ACTA ENTOMOLOGICA MUSEI NATIONALIS PRAGAE
Published 15.vii.2016 Volume 56(1), pp. 167–193 ISSN 0374-1036
http://zoobank.org/urn:lsid:zoobank.org:pub:272A8C9D-6190-4E24-A4E2-2981985266B2

Primary chaetotaxy and larval morphometry of *Phaenonotum exstriatum* and *Dactylosternum cacti* (Coleoptera: Hydrophilidae)

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Abstract. The primary and secondary chaetotaxy of the head capsule and head appendages of the three larval instars of *Dactylosternum cacti* (LeConte, 1855) and *Phaenonotum exstriatum* (Say, 1835) (Coleoptera: Hydrophilidae: Sphaeridiinae) are described for the first time. Morphometric characters derived from the head capsule, mouthparts and legs are also included, together with detailed illustrations of all characters. Morphology and chaetotaxy of these larvae are compared to that of other described Coelostomatini larvae.

Key words. Hydrophilidae, Sphaeridiinae, Coelostomatini, larva, morphology, primary chaetotaxy, aquatic beetles, water scavenger beetles, Neotropical Region

Introduction

Hydrophilids are well known for their aquatic members, hence the common name given to them in English speaking countries: "water scavenger beetles". Less known are their terrestrial members most of which are included within the subfamily Sphaeridiinae. These terrestrial species can be found in a variety of habitats such as dung, decomposing plant material, carcasses, rotting fungi, and a few species are known to be associated with ant nests (Fikáček et al. 2013). Sphaeridiinae is a rather large group, including about one third of the known hydrophilid species (Short & Fikáček 2013).

Knowledge of larval Sphaeridiinae is rather poor; most of the genera included in this subfamily have undescribed larvae. Within the tribe Coelostomatini, which includes 17 genera (Short & Fikáček 2013), larvae have been described for only five genera: *Coelostoma* Brullé, 1835, *Dactylosternum* Wollaston, 1854, *Hydroglobus* Knisch, 1921, *Lachnodacnun*

Table 1. Coelostomatini species for which larval descriptions are available.

Species	Morphology	Chaetotaxy	References
Coelostoma orbiculare (Fabricius, 1775)	×	×	Böving & Henriksen (1938) Hrbáček (1943) Fikáček (2006)
Dactylosternum abdominale (Fabricius, 1792)	×	–	De Marzo (2000)
Dactylosternum cacti (LeConte, 1855)	×	×*	Archangelsky (1994, 1997)
Dactylosternum subrotundum (Fabricius, 1792)	×	–	Costa et al. (1988)
Dactylosternum sp.	×	–	Archangelsky (1997)
Hydroglobus puncticollis (Bruch, 1915)	×	–	Archangelsky & Fernández (1994)
Lachnodacnum luederwaldti Orchymont, 1937	×	×	Clarkson et al. (2014)
Phaenonotum exstriatum (Say, 1835)	×	×*	Archangelsky & Durand (1992) Archangelsky (1997)

* described in the present paper.

Orchymont, 1937, and *Phaenonotum* Sharp, 1882 (see Table 1). These descriptions are detailed, especially for third instar larvae, but they do not include chaetotaxic characters, except for *Coelostoma orbiculare* (Fabricius, 1792) and *Lachnodacnum luederwaldti* (Orchymont, 1937) (Fikáček 2006, unpublished; Clarkson et al. 2014).

This paper focuses on the description of the chaetotaxic characters of *Dactylosternum cacti* (LeConte, 1855) and *Phaenonotum exstriatum* (Say, 1835), following the chaetotaxic system implemented by Fikáček et al. (2008). For general morphological characters of these two species the original descriptions should be consulted (Archangelsky & Durand 1992; Archangelsky 1994, 1997). Comparative notes with known larvae of the other Coelostomatini genera are included.

Materials and methods

Larvae were killed in boiling water and preserved in 75% ethyl alcohol. Larval specimens were cleared in warm lactic acid, dissected and mounted on glass slides with Hoyer's medium. Observations (up to 1000×) and drawings were made using a Leica S6D dissecting microscope and a Leica DMLB compound microscope, both with camera lucida and a photographic camera attached. Drawings were scanned and digitally edited, photographs were assembled using the freeware program CombineZP (Hadley 2010). The material studied is held in the larval collection of one of the authors (M.A.). Identification of adults was done using the revision of the subfamily Sphaeridiinae by Smetana (1978). Since *D. cacti* had not been previously recorded from Guatemala, the aedeagus of those specimens was dissected and their morphology completely agrees with that illustrated in Smetana's revision; also, considering that the specimens from Guatemala and Arizona were collected in rotting cacti, there is no doubt that the identification is correct.

Morphometry. Measurements of the head capsule and head appendages were taken with a micrometer adapted to the ocular of the microscope. Different measurements were used to calculate ratios, which are practical to characterize shapes. Measured structures were adjusted as parallel as possible to the plane of the objective. The following measurements were taken.

AL length of antenna, derived by adding the lengths of the first (A1L), second (A2L) and third (A3L) antennomeres;
HL head length, measured medially along epicranial stem from anterior margin of frontoclypeus to occipital foramen;
HW maximum head width;
ML length of maxilla, derived by adding SL and MPL, cardo omitted;
MPL length of maxillary palpus, obtained by adding the lengths of the first (MP1L), second (MP2L), third (MP3L) and fourth (MP4L) palpomeres;
MtW maximum width of mentum;
MW maximum body width, measured at level of prothorax;
Leg 1L length of prothoracic leg derived by adding the lengths of coxa (CO), trochanter (TR), femur (FE), tibiotarsus (TITA) and claw (CL). The length of trochanter includes only the proximal portion, the length of distal portion is included in the femoral length.
Leg 2L length of mesothoracic leg;
Leg 3L length of metathoracic leg;
LigL length of ligula;
LPL length of labial palpus, obtained by adding the lengths of the first (LP1L) and second (LP2) palpomeres;
PrmtL length of prementum, measured from its base to the base of LP1;
PrmtW maximum width of prementum;
SeL length of antennal sensorium;
SL length of stipes;
TL total body length;

Chaetotaxy. Primary (present in first-instar larva) and secondary (arising in later instars) setae and pores were identified in the cephalic capsule and head appendages. Sensilla present in first-instar larvae of *Phaenonotum exstriatum* and *Dactylosternum cacti* were labeled by comparison with the ground plan of chaetotaxy of the family Hydrophilidae (Fikáček et al. 2008, Byttebier & Torres 2009), additional setae were highlighted with a black square. Homologies were established using the criterion of similarity of position (Wiley 1981). Sensilla were coded with a number and two capital letters, usually corresponding to the first two letters of the name of the structure on which they are located. The following abbreviations were used: AN – antenna; FR – frontale; LA – labium; MN – mandible; MX – maxilla; PA – parietale; gAN – group of antennal sensilla; gAPP – group of sensilla on the inner appendage of the maxilla; gFR1, gFR2 – group of sensilla on the frontale; gLA – group of sensilla on the labial palp; gMX – group of sensilla on the maxillary palp; gMX2 – group of sensilla on inner margin of maxillary stipes. Sensilla on the legs were named considering their position (anterior or posterior) on each segment.

Results

Dactylosternum cacti (LeConte, 1855)

Examined larvae. Nine 1st instar larvae (L1), three 2nd instar larvae (L2) and 6 3rd instar larvae (L3) reared from the adults collected in the following localities: **USA: Arizona:** Maricopa Co., 29.vii.1995, M. Archangelsky lgt. **GUATEMALA:** El Progreso, 5 km W junction CA14 and CA9, 7.viii.1991, T. K. Philips and P. W. Kovarik lgt. Adults and larvae were reared in laboratory and the complete life cycle was obtained (Archangelsky 1994).

First instar larva (Figs 7, 11–22). ***Diagnosis*.** Head capsule suboval; frontal lines inversely bell-shaped, merging before occipital foramen, coronal line present, extremely short (Fig. 11); clypeolabrum asymmetrical, nasale slightly asymmetrical, shorter than lateral lobes (Figs 11, 13); lateral lobes of epistome asymmetrical, projecting farther than nasale, left lobe larger than right lobe, slightly serrated on inner margin (Fig. 11); posterior tentorial grooves close to midline, before basal half (Fig. 12). Cervical sclerites present (Fig. 11). Antenna short (Fig. 14),


1

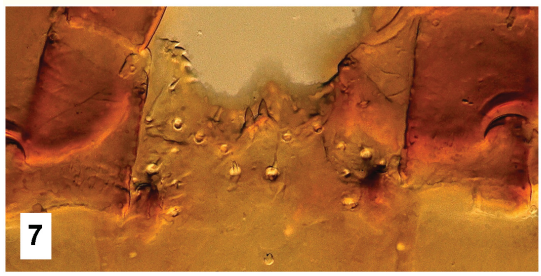

2


3


4


5


6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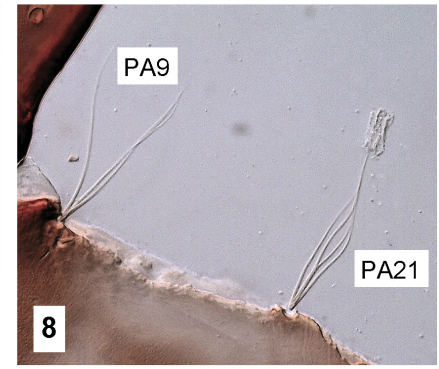

