certain body parts, especially the head width, three distinct size intervals were established, which indicate that the larval development of this species involves three instars (table 1). Apart from body size, the differences between the first and last larval instars relate to: (i) the length proportions of the antennal articles - particularly the rather longer last article in L_3 than in L_1; (ii) the shape of the labrum; (iii) the structure of the legs - in L_3 they are more slender and longer than in L_1; (iv) the microsculpture of the body surface - far more delicate and less differentiated in L_1 than in L_3. On the other hand, no apparent differences in the chaetotaxy were found between L_1 and L_3. This condition distinguishes the larvae of this species from known larval instars of some other coleopteran species like staphylinids, where such differences are the rule (Ashe and Watrous, 1984; Zagaja *et al*., 2014; Staniec *et al*., 2016; 2018).

Hitherto available data on the morphology of monotomid larvae relate solely to *Monotoma producta* LeConte and *Monotoma americana* Aube (Chandler, 1983; Lawrence *et al*., 1991, 2011). Even so, they are fragmentary, with few, rather schematic drawings, and therefore wholly insufficient in the context of contemporary comparative analyses at different taxonomic levels. The description of the larva of the former species contains just a few schematic drawings of the habitus, the appearance of the head, maxillae, labium, mandibles and antennae. The only information available on the latter species consists of drawings illustrating the body and mandibles (Chandler, 1983; Lawrence *et al*., 1991; 2011).

If we take the family Monotomidae as a whole, then to date the preimaginal stages, mostly larvae, have been at least partially described in just 7 of the 36 known genera (Lawrence, 1991). All monotomid larvae examined so far share the following diagnostic characters: (1) extended, cylindrical or slightly flattened body, covered with usually characteristic grainy/tuberose processes with long, straight setae; (2) head narrower than the thoracic segments, without a frontal suture; (3) three articled antennae; (4) symmetrical mandibles with a smooth or toothed incisor, an additional tooth ventrally and a narrow, straight or toothed prostheca; (5) three articled maxillary palp; (6) falcate maxillary galea; (7) one- or two articled labial palp; (8) ten segmented abdomen with characteristically complex abdominal processes on segment IX; (9) absence of anal hooks (Bousquet, 2001; 2010; Sen Gupta, 1988, Lawrence, 1991; McElrath *et al*., 2012).

The larva of *M. angusticollis* closely resembles other monotomid larvae. One character, however, that distinguishes the larva of *M. angusticollis* form other larvae of this genus and other monotomids relates to the unique short, mace-shaped setae. Along with the larva's characteristic, well-developed surface microsculpture, they probably make for the better adherence of large amounts of ant-nest material, which is saturated with the hosts' odour. This character, equally well-developed in the imago (figure 73a), may facilitate effective camouflage and thus the survival of this symbiont in the inhospitable anthill environment. In addition, this masking effect is potentiated by the slow movements of both larva and imago, and, in the case of the latter, the ability, if threatened, to pass into an inactive cataleptic state (Parmentier *et al*., 2014; own observations).

Hence, even though the cuticles of both larvae and imagines of *M. angusticollis* contain minimal amounts of the cuticular hydrocarbons (CHC) characteristic of ants, their hosts probably ignore them for the reason stated in the previous paragraph. This stands in contrast to other myrmecophilous species, equally poor in cuticular CHCs, e.g. *Quedius brevis* Erichson (Staphylinidae) or the spider *Mastigusa arietina* (Thorell), individuals of which are immediately attacked by ants on being discovered by them (Parmentier *et al*., 2017).

The clavate setae, typical of *M. angusticollis*, are also present in members of other Coleoptera, such as *Corticaria* sp. from Latridiidae or *Orthoperus* sp. from Corylophidae (Chandler, 1983). It is precisely this structure of the setae that may have been one of the key evolutionary characters, as an advantageous pre-adaptation, that enabled the symbiosis between studied beetle and ants to come about. As the literature (Burakowski *et al*., 1986b) and authors' observations showed, the mentioned genus (*Corticaria* sp. and *Orthoperus* sp.) are also observed occasionally in the ant nests, but so far there is no mention of myrmecophilism or it is a very early stage. However, this is consistent with the proposed theory.

