



Primary chaetotaxy of the larval head capsule and head appendages of the Hydrophilidae (Coleoptera) based on larva of *Hydrobius fuscipes* (Linnaeus, 1758)

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Abstract

The primary chaetotaxy of the larval head capsule and head appendages of the family Hydrophilidae (Insecta: Coleoptera) is described and illustrated using the larva of *Hydrobius fuscipes* (Linnaeus, 1758) as a model, and compared with fifteen hydrophilid taxa representing all main taxonomic groups within the family; brief comparative notes with representatives of the families Helophoridae, Spercheidae, Hydrochidae and Histeridae are also provided. Primary chaetotaxonomic nomenclature is developed for the Hydrophilidae, allowing the use of chaetotaxonomic characters for phylogenetic studies as well as diagnostic purposes. The study of representatives of the families Helophoridae, Hydrochidae and Spercheidae suggests that this nomenclature can also be effectively applied to other hydrophiloid families. Chaetotaxonomic nomenclature systems used in larvae of other groups of Coleoptera are briefly reviewed.

Key words: chaetotaxy, head capsule, head appendages, Hydrophilidae, Coleoptera, Insecta

Introduction

Hydrophiloidea (*s. str.*) comprises a large group of beetles, worldwide in distribution, containing six families, 180 genera and about 3150 described species (Hansen 1999; Short & Hebauer 2006). Bionomically, they are a very diverse group of beetles, inhabiting both aquatic and terrestrial habitats. Adults and larvae are common in freshwater, riparian habitats, phytotelmata, decaying plant material, carrion, dung, etc. Feeding habits are contrasting: adults are mostly scavengers (including necrophagy) or herbivores, predatory in a few cases (Wilson 1923a,b; Miller 1963), while larvae are almost always predatory (Balduf 1935; Böving & Henriksen 1938; Miller 1963; Spangler 1991; Archangelsky 1997; Archangelsky et al. 2005).

The family Hydrophilidae (*s. str.*) comprises over 2650 species (Hansen 1999; Short & Hebauer 2006) and has been subdivided into four subfamilies. Of these subfamilies, Hydrophilinae and Sphaeridiinae are the most diverse and include several tribes each. Adults and larvae of Hydrophilidae are quite common, their size ranging from about 1.5 mm to about 50 mm in some genera (e.g. *Hydrophilus* Geoffroy, 1762).

For most beetle families, knowledge of the larval stages is generally very poor. Although immature stages of hydrophilids are better known than in other groups, there remains a lot of work to do within the family (Archangelsky 1999). Most work on immatures of this family has focused on their biology and general mor-

phology of larvae, pupae and egg cases (Fikáček 2006). This information has recently been applied to several phylogenetic studies (Hansen 1991; Beutel 1994, 1999; Archangelsky 1998, 2004; Beutel & Leschen 2005; Bernhard et al. 2006). These studies have relied mostly on morphological characters, including in a few cases anatomical characters such as musculature (Beutel 1999). Until now, no chaetotaxic characters have been used since no detailed chaetotaxic system for hydrophilids was available (Fikáček 2006).

The aim of this paper is to present a chaetotaxic system for first instar larvae of Hydrophilidae, using larvae of the genus *Hydrobius* Leach, 1815 as a reference. This genus is included in the subfamily Hydrophilinae, and following Hansen (1999) in the tribe Hydrophilini, although this tribal placement has been questioned by Archangelsky (2004). In this paper, a detailed description of the primary chaetotaxy of the head capsule and mouthparts of *Hydrobius fuscipes* (Linnaeus, 1758) is performed; this information is compared with larvae of fifteen additional hydrophilid taxa and with representatives of the Helophoridae, Hydrochidae, Spercheidae and Histeridae.