PA9
PA21
8


9

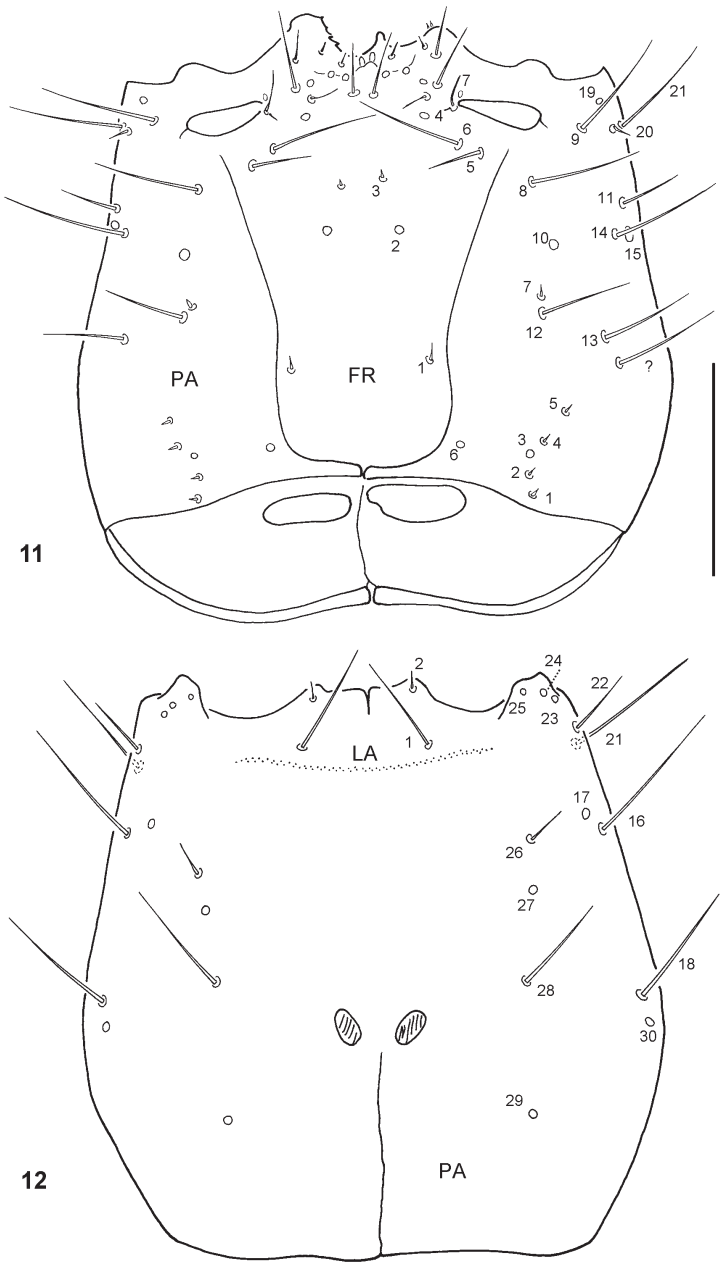

10

basal antennomere the longest, sensory appendage 0.55–0.63× as long as third antennomere. Mandibles asymmetrical (Figs 15, 16), right one slightly smaller (Fig. 16), with a stout inner tooth serrated distally; left mandible with two sharp inner teeth on basal half, covered by a short pubescence (Fig. 15); both mandibles serrated on distal inner margin. Maxilla (Figs 17, 18) with large stipes, longer than palpus, inner margin with dense pubescence (formed by fine spinulae) on inner and outer margins; first palpomere the longest, wider than long, dorsally pubescent; second and third palpomeres shorter than both first and fourth palpomeres. Labium with submentum completely fused to head capsule, lines of fusion not evident, mentum slightly wider than prementum (Fig. 12); basal palpomere the shortest; ligula reduced (Figs 19, 20); dorsally with sharp cuticular spines on membrane between mentum and prementum, and between prementum and first palpomere (Fig. 19). Hypopharynx asymmetrical, membranous and pubescent, developed as a lobe on left side (Fig. 9, third instar larva). Pronotal plate large, covering most of pronotum; those of meso- and metathorax shorter. First abdominal tergum membranous (see Fig. 1, third instar larva); abdominal segments one to seven with two dorsal rows of spines; dorsal plate on abdominal segment eight large, suboval; abdominal segments one to eight with two horizontal rows of strong spines on ventral face, laterally ending in lobed projections or "prolegs" which bear larger spines (Figs 2, 3,10 show the character in third instar larva); legs short, five-segmented (Figs 3, 21, 22).

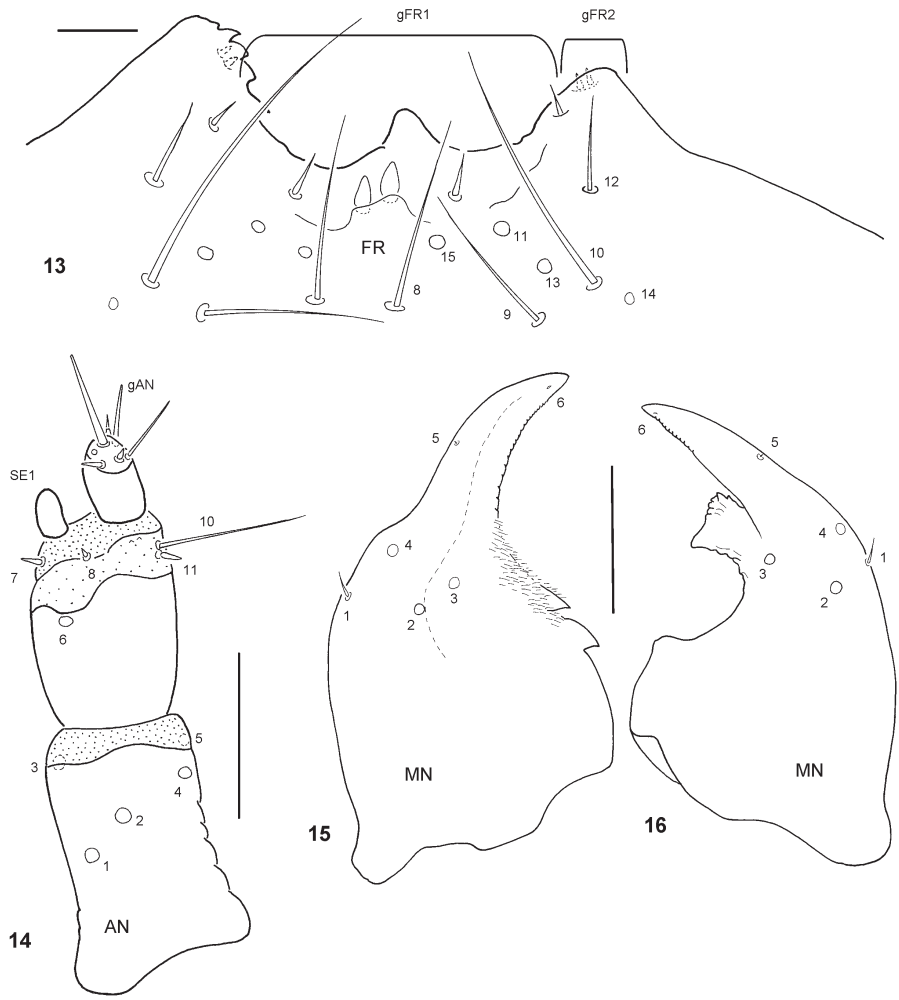
Chaetotaxy: Two innermost seta of gFR1 short and stout, placed on small lobe (Figs 7, 13); PA26+27+28 not closely aggregated (Fig. 12); seta AN9 absent (Fig. 14); inner margin of stipes with row of additional unifid setae (gMX2) (Fig. 17); pore LA8 located in a distal position (Fig. 19); with additional seta near LA10 (Fig. 19); sensilla LA11 and LA12 absent (Figs 19, 20). The illustrated specimen (Fig. 11) has an extra seta (PA?) near PA13, this seta is not present on the left side nor in any other examined specimens, therefore it is not considered an additional seta.

Primary chaetotaxy (Figs 11–22). *Head capsule* (Figs 11–13). Frontale with 30 sensilla: two very short setae on basal third, close to frontal lines (FR1); two pores (FR2) and two minute setae (FR3) close to midline on distal half; five pairs of setae (FR5 rather long, FR6 long, FR7 short, FR9 rather long, FR10 long) and two pairs of pores (FR4, FR14) close to base of each antenna; distal area of frontale with two pairs of setae (FR8 long, FR12 short) and three pairs of pores (FR11, FR13, FR15); nasale with six short setae (gFR1), middle two stouter and placed on a small lobe (Figs 7, 13), each epistomal lobe with two short anterior setae (gFR2). Each parietale with 31 sensilla. Dorsal surface with a basal longitudinal row of four very short setae (PA1, PA2, PA4, PA5) and one pore (PA3); one subbasal pore (PA6) close to frontal lines; three long setae (PA12, PA13, PA14) and one very short seta (PA7) arranged in a transverse row posterior to midlength; three long setae

Figs 1–10. 1–3 – habitus of the third instar larva of *Dactylosternum cacti* (LeConte, 1855) (1 – dorsal view; 2 – ventral view; 3 – lateroventral view). 4–6 – habitus of the third instar larva of *Phaenonotum exstriatum* (Say, 1835) (4 – dorsal view; 5 – ventral view; 6 – lateral view). 7 – middle setae of gFR1 of *Dactylosternum cacti*; 8 – branched setae on head capsule of *Phaenonotum exstriatum* (second instar larva); 9 – labium with hypopharyngeal lobe of *D. cacti* (third instar larva, ventral view); 10 – rows of spines and 'proleg' of *D. cacti* (third instar larva, ventral view). Scale bars: Figs 1–6 = 1 mm, Fig. 9 = 0.05 mm.

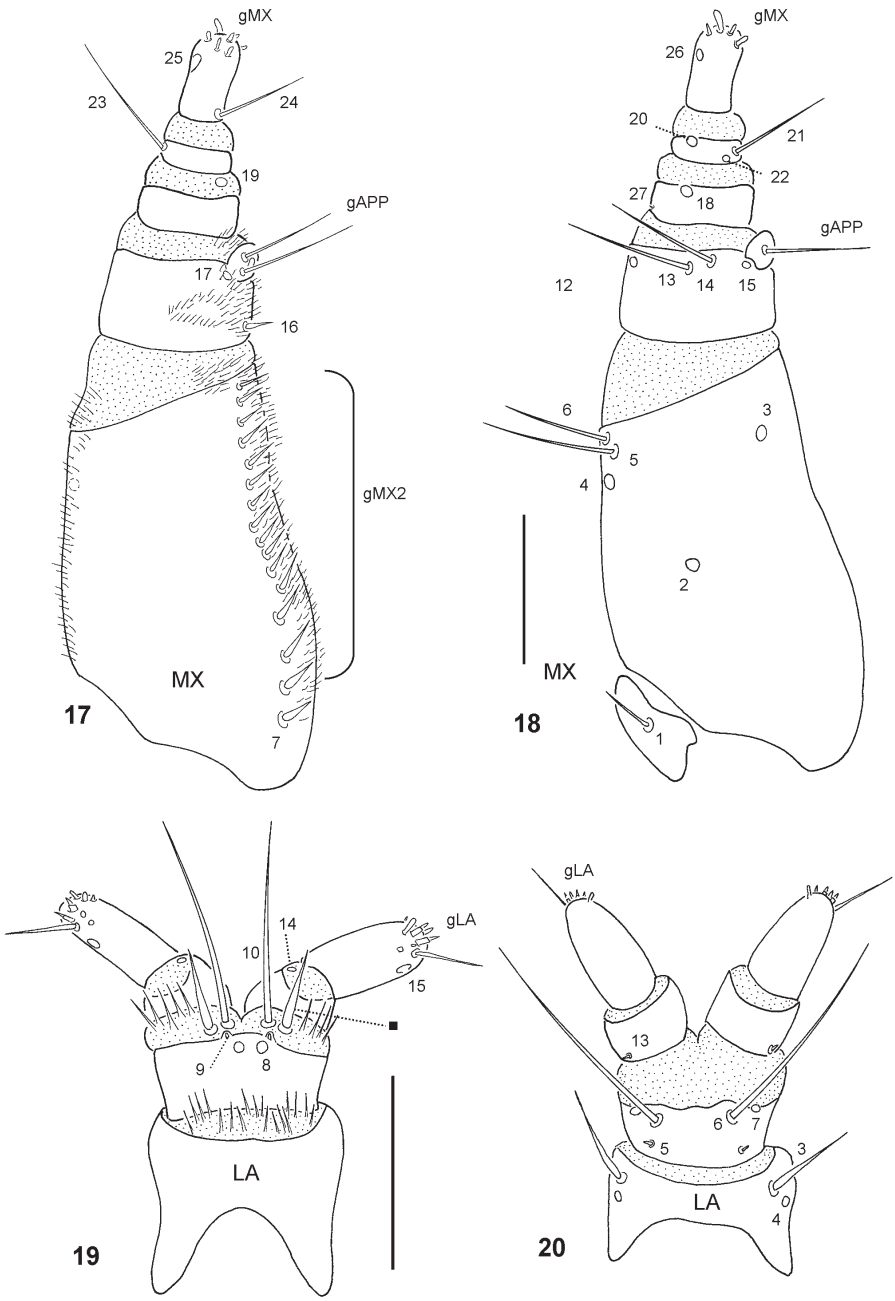


Figs 11–12. *Dactylosternum cacti* (LeConte, 1855), chaetotaxy of the head capsule of the first instar larva. 11 – dorsal view; 12 – ventral view. Scale bar = 0.1 mm.