Most monotomid beetles normally inhabit decomposing organic matter, but their precise trophic requirements are not well known. It is known that *Bactridium*, *Monotoma* and *Hesperobaenus* species feed mainly on fungi - members of Ascomycota like *Hypoxylon* and *Daldinia* (Lawrence, 1977; Chandler, 1983). The imagines of these beetles can usually be found on the fruiting bodies of these fungi or in sites where they commonly occur. It is thought that most beetle species inhabiting environments beneath tree bark are also fungivorous. Some species from the genera *Rhizophagus* Herbst and *Mimemodes* Reitter are known predators that feed on the eggs of bark beetles (Gregoire *et al*., 1985). But it is also considered that species from these genera also consume any mycelium that they come across in the bark-beetle corridors. Beetles of the genus *Rhizophagus* are known vectors of fungi from the genera *Ceratocystis* and *Ophiostoma* (Hinds, 1972).

In the light of the above information, the myrmecophilous *M. angusticollis* is distinguished from other members of the family by its somewhat different trophic requirements. Even though both imago and larva prefer partially decomposed organic matter such as dead ants, they feed (in the laboratory, too) on their hosts' eggs and larvae, and also on whatever items the ants manage to bring back to the nest (Parmentier *et al*., 2016a; own observations). There is probably a connection between this manner of feeding and the unique structure of this beetle's mandibles which, compared to the other monotomids examined to date, are exceptionally asymmetrical (Lawrence, 1991). Nonetheless, a convincing explanation of this interdependence will require more detailed study.

Recapitulating, we can state that the morphological, behavioural and trophic adaptations of larvae and imagines of *M. angusticollis* facilitate its survival within the ant nest (Parmentier *et al*., 2016b; own observations). Adaptations to life among social insects are exhibited by other members of Monotomidae, e.g. from the genus *Crowsonius* Pakaluk et Slipinski, which colonise the nests of South American *Trigona* Jurine bees. The morphology of these beetles has become substantially modified, enabling them to adopt this lifestyle. They are practically blind (strongly reduced eyes) and flightless (no second pair of wings). In addition, the structure of their mandibles has undergone significant adaptation, enabling imagines to attach themselves to their hosts' legs in order to move around (phoresis) (Pakaluk and Slipinski, 1993, 1995).

Larvae of the symphilous beetles from the genus *Lomechusa* Gravenhorst (Staphylinidae) possess by far the greatest number of adaptive characters for life among ants. Both their imagines and their larvae are completely integrated with their hosts. The evidence for this includes the lack of eyes in the larvae, as well as their grub-like body shape resembling that of ant larvae, the absence of abdominal processes, shortened legs, and reduced mouthparts that are adapted to imbibing liquid food from worker ants (trophallaxis). This characteristic structure of *Lomechusa* larvae is augmented by their passive lifestyle and chemical mimicry (Hölldobler, 1967; 1970, Parmentier *et al*., 2014, Parker, 2016; Staniec *et al*., 2017).

Unlike *Lomechusa*, *M. angusticollis* does not display such far-reaching integration with its host: no special morphological adaptations have developed in this species as a consequence of myrmecophily. It would seem, however, that this beetle does possess a certain set of characters enabling it to be a permanent resident of ant nests, one that is tolerated, overlooked or ignored by its hosts. One can therefore treat this case as a typical illustration of Parker (2016) preadaptation hypothesis, which assumes that a set of characters that evolved in one environment enable its possessor to exist equally well in another, such as the interior of an anthill. The trophic aspect is also important here. *M. angusticollis* belongs to a family of saprophagous/mycophagous beetles. Its adaptation to life within an ant colony therefore did not require any drastic change in its feeding mode, since the type of food preferred by monotomids, i.e. organic detritus and fungi, is plentiful in ant nests (Leschen, 1999).