Review of larval chaetotaxic studies in Coleoptera

A sensillum (pl. sensilla) is any cuticular structure (seta, “pore”, etc.) associated with primary external receptors (Makarov 1996). Sensilla serve as mechano- and/or chemoreceptors, informing the larva about its environment (Chapman 1998; Makarov 1996). The arrangement of these sensilla on any part of the insect exoskeleton, i.e. so-called chaetotaxy (Nichols et al. 1989), is often characteristic of a given taxon or group of taxa, and is used for diagnostic purposes or as a source of phylogenetically informative characters. For these reasons, chaetotaxy has been extensively studied in many groups of Staphyliniformia and Adephaga, but very few studies have been performed for Hydrophiloidea (*s. str.*). The value of chaetotaxic characters for phylogenetic studies has been questioned by some authors (e.g. Makarov (1996) for the Carabidae), but results of other authors (e.g. Alarie 1995; Alarie & Bilton 2005; Alarie et al. 1999, 2000, 2002; Delgado & Archangelsky 2005) demonstrate that the rejection of the use of these characters for phylogenetic studies is not justified. Solodovnikov (2007) analyzed the problems of using chaetotaxy for phylogenetic studies in detail, defined the factors that complicate the study and suggested possible solutions.

The first attempt to develop a broadly applicable system and nomenclature of sensilla intended for beetle larvae was made by Bousquet & Goulet (1984) for carabid larvae. These authors based their system on the sensilla present in first-instar larvae (primary chaetotaxy), which are represented by setae and pores. Primary sensilla are further subdivided into those associated with an “ancestral pattern” of chaetotaxy (i.e. those found in most carabid taxa or at least in one carabid taxon and in at least one outgroup taxon studied by the authors) called ancestral, and those restricted to one genus or tribe studied called additional. Only ancestral primary sensilla are classified, named by a two-letter abbreviation of the sclerite or body part and numbered for setae or alphabetized for pores. Those sensilla of higher instars not having their homologues in first-instar larvae are called secondary.

Homologization of sensilla found within Adephaga with those found in Polyphaga is partially possible only for groups with prognathous predatory larvae, but it is usually very difficult for all other Polyphaga (Makarov 1996; Fikáček, pers. observ.). For this reason, Bousquet & Goulet’s system was not used for other groups of beetles. Instead, alternative chaetotaxic systems were developed for these groups.

Within Staphyliniformia three alternative systems were developed, each for a different taxonomic group. The most broadly applied system was that developed by Ashe & Watrous (1984) for larvae of the aleocharine Staphylinidae. This system is based on third-instar larvae; sensilla are named according to their position on the body, distinguished into setae and campaniform sensilla (the latter corresponding with “pores” sensu Bousquet & Goulet (1984)), setae are grouped in longitudinal groups on the head and tergites or in groups reflecting their position on the body, and are numbered for each recognized group. In contrast to Bousquet &

Goulet (1984), the antennomeres, segments of maxilla as well as sclerites of labium are distinguished as separate areas in this case. This system is at present widely used for aleocharine larvae (Ashe 1985; Ahn & Ashe 1996; Thayer et al. 2004) and only rarely applied to other staphylinid larvae (Paederinae: Frania (1986); Oxyporinae: Hanley & Goodrich (1994)). Within the Staphylinoidea, the system was also applied to larval Hydraenidae (Delgado & Soler 1997a, b; Delgado & Archangelsky 2005), with the difference that the chaetotaxic pattern of this family is based on first-instar larvae. In many other studies of staphylinoid larvae, the arbitrary numbering/alphabetizing of sensilla is presented allowing the homologization at least among closely allied taxa (e.g. Staphylinidae: Arrowinini: Solodovnikov & Newton (2005); Ptiliidae: Grebennikov & Beutel (2002)). The same approach was used also by Grebennikov (2004) for larvae of Archostemata.

A different system resembling that of Ashe & Watrous (1984) was developed by Wheeler (1990) for larval Leiodidae. In this case sensilla are recognized for first-instar larvae, additional setae of higher instars are marked with an asterisk, pore-like sensilla are omitted and the names of body parts and/or areas are different than those used by Ashe & Watrous (1984). This system, with slight modifications, is used exclusively for leiodid larvae by recent authors (e.g. Ratajczak 1995, 1996; Kilian 1998, 2001, 2007).

Kovarik & Passoa (1993) developed a different nomenclature for histerid larvae based on the larva of *Onthophilus nodatus* LeConte, 1845. Their system follows Bousquet & Goulet (1984) in dividing the body into well defined areas/sclerites (maxilla, labium and antenna are not subdivided) indicated by a two-letter abbreviation, and in numbering of setae and alphabetizing of pores of each of these areas/sclerites. Moreover, their study is also based on first-instar larvae and the proposed system concerns thus primary chaetotaxy. The nomenclature developed by Kovarik & Passoa was recently applied to some Hetaeriinae larvae by Caterino & Tishechkin (2006).

