Chaetotaxy and larval morphometry of *Cercyon praetextatus* (Say) and *C. quisquilius* (Linnaeus) (Coleoptera: Hydrophilidae: Sphaeridiinae) and their phylogenetic implications

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Abstract

The primary and secondary chaetotaxy of the head capsule and head appendages of the three larval instars of *Cercyon praetextatus* (Say, 1825) and *Cercyon quisquilius* (Linnaeus, 1761) are described for the first time. Morphometric characters derived from the head capsule and mouthparts are also included, together with detailed illustrations of all characters. Morphology and chaetotaxy of these larvae is compared to that of *Cercyon convexiusculus* Stephens, 1829. Comparison of character states with other larvae of the tribes Megasternini, Coelostomatini, Protosternini and Shaeridiini confirms a well supported Megasternini, and a close relationship between Megasternini and Sphaeridiini.

Key words

Hydrophilidae, Sphaeridiinae, water scavenger beetles, larva, head, primary chaetotaxy, morphology, phylogeny.

1.　Introduction

The family Hydrophilidae is better known for its aquatic members, which inhabit all kind of freshwater environments. On the other hand, one of the most diverse hydrophilid subfamilies, Sphaeridiinae, includes mostly terrestrial species and has received less attention than the remaining, predominantly aquatic subfamilies (SHORT & FIKÁČEK 2011, 2013; BLOOM et al. 2014). Knowledge of larval Sphaeridiinae is inconsistent and larvae of most genera are unknown. Within the tribe Megasternini, which includes about 50 genera (SHORT & FIKÁČEK 2013), larval descriptions have been published for only five genera: *Cercyon* Leach, *Cryptopleurum* Mulsant, *Megasternum* Mulsant, *Oosternum* (Sharp) and *Pelosoma* Mulsant (PHILLIPS 1923; BÖVING & HENRIKSEN 1938; HAFEZ 1939; QUENNEDEY 1965; PRINS 1984; SCHULTE 1985; ARCHAN-GELSKY 1997; FUHRMANN et al. 2013). Most of these descriptions focus on third-instar larvae and do not include chaetotaxic characters (Table 1).

Cercyon, a speciose genus with a worldwide distribution and more than 250 species (SHORT & FIKÁČEK 2011), has received more attention than the remaining megasternine genera and several larval descriptions have been published by different authors. As mentioned above, most of those descriptions are brief and deal mostly with the general morphology of third-instar larvae (Table 1). Chaetotaxic characters have been studied only for *C. convexiusculus* Stephens, 1829 (FIKÁČEK 2006, unpublished; FIKÁČEK et al. 2008). In order to increase our knowledge of larval Megasternini, the present paper focuses on the description of chaetotaxic characters

Table 1. Megasternini species for which larval descriptions are available. * Chaetotaxy described in the present paper.

Species	Morphology	Chaetotaxy	References
Cercyon (*C.*) *convexiusculus*	X	X	FIKÁČEK 2006
Cercyon (*C.*) *haemorrhoidalis*	X	–	DE MARZO 2000; SCHULTE 1985
Cercyon (*C.*) *lateralis*	X	–	SCHULTE 1985
Cercyon (*C.*) *littoralis*	X	–	THOMSON 1860; SCHIÖDTE 1862, 1872; MJÖBERG 1906; BÖVING & HENRIKSEN 1938
Cercyon (*C.*) *maritimus*	X	–	PRINS 1984
Cercyon (*C.*) *melanocephalus*	X	–	DE MARZO 2000; SCHULTE 1985
Cercyon (*C.*) *praetextatus*	X	X*	ARCHANGELSKY 1997
Cercyon (*C.*) *pygmaeus*	X	–	SCHULTE 1985
Cercyon (*C.*) *quisquilius*	X	X*	HAFEZ 1939; SCHULTE 1985
Cercyon (*C.*) *unipunctatus*	X	–	SCHULTE 1985
Cercyon (*P.*) *analis*	X	–	SCHIÖDTE 1862 1872; BÖVING & HENRIKSEN 1938
Cercyon sp.	X	–	QUENNEDEY 1965
Cryptopleurum minutum	X	–	ARCHANGELSKY 1997
Megasternum concinuum	X	–	PHILLIPS 1923 (as *M. boletophagum*?); BÖVING & HENRIKSEN 1938 (as *Cryptopleurum* or *Megasternum*); QUENNEDEY 1965
Oosternum costatum	X	–	ARCHANGELSKY 1997 (as *Pemelus costatus*)
Pelosoma sp.	X	–	ARCHANGELSKY 1997
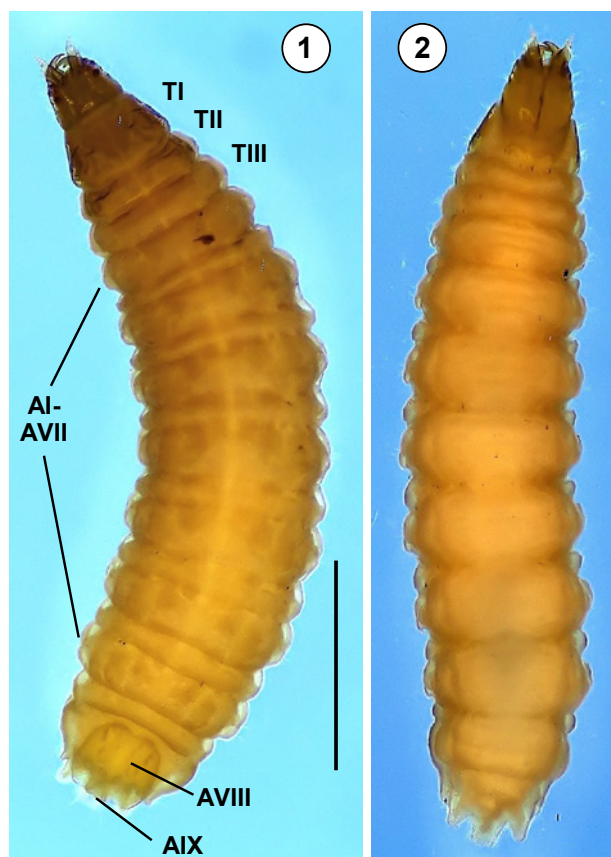
Figs. 1, 2. *Cercyon praetextatus*, habitus third instar larva. **1**: dorsal view. **2**: ventral view. (Scale bar: 2 mm)

and morphometry of *Cercyon praetextatus* (Say, 1825) and *Cercyon quisquilius* (Linnaeus, 1761), following the chaetotaxic system implemented by FIKÁČEK et al. (2008) and BYTTEBIER & TORRES (2009); for general morphological characters of these two species previous descriptions should be consulted (HAFEZ 1939; SCHULTE 1985; ARCHANGELSKY 1997). Comparative notes with other

Megasternini, Coelostomatini, Protosternini and Sphaeridiini genera are included, together with some phylogenetic considerations.

2. Material and methods

Source of material. Adults of *Cercyon praetextatus* were collected in USA, Holmes Co., Ohio, 21.vii.1990 (P.W. Kovarik, S. Wells, M. Archangelsky leg.); those of *Cercyon quisquilius* were collected in Argentina, Aldea Escolar, West of Trevelin, Chubut 28.ii.2015 (Archangelsky leg.). For the descriptions 7 L1, 3 L2 and 6 L3 of *C. praetextatus* and 6 L1, 4 L2 and 6 L3 of *C. quisquilius* were examined (L1–L3 being the larval instars, while later larval instars do not exist).

For comparison, larvae of other sphaeridiine genera were examined. *Cryptopleurum minutum* (Fabricius, 1775) (1 L1, 2 L3); USA, Ohio, Fayette Co., *ex* donkey and horse manure, v–vi.1995, B. Gerdeman leg. – *Oosternum costatum* (LeConte, 1855) (1 L1, 2 L3); USA, Ohio, Lawrence Co. Wayne National Forest, Sharps creek, Bluegrass trail, *ex* pig manure, v–vi.1995, P.W. Kovarik leg. – *Pelosoma* sp. (3 L1, 2 L3); Venezuela, Aragua, H. Pittier National Park, Rancho Grande Biological Station: La Toma trail 1100 m, and La Trilla cacao plantation 300–400 m (*ex Heliconia* flowers), 4–21.viii.1994, M. Archangelsky leg. – *Sphaeridium* spp. (3 L2 or L3); USA, Ohio, Lancaster Co., *ex* horse and cow manure, 19.vi.1994, D.L. Wrensch leg.; USA, Ohio, Fayette Co., *ex* donkey and horse manure, vi.1995, B. Gerdeman leg.

Methods. *Cercyon praetextatus* adults were reared in laboratory, where the complete life cycle was obtained. Larvae (L2 and L3) and adults of *C. quisquilius* were collected from horse manure using a Berlese funnel; egg