In contrast to the larvae and imagines of Monotomidae, the general characters of which are still imperfectly known (Nunberg, 1967; Leschen *et al*., 2010; Lawrence and Slipinski, 2013), information on their pupae is practically non-existent in the literature. This applies in equal measure to related families, the members of which lead a similar saprophagous or mycophagous lifestyle, e.g. Cerylonidae Billberg, Rhizophaginae Redtenbacher and Phalacridae Leach. Consequently, the need for such data is urgent (Nunberg, 1967; Burakowski and Ślipiński, 1986; Cmoluch, 1997). Only a few crop pest species from the closely related family Nitidulidae have been described in greater detail (e.g. Nunberg, 1976; Neumann *et al*., 2004; Okada and Miyatake, 2007; Ellis and Ellis, 2010). The description of the pupa of *M. angusticollis* provided here can thus be regarded as the first report of its kind for the family Monotomidae.

In the laboratory, the development of this species takes place in spring (April, May), like that of some other myrmecophilous beetles associated with ants from the *F. rufa* group (Zagaja *et al*., 2017; Staniec *et al*., 2018).

The described species is a typical myrmecophilous, so many morphological or behavioural features could be developed as a specialization and do not necessarily have to be complementary to other *Monotoma* genus representatives. Thus, further research is needed on both the biology and morphology of other monotomids inhabiting different niches.

Acknowledgements

The authors gratefully acknowledge the State Forests National Forest Holding (SFNFH), Poland, for funding the research and the Management of the Polesie National Park (PNP) for its cooperation. The project was carried out with the cooperation of the Polesie National Park and the Maria Curie-Skłodowska University (MCSU) in Lublin; the numbers of the relevant agreements are: EZ.0290.1.28.2017 (between PNP and SFNFH); 6, NB 520-3/2017 (between PNP and MCSU).

References

ASHE J. S., 1986.- Structural features and phylogenetic relationships among larvae of genera of gyrophaenine staphylinids (Coleoptera: Staphylinidae: Aleocharinae).- *Fieldiana, Zoology*, 30: 1-60.

ASHE J. S., WATROUS L. E., 1984.- Larval chaetotaxy of Aleocharinae (Staphylinidae) based on a description of *Atheta coriaria* Kraatz.- *Coleopterists' Bulletin*, 38: 165-179.

BOUSQUET Y., 2001.- 79. Monotomidae Laporte 1840. pp. 319-321. In: *American beetles. Volume 2. Polyphaga: Scarabaeoidea through Curculionoidea* (ARNETT R. H., THOMAS M. C., SKELLEY P. E., FRANK J. H., Eds).- CRC Press, Boca Raton, USA.

BOUSQUET Y. 2010.- 10.8. Monotomidae Laporte, 1840. pp. 319-324. In: *Handbook of zoology - Coleoptera, vol. 2. Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim)* (LESCHEN R. A. B., BEUTEL R. G., LAWRENCE J. F., Eds).- De Gruyter, Berlin, Germany.

Burakowski B., Ślipiński S. A., 1986.- *Klucze do oznaczania owadów Polski*. Część XIX, Chrząszcze - Coleoptera. Zeszyt 59: Gwozdnikowate - Colydiidae, Bothrideridae, Cerylidae, Anommatidae. Państwowe Wydawnictwo Naukowe. Warszawa, Wrocław.

Burakowski B., Mroczkowski M., Stefańska J., 1986a.- Chrząszcze - Coleoptera. Cucujoidea, część 1.- *Katalog Fauny Polski*, XXIII, 12, Warszawa.

Burakowski B., Mroczkowski M., Stefańska J. 1986b.- Chrząszcze - Coleoptera. Cucujoidea, część 2. *Katalog Fauny Polski*, XXIII, 13, Warszawa.