Figs 13–16. *Dactylosternum cacti* (LeConte, 1855), chaetotaxy of first instar larva. 13 – detail of clypeolabrum; 14 – left antenna, dorsal view; 15 – left mandible, dorsal view; 16 – right mandible, dorsal view. Scale bars: Fig. 13 = 0.1 mm, Figs 14–16 = 0.05 mm.

(PA8, PA11 and PA14) and two pores (PA10, PA15) in a transverse row in the area surrounding the stemmata; three setae (PA9 long, PA20 short, PA21 long) and one pore (PA19) on anterolateral corner of head capsule. Ventral surface with three pores (PA23, PA24, PA25) and one rather long seta (PA22) on anterolateral corner, close to mandibular acetabulum; two long setae (PA16, PA18) and two pores (PA17, PA30) along outer margin; one short seta (PA26), one long seta (PA28), and two pores (PA27, PA29) forming a longitudinal row closer to midline.



Figs 17–20. *Dactylosternum cacti* (LeConte, 1855), chaetotaxy of first instar larva. 17 – left maxilla, dorsal view; 18 – maxilla, ventral view; 19 – labium, ventral view; 20 – labium, dorsal view. Scale bars = 0.05 mm.

Antenna (Fig. 14). A1 bare, with five pores, three dorsal on distal half (AN1 at midlength on outer margin, AN2 close to midline, AN4 distally on inner margin) and two ventral, on distal margin (AN3, AN5). A2 with one dorsal pore (AN6) on distal third, two short subapical setae (AN7 on outer margin, AN8 close to midline) close to base of SE1, and two subapical setae on inner margin (AN10 long, AN11 short); AN9 absent. A3 with a group of at least three short setae, three long setae and one pore (gAN).

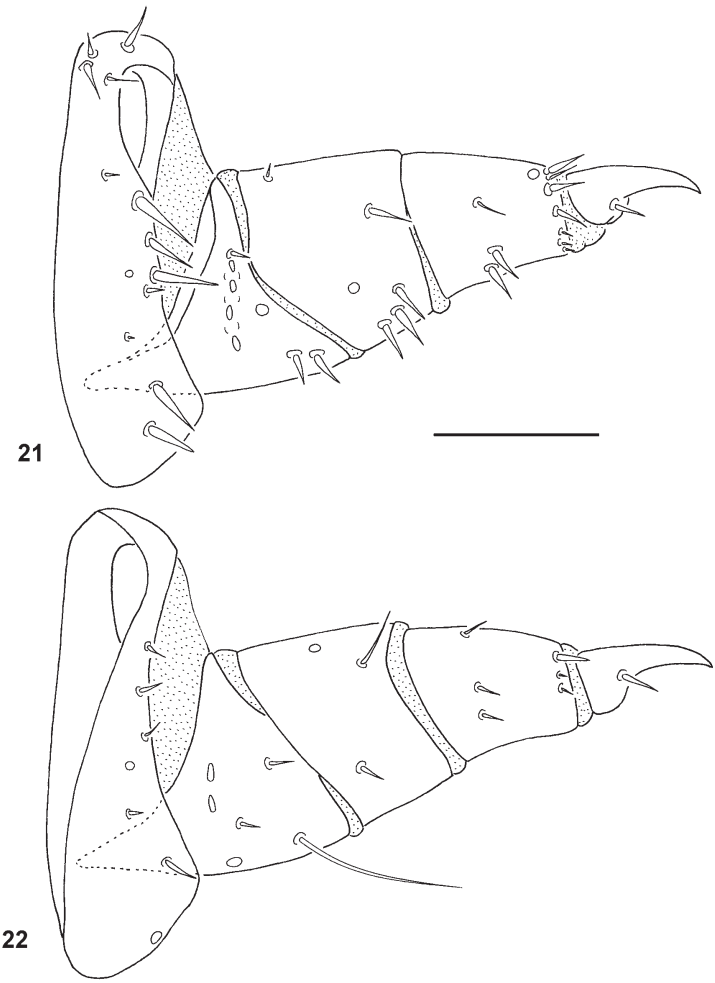
Mandibles (Figs 15–16). Both mandibles with six sensilla: one short seta on outer margin at midlength (MN1), one minute seta on outer margin at distal quarter (MN5), three dorsal pores at level of inner retinaculum (MN2, MN3, MN4); MN6 minute, difficult to see, located subapically close to inner margin.

Maxilla (Figs 17–18). Cardo with one rather long seta (MX1). Stipes with a row of ca. 16–17 stout and short setae along inner margin (gMX2), those at midlength closely aggregated, basal seta of that row likely homologous to MX7; ventral face of stipes with three pores, one at midlength (MX2), one subapical close to inner margin (MX3) and one subapical on outer margin (MX4); two long setae distal to pore MX4 (MX5, MX6). MP1 dorsally with one subbasal spiniform seta (MX16) on inner margin and one pore close to base of appendage (MX17); ventrally with two long subapical setae (MX13, MX14) and two pores (MX12 on outer margin, MX15 at base of appendage); inner appendage with three long setae and one short sensillum (gAPP). MP2 with two pores, one ventral and apical (MX18) and one dorsal on membrane connecting with MP3 (MX19); subbasal minute seta present on outer margin (MX27). MP3 with two long setae and two pores, one seta dorsal, on outer margin (MX23), the other ventral on mesal margin (MX21); both pores on ventral surface, one close to seta MX21 (MX22), the other apical, close to outer margin (MX20). MP4 with one long basal seta dorsally (MX24) on inner margin and two subapical pores on outer margin (MX25 digitiform and dorsal, MX26 ventral); a group of at least six or seven short setae constitute gMX.

Labium (Figs 12, 19–20). Submentum with two pairs of setae on anterior margin (Fig. 12), one long (LA1), the other minute (LA2). Mentum with two rather long setae (LA3) and two pores (LA4) on ventral surface close to anterolateral angle, LA3 anterior to LA4. Prementum ventrally with two pairs of setae (LA5 minute and basal, LA6 long and subapical) and one pair of subapical pores (LA7); dorsally with one apical pair of pores (LA8), one apical pair of minute seta-like sensilla (LA9) and two pairs of stout setae distally on membrane connecting with labial palpi, inner pair very long (LA10), outer pair additional (LA■). Sensilla associated with ligula absent (LA11, LA12). LP1 with one minute seta (LA13, ventral) and one distal pore (LA14, dorsal) on membrane connecting with LP2; LP2 with one subapical pore on outer face (LA15) and a group of at least five setae and two pores in the apex constitute (gLA), four setae short, one rather long.

Legs (Figs 21–22). The number and position of pores are the same in pro-, meso-, and metathoracic legs. Coxa with 3 pores (1 anterodorsal, 2 posterior) and 17 setae (12 anterior, 5 posterior); trochanter with 8 pores (5 anterior, 3 posterior) and 6 setae (3 anterior, 3 posterior); femur with 2 pores (1 anterior, 1 posterior) and 7 setae (5 anterior, 2 posterior); tibiotarsus with 1 anterior pore and 16 setae (10 anterior, 6 posterior); pretarsus with two subbasal setae (1 anterior, 1 posterior).

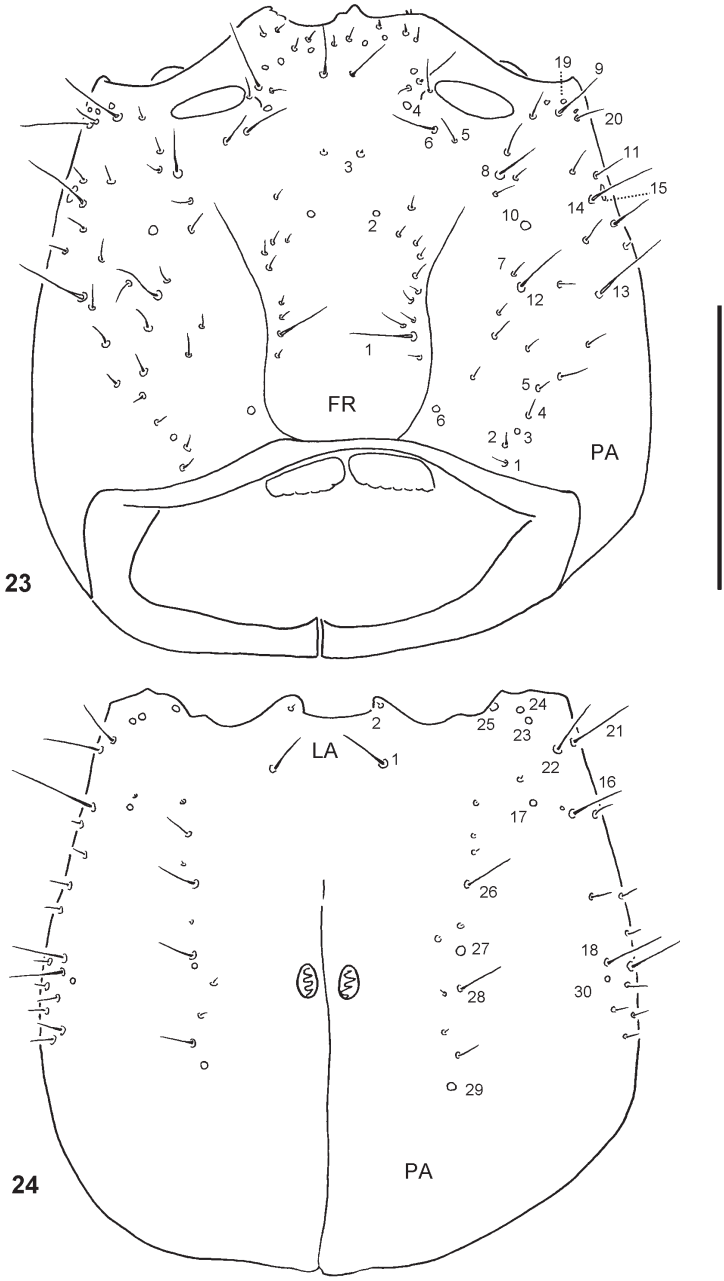
Morphometry. See Table 2.