Table 2. Measurements (in mm) and ratios for the three larval instars of *Cercyon praetextatus* and *C. quisquilius*.
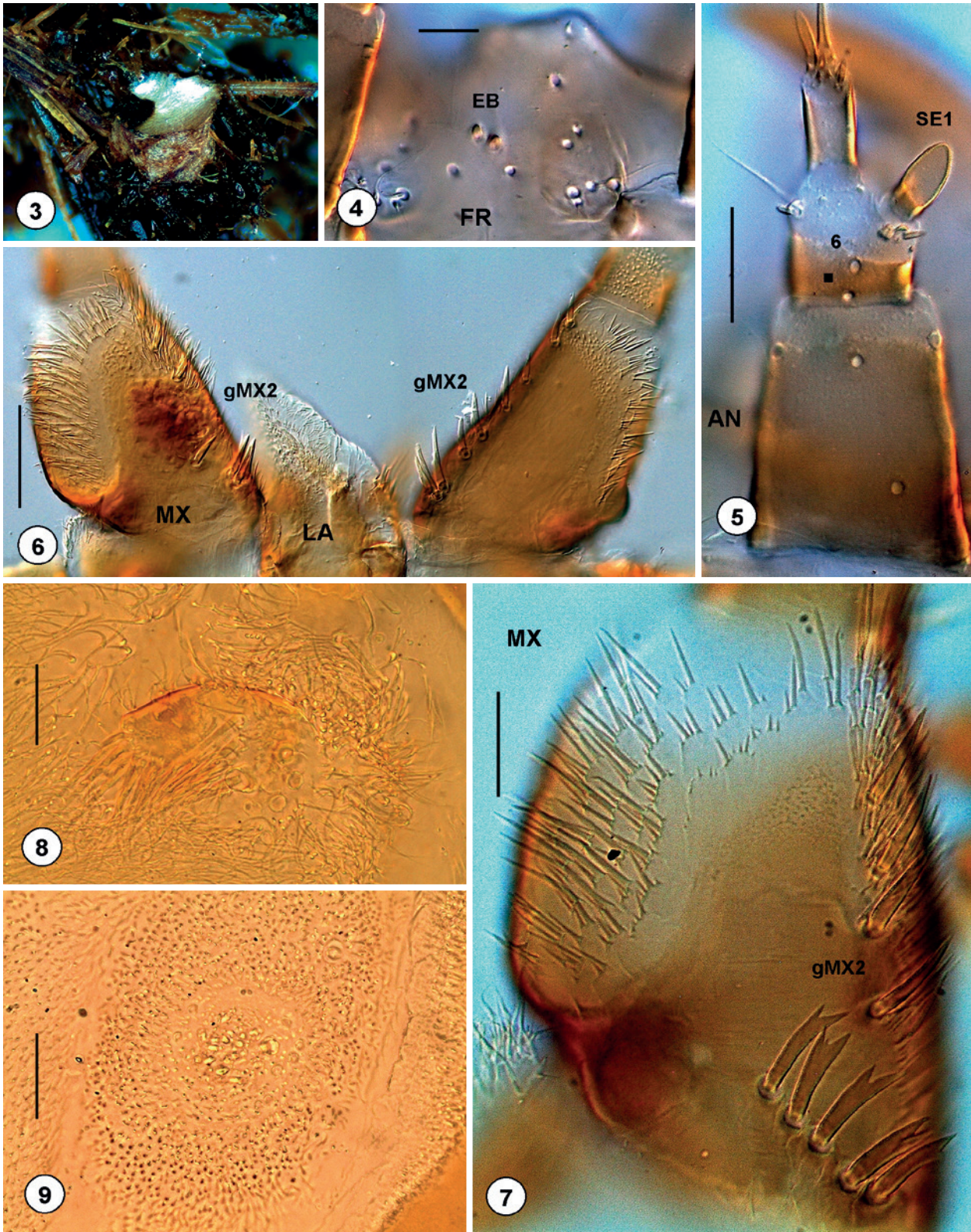
Measure	*Cercyon praetextatus*			*Cercyon quisquilius*		
	Instar I	Instar II	Instar III	Instar I	Instar II	Instar III
TL	2.00–3.10	3.60–4.90	6.30–7.40	1.3–2.0	2.8–3.4	3.8–4.5
MW	0.30–0.55	0.70–1.00	1.40–1.50	0.29–0.32	0.52–0.59	0.61–0.83
HL	0.18–0.19	0.22–0.23	0.29–0.30	0.16–0.17	0.19–0.20	0.24
HW	0.24–0.25	0.33–0.34	0.45	0.22–0.23	0.26–0.28	0.36
HL/HW	0.71–0.78	0.66–0.69	0.65–0.67	0.73–0.75	0.71	0.66
AL	0.08	0.09–0.10	0.13–0.14	0.07	0.09	0.11
A1L	0.04–0.05	0.05–0.06	0.08	0.04	0.05	0.06
A2L	0.02	0.02	0.03	0.01	0.02	0.02
A3L	0.02	0.02	0.03	0.02	0.02	0.03
SEL	0.02	0.02	0.02	0.02	0.02	0.02
SEL/A3L	0.94–1.06	0.79–0.85	0.63–0.75	0.84–0.94	0.75–0.82	0.61–0.63
A1L/A2L	2.53–2.93	2.79–3.00	2.78–3.00	3.08–3.50	2.45–2.89	3.00–3.47
A1L/(A2L+A3L)	1.23–1.42	1.43–1.46	1.36–1.47	1.25–1.45	1.11–1.30	1.15–1.23
HL/AL	2.31–2.45	2.38–2.53	2.12–2.29	2.25–2.39	2.02–2.17	2.11–2.21
HW/AL	3.08–3.36	3.46–3.82	3.25–3.57	3.07–3.21	2.84–3.04	3.18–3.33
SL	0.08–0.09	0.1–0.11	0.14–0.15	0.07–0.08	0.08–0.09	0.10
MPL	0.05–0.06	0.06	0.07–0.08	0.05–0.06	0.06–0–07	0.07
SL/MPL	1.46–1.89	1.75–1.86	1.82–1.96	1.23–1.34	1.31–1.37	1.46–1.50
MP1L	0.02	0.02	0.03	0.02	0.02	0.02
MP2L	0.01	0.01	0.01	0.01	0.01	0.01
MP3L	0.01	0.01	0.01	0.01	0.01	0.01
MP4L	0.01–0.02	0.02	0.02	0.02	0.02	0.02
ML	0.13–0.14	0.16–0.17	0.21–0.23	0.12–0.13	0.14–0.15	0.17
LPL	0.03	0.03	0.05	0.02	0.03	0.04
LP1L	0.01	0.01	0.02	0.01	0.01	0.01
LP2L	0.02	0.02	0.03	0.01–0.02	0.02	0.02–0.03
LP2L/LP1L	1.67–1.91	2.00	1.56–1.61	1.56–1.88	2.00–2.11	2.17–2.18
MtW	0.03	0.04	0.06	0.03	0.03	0.05
PrmtW	0.02	0.03	0.04	0.02	0.03	0.03
PrmtL	0.01	0.01	0.02	0.01	0.01	0.01
PrmtW/PrmtL	3.17–4.00	4.29	2.67	3.67–4.00	3.86–4.29	4.86
PrmtW/MtW	0.60–0.67	0.75	0.69	0.74–0.82	0.84–0.88	0.74

cases (Fig. 3) were also collected from the same patch of fresh horse manure and were reared in order to obtain first-instar larvae (no other sphaeridiines were present in the manure). Rearing techniques follow those of ARCH-ANGELSKY (1997). Larvae were killed in boiling water and preserved in 75% ethyl alcohol. They were cleared in warm lactic acid, dissected and mounted on glass slides with Hoyer's medium. Observations (up to 1000 x) 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 the author. Identification of adults was done using the revision of Sphaeridiinae by SMETANA (1978); argentine adults of *C. quisquilius* were also compared with adults of *C. quisquilius* from USA.

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: **TL**: total body length; **MW**: maximum body width, measured at level of prothorax; **HL**: head length, measured medially along epicranial stem from anterior margin of frontoclypeus to occipital foramen; **HW**: maximum head width; **AL**: length of antenna, derived by adding the lengths of the first (A1), second (A2) and third (A3) antennomeres; **SeL**: length of antennal sensorium; **SL**: length of stipes; **MPL**; length of maxillary palpus, obtained by adding the lengths of the first (MP1), second (MP2), third (MP3) and fourth (MP4) palpomeres; **ML**: length of maxilla, derived by adding SL and MPL; cardo omitted; **LPL**: length of labial palpus, obtained by adding the lengths of the first (LP1) and second (LP2) palpomeres; **LigL**: length of ligula; **MtW**: maximum width of mentum; **PrmtL**: length of prementum, measured from its base to the base of LP1; **PrmtW**: maximum width of prementum. Legs and leg segments were not measured due to the extreme leg reduction that *Cercyon* larvae exhibit.

Figs. 3–9. 3: *Cercyon quisquilius*, egg case, laterodorsal view. **4**: *C. quisquilius*, frons of first instar larva with egg-bursters (EG). **5**: *C. quisquilius*, antenna of first instar larva with additional pore (■) at base of A2, dorsal view. **6**: *C. praetextatus*, maxillae and labium of third instar larva depicting asymmetry of maxillae, dorsal view. **7**: *C. quisquilius*, left stipes of third instar larva showing gMX2, dorsal view. **8**: *C. praetextatus*, proleg of third instar larva. **9**: *C. quisquilius*, proleg of third instar larva. (Scale bars for Figs. 4–9: 0.02 mm)

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 were labeled by comparison with the ground plan of chaetotaxy of Hydrophilidae (FIKÁČEK et al. 2008; BYTTEBIER & TORRES 2009).

Homologies were established using the criterion of similarity of position (WILEY 1981). Sensilla are 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. Additional sensilla are coded with a black square (■).

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.

3.   Results

3.1.   First-instar larvae of *Cercyon praetextatus* and *C. quisquilius*

Morphology. Measurements and ratios in Table 2. ***Color***. Head capsule, head appendages, thoracic and abdominal sclerotized structures yellowish to light brown in older specimens; membranous areas whitish. Non-sclerotized integument covered by fine and short microtrichiae.

Body. Subcylindrical, slightly narrowing towards anterior end (as in Figs. 1, 2 of third instar larva).