Chaetotaxy is rarely used for diagnostic or phylogenetic purposes in the remaining groups of Polyphaga, with the one exception being the Curculionoidea, in which the chaetotaxic system was developed by May (1967, 1994) and is currently widely used (e.g., Marvaldi 1999, 2003; Skuhrovec 2006, 2007). In other polyphagan groups, at most a very limited set of chaetotaxic characters is used, partly because of the polysetose type of chaetotaxy which complicates or completely excludes homologization of particular sensilla (e.g., Kiselyova & McHugh 2006, Lee et al. 2007, Micó et al. 2008).

Within the Hydrophiloidea, chaetotaxy was never adequately studied, and only a number of setae situated on the anterior margin of the nasale and epistomal lobes are mentioned in some of the published papers (Richmond 1920; Archangelsky 1997). The only attempt to describe the chaetotaxy of the head capsule of *Enochrus* Thomson, 1859 was published by Moulins (1959). He recognized four groups of setae (lateral setae, clypeolabral setae, oral setae, and microtrichia) but his results seem doubtful as he figured many additional setae to those named by him on the head of the examined species. The present study is therefore the first detailed study addressing the chaetotaxy of Hydrophilidae.

Material and methods

The chaetotaxic nomenclature was developed after consulting studies on larvae of different beetle families (Ashe & Watrous 1984; Bousquet & Goulet 1984; Alarie 1991, 1998; Wheeler 1990; Bousquet & Tchang 1992; Kovarik & Passoa 1993; May 1994; Delgado & Soler 1997a,b; Alarie et al. 2004; Alarie & Bilton 2005). First-instar larvae of 18 genera of Hydrophiloidea and one histerid species (Table 1) were examined in order to observe the variations in head chaetotaxy.

Larvae examined for this study were obtained through laboratory rearing; this assured correct association between the preimaginal stages and the adults. The only exception are larvae of *Sphaeridium* sp. and *Teretrius fabricii* Mazur, 1972, which were collected in the field and associated with adults, first instars were identified by sorting larvae into groups according to the size of their head capsules. Rearing techniques are described in

detail by Archangelsky (1997). Larvae were fixed in boiling water and stored in 75% ethyl alcohol. Specimens were cleared in warm lactic acid or cold 10% KOH, dissected and mounted on standard glass slides with Hoyer's medium for examination. Temporary slides (prepared with glycerin or lactic acid) were used for examination of head capsules in lateral view. Observation (at magnifications up to 1000×) and drawings were made using a Leica DMLB and Olympus BX40 compound microscopes equipped with camera lucida.

TABLE 1. List of taxa examined for this study.

Family	Species	Abbreviation
Histeridae	<i>Teretrius fabricii</i> Mazur, 1972	TeF
Helophoridae	<i>Helophorus liguricus</i> Angus, 1970	HeL
Spercheidae	<i>Spercheus emarginatus</i> (Schaller, 1783)	SpE
Hydrochidae	<i>Hydrochus megaphallus</i> Berge Henegouwen, 1988	HcM
Hydrophilidae	<i>Berosus signaticollis</i> (Charpentier, 1825)	BeS
	<i>Laccobius striatulus</i> (Fabricius, 1801)	LaS
	<i>Paracymus subcupreus</i> (Say, 1825)	PaS
	<i>Chaetarthria seminulum</i> (Herbst, 1797)	ChS
	<i>Cymbiodyta marginella</i> (Fabricius, 1792)	CyM
	<i>Enochrus coarctatus</i> (Gredler, 1863)	EnC
	<i>Helochares obscurus</i> (Müller, 1776)	HcO
	<i>Hydrobius fuscipes</i> (Linnaeus, 1758)	HdF
	<i>Hydrobius melaenus</i> (Germar, 1824)	HdM
	<i>Hydramara argentina</i> (Knisch, 1925)	HaA
	<i>Hydrochara caraboides</i> (Linnaeus, 1758)	HrC
	<i>Hydrophilus piceus</i> (Linnaeus, 1758)	HyP
	<i>Tropisternus lateralis</i> (Fabricius, 1775)	TrL
	<i>Coelostoma orbiculare</i> (Fabricius, 1775)	CoO
<i>Cercyon convexiusculus</i> Stephens, 1829	CeC	
	<i>Sphaeridium</i> sp.	Sph