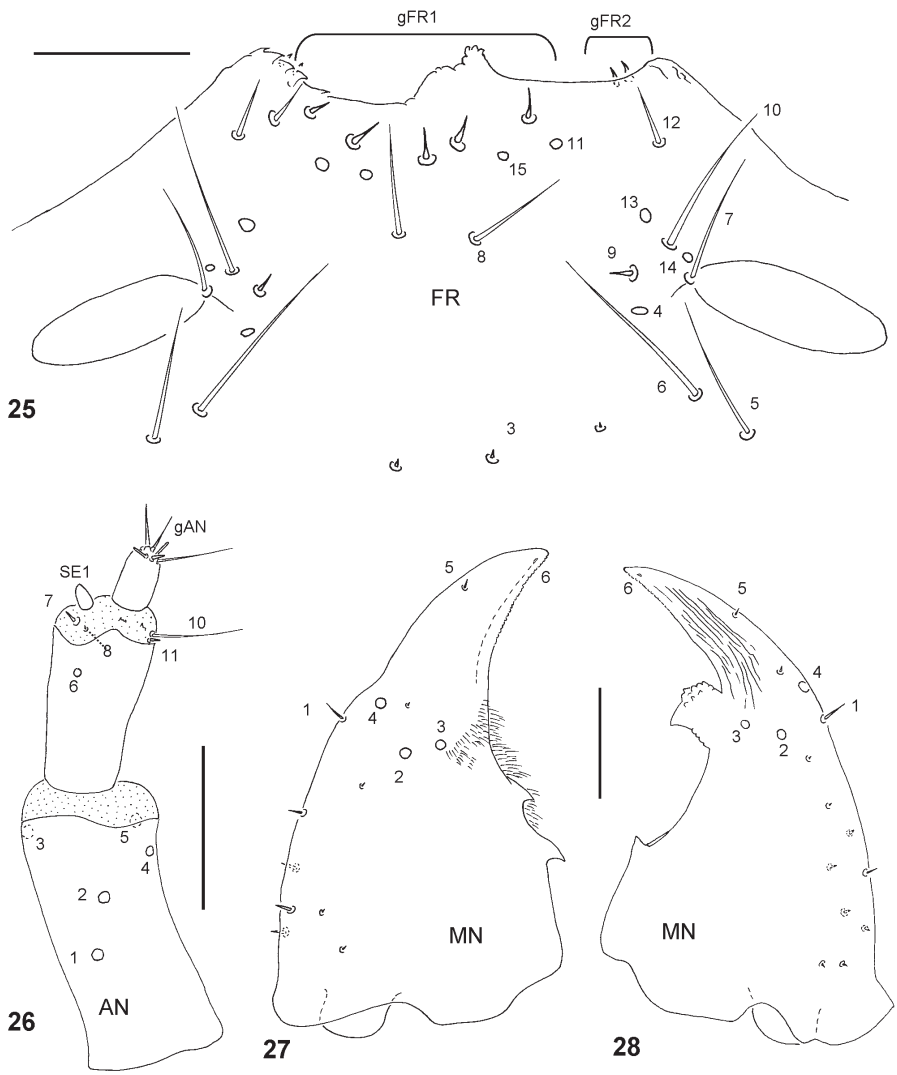
Figs 21–22. *Dactylosternum cacti* (LeConte, 1855), prothoracic leg of first instar larva. 21 – anterior view; 22 – posterior view. Scale bar = 0.05 mm.

Second instar larva. ***Chaetotaxy.*** More similar to the third instar than to the first. *Head capsule*. Frontale and parietale bearing several small secondary sensilla; middle setae of gFR1 not stout, lobe absent. *Antenna*. Without secondary sensilla; sensory appendage proportionally longer than in third instar. *Mandible.* With several minute secondary sensilla on outer face. *Maxilla*. With two or three minute secondary setae on ventral face of stipes, gMX2 with 17–18 setae, distal ones slightly longer and narrower than basal ones. *Labium*. Without secondary sensilla. Number and distribution of pores and setae in legs similar to first instar larva.

Morphometry. See Table 2.

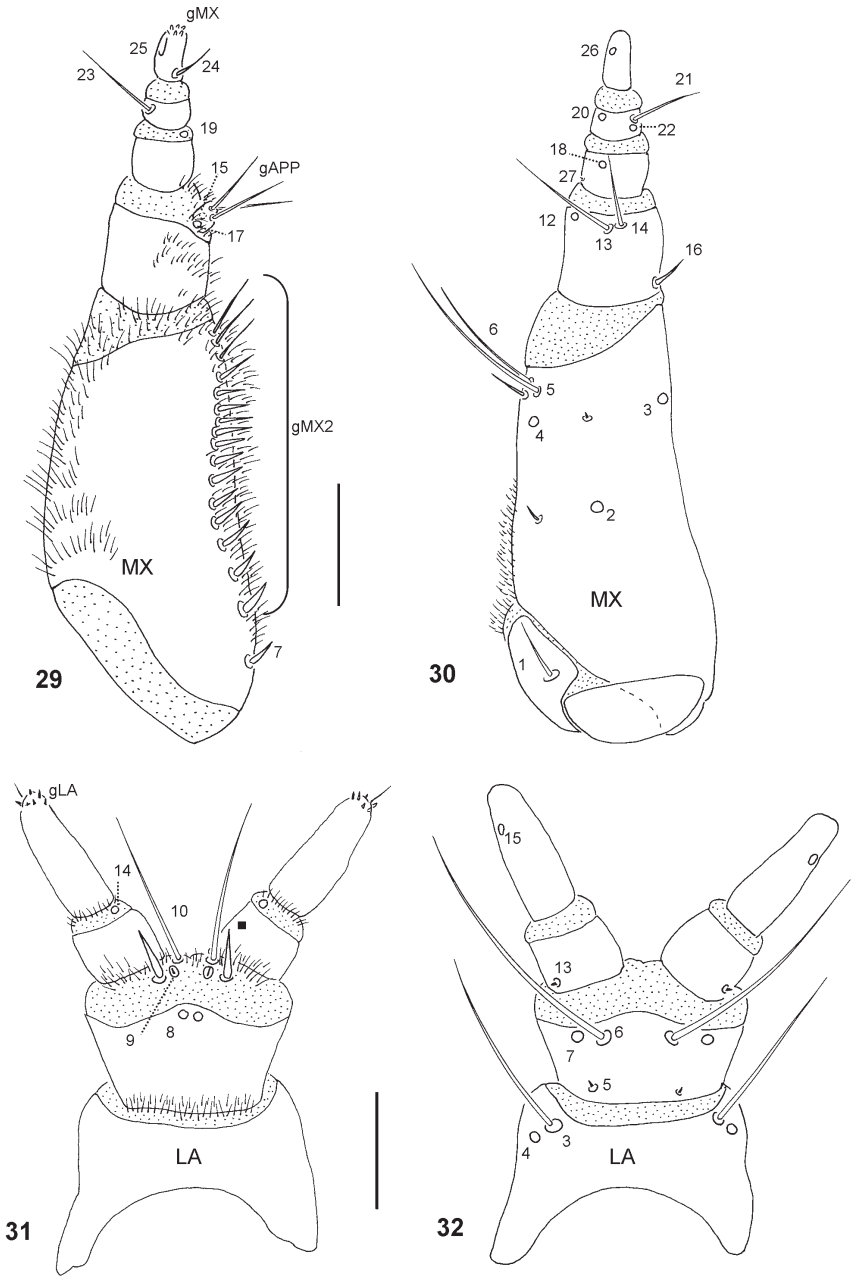


Figs 23–24. *Dactylosternum cacti* (LeConte, 1855), chaetotaxy of the head capsule of the third instar larva. 23 – dorsal view; 24 – ventral view. Scale bar = 0.5 mm.



Figs 25–28. *Dactylosternum cacti* (LeConte, 1855), chaetotaxy of third instar larva. 25 – detail of clypeolabrum; 26 – left antenna, dorsal view; 27 – left mandible, dorsal view; 28 – right mandible, dorsal view. Scale bars = 0.1 mm.

Third instar larva (Figs 23–32). ***Chaetotaxy.*** *Head capsule* (Figs 23–25). Frontale with eight to 10 secondary sensilla arranged in a row subparallel to each frontal line starting behind FR1 and extending slightly past pore FR2; a minute secondary seta present in some specimens between FR3 and FR6 (Fig. 25); middle setae of gFR1 not stout, lobe absent. Each parietale with 15 to 17 short secondary setae and one or two small secondary pores on dorsal surface; ventrally with 17 to 18 short or minute secondary setae and one secondary pore in



Figs 29–32. *Dactylosternum cacti* (LeConte, 1855), chaetotaxy of third instar larva. 29 – maxilla, dorsal view; 30 – maxilla, ventral view; 31 – labium, dorsal view; 32 – labium, ventral view. Scale bars: Figs 29–30 = 0.1 mm, Figs 31–32 = 0.05 mm.

some specimens. Posterior tentorial grooves at midlength, slightly more distally placed than in first instar larvae. *Antenna* (Fig. 26) without secondary sensilla, sensory appendage shorter, 0.42–0.50× as long as third antennomere. *Mandibles* (Figs 27–28). Each mandible with eight to nine short secondary setae, most of them on basal outer face. *Maxilla* (Figs 29–30).

Table 2. Measurements (in mm) and ratios for the three larval instars of *D. cacti* (LeConte, 1855) and *P. exstriatum* (Say, 1835). For abbreviations see Material and methods.