Chandler D. S., 1983.- Larvae of wrack Coleoptera in the families Corylophidae, Rhizophagidae, and Lathridiidae.- *Psyche*, 90: 287-296.

Cmoluch Z., 1997.- *Klucze do oznaczania owadów Polski*. Część XIX, Chrząszcze - Coleoptera. Zeszyt 58: *Phalacridae*. Oficyna Wydawnicza Turpress, Toruń.

Di Giulio A., Fattorini S., Kaupp A., Vigna Taglianti A., Nagel P., 2003.- Review of competing hypotheses of phylogenetic relationships of Paussinae (Coleoptera: Carabidae) based on larval characters.- *Systematic Entomology*, 28: 509-537.

Di Giulio A., Maurizi E., Hlaváč P., Moore W., 2011.- The long-awaited first instar larva of *Paussus favieri* (Coleoptera: Carabidae: Paussini).- *European Journal of Entomology*, 108: 127-138.

Ellis J. D., Ellis A., 2010.- Featured creatures, small hive beetle, *Aethina tumida* Murray (Insecta: Coleoptera: Nitidulidae). University of Florida, IFAS and Florida Department of Agriculture and Consumer Services.- [online] URL: http://entomology.ifas.ufl.edu/creatures/misc/bees/small_hive_beetle.htm Accessed on 4 August 2010.

Fikáček M., Maruyama M., Komatsu T., von Beeren C., Vondráček D., Short A. E. Z., 2015.- Protosternini (Coleoptera: Hydrophilidae) corroborated as monophyletic and its larva described for the first time: a review of the myrmecophilous genus *Sphaerocetum*.- *Invertebrate Systematics*, 29: 23-36.

Goczał J., Rossa R., Tofilski A., 2018.- Elytra reduction may affect the evolution of beetle hind wings.- *Zoomorphology*, 137: 131-138.

Gregoire J. C., Merlin J., Pasteels J. M., Jaffuel R., Vouland G., Schvester D., 1985.- Biocontrol of *Dendroctonus micans* by *Rhizophagus grandis* Gyll. (Col., Rhizophagidae) in the Massif Central (France): a first appraisal of the mass-rearing and release methods.- *Zeitschrift fur Angewandte Entomologie*, 99: 182-190.

Härkönen S. K., Sorvari J., 2014.- Species richness of associates of ants in the nests of red wood ant *Formica polyctena* (Hymenoptera, Formicidae).- *Insect Conservation and Diversity*, 7: 485-495.

Hinds T. E., 1972.- Insect transmission of *Ceratocystis* species associated with aspen cankers.- *Phytopathology*, 62: 221-225.

Hölldobler B., 1967.- Zur Physiologie der Gast-Wirt-Beziehung (Myrmecophilie) bei Ameisen. Das Gastverhältnis der *Atemeles*- und *Lomechusa*- Larven (Col. Staphylinidae) zu *Formica* (Hym. Formicidae).- *Zeitschrift für Vergleichende Physiologie*, 56: 1-21.

Hölldobler B., 1970.- Zur Physiologie der Gast-Wirt-Beziehungen (Myrmecophilie) bei Ameisen. II. Das Gastverhältnis des imaginalen *Atemeles pubicollis* Bris. (Col. Staphylinidae) zu *Myrmica* und *Formica* (Hym. Formicidae).- *Zeitschrift für Vergleichende Physiologie*, 66: 215-250.

Hölldobler B., Wilson E. O., 1990.- *The ants*.- Harvard University Press, Cambridge, USA.

Kistner D. H., 1979.- Social and evolutionary significance of social insect symbionts, pp. 339-413. In: *Social insects* (Hermann H. R., Ed.).- Academic Press, New York, USA.

Kistner D. H., 1982.- The social insects' bestiary, pp. 1-244. In: *Social insects* (Hermann H. R., Ed.).- Academic Press, New York, USA.