Head capsule (Figs. 4, 10–12, 28–30). Suboval, broader than long; occipital foramen wide. Coronal line absent, area enclosed by frontal lines inversely bell-shaped. Stemmata closely aggregated. Clypeolabrum asymmetrical, right side concave to slightly concave, left side with small notch bearing dense pubescence (formed by fine microtrichiae); lateral lobes of epistome short, rounded, not projecting farther than nasale; clypeolabrum bearing two sharp cuticular projections interpreted as egg-bursters. ***Antenna*** (Figs. 5, 13, 31). Three-segmented, A1 the longest and widest segment; A2 short, slightly narrower than A1; A3 subequal to A2 in length, very narrow; SE1 either subequal to A3 in length (*C. praetextatus*) or slightly shorter, narrower and cone-shaped (*C. quisquilius*). ***Mandibles*** (Figs. 14, 15, 32, 33). Strongly asymmetrical, right one slightly smaller than left one, bearing one strongly serrated inner tooth, either distal inner margin finely serrated (*C. praetextatus*) or inner margin and inner tooth of right mandible more feebly serrated (*C. quisquilius*); left mandible lacking inner tooth, finely serrated distally on inner margin, serration becoming stronger on central and subbasal area of inner margin, a patch of sharp cuticular projections either present centrally on inner margin (*C. praetextatus*) or absent (*C. quisquilius*). ***Maxilla*** (Figs. 17, 18, 35, 36). Six-segmented, longer than antenna, cardo subtriangular, partially covered by submentum and parietale. Stipes large, longer than palpus, either slightly asymmetrical (*C. praetextatus*) or strongly asymmetrical (*C. quisquilius*);

left stipes broader than right one. Palpus four-segmented, first palpomere the largest, subquadrate, with inner appendage reduced; second and third palpomeres shorter, wider than long; fourth palpomere subconical, slightly longer than previous two palpomeres. ***Labium*** (Figs. 11, 16, 29, 34). Submentum large, subtriangular, fused to head capsule, with a pair of deep lateral, subapical notches. Mentum short, narrower than submentum, transversely subrectangular. Prementum reduced, as a wide and narrow plate on ventral face. Palpi two-segmented, basal palpomere short, distal palpomere either longer (*C. praetextatus*), or shorter (*C. quisquilius*). Ligula reduced, not sclerotized. Asymmetrical hypopharyngeal lobe as a membranous pubescent lobe developed on left side (as in Fig. 6 of third-instar larva). ***Cervical sclerites*** (Figs. 10, 28) dorsal, narrow and transverse.

Thorax. Wider than head capsule (as in Fig. 1 of third-instar larva). Pronotal plate large, covering most of prothorax, divided by fine sagittal line; mesonotal plate narrower and shorter, either ca. 1/3 (*C. praetextatus*) or ca. 1/6 (*C. quisquilius*) the length of pronotal plate, with sagittal line; metanotal plate either half the length and width of mesonotal plate, with sagittal line (*C. praetextatus*), or indistinguishable (*C. quisquilius*: metathorax membranous). Prosternal plate subtrapezoidal, narrowly transverse, ca. 1/2 the length of pronotal plate; meso- and metasternum membranous. Legs either minute, represented by two minute sclerotized segments, coxal area large, membranous (*C. praetextatus*, as in Fig. 8 of third-instar larva); or legs strongly reduced, unsclerotized (*C. quisquilius*, as in Fig. 9 of third instar larva). Mesothoracic spiracles non-functional.

Abdomen. Ten-segmented, segments IX and X modified (as in Fig. 1 of third-instar larva). Segments I to VII subequal in size and shape, lacking sclerites, subdivided by transverse folds. Segment VIII with large dorsal plate, posteriorly lobed; with a short pair of procerci laterad to dorsal plate. Segment IX trilobed, with a pair of one-segmented urogomphi. Spiracles on segments I–VII biforous, non-functional; those on segment VIII large, annular.

Primary chaetotaxy. ***Head capsule*** (Figs. 10–12, 28–30). Frontale with 28 sensilla: two setae on basal third, close to frontal lines (FR1, long in *C. praetextatus*, short in *C. quisquilius*); two pores (FR2) and two very short setae (FR3) close to midline at about midlength; two pairs of setae laterad to FR3 (FR5 long in *C. praetextatus*, shorter in *C. quisquilius*, FR6 short), FR5 and FR6 more closely aggregated in *C. quisquilius*; one pair of pores posterior to inner margin of antennal sockets (FR4); one pair of pores (FR15) posterior to egg-bursters (EB); five pairs of sensilla close to base of antennae, two rather long setae (FR8, FR9), two pores (FR13, FR14) and one very short seta (FR10); slightly distal to this group one very short seta (FR12) and a pore (FR11); nasale with gFR1 bearing four dorsal short and stout setae, and a pair of small setae inserted ventrally; left two setae of gFR1 more slender in *C. quisquilius*. Epistomal lobes lacking
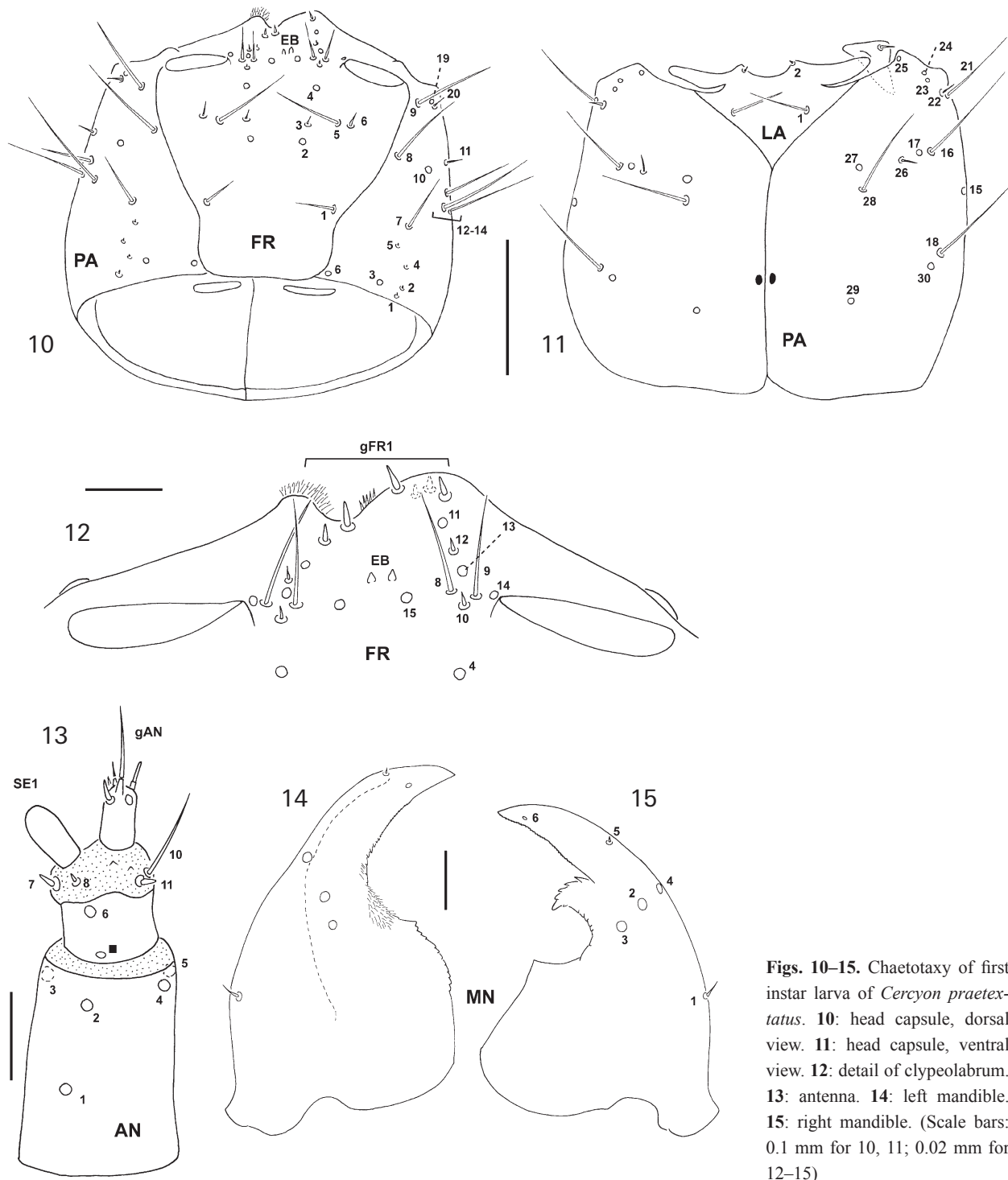
Figs. 10–15. Chaetotaxy of first instar larva of *Cercyon praetextatus*. **10**: head capsule, dorsal view. **11**: head capsule, ventral view. **12**: detail of clypeolabrum. **13**: antenna. **14**: left mandible. **15**: right mandible. (Scale bars: 0.1 mm for 10, 11; 0.02 mm for 12–15)

sensilla, therefore gFR2 absent. Seta FR7 apparently absent. Each parietale with 30 sensilla: dorsal surface with a basal longitudinal row of four minute setae (PA1, PA2, PA4, PA5) and one pore (PA3) located closer to frontal line; one basal pore (PA6) close to frontal line; seta PA7 either long (*C. praetextatus*) or short (*C. quisquilius*), distal to PA5; setae PA12, PA13, PA14 closely aggregated on lateral margin at about midlength, either all long (*C. praetextatus*), or one long and two short (*C. quisquilius*); setae PA8 (long), PA11 (short) and one pore (PA10) in a transverse row past midlength; two setae (PA9 long,