Measurement	*Dactylosternum cacti*			*Phaenonotum exstriatum*		
	Instar I	**Instar II**	**Instar III**	**Instar I**	**Instar II**	**Instar III**
TL	1.9–3.4	4.2–5.9	6.7–8.5	2.3–3.8	3.6–5.4	5.5–7.5
MW	0.6–0.7	1.0–1.1	1.3–1.6	0.5–0.6	0.7–0.8	0.9–1.1
HL	0.27–0.28	0.44–0.46	0.65–0.70	0.21–0.22	0.28–0.30	0.35–0.39
HW	0.37–0.38	0.60	0.71–0.81	0.25–0.26	0.36–0.38	0.45–0.50
HL/HW	0.72–0.75	0.73–0.77	0.80–0.99	0.84–0.86	0.77–0.80	0.78
AL	0.15–0.16	0.21–0.22	0.32–0.34	0.11	0.14	0.16
A1L	0.07	0.10–0.11	0.16–0.18	0.06	0.08	0.09
A2L	0.04	0.06–0.07	0.10–0.11	0.03	0.03	0.04
A3L	0.03	0.03–0.04	0.04–0.05	0.03	0.03	0.03–0.04
SEL	0.02	0.02	0.02	0.02–0.03	0.03	0.03
SEL/A3L	0.55–0.63	0.46–0.47	0.42–0.50	0.90–1.00	0.79–0.87	0.88–0.91
A1L/A2L	1.67–1.70	1.58–1.59	1.48–1.70	2.32–2.52	2.42–2.52	2.20–2.51
A1L/(A2L+A3L)	1.01–1.03	1.01–1.04	1.05–1.23	1.14–1.26	1.19–1.22	1.21–1.31
HL/AL	1.69–1.82	2.06–2.09	1.94–2.09	1.93–1.98	2.03–2.17	2.13–2.38
HW/AL	2.08–2.48	2.69–2.84	2.08–2.52	2.30–2.31	2.62–2.73	2.74–3.05
SL	0.13–0.14	0.18–0.20	0.30–0.33	0.12–0.13	0.16–0.17	0.20–0.21
MPL	0.08	0.12	0.15–0.16	0.05–0.06	0.06–0–07	0.07–0.08
SL/MPL	1.62–69	1.69–1.74	1.81–2.20	2.20–2.36	2.51–2.58	2.65–2.81
MP1L	0.03–0.04	0.05	0.07–0.08	0.02	0.02	0.02–0.03
MP2L	0.01–0.02	0.02–0.03	0.03	0.01	0.01	0.01
MP3L	0.01	0.01–0.02	0.02	0.01	0.01	0.01
MP4L	0.02–0.03	0.03	0.04	0.02	0.02–0.03	0.03
ML	0.21–0.22	0.32	0.46–0.48	0.18–0.19	0.23	0.28–0.29
LPL	0.04–0.05	0.06–0.07	0.10–0.11	0.03–0.04	0.04	0.06
LP1L	0.01–0.02	0.01–0.02	0.03	0.01	0.01	0.02
LP2L	0.03	0.05	0.07–0.08	0.03	0.03	0.04
LP2L/LP1L	2.20–2.39	3.33–3.50	2.79–3.00	3.22–3.86	2.91–3.30	2.35–2.87
LigL	N/A	N/A	N/A	0.02	0.02	0.03
LigL/LPL	N/A	N/A	N/A	0.45–0.56	0.47–0.53	0.52–0.53
MtW	0.05	0.08	0.10–0.11	0.04–0.05	0.05	0.10
PrmtW	0.04	0.06	0.09–0.10	0.03–0.04	0.04	0.05
PrmtL	0.02	0.03	0.05–0.06	0.02	0.02	0.03
PrmtW/PrmtL	1.96–2.21	2.03	1.69–1.94	1.94–2.25	2.00–2.28	1.80
PrmtW/MtW	0.83–0.87	0.80	0.90–0.91	0.74–0.78	0.77–0.79	0.56
LEG 1 L	0.31	0.44–0.47	0.65	0.25–0.28	0.33–0.34	0.46
LEG 2 L	0.30	0.41–0.47	0.64–0.66	0.26–0.28	0.32–0.34	0.44
LEG 3 L	0.29–0.30	0.43–0.45	0.64	0.26–0.28	0.32–0.34	0.43
LEG 3/LEG 1	0.93–0.99	0.91–1.01	0.98–0.99	0.99–1.04	0.95–1.00	0.94
LEG 3/LEG 2	0.96–1.00	0.96–1.08	0.98–0.99	0.97–1.03	0.98–1.01	0.99
LEG 1 (CO/FE)	2.26–2.60	2.81–2.86	2.63–2.81	1.66–2.00	1.93–2.12	1.84–1.94
LEG 2 (CO/FE)	2.23–2.67	2.65–3.00	2.72–2.80	2.00–2.25	2.06–2.50	2.15
LEG 3 (CO/FE)	2.40–2.67	2.71–3.14	2.68–2.72	2.04–2.25	2.08–2.30	1.95–2.09
LEG 1 (TITA/FE)	0.90–1.00	0.83–0.90	0.78–0.81	0.66–0.76	0.66–0.77	0.61–0.66
LEG 2 (TITA/FE)	0.81–1.07	0.85–0.92	0.88–0.92	0.80–0.90	0.84–0.86	0.68
LEG 3 (TITA/FE)	0.94–1.07	0.86–1.03	0.88–0.92	0.83–1.00	0.88–0.91	0.72–0.74
LEG 1 (CL/TITA)	0.78–0.89	0.74–0.79	0.76–0.81	0.70–0.87	0.69–0.78	0.66–0.67
LEG 2 (CL/TITA)	0.79–0.89	0.75–0.88	0.77–0.78	0.83–0.95	0.70–0.76	0.74
LEG 3 (CL/TITA)	0.83–0.89	0.71–0.77	0.74–0.86	0.83–1.00	0.72–0.76	0.74–0.76

Stipes with three secondary setae on ventral face, one very short close to outer margin, one minute at midlength between MX3 and MX4, and one short on outer margin close to MX5 and MX6; inner row of setae on stipes with ca. 18–19 setae (gMX2), distal ones longer and more slender, basal one slightly apart from others, probably homologous to MX7. *Labium* (Figs 31–32) without secondary sensilla. Number and distribution of pores and setae in legs similar to first instar larva.

Morphometry. See Table 2.

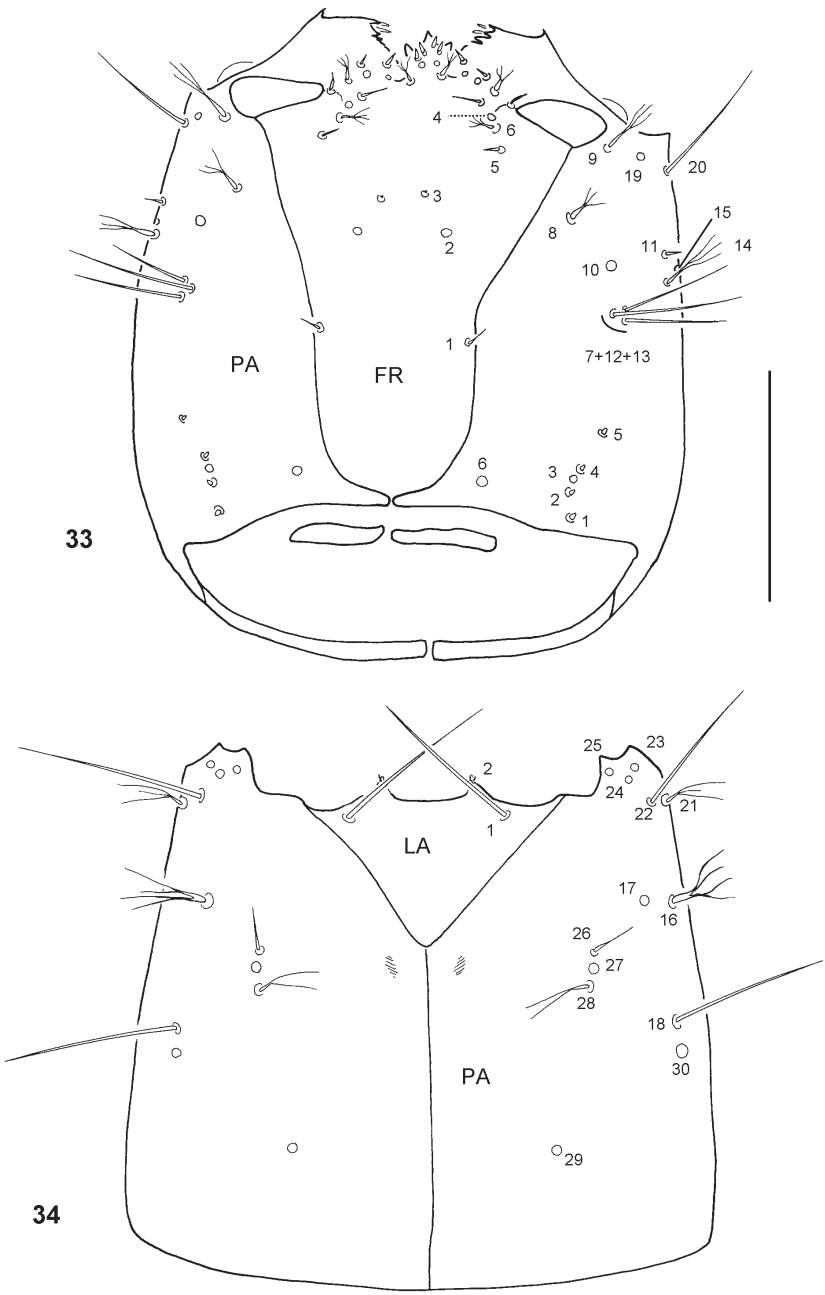
Phaenonotum exstriatum (Say, 1835)

Examined larvae. Seven L1, four L2 and seven L3 reared from the adults collected in the following locality: **USA: Oklahoma:** Latimer Co., vi.1990, K. Stephan lgt. Adults and larvae were reared in laboratory and the complete life cycle was obtained (Archangelsky & Durand 1992).

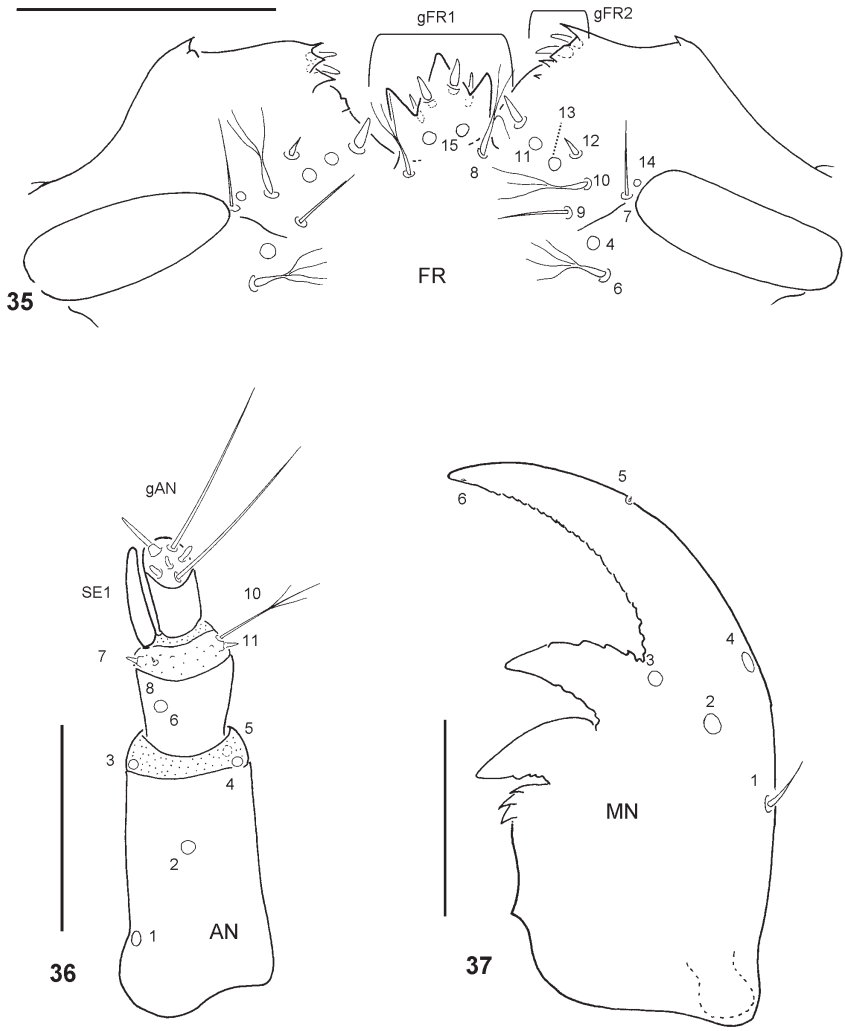
First instar larva (Figs 33–43). ***Diagnosis.*** Head capsule subquadrate to slightly suboval; frontal lines inversely bell-shaped, merging just before occipital foramen, coronal line present, extremely short (Fig. 33); clypeolabrum symmetrical, bearing three short teeth, middle one projecting farther than lateral ones (Figs 33, 35); lateral lobes of epistome almost symmetrical, projecting farther than nasale, slightly serrated on inner margin, with a sharp short spine on outer angle pointing mediad (Figs 33, 35); posterior tentorial grooves close to midline, past midlength, just behind submentum (Fig. 34). Cervical sclerites present, narrow and elongate (Fig. 33). Antenna short (Fig 36), basal antennomere the longest, sensory appendage as long as third antennomere. Mandibles symmetrical (Fig. 37), with two inner teeth and inner border serrated. Maxilla (Figs 38, 39) with large stipes, longer than palpus, with strong cuticular spines on outer face dorsally and an apical stout and sharp projection on inner margin; first and fourth palpomeres subequal in length, longer than second and third. Labium with submentum fused to head capsule, subtriangular; mentum slightly wider than prementum, with strong cuticular spines dorsally (Fig. 40); basal palpomere the shortest, membranous area at base of both palpomeres with sharp cuticular spines; ligula twice as long as first palpomere (Figs 40, 41). Pronotal plate large, covering most of pronotum; those of meso- and metathorax shorter (see Figs 4, 6, third instar larva). First abdominal segment dorsally with a pair of narrow, poorly sclerotized sclerites (Figs 4, 6, third instar larva); dorsal plate on abdominal segment eight subdivided (Fig. 4, third instar larva); abdominal segments two to seven ventrally not strongly lobed (Figs 5, 6, third instar larva), with two rows of short spines but not "prolegs"; legs short, five-segmented (Figs 42, 43).