Koch K. 1989.- *Die Käfer Mitteleuropas*. Ökologie, 1.- Goecke & Evers Verlag, Krefeld, Germany.

Lawrence J. F., 1977.- Coleoptera associated with an *Hypoxylon* species (Ascomycetes: Xylariaceae) on oak.- *The Coleopterists Bulletin*, 31: 309-312.

Lawrence J. F., 1991.- Rhizophagidae (Cucujoidea) (including Monotomidae), pp. 460-462. In: *Immature insects. Vol. 2* (Stehr F.W., Ed.).- Kendall/Hunt Publishing Co., Dubuque, Iowa, USA.

Lawrence J. F., Slipinski A., 2013.- *Australian beetles. Vol. 1: morphology, classification and keys*.- CSIRO Publishing, Australia.

Lawrence J. F., Slipinski A., Seago A. E., Thayer M. K., Newton A. F., Marvaldi A. E., 2011.- Phylogeny of the Coleoptera based on morphological characters of adults and larvae.- *Annales Zoologici*, 61: 1-217.

Leschen R. A. B., 1999.- Origins of symbiosis: phylogenetic patterns of social insect inquilinism in Cryptophagidae (Coleoptera: Cucujoidea).- *University of Kansas Natural History Museum Special Publication*, 24: 85-101.

Leschen R. A. B., Beutel R. G., Lawrence J. F., 2010.- *Handbuch der Zoologie / Handbook of Zoology*, Vol. IV (Arthropoda: Insecta), Part 38 Coleoptera, Beetles. Volume 2: Morphology and systematics (Elateroidea, Bostrichiformia, Cucujiformia partim.).- Walter de Gruyter, Berlin.

Linz D. M., Hu A. W., Sitvarin M. I., Tomoyasu Y., 2016.- Functional value of elytra under various stresses in the red flour beetle, *Tribolium castaneum*.- *Scientific Reports*, 6: 34813.

McElrath T., Bousquet Y., McHugh J. V., 2012.- *Monotomidae. Root-eating beetles*. Version 06 December 2012 (temporary). http://tolweb.org/Monotomidae/9147/2012.12.06 in The Tree of Life Web Project, http://tolweb.org/.

Moore W., Song X. B., Di Giulio A., 2011.- The larva of *Eustra* (Coleoptera, Paussinae, Ozaenini): a facultative associate of ants.- *ZooKeys*, 90: 63-82.

Neumann P., Elzen P. J., 2004.- The biology of the small hive beetle (*Aethina tumida*, Coleoptera: Nitidulidae): gaps in our knowledge of an invasive species.- *Apidologie*, 35: 229-247.

Nunberg M., 1967.- *Klucze do oznaczania owadów Polski*. Część XIX, Chrząszcze - Coleoptera. Zeszyt 64: Obumierki - *Rhizophagidae*. Państwowe Wydawnictwo Naukowe, Warszawa.

Nunberg M., 1976.- *Klucze do oznaczania owadów Polski*. Część XIX, Chrząszcze - Coleoptera. Zeszyt 65: Łyszczynkowate - *Nitidulidae*. Państwowe Wydawnictwo Naukowe, Warszawa.

Okada K., Miyatake T., 2007.- *Librodor japonicus* (Coleoptera: Nitidulidae): life history, effect of temperature on development, and seasonal abundance.- *Applied Entomology and Zooogy*, 42 (3): 411-417.

Päivinen J., Ahlroth P., Kaitala V., 2002.- Ant-associated beetles of Fennoscandia and Denmark.- *Entomologica Fennica*, 13: 20-40.

Päivinen J., Ahlroth P., Kaitala V., Kotiaho J. S., Suhonen J., Virola T., 2003.- Species richness and regional distribution of myrmecophilous beetles.- *Oecologia*, 134: 587-595.