PA20 short) and one pore (PA19) in a transverse row on anterolateral corner of head capsule. Ventral surface with three pores (PA23, PA24, PA25) and two setae PA21 (long in *C. praetextatus*, short in *C. quisquilius*) and PA22 (short in *C. praetextatus*, long in *C. quisquilius*) on anterolateral corner, close to mandibular acetabulum; one pore (PA15) on lateral margin at about midlength; setae PA16, and PA18 (long in *C. praetextatus*, short in *C. quisquilius*) and two pores (PA17, PA30) along outer margin; one short seta (PA26) close to pore PA17; pore PA17 placed either between setae PA16 and PA26 (*C.*
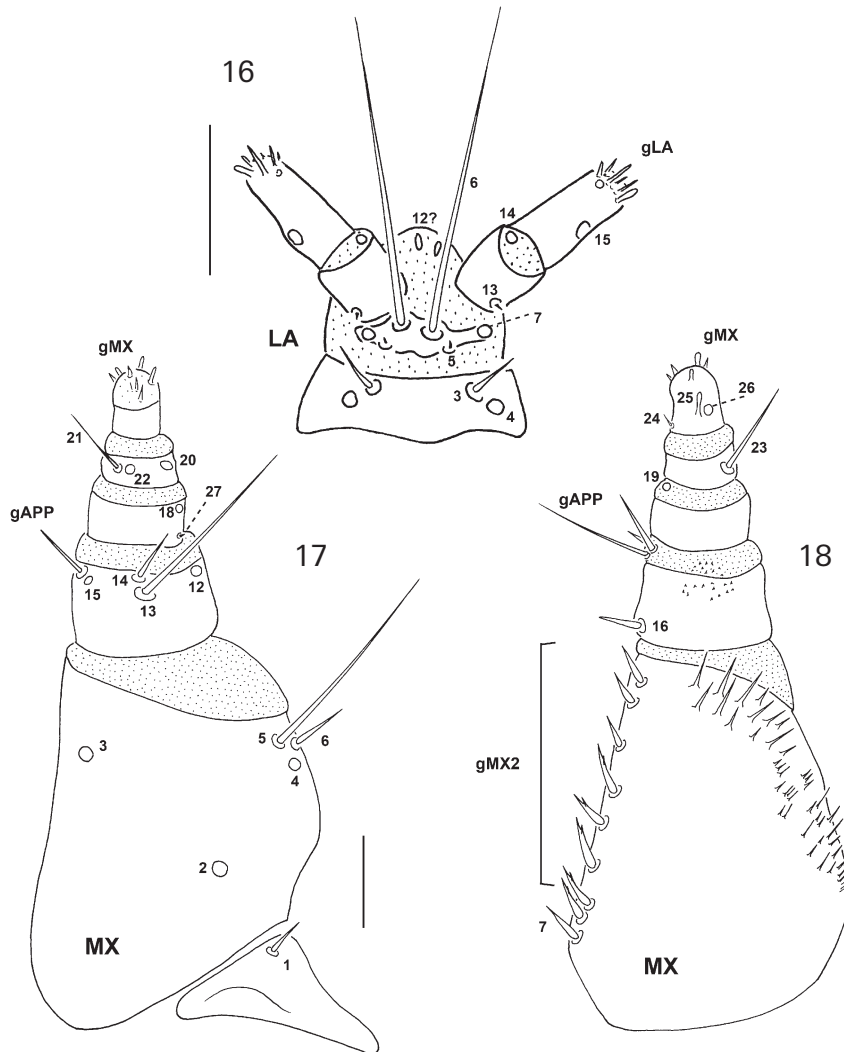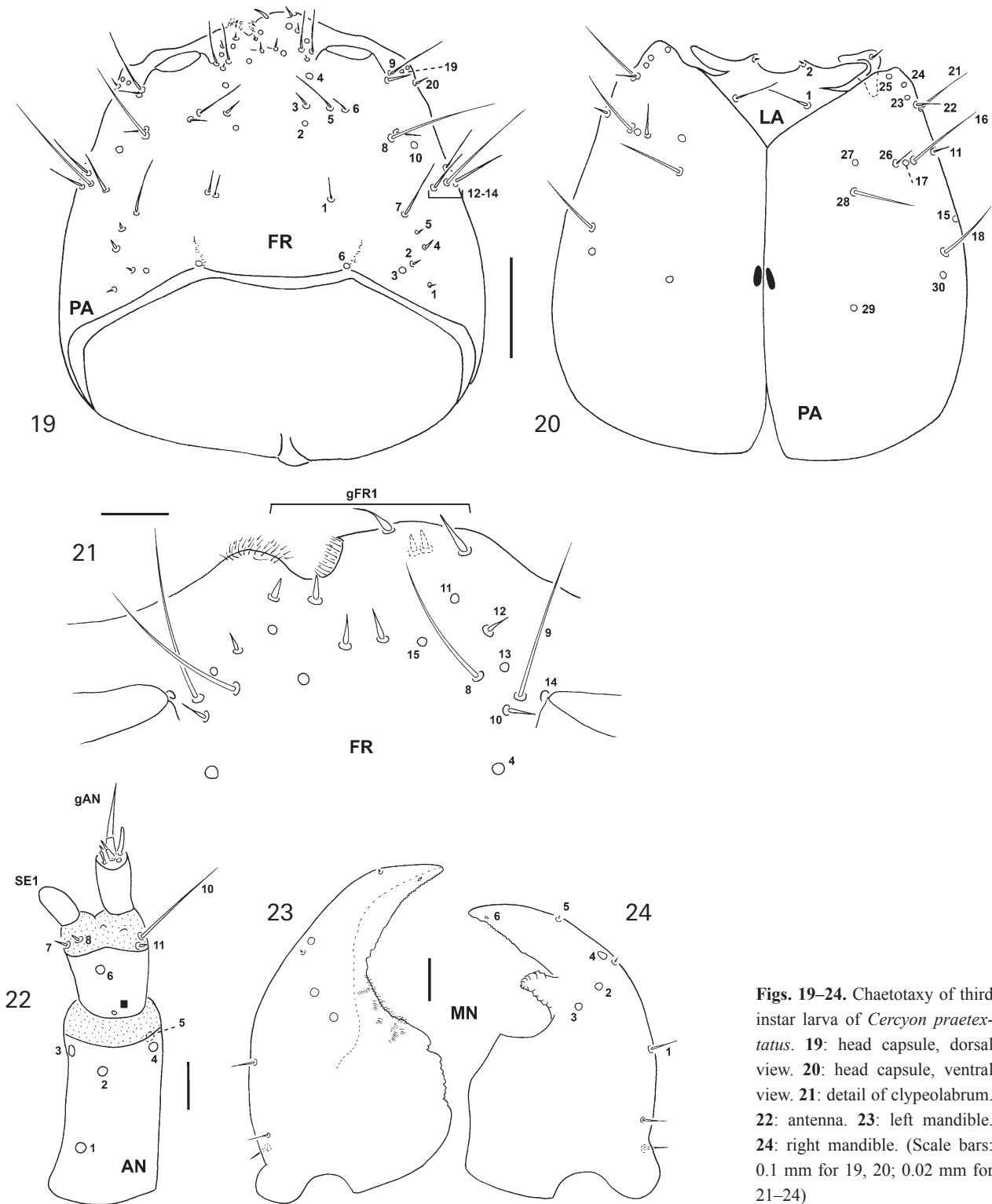
Figs. 16–18. Chaetotaxy of first instar larva of *Cercyon praetextatus*. **16**: labium, ventral view. **17**: left maxilla, ventral view. **18**: left maxilla, dorsal view. (Scale bars: 0.02 mm)

praetextatus) or laterad to PA26 (*C. quisquilius*); two pores (PA27, PA29) and seta PA28 (long in *C. praetextatus*, short in *C. quisquilius*) forming a longitudinal row closer to midline.

Antenna (Figs. 5, 13, 31). A1 bare, with five pores, three dorsal ones on distal half (AN1 and AN2 close to midline, AN4 distally on inner margin) and two ventral ones on distal margin (AN3, AN5). A2 with two pores, one distal (AN6) and one subbasal (■), and four setae, two very short subapical on outer margin (AN7, AN8) close to base of SE1, and two subapical on inner margin (AN10 long, AN11 very short). A3 with a group of at least four short setae, one long seta and one pore (gAN).

Mandibles (Figs. 14, 15, 32, 33). Both mandibles with six sensilla; one short seta on outer margin at basal third (MN1), one minute seta on outer margin at distal quarter (MN5) in right mandible (closer to apex in left mandible), three dorsal pores (MN2, MN3, MN4) forming an oblique row at level of inner retinaculum of right mandible (equidistant in *C. praetextatus*, MN2 closer to MN4 than to MN3 in *C. quisquilius*), MN3 closer to inner margin, more basal, MN4 on outer margin, more distal; pore MN6 small, subapical on inner margin.

Maxilla (Figs. 17, 18, 35, 36). Cardo with one short seta (MX1). Stipes with a row of stout and short setae along inner margin (9 in *C. praetextatus*, 7 in *C. quisquilius*), those at base more closely aggregated; basal seta of that row simple, likely homologous to MX7, remaining setae forming (gMX2), with basal four or five setae bifid distally; left stipes in *C. quisquilius* with setae of gMX2 arranged in two groups: basal 4 in an oblique row, distal 3 in a longitudinal row (as in Fig. 7 of third-instar larva); ventral face with three pores, one on basal half (MX2), one subapical close to inner margin (MX3) and one subapical on outer margin (MX4), and two setae distal to pore MX4 (MX5 very long, MX6 short). MP1 dorsally with one basal spiniform seta (MX16), MX17 apparently absent; ventrally with two subapical setae MX13 (very long in *C. praetextatus*, shorter in *C. quisquilius*) and MX14 (short) and two pores (MX12 on outer margin, MX15 on inner margin at base of gAPP); inner appendage reduced, with four setae of different lengths (gAPP). MP2 with two pores, one ventral and apical on outer margin (MX18) and one dorsal at inner margin on membrane connecting with MP3 (MX19); one basal minute seta (MX27) on outer margin. MP3 with two rather long setae and two pores, one seta dorsal, on outer mar-
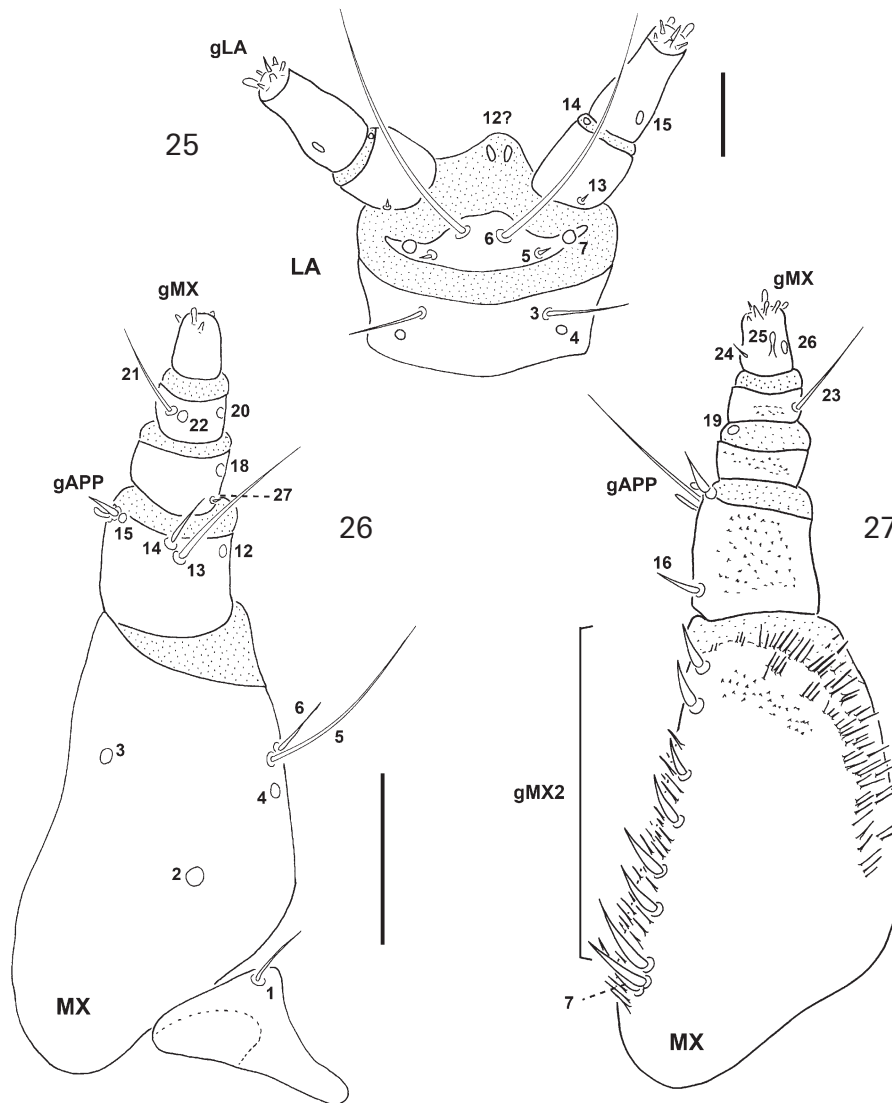
Figs. 19–24. Chaetotaxy of third instar larva of *Cercyon praetextatus*. **19**: head capsule, dorsal view. **20**: head capsule, ventral view. **21**: detail of clypeolabrum. **22**: antenna. **23**: left mandible. **24**: right mandible. (Scale bars: 0.1 mm for 19, 20; 0.02 mm for 21–24)