Chaetotaxy. Setae PA8, PA9, PA14, PA16, PA21, PA28, FR6, FR10, FR8 and AN10 branched (as in Fig 8); setae PA7, PA12, PA13 closely aggregated; seta AN9 absent; inner margin of stipes with row of additional bifid setae (gMX2).

Primary chaetotaxy (Figs 33–43). *Head capsule* (Figs 33–35). Frontale with 30 sensilla: two short setae on basal third, close to frontal lines (FR1); two pores (FR2) and two minute setae (FR3) closer to midline on distal half; five pairs of setae (FR5 short, FR6 short and branched, FR7 short, FR9 short, FR10 short and branched) and two pairs of pores (FR4, FR14) close to base of each antenna; distal area of frontale with two pairs of setae (FR8 short and branched, FR12 very short) and three pairs of pores (FR11, FR13, FR15); nasale with six short and stout setae (gFR1), each epistomal lobe with two anterior setae pointing mediad

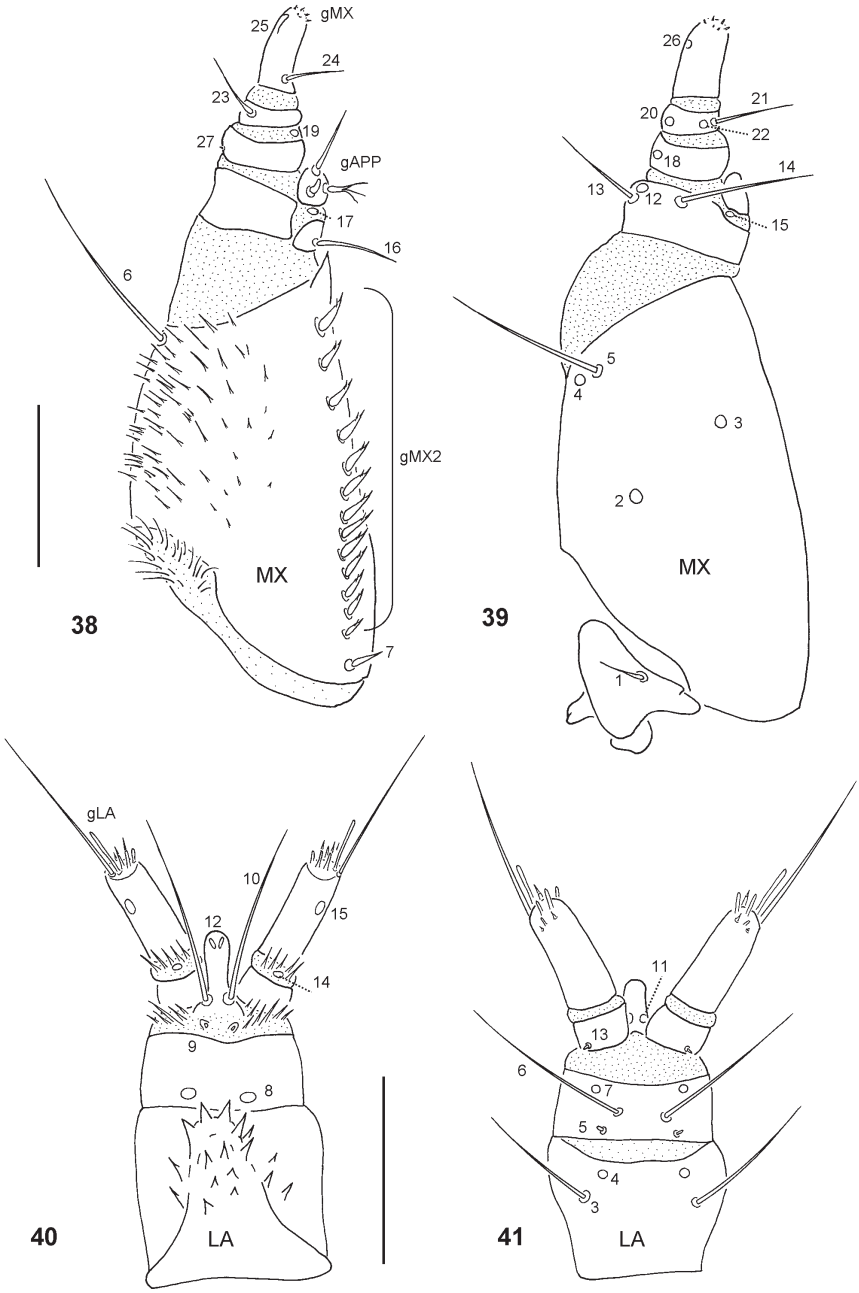


Figs 33–34. *Phaenonotum exstriatum* (Say, 1835), chaetotaxy of the head capsule of the first instar larva. 33 – dorsal view; 34 – ventral view. Scale bar = 0.1 mm.



Figs 35–37. *Phaenonotum exstriatum* (Say, 1835), chaetotaxy of first instar larva. 35 – detail of clypeolabrum; 36 – left antenna, dorsal view; 37 – right mandible, dorsal view. Scale bars = 0.05 mm.

(gFR2). Each parietale with 30 sensilla. Dorsal surface: with a basal longitudinal row of four very short setae (PA1, PA2, PA4, PA5) and one pore (PA3); one subbasal pore (PA6) close to frontal line; three closely aggregated long setae at midlength (PA7, PA12, PA13); two pores (PA10, PA15) and two setae at distal third (PA11 short, PA14 rather long and branched) in the area surrounding the stemmata; one short branched seta close to frontal line behind antennal socket (PA8) and one pore (PA19) and three setae on anterolateral corner of head capsule (PA9 rather long and branched, PA20 long, and PA21 rather long and branched). Ventral sur-



Figs 38–41. *Phaenonotum exstriatum* (Say, 1835), chaetotaxy of first instar larva. 38–39 – maxilla (38– dorsal view; 39 – ventral view). 40–41 – labium (40 – dorsal view; 41 – labium, ventral view). Scale bars = 0.05 mm.

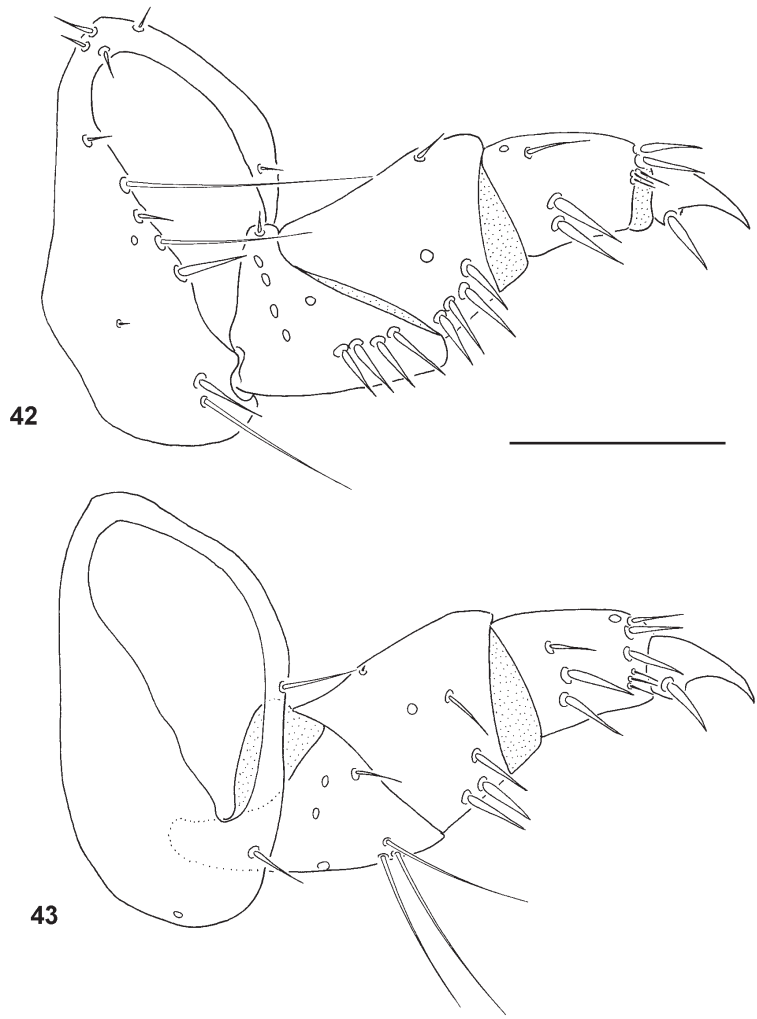
face with three pores (PA23, PA24, PA25) and one long seta (PA22) on anterolateral corner, close to mandibular acetabulum; two pores (PA17, PA30) and two setae (PA16 rather long and branched, PA18 long) along outer margin; two pores (PA27, PA29) and two setae (PA26 short, PA 28 rather long and branched) forming a longitudinal row closer to midline, PA26, PA27 and PA28 very close together at about midlength, PA29 at basal fourth.

Antenna (Fig. 36). A1 bare, with five pores, four on dorsal face (AN1 basal on outer margin, AN2 at midlength, AN3 distally on outer margin, AN4 distally on inner margin) and one on ventral face (AN5 on inner distal margin). A2 with one dorsal pore (AN6) on distal half, two subapical setae (AN7 short, AN8 minute) on outer margin close to base of SE1, and two subapical setae on inner margin (AN10 long and branched, AN11 short); AN9 absent. A3 with a group of at least six setae (two long, one short and three very short).

Mandible (Fig. 37) with six sensilla, one short seta on outer face at basal third (MN1), one minute seta on outer margin at distal quarter (MN5), and three dorsal pores at level of distal retinaculum (MN2, MN3, MN4). MN6 minute, difficult to see, located subapically close to inner margin.