Pakaluk J., Slipinski S. A., 1993.- A new genus and two new species of Neotropical Rhizophagidae (Coleoptera) from *Trigona* (Hymenoptera: Apidae) nests, with a review of rhizophagid biology.- *The Coleopterists Bulletin*, 47: 349-358.

PAKALUK J., SLIPINSKI S. A., 1995.- *Crowsonius parensis*, a new species of Neotropical Rhizophagidae from the nest of the stingless bee *Trigona dallatorreana* Friese (Hymenoptera: Apidae) (Coleoptera: Cucujoidea).- *Genus*, 5: 337-340.

PARKER J., 2016.- Myrmecophily in beetles (Coleoptera): evolutionary patterns and biological mechanisms.- *Myrmecological News*, 22: 65-108.

PARMENTIER T., DEKONINCK W., WENSELEERS T., 2014.- A highly diverse microcosm in a hostile world: a review on the associates of red wood ants (*Formica rufa* group).- *Insectes Sociaux*, 61: 229-237.

PARMENTIER T., BOUILLON S., DEKONINCK W., WENSELEERS T., 2016a.- Trophic interactions in an ant nest microcosm: a combined experimental and stable isotope (δ13C/δ15N) approach.- *Oikos*, 125 (8): 1182-1192.

PARMENTIER T., DEKONINCK W., WENSELEERS T., 2016b.- Do well-integrated species of an inquiline community have a lower brood predation tendency? A test using red wood ant myrmecophiles.- *BMC Evolutionary Biology*, 16 (1): 12.

PARMENTIER T., DEKONINCK W., WENSELEERS T., 2017.- Arthropods associate with their red wood ant host without matching nestmate recognition cues.- *Journal of Chemical Ecology*, 43 (7): 644-661.

PEACOCK E. R., 1977.- *Coleoptera Rhizophagidae. Handbooks for the ldentification of British Insects*.- Vol. V, part 5(a). Royal Entomological Society of London, London, UK.

PIETRYKOWSKA-TUDRUJ E., STANIEC B., 2012.- Comparative larval morphology of *Platydracus* and *Staphylinus* (Staphylinidae: Staphylinini: Staphylinina) with notes on their biology and redescription of the pupa of *Staphylinus*.- *Zootaxa*, 3580: 24-42.

RATCLIFFE B. C., 1977.- Description of the larva and pupa of *Osmoderma subplanata* (Casey) and *Cremastocheilus wheeleri* LeConte (Coleoptera: Scarabaeidae).- *Journal of the Kansas Entomological Society*, 50: 363-370.

ROBERTSON J. A., ŚLIPIŃSKI A., MOULTON M., SHOCKLEY F. W., GIORGI A., LORD N. P., MCKENNA D. D., TOMASZEWSKA W., FORRESTER J., MILLER K. B., WHITING M. F., MCHUGH J. V., 2015.- Phylogeny and classification of Cucujoidea and the recognition of a new superfamily Coccinelloidea (Coleoptera: Cucujiformia).- *Systematic Entomology*, 40: 745-778.

SCARPARO G., CERRETTI P., MEI M., DI GIULIO A., 2017.- Detailed morphological descriptions of the immature stages of the ant parasite *Microdon mutabilis* (Diptera: Syrphidae: Microdontinae) and a discussion of its functional morphology, behaviour and host specificity.- *European Journal of Entomology*, 114: 565-586.

SEN GUPTA T., 1988.- Review of the genera of the family Rhizophagidae (Clavicornia: Coleoptera) of the world.- *Memoirs of the Zoological Survey of India*, 17: 1-58.

ŚLIPIŃSKI S. A. 1981.- *Klucze do Oznaczania Owadów Polski*, Część XIX. Chrząszcze - Coleoptera. Monotomidae. 119, 63, Warszawa.

STANIEC B., 2004.- Description of the developmental stages of *Hesperus rufipennis* (Gravenhorst, 1802) (Coleoptera, Staphylinidae), with comments on its biology.- *Annales Zoologici*, 54: 287-500.