gin (MX23), the other ventral on inner margin (MX21); both pores on ventral surface, one close to seta MX21 (MX22), the other apical, close to outer margin (MX20). MP4 with one short basal seta dorsally (MX24) and two dorsal subapical pores (MX25 central, digitiform, MX26 closer to outer margin); a group of at least seven or eight very short sensilla constitute gMX1.

Labium (Figs. 11, 16, 29, 34). Submentum with two pairs of setae (Fig. 11), one long (LA1), the other minute, on anterior margin (LA2). Mentum ventrally with one pair of short setae (LA3) and one pair of lateral pores (LA4). Prementum with two pairs of setae (LA5 minute, almost pore-like, LA6 very long in *C. praetextatus*, shorter in *C. quisquilius*) and one pair of lateral pores (LA7). Sensilla associated with ligula absent (LA9–12) except for one pair of pores (LA12?), resembling LA12 placed on membranous lobe between labial palpi (behind palpi in ventral view). LP1 with one minute seta (LA13,

Figs. 25–27. Chaetotaxy of third instar larva of *Cercyon praetextatus*. **25**: labium, ventral view. **26**: left maxilla, ventral view. **27**: left maxilla, dorsal view. (Scale bars: 0.025 mm for 25; 0.05 mm for 26, 27)

ventral) and one distal pore (LA14, on inner margin); LP2 with one subapical pore on outer face (LA15) and a group of at least seven short sensilla that constitute gLA.

3.2. Second-instar larvae of *Cercyon praetextatus* and *C. quisquilius*

Morphology. Measurements and ratios in Table 2. Very similar to third-instar larva, but with frontal lines well developed. Mesonotal plate proportionally larger, either ca. 1/2 (*C. praetextatus*) or ca. 1/3 (*C. quisquilius*) the length of pronotal plate; metanotal plate present in both species, ca. 2/3 the length of mesonotal plate. Prosternal plate larger, either slightly shorter (*C. praetextatus*) or ca. 2/3 (*C. quisquilius*) the length of pronotal plate.

Chaetotaxy. *Head capsule*. Frontale without secondary sensilla (only one specimen of *C. quisquilius* has one on left side by FR1, probably a duplication of the structure). Each parietale with three (*C. praetextatus*) or four (*C. quisquilius*) secondary sensilla as those of

third-instar larva. *Antenna*. Without secondary sensilla, sensory appendage proportionally shorter than third antennomere. *Mandibles*. Each mandible with three secondary setae as those of third-instar larva. *Maxilla*. Similar to that of third-instar larva. *Labium*. Similar to that of third-instar larva.

3.3. Third-instar larvae of *Cercyon praetextatus* and *C. quisquilius*

Morphology. Figs. 1, 2, 6, 19–27, 37–46. Measurements and ratios in Table 2. Frontal lines absent. Mesonotal plate proportionally larger, ca. 1/2 the length of pronotal plate; metanotal plate present. Prosternal plate larger, either slightly shorter than pronotal plate (*C. praetextatus*) or ca. 2/3 the length of pronotal plate (*C. quisquilius*). Inner margin of right stipes either with (*C. praetextatus*) or without (*C. quisquilius*) short and fine cuticular projections surrounding setae of gMX2; dorsal cuticular projections of left stipes longer, covering outer and inner margins of stipes (*C. quisquilius*).
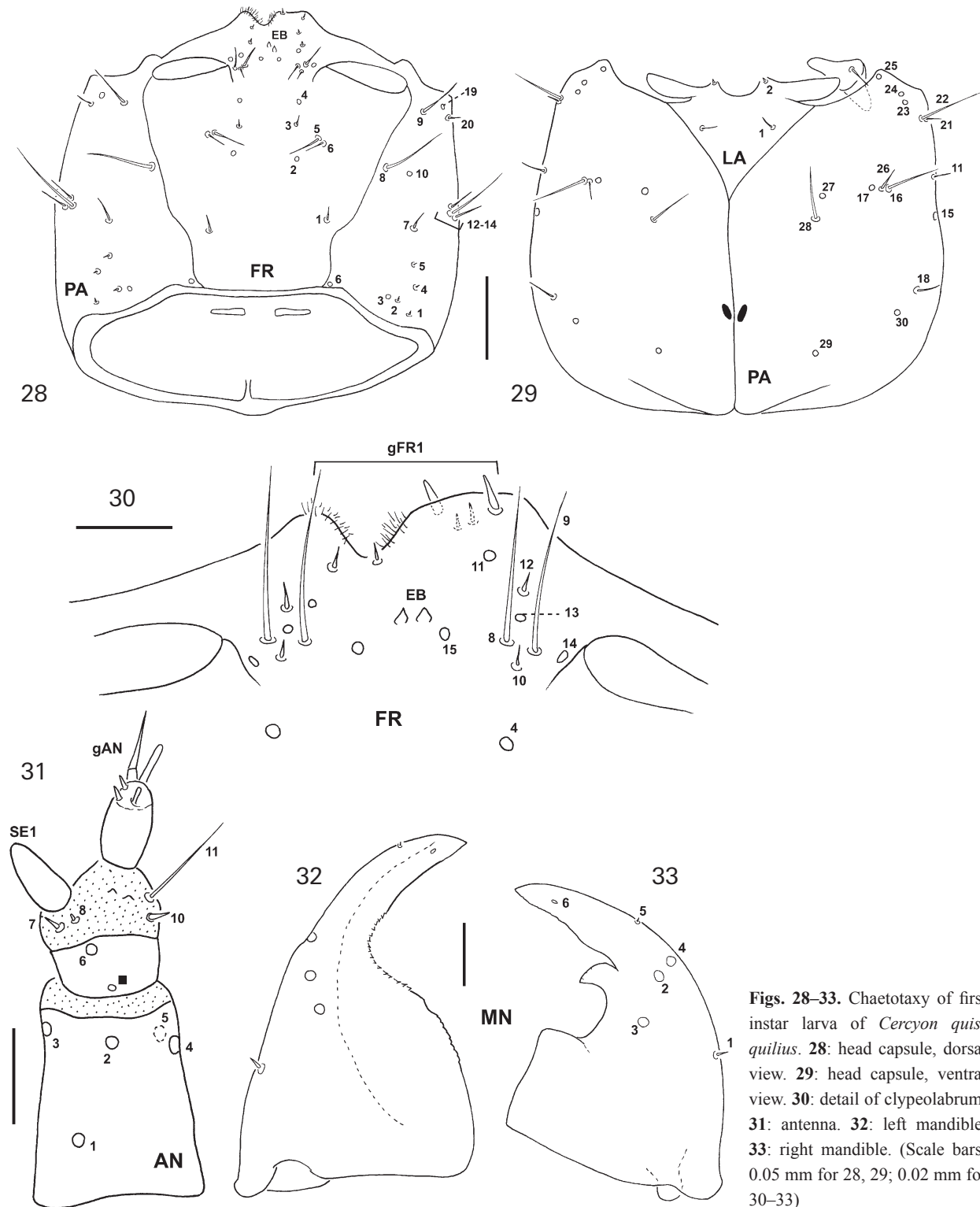
Figs. 28–33. Chaetotaxy of first instar larva of *Cercyon quisquilius*. **28**: head capsule, dorsal view. **29**: head capsule, ventral view. **30**: detail of clypeolabrum. **31**: antenna. **32**: left mandible. **33**: right mandible. (Scale bars: 0.05 mm for 28, 29; 0.02 mm for 30–33)