Maxilla (Figs 38–39). Cardo with one rather long seta (MX1). Stipes with a row of 14 short and stout setae, distal 13 (gMX2) bearing a subapical spine and separated by a longer distance, becoming closer to each other basally, basal seta simple (homologous to MX7) slightly more distant from others; apical outer face of stipes with two long setae (MX6 dorsal, MX5 ventral) and one pore (MX4 ventral); ventral face with two pores (MX2 at midlength closer to outer margin, MX3 more distally and closer to inner margin). MP1 dorsally with one subbasal rather long seta (MX16) on inner margin and one pore close to base of appendage (MX17); ventrally with two long subapical setae (MX13, MX14) and two pores (MX12 on outer margin, MX15 at base of appendage); inner appendage with at least three sensoria (gAPP, one rather long seta, one short branched seta, one short stout seta). MP2 with two pores, one dorsal and apical on inner margin (MX19) and one ventral on outer margin (MX18), and one minute seta basally on outer margin (MX 27). MP3 with two rather long setae and two pores, one seta dorsal, on outer margin (MX23), the other ventral on inner margin (MX21); both pores on ventral surface, one close to outer margin (MX20) the other (MX22) close to seta MX21. MP4 with one rather long basal seta dorsally on inner margin (MX24) and two subapical pores on outer margin (MX25 digitiform and dorsal, MX26 ventral); a group of six or seven short setae constitute gMX.

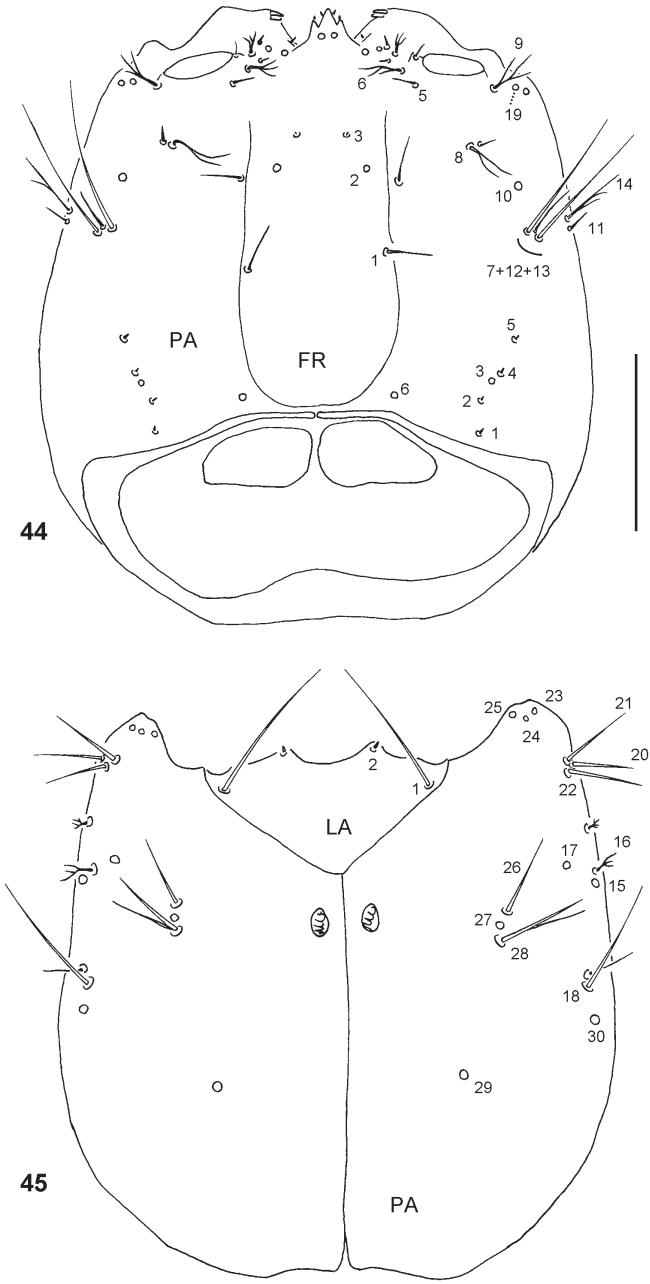
Labium (Figs 34, 40–41). Submentum with two pairs of setae on anterior margin (Fig. 34), one long (LA1), the other minute (LA2). Mentum with two long setae (LA3) and two pores (LA4) on ventral surface, LA4 close to anterior margin, anterior to LA3. Prementum ventrally with two pairs of setae (LA5 minute and basal, LA6 long at midlength) and one pair of subapical pores (LA7); dorsally with one basal pair of pores (LA8) and one pair of minute seta-like sensilla (LA9) on membrane connecting with labial palpi and ligula. Ligula with one pair of long setae at the base (LA10) and two pairs of sensilla (LA12 cone-like, apical on dorsal face and LA11 pore-like, at midlength on ventral face). LP1 with one minute seta (LA13, ventral) and one distal pore (LA14 dorsal) on membrane connecting with LP2; LP2 with one subapical pore on outer face (LA15) and a group of at least nine setae at the apex constitute gLA, three setae minute, four setae short, one rather long and one long seta.



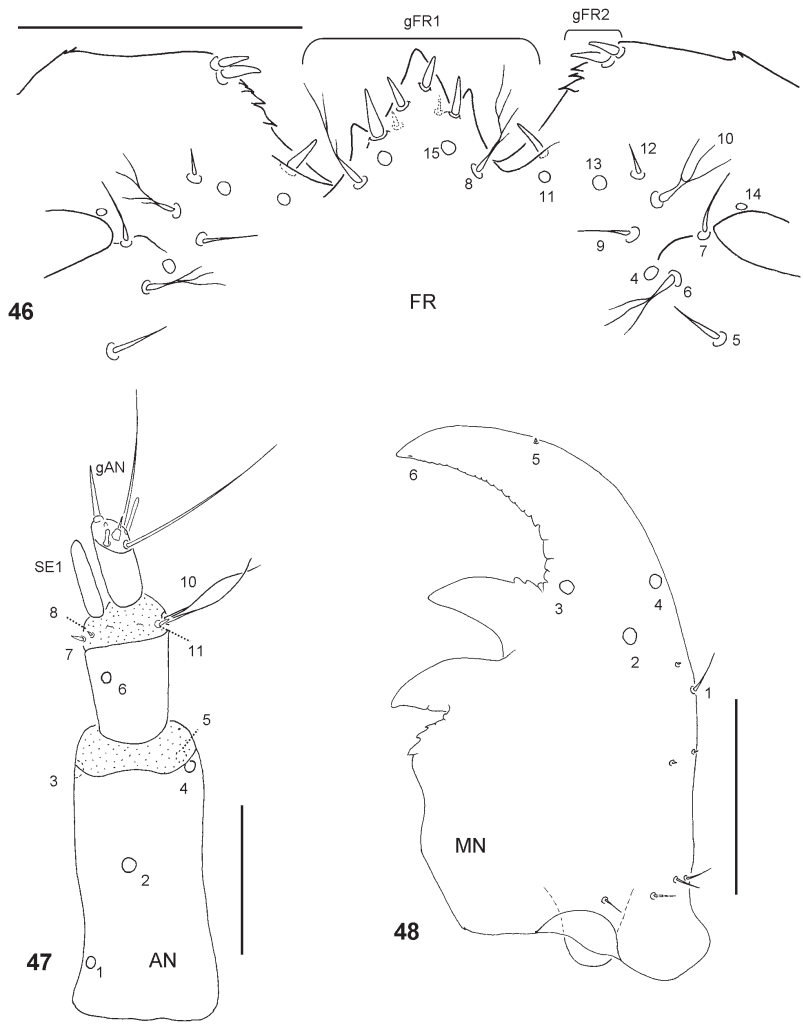
Figs 42–43. *Phaenonotum exstriatum* (Say, 1835), prothoracic leg of first instar larva. 42 – anterior view; 43 – posterior view. Scale bar = 0.05 mm.

Legs (Figs 42–43). The number and position of pores are the same in pro-, meso-, and metathoracic legs. Coxa with 2 pores (1 anterodorsal, 1 posterior) and 14 setae (12 anterior, 2 posterior); trochanter with 8 pores (5 anterior, 3 posterior) and 9 setae (5 anterior, 4 posterior); femur with 2 pores (1 anterior, 1 posterior) and 10 setae (5 anterior, 5 posterior); tibiotarsus with 2 pores (1 anterior, 1 posterior) and 17 setae (8 anterior, 9 posterior); pretarsus with two setae (1 anterior, 1 posterior).

Morphometry. See Table 2.

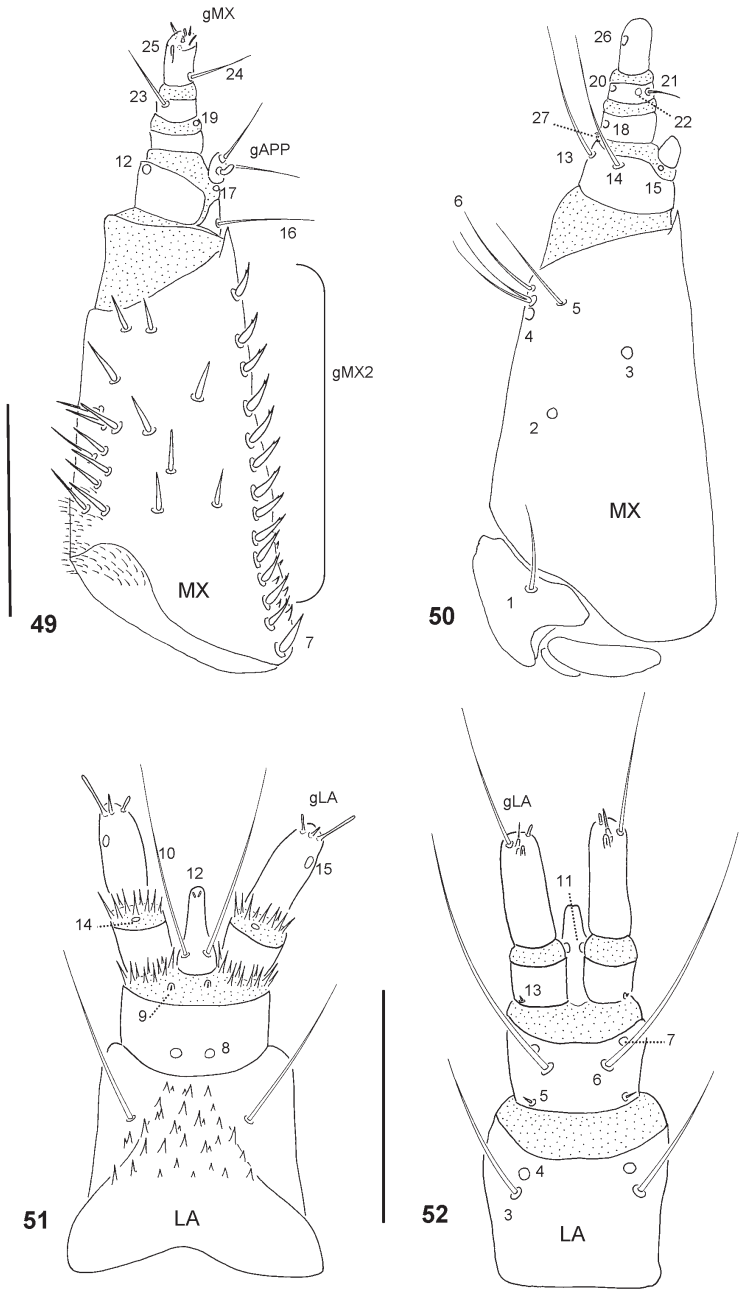


Figs 44–45. *Phaenonotum exstriatum* (Say, 1835), chaetotaxy of the head capsule of the third instar larva. 44 – dorsal view; 45 – ventral view. Scale bar = 0.2 mm.