STANIEC B., PIETRYKOWSKA-TUDRUJ E., PILIPCZUK J., 2009.- Morphology of the developmental stages of *Pella* (=*Zyras*) *laticollis* (Märkell, 1844) with remarks on its biology (Coleoptera: Staphylinidae).- *Genus*, 20: 225-242.

STANIEC B., PIETRYKOWSKA-TUDRUJ E., CZEPIEL-MIL K., 2016.- Larva of *Gyrophaena boleti* (Linnaeus, 1758) (Coleoptera: Staphylinidae) - an obligatory saproxylic and mycophagous species associated with *Fomitopsis pinicola*: notes on tergal gland system and behavior.- *Annales Zoologici*, 66 (1): 83-100.

STANIEC B., PIETRYKOWSKA-TUDRUJ E., ZAGAJA M., 2017.- Adaptive external larval ultrastructure of *Lomechusa* Gravenhorst, 1806 (Coleoptera: Staphylinidae: Aleocharinae), an obligate myrmecophilous genus.- *Annales Zoologici*, 67 (3): 609-626.

STANIEC B., ZAGAJA M., PIETRYKOWSKA-TUDRUJ E., WAGNER G. K., 2018.- Comparative larval ultramorphology of some myrmecophilous Aleocharinae (Coleoptera, Staphylinidae), with a first description of the larvae of *Amidobia talpa* (Heer O, 1841) and *Oxypoda haemorrhoa* (Mannerheim C.G., 1830), associated with the *Formica rufa* species group.- *ZooKeys*, 808: 93-114.

WAGNER G. K., GOSIK R., 2016.- Comparative morphology of immature stages two sympatric Tenebrionidae species, with comments on their biology.- *Zootaxa*, 4111 (3): 201-222.

WASMANN E., 1894.- *Kritisches Verzeichniss der Myrmekophilen und Termitophilen Arthropoden*.- Felix Dames, Berlin, Germany.

WILTS B. D., MICHIELSEN K., KUIPERS J., DE RAEDT H., STAVENGA D. G., 2012.- Brilliant camouflage: photonic crystals in the diamond weevil, *Entimus imperialis*.- *Proceedings of the Royal Society B: Biological Sciences*, 279: 2524-2530.

WITEK M., SKÓRKA P., ŚLIWINSKA B. E., NOWICKI P., MOROŃ D., SETTELE J., WOYCIECHOWSKI M., 2011.- Development of parasitic *Maculinea teleius* (Lepidoptera: Lycaenidae) larvae in laboratory nests of four *Myrmica* ant host species.- *Insectes Sociaux*, 58: 403-411.

ZAGAJA M., STANIEC B., PIETRYKOWSKA-TUDRUJ E., 2014.- The first morphological description of the immature stages of *Thiasophila* Kraatz, 1856 (Coleoptera; Staphylinidae) inhabiting ant colonies of the *Formica rufa* group.- *Zootaxa*, 3774: 301-323.

ZAGAJA M., STANIEC B., PIETRYKOWSKA-TUDRUJ E., TRYTEK M., 2017.- Biology and defensive secretion of myrmecophilous *Thiasophila* spp. (Coleoptera: Staphylinidae: Aleocharinae) associated with the *Formica rufa* species group.- *Journal of Natural History*, 51: 2759-2777.

Authors' addresses: Grzegorz K. WAGNER (corresponding author: grzegorz.wagner@poczta.umcs.lublin.pl), Bernard STANIEC, Ewa PIETRYKOWSKA-TUDRUJ, Department of Zoology, Maria-Curie Skłodowska University, Akademicka 19, 20-033 Lublin, Poland; Mirosław ZAGAJA, Isobolographic Analysis Laboratory, Institute of Rural Health, Jaczewskiego 2, 20-090 Lublin, Poland.

Received April 30, 2019. Accepted October 29, 2019.