Chaetotaxy. *Head capsule* (Figs. 19–21, 37–39). Frontale without secondary sensilla (only the illustrated specimen of *C. praetextatus* has one on left side by FR1, probably a duplication of the structure); FR8 and FR9 in *C. quisquilius* shorter; gFR1 with either six (*C. praetextatus*) or five (*C. quisquilius*) dorsal and two ventral setae. Each parietale with four secondary sensilla; one short seta near PA9, one pore between pore PA19 and seta PA20, one seta near PA8 (short in *C. praetextatus*,

long in *C. quisquilius*), and one short seta either close to group formed by PA12–14 (*C. praetextatus*) or near PA11 (*C. quisquilius*). *Antenna* (Figs. 22, 40). Without secondary sensilla, sensory appendage shorter than third antennomere. *Mandibles* (Figs. 23, 24, 41, 42). Each mandible with three secondary setae, two short setae on basal outer face, behind MN1, third one minute, close to pore MN4. *Maxilla* (Figs. 7, 26, 27, 43–45). Stipes without secondary setae on ventral face; right stipes
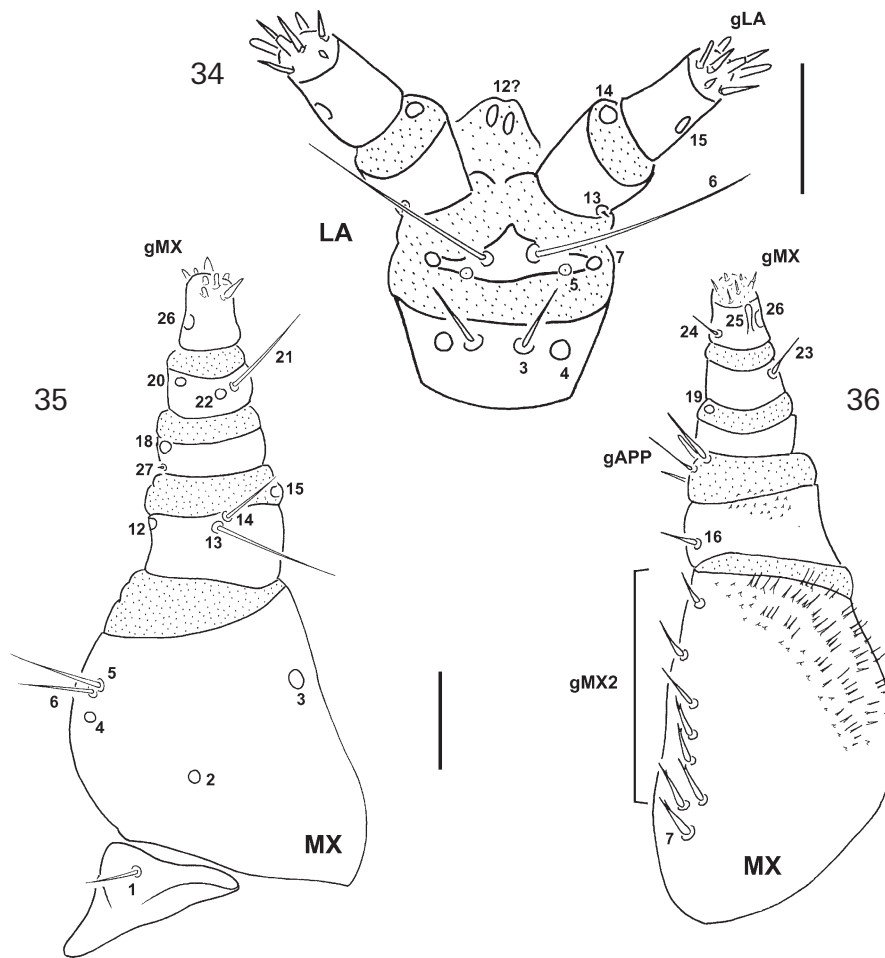
Figs. 34–36. Chaetotaxy of first instar larva of *Cercyon quisquilius*. **34**: labium, ventral view. **35**: left maxilla, ventral view. **36**: right maxilla, dorsal view. (Scale bars: 0.02 mm)

without (*C. praetextatus*) or with one (*C. quisquilius*) secondary seta on gMX2, basal setae of gMX2 slightly stouter, either not bifid apically (*C. praetextatus*) or basal five setae bifid apically (*C. quisquilius*); left stipes without (*C. praetextatus*) or with two secondary setae (*C. quisquilius*) on gMX2; setae of gMX2 of left stipes almost in a straight line (*C. praetextatus*), or as in *C. quisquilius* with basal five setae of gMX2 strongly bifid, forming an oblique row, remaining four setae forming a longitudinal line. ***Labium*** (Figs. 20, 25, 38, 46). Without secondary sensilla, LA6 proportionally shorter in *C. praetextatus*.

4. Discussion

Egg-bursters. These structures have been reported for only a few genera of hydrophilids, and all of them within Sphaeridiinae: *Cercyon*, *Sphaeridium* Fabricius, and *Dactylosternum* Wollaston, at least in *D. cacti* (LeConte, 1855) (Fikáček 2006, unpublished; Archangelsky et al. 2016). The egg-bursters of these three genera are different, but show a similar position, in front and between sensilla FR8 and FR15. *Cercyon* larvae present two small but stout toothlets pointing forward (Fig. 4); *Sphaeridium*

larvae have a short longitudinal row of four sharp toothlets; *Dactylosternum cacti* larvae show two strong spines placed on a small lobe, which belong to gFR1, in later instars these two stout setae become more slender and the small lobe that bears them disappears. First-instar larvae of the megasternine genera *Cryptopleurum*, *Oosternum* and *Pelosoma* also have egg-bursters similar in structure and position to those found in *Cercyon*. I cannot think of any reason why these structures occur in a group of predominantly terrestrial hydrophilids except that these egg-bursters occur in larvae which show a reduction of the teeth of the nasale, for example *Phaenonotum exstriatum*, with well developed nasal teeth, lacks egg-bursters; M. Fikáček has suggested (in litt.) that terrestrial species perhaps have thicker chorions, this would explain the presence of egg-bursters. Nonetheless, even though their structure is variable, this should be considered a character of phylogenetic importance within Sphaeridiinae, and for Megasternini they could represent a synapomorphy since in the abovementioned genera they are morphologically similar.

Chaetotaxy. Based on the sample of *C. praetextatus* and *C. quisquilius* specimens here studied (see Material and Methods), all the characters documented in the description and mentioned in the preceding comparison were found invariable in a particular species and instar with
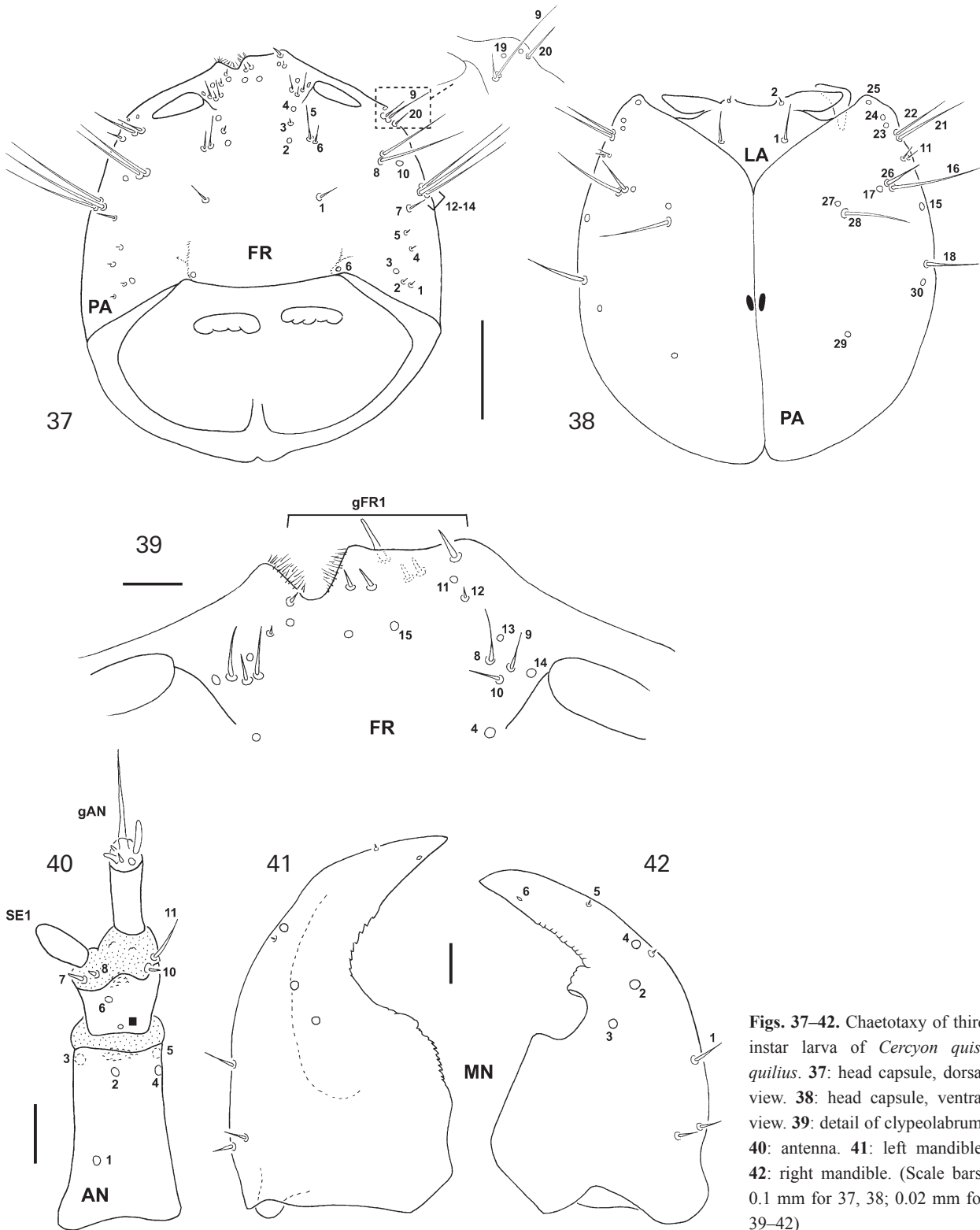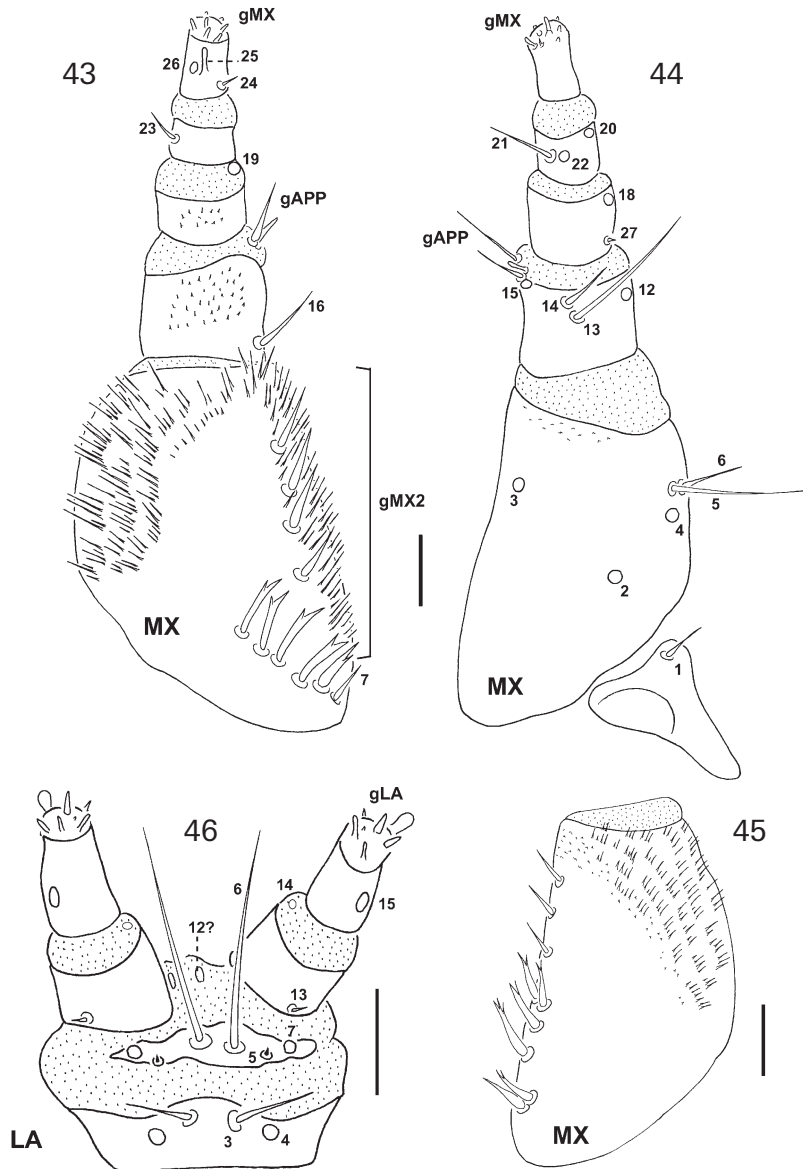
Figs. 37–42. Chaetotaxy of third instar larva of *Cercyon quisquilius*. **37**: head capsule, dorsal view. **38**: head capsule, ventral view. **39**: detail of clypeolabrum. **40**: antenna. **41**: left mandible. **42**: right mandible. (Scale bars: 0.1 mm for 37, 38; 0.02 mm for 39–42)