Figs 46–48. *Phaenonotum exstriatum* (Say, 1835), chaetotaxy of third instar larva. 46 – detail of clypeolabrum; 47 – left antenna, dorsal view; 48 – right mandible, dorsal view. Scale bars: Figs 46, 48 = 0.1 mm, Fig. 47 = 0.05 mm.

Second instar larva. ***Chaetotaxy*** more similar to the third instar than to the first. *Head capsule*. Frontale lacking secondary setae; parietale bearing four small secondary sensilla in similar positions than those of third instar (except for the one close to the frontal line that is absent). *Antenna*. Without secondary sensilla. *Mandible* with five or six short secondary sensilla on outer face. *Maxilla*. Stipes with 12–13 stout secondary setae on dorsal surface and one branched ventral secondary seta close to MX4 and MX6; gMX2 with ca. 13 setae. *Labium*. Mentum with one pair of long secondary setae dorsally on distal half. Number and distribution of pores and setae in legs similar to first instar larva.



Figs 49–52. *Phaenonotum exstriatum* (Say, 1835), chaetotaxy of third instar larva. 49–50 – maxilla (49 – dorsal view; 50 – ventral view); 51–52 – labium (51 – dorsal view; 52 – ventral view). Scale bars = 0.1 mm.

Morphometry. See Table 2.

Third instar larva (Figs 44–52). Lateral lobes of epistome projecting slightly farther than nasale, slightly serrated on inner margin but with spine on outer angle much smaller.

Chaetotaxy. *Head capsule* (Figs 44–46). Frontale without secondary sensilla. Parietale with five secondary sensilla, one ventral seta close to PA18, one dorsal pore near PA19 and two dorsal setae, one close to PA8, the other close to frontal line, near pore FR2; PA21 apparently simple in examined specimens (branched in first and second instars). *Antenna* (Fig. 47) without secondary sensilla. *Mandible* (Fig. 48) with four short basal secondary setae close to outer face, and three or four minute secondary setae close to MN1. *Maxilla* (Figs 49–50). Stipes with ca. 17 stout secondary setae on dorsal surface and one branched ventral secondary seta between pore MX4 and seta MX6; gMX2 with 13–14 setae. *Labium* (Figs 51–52). Mentum with one pair of long secondary setae dorsally on distal half. Number and distribution of pores and setae in legs similar to first instar larva.

Morphometry. See Table 2.

Discussion

A morphological comparative analysis among the known Coelostomatini larvae has been presented by Clarkson et al. (2014). In addition to the characters discussed by Clarkson et al. (2014) we have found several additional characters that deserve to be mentioned (all summarized in Table 3). The first character is the relative size of the antennal sensorium when compared to the third antennomere; in all known *Dactylosternum* larvae this sensorium is clearly shorter than the third antennomere; in the remaining genera (*Coelostoma*, *Hydroglobus*, *Lachnodacnum* and *Phaenonotum*) the sensorium is subequal to the third antennomere. The degree of fusion of the submentum is also informative, in *Dactylosternum cacti* it is strongly fused, and the lines of fusion have been lost; in *Dactylosternum subrotundum*, one unidentified species of *Dactylosternum* (*Dactylosternum* B in Archangelsky 1997), *Coelostoma*, *Hydroglobus*, *Lachnodacnum* and *Phaenonotum* it is fused to the head capsule, but the lines separating both structures are distinctly visible. Another character from the labium is the presence of strong cuticular spines on the dorsal face of the mentum, which are present in *Dactylosternum* B, *Dactylosternum subrotundum*, *Lachnodacnum* and *Phaenonotum*; but are absent in *Coelostoma orbiculare*, *Dactylosternum cacti* and *Hydroglobus*. Finally, the presence of a pubescent left hypopharyngeal lobe in *Dactylosternum cacti* and *Dactylosternum* B should be mentioned; this lobe is absent in the remaining species (in *Dactylosternum abdominale* the state of this character is not known).

While considering probable chaetotaxic characters, Clarkson et al. (2014) mentioned as a possible synapomorphy of Coelostomatini the closely aggregated setae PA7+12+13, they compared this character only between *Coelostoma orbiculare* and *Lachnodacnum luederwaldti*, the only larvae with known chaetotaxy at the time. This character is also present in *Phaenonotum exstriatum* (Figs 33, 44), but in *Dactylosternum cacti*, even though PA7 and PA12 are close to each other, PA13 is far from these two setae (Figs 11, 23). It is worth mentioning that larvae of *Horelophopsis* Hansen, 1997 and *Agraphydrus* Régimbart, 1903, also show setae PA7+12+13 closely aggregated, but this is probably a convergence since both genera, closely related, belong to the subfamily Acidocerinae (Minoshima & Hayashi 2011,

Table 3. Comparative table of morphological characters of third instar larvae of Coelostomatini.

	Coelostoma orbiculare	*Dactylosternum abdominale*	*Dactylosternum cacti*	*Dactylosternum subrotundum*	*Dactylosternum* sp.	*Hydroglobus puncticollis*	*Lachnodacnum luederwaldti*	*Phaenonotum exstriatum*
Head capsule	not depressed	not depressed	not depressed	not depressed	not depressed	not depressed	depressed	not depressed
Teeth on nasale	one tooth	one tooth?	one tooth	3 teeth[2]	3 teeth	one tooth	3 teeth	3 teeth
Epistomal lobes	symmetrical	symmetrical	asymmetrical	asymmetrical	asymmetrical	symmetrical	symmetrical	symmetrical
Antennal sensorium[1]	subequal to A3	shorter than A3	shorter than A3	shorter than A3	shorter than A3	subequal to A3	subequal to A3	subequal to A3
Mandibles	symmetrical	asymmetrical	asymmetrical	subsymmetrical	subsymmetrical	symmetrical	symmetrical	symmetrical
Submentum[1]	defined	defined?	completely fused	defined	defined	defined	defined	defined
Cuticular spines on mentum[1]	absent	?	absent	present	present	absent	present	present
Ligula	present	?	reduced	present	present	present	present	present
Hypopharyngeal lobe[1]	absent	?	present	absent	present	absent	absent	absent
Tergite VIII	subdivided	entire	entire	entire	entire	entire	subdivided	subdivided

[1] Characters not discussed by Clarkson et al. (2014).
[2] In the illustrations of *D. subrotundum* the nasale appears as slightly asymmetrical (Costa et al. 1998), with two well defined teeth on the right and a minute tooth on the left.

Minoshima et al. 2013). A similar distribution of character states is seen ventrally in the parietale; PA26+27+28 are closely aggregated in *Coelostoma orbiculare*, *Phaenonotum exstriatum* (Figs 34, 45) and *Lachnodacnum luederwaldti*, but in *Dactylosternum cacti* these setae are not closely aggregated (Figs 12, 24). One character shared by *Coelostoma*, *Dactylosternum* and *Phaenonotum* is the absence of AN9; according to Clarkson et al. (2014) in first instar larvae of *Lachnodacnum*, they could not confirm the presence of AN9, therefore they highlighted its probable presence with a "?"; while in third instars it is clearly present and is properly illustrated and labelled. The absence of AN9 is also seen in other sphaeridiines (e.g. *Cercyon* larvae), so its absence could be a common situation within Sphaeridiinae. The prementum of *Dactylosternum cacti* has pore LA8 situated in a distal position (Figs 20, 31) while in the remaining genera LA8 is basal (e.g. *Phaenonotum exstriatum*, Figs 40, 51). The above mentioned chaetotaxic characters group the genera *Coelostoma*, *Lachnodacnum* and *Phaenonotum*, leaving *Dactylosternum* apart. Nevertheless, several other chaetotaxic characters show a different distribution. *Phaenonotum exstriatum*, *Lachnodacnum* and also *Coelostoma* (M. Fikáček, personal communication, also see Böving & Henriksen 1938: Fig. 18) third instar larvae have many secondary setae on the dorsolateral area of the stipes (Fig. 49), this fact was already noted by Clarkson et al. (2014); these setae are not present in third instar larvae of *Dactylosternum cacti* (Fig. 29). This seems to be a transformation series since first instar larvae have short cuticular projections that become longer in second instar larvae, becoming articulated setae in the third instar (Clarkson et al. 2014).

One character state shared by *Phaenonotum exstriatum* and *Coelostoma orbiculare* are the bifid setae present in gMX2 (except for MX7 that is simple); nonetheless, this character state should be considered with care since it is common within Hydrophilidae and is present in genera belonging to other subfamilies (e.g. *Agraphydrus*, *Enochrus* Thomson, 1859, *Helochares* Mulsant, 1844, *Paracymus* Thomson, 1867) (Archangelsky 1997, Minoshima & Hayashi 2011). *Dactylosternum cacti* and *Lachnodacnum luederwaldti* have simple setae in gMX2. *Phaenonotum exstriatum* has several branched setae in the head capsule (Figs 8, 33, 34), something not shared with the other three genera (this could be an autapomorphy of *Phaenonotum* larvae). Associated to the reduction of the ligula in *Dactylosternum cacti*, we have the loss of pore-like sensilla LA11 and LA12; these sensilla are present in the other known coelostomatine larvae. Finally, an interesting character state unique of *Dactylosternum cacti* is the shape of the two innermost setae of gFR1 (in first instar larvae), which are short and stout (Figs 7, 13), and are placed on a small lobe, these setae are slender in second and third instar larvae. These setae could represent egg-bursters and if that is their function, this is the first time they are mentioned for Coelostomatini larvae. Within Hydrophilidae egg-bursters have been reported for larvae of the tribes Sphaeridiini and Megasternini (Fikáček 2006, unpublished, personal observations by M. Archangelsky); the only difference is that the egg-bursters of Megasternini and Sphaeridiini are sharp, triangular cuticular projections, while those of *Dactylosternum cacti* are short and stout setae). Besides the presence of egg-bursters, larvae of *Dactylosternum cacti* share two other characters with known Megasternini larvae: the presence of the hypopharyngeal lobe, and the reduction of the ligula; Sphaeridiini larvae also have a hypopharyngeal lobe, but their ligula is not reduced; additionally, larvae of *Austrotypus* Fikáček, Minoshima & Newton, 2014 (Cylominae) have a well developed hypopharyngeal lobe, and although the ligula is present, it is small and membranous (Fikáček et al. 2014).

Acknowledgements

We would like to thank P. W. Kovarik, T. K. Philips and K. Stephan for providing living adults (for rearing) of the two species studied here. We also thank Bruno Clarkson, Yûsuke Minoshima and Martin Fikáček for their comments and corrections of the manuscript. Martin Fikáček provided useful information on the maxilla of *Coelostoma orbiculare*. This is contribution # 115 from LIESA.

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