the exception of two situations discussed below in the section on intra-specific variation.

Larvae of *C. praetextatus* and *C. quisquilius* are very similar in gross morphology and in their chaetotaxy. Nonetheless some differences in chaetotaxy can be found in the head capsule and in the head appendages of first instar larvae. In the head capsule FR1 is long in *C. praetextatus* but short in *C. quisquilius*; FR5 is also long in

C. praetextatus and shorter in *C. quisquilius*; FR5 and FR6 are more closely aggregated in *C. quisquilius*, their bases almost touching each other; the left two setae of gFR1 in *C. quisquilius* are more slender; seta PA7 is long in *C. praetextatus* and short in *C. quisquilius*; closely aggregated setae PA12, PA13, PA14 are long in *C. praetextatus* while in *C. quisquilius* one is long and two are short; seta PA21 is long in *C. praetextatus* and short in

Figs. 43–46. Chaetotaxy of third instar larva of *Cercyon quisquilius*. **43**: left maxilla, dorsal view. **44**: right maxilla, ventral view. **45**: right stipes, dorsal view. **46**: labium, ventral view. (Scale bars: 0.02 mm)

C. quisquilius; seta PA22 is short in *C. praetextatus* but long in *C. quisquilius*; setae PA16 and PA18 are long in *C. praetextatus* but shorter in *C. quisquilius*; pore PA17 is placed between setae PA16 and PA26 in *C. praetextatus* while in *C. quisquilius* seta PA26 placed between pore PA17 and seta PA16; seta PA28 is long in *C. praetextatus* and short in *C. quisquilius*. In the antenna the only difference is the ratio SEL/A3L, which is larger in *C. praetextatus* (in all larval instars, Table 2). The mandible also has one difference concerning pores MN2–4: equidistant in *C. praetextatus*, but MN2 being closer to MN4 than to MN3 in *C. quisquilius*. The maxilla presents several differences, the most distinctive are found in the stipes, the number of setae on gMX2 is 9 in *C. praetextatus* but 7 in *C. quisquilius*; additionally in *C. quisquilius* the basal four setae of the left gMX2 are arranged in a well defined oblique row, and not almost in line with the remaining setae of gMX2 as in *C. praetextatus*. In the labium the only difference is seta LA6, which is very long in *C. praetextatus* and slightly shorter in *C. quisquilius*.

The chaetotaxy of second and third instar larvae is very similar, but some differences can be mentioned. In third-instar larvae FR8 and FR9 are long in *C. praetextatus* and short in *C. quisquilius*; gFR1 has eight setae in *C. praetextatus* and seven in *C. quisquilius*; the parietale has three secondary sensilla in second-instar larvae of *C.praetextatus*, and four in *C. quisquilius*; in third-instar larvae both species have four secondary sensilla on the parietale; the additional seta near PA8 in *C. praetextatus* is short, but long in *C. quisquilius*; *C. praetextatus* has one secondary short seta close to the group formed by PA12–14 (absent in *C. quisquilius*); and *C. quisquilius* has one secondary short seta near PA11 (absent in *C. praetextatus*). The stipes includes some distinctive characters: gMX2 in the right stipes of *C. quisquilius* has one secondary seta (none in *C. praetextatus*) and the basal five setae of gMX2 in *C. quisquilius* are bifid (simple in *C. praetextatus*); gMX2 in the left stipes has two secondary setae in *C. quisquilius* (none in *C. praetextatus*).

Larvae of *C. praetextatus* and *C. quisquilius* share several chaetotaxic characters with *C. convexiusculus* (FIKÁČEK 2006, unpublished). Sensilla FR3, FR5 and FR6 form a more or less transverse row; FR7 and gFR2 are absent; PA3 is located further mesad and not in line with PA1, PA2, PA4 and PA5; PA6 is located basally close to frontal line; PA12–14 appear closely grouped making it difficult to differentiate each one; PA16, PA17 and PA26 are close to each other, forming a transverse row; PA16 is not aligned longitudinally with PA27 and PA28; seta MN1 is located at basal third of mandible; MN5 is positioned more apically in the left mandible than in the right one; MN2–4 are arranged in an almost oblique row instead of forming a triangle as in most hydrophilid larvae; gMX2 on stipes is composed of 7–9 stout setae, with the basal ones sometimes bifid distally. Some differences can also be observed. The small additional pore on A2 present in *C. praetextatus* and *C. quisquilius* is not present in *C. convexiusculus*; instead, in the same place, FIKÁČEK (2006, unpublished) shows a small triangular cuticular spine, which could be homologous with the additional pore. In *C. praetextatus* and *C. quisquilius* this pore is smaller than the other pores on the antenna, but it does not resemble a cuticular spine or projection; at most it could represent an inner muscular insertion, but since it is not present in other hydrophilid larvae (except for other megasternine genera, see Table 3), and it is found in all three larval instars, it should be considered a diagnostic character. In *C. convexiusculus* sensilla MX25 and MX26 are not contiguous (actually MX26 is not shown), and pore MX17 is present (in *C. praetextatus* and *C. quisquilius* I could not locate this pore, but there is a chance that its presence is obscured by the sensoria of the gAPP). On the labium of *C. convexiusculus* LA5 is apparently absent (FIKÁČEK 2006, unpublished), and one pair of sensoria resembling LA12 are apparently absent too (these sensoria were perhaps overlooked). These differences in chaetotaxy are therefore important to allow differentiation among larvae of *Cercyon* species as well as among larval instars.

Comparative notes on the chaetotaxy with other Megasternini is not easy to perform since no other genera have been studied in detail. FUHRMANN et al. (2013) published a brief note on the morphology of third-instar larvae of a Brazilian species of *Pelosoma*, but they did not detail the chaetotaxic characters. I did compare larvae of *Cercyon* with those of the genera *Pelosoma*, *Cryptopleurum* and *Oosternum*; based on this material, I have made some brief generalizations which are summarized in Table 3. Most of these characters are similar in all these four genera. One character that shows a slight variation is the arrangement of the basal setae of gMX2 on the left stipes, in *Cercyon* and *Oosternum* they are clearly arranged in a transverse row while in *Cryptopleurum* and *Pelosoma* the transverse row is less obvious.

Additionally, some comparative notes can be made with the chaetotaxy of some known Coelostomatini, Protosternini and Sphaeridiini larvae. Detailed chaetotaxic descriptions are available for *Coelostoma orbiculare*

(Fabricius, 1775), *Dactylosternum cacti*, *Lachnodacnum luederwaldti* Orchymont, 1937, *Phaenonotum exstriatum* (Say, 1835), *Sphaeridium* spp. and *Sphaerocetum arboreum* Fikáček et al., 2015 (FIKÁČEK 2006, unpublished; CLARKSON et al. 2014; FIKÁČEK et al. 2015; ARCHANGELSKY et al. 2016). Table 3 summarizes some characters of importance and compares them with character states shared by the four Megasternini genera.

Asymmetry of stipes within Megasternini. Larvae of *Cercyon* display a very interesting modification in the morphology of the left stipes, which results in a stipital asymmetry. This asymmetry involves three modifications: 1) the left stipes becomes slightly wider than the right one; 2) the development of the dorsal cuticular spines and microtrichiae on the left stipes is more pronounced, covering the outer, the distal and the inner margins; 3) on the left stipes the basal setae of gMX2 assume a different arrangement, forming an oblique row instead of being in line (and pointing mediad) with the distal setae as occurs on the right stipes. These three modifications are to be considered apomorphic character states, which contrast with the condition found in most hydrophiloid larvae, that is both stipites being similar in size, shape, and distribution of setae and microtrichiae. This asymmetry has been reported only once, for *C. quisquilius*, by HAFEZ (1939), and to my knowledge no other mention of this particular character has been made in the literature; moreover it has not been mentioned for any other hydrophilid larvae. The larval asymmetry is more evident in *C. quisquilius* than in *C. praetextatus* (see Figs. 6 and 7), and is more strongly developed in third-instar larvae than in first-instar larvae (second-instar larvae are quite similar to third-instar ones). The maxillary asymmetry was not mentioned by FIKÁČEK (2006, unpublished) for first-instar larvae of *C. convexiusculus*; perhaps it is less evident than that of *C. quisquilius* and is closer to what is observed in *C. praetextatus* and therefore was less obvious. In order to confirm if this modification was exclusive of *Cercyon*, larvae of other Megasternini genera were examined, and similar modifications of the left stipes were observed in *Cryptopleurum*, *Oosternum* and *Pelosoma*. Additionally, larvae of *Sphaeridium* (Sphaeridiini) also display the first two modifications (left stipes wider, and distribution of microtrichiae more pronounced), but the setae on the inner margin retain the plesiomorphic condition, being in line along the inner margin. These modifications could be correlated with the development of the hypopharyngeal lobe, characteristic of many Sphaeridiinae larvae, which is developed on the left side (Fig. 6). These combined structures, acting as a sponge, probably improve the absorption of externally predigested fluids in all these terrestrial hydrophilids (ARCHANGELSKY 1999; FIKÁČEK et al. 2013). The development of similar setose or spinose structures is known to occur in other beetle larvae such as Lampyridae (e.g. ARCHANGELSKY & BRANHAM 1998) and in adults of liquid feeding beetles (LAWRENCE 1989; LESCHEN 1993). This character deserves special attention in future larval studies of Sphaeridiinae.

Table 3. Comparative table of selected chaetotaxic characters among larvae of Megasternini, Coelostomatini, Protosternini* and Sphaeridiini. * *Sphaerocetum* is known from a third instar larva, therefore recognition of primary sensilla is obscured.

Character	Megasternini				Coelostomatini				Proto-sternini	Sphaeridiini
	Cercyon	*Cryptopleu-rum*	*Oosternum*	*Pelosoma*	*Coelostoma*	*Dactylo-sternum*	*Lachno-dacnum*	*Phaeno-notum*	*Sphaero-cetum**	*Sphaeri-dium*
gFR2	absent	absent	absent	absent	present	present	present	present	present	absent
FR7	absent	absent	absent	absent	present	present	present	present	present	absent
PA1−3	in a trans-verse row not in line with PA4−5	in a trans-verse row not in line with PA4−5	in a oblique row not in line with PA4−5	in a trans-verse row not in line with PA4−5	in a longi-tudinal row with PA4−5	in a longi-tudinal row with PA4−5	in a longi-tudinal row with PA4−5	in a longi-tudinal row with PA4−5	in a longi-tudinal row with PA4−5	in a trans-verse row not in line with PA4−5
PA6	basal, almost touching frontal line	basal, almost touching frontal line	basal, almost touching frontal line	basal, almost touching frontal line	subbasal, far from frontal line	subbasal, rather close to frontal line	subbasal, far from frontal line	subbasal, far from frontal line	subbasal, far from frontal line	basal, almost touching frontal line
PA12−14	closely grouped	closely grouped	closely grouped	not closely grouped	not closely grouped	not closely grouped	not closely grouped	not closely grouped	appar-ently closely grouped	not closely grouped
PA26−28	not closely aggregated	not closely aggregated	not closely aggregated	not closely aggregated	closely ag-gregated	closely ag-gregated	closely ag-gregated	closely ag-gregated	rather closely aggregated	not closely aggregated
SE1 length	subequal to A3	subequal to A3	subequal to A3	subequal to A3	subequal to A3	half the length of A3	subequal to A3	subequal to A3	subequal to A3	much shorter than A3
Additional pore on A2	present	present	present	present	absent	absent	absent	absent	absent	absent
MN2−4	in an oblique row	in an oblique row	in an oblique row	in an oblique row	forming a triangle	forming a triangle	forming a triangle	forming a triangle	forming a triangle	in an oblique row
MN5	more apical in left mandible	more apical in left mandible	more apical in left mandible	more apical in left mandible	far from apex in both mandibles	far from apex in both mandibles	far from apex in both mandibles	far from apex in both mandibles	far from apex in both mandibles	more apical in left mandible
Stipital asym-metry	present	present	present	present	absent	absent	absent	absent	absent	present
MX25−26	placed dorsally, contiguous	placed dorsally, contiguous	placed dorsally, contiguous	placed dorsally, contiguous	MX25 dorsal, MX26 ventral	MX25 dorsal, MX26 ventral	MX25 dorsal, MX26 ventral	MX25 dorsal, MX26 ventral	?	placed dorsally, contiguous
Dorsal sec-ondary setae on disk of stipes (L3)	absent	absent	absent	absent	present	absent	present	present	absent	absent

Intra-specific variation. There are some incidental asymmetries that are of interest and are related to the secondary chaetotaxy; they have already been mentioned in the chaetotaxic descriptions of second and third-instar larvae. Both asymmetries are similar and are related to an extra seta near FR1; the first asymmetry occurs in one third-instar larva of *C. praetextatus* (Fig. 19), the second one occurs in one second-instar larva of *C. quisqui-lius* (not illustrated but similar to Fig. 19). These asym-metries occur only on the left side of the frons and in only one specimen of each species, therefore this can be interpreted as a duplication of FR1. Nevertheless in-traspecific variation in the number of secondary setae has been reported for other hydrophilid species (MINOSHIMA & HAYASHI 2011). For example *Enochrus* (*Holcophily-drus*) *simulans* (Sharp, 1873) may have one, two or three secondary setae between PA6 and PA7 in second-instar larvae, and in the same position may have three, four or five secondary setae in third-instar larvae (MINOSHIMA & HAYASHI 2011); comparable variations were also reported for other species of *Enochrus* Thomson and *Helochares* Mulsant (MINOSHIMA & HAYASHI 2011). ARCHANGELSKY et al. (2016) also mentioned an asymmetry in a first-instar larva of *Dactylosternum cacti* where an extra seta near PA13 appears on the right side of just one of the exam-ined specimens.

Phylogenetic considerations. The most recent and com-prehensive analysis of Hydrophilidae is that of SHORT & FIKÁČEK (2013), who recognize a well supported sub-family Sphaeridiinae; similar results were obtained by MADARIĆ et al. (2013) in a more restricted analysis. In both studies the Megasternini genera form the sister-group of *Sphaeridium* (Sphaeridiini), and Coelostomatini joins them more basally. A comparison of the chaetotaxy of the *Cercyon* species with that of other Megasternini, Coelostomatini and Sphaeridiini reveals some interest-ing aspects (some of these were already considered by FIKÁČEK 2006 and unpublished, before the chaetotaxic system was completely developed by FIKÁČEK et al. 2008).

In first place, larvae of *Cercyon*, *Cryptopleurum*, *Oosternum* and *Pelosoma* share several unique chaeto-taxic and morphological characters: 1) PA12–14 closely grouped (except *Pelosoma*); 2) additional pore on A2 present; 3) basal setae of gMX2 of left maxilla arranged

in an oblique row; 4) gMX2 with 5–9 setae; 5) legs strongly reduced, with two or less segments. Considering that almost all these characters are shared by the four genera they can be considered probable synapomorphies supporting the monophyly of the tribe Megasternini. To confirm this, it is of upmost importance to conduct more studies on the morphology and chaetotaxy of other genera of Megasternini.

In second place, several characters are shared by larvae of Megasternini and *Sphaeridium*: 1) gFR2 absent; 2) FR7 absent; 3) PA1–3 in a transverse row; 4) PA6 basal, almost touching frontal line; 5) PA26–28 not closely aggregated; 6) MN2–4 in an oblique row; 7) MN5 placed more apical in left mandible; 8) stipital asymmetry present (although less marked in *Sphaeridium*); 9) MX25–26 dorsal and contiguous. All these characters strongly support the sister-group relationship proposed by SHORT & FIKÁČEK (2013), MADARIĆ et al. (2013), FIKÁČEK et al. (2015) and also FIKÁČEK (2006, unpublished); in all these studies the two tribes appear as sister-groups with strong support.

Finally, based on the morphological and chaetotaxic information presented in this paper, the position of Coelostomatini and Protosternini is confirmed as more basal to the clade formed by Megasternini and Sphaeridiini as suggested by the studies of SHORT & FIKÁČEK (2013), MADARIĆ et al. (2013), FIKÁČEK et al. (2015) and FIKÁČEK (2006, unpublished). The larva of *Sphaerocetum* (Protosternini) described by FIKÁČEK et al. (2015) is of the third instar, this fact unfortunately obscures the interpretation of the primary chaetotaxy on the head capsule since this larva has numerous setae on it; nonetheless many of the characters listed on Table 3 are shared by *Sphaerocetum* and most of the Coelostomatini larvae included there, supporting a close relationship between these two tribes. Larvae of Omicrini are only known from second and third-instar larvae of *Omicrus ingens* Hansen & Richardson, 1998 described by HANSEN & RICHARDSON (1998); only the gross morphology of these larvae is available, therefore the chaetotaxic characters remain unknown. M. Fikáček (personal communication) has provided me with a brief description and some illustrations of an unidentified larva associated with adults of *Noteropagus* and *Paromicrus* (Omicrini), but the chaetotaxy of this larva is not complete, which makes it difficult to perform in-depth comparisons; in addition, the monophyly of Omicrini is still not fully resolved (SHORT & FIKÁČEK 2013; FIKÁČEK et al. 2013, 2015). Nonetheless these facts give a direction towards selecting groups of Sphaeridiinae to be studied from the point of view of larval morphology and chaetotaxy in order to reach a better understanding of the relationships within Sphaeridiinae.

5. Acknowledgements

6. References

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