The chaetotaxic nomenclature developed for Hydrophilidae is derived, in part, from that used for Carabidae by Bousquet & Goulet (1984) and for Aleocharinae by Ashe & Watrous (1984), but adapted for Hydrophilidae. A unique code is used for each sensillum, composed of its localization and a number. No distinction is made between setae and “pores” (i.e., pore-like sensilla), therefore sensilla are numbered consecutively. The following abbreviations are used: AN= antenna; APP= inner appendage of maxilla; FR= frontale; LA= labium; MN= mandible; MX= maxilla; PA= parietale; SE= sensorium. Sensilla on intersegmentary membranes are considered as belonging to the segment situated proximal to the membrane.

Following Bousquet & Goulet (1984), two types of primary sensilla are recognized: ancestral (recognized and homologized in most or all examined taxa) and additional (restricted to a genus or a tribe only, non-homologisable to any ancestral sensilla); only ancestral sensilla are numbered. Additional sensilla are marked by a black square in all drawings. Bousquet & Goulet (1984) did not define the term “ancestral sensillum” in a phylogenetic context (i.e., it does not refer to the presence of the sensillum in a presumed ancestor of the studied group). Although the term “ancestral” is therefore misleading in this sense, it is widely used in studies concerning the chaetotaxy of Coleoptera, in all cases sensu Bousquet & Goulet (1984). For that reason, we also decided to use the term “ancestral” sensu Bousquet & Goulet (1984) throughout this study. The phylogenetic significance of the primary sensilla recognized and named in this paper will be formally tested later on

by a phylogenetic analysis (Archangelsky, Torres, & Fikáček, in prep.). However, preliminary results based on a limited number of taxa suggest that all sensilla of *Hydrobius fuscipes* recognized here as “ancestral” sensu Bousquet & Goulet (1984) were really present in an presumed ancestor of the Hydrophilidae (Fikáček 2006).

Groups of sensilla whose homology could not be defined separately are marked by: g + abbreviation for localization + number (e.g. group of frontal setae of nasale: gFR1). Sensilla of apical membranous fields of antennomere III, maxillary palpomere IV and labial palpomere II were not compared in detail among taxa even though differences in number, size and shape of these sensilla may occur (Alekseev et al. 2006). We did not carry out SEM studies of these sensilla and refer to them as groups of sensilla (gAN, gMX1 and gLA, respectively) throughout this study.

The larva of *Hydrobius fuscipes* was chosen for the basic description of hydrophiloid chaetotaxy. Reasons for this choice are as follows

(1) Based on the examination of other hydrophilid taxa (Table 1), *Hydrobius fuscipes* bears all ancestral sensilla (sensu Bousquet & Goulet (1984)) present in the primary chaetotaxy of larval Hydrophilidae and does not bear any additional sensillum;

(2) The moderate size of the larva - the chaetotaxy can be more easily examined in first instars of *Hydrobius* than in many other Hydrophilidae;

(3) *Hydrobius* is a common Holarctic genus occurring broadly in the region; it is easy to rear and to collect in larval stage.

The criteria of position, special similarity, and transformation were used to hypothesize the homology of sensilla (Remane 1956). Concerning the position of a sensillum, its relative position to other adjacent sensilla as well as its relative position to non-chaetotaxic structures were evaluated. When more than one hypothesis of homology exists for a particular sensillum or group of sensilla, the hypothesis breaking the least number of criteria was chosen.

Three hypotheses explaining the structure of maxillary palpus have been proposed so far, which differ especially in the interpretation of the third maxillary segment: (1) Moulins (1959) interpreted the segment as the first palpomere based on maxillary musculature, considering the palpus as tetramerous; (2) Kovarik & Passoa (1993) regarded the segment as a fusion of sclerites from both the galea and palp; and (3) Beutel (1994, 1999) interpreted the segment as palpifer and deemed the palpus as trimerous. We do not favor any hypothesis over the others. Instead, we use the hypothesis by Moulins (1959) and consider the palpus as tetramerous in this paper to make the descriptions compatible with other descriptions of larval Hydrophilidae published recently (e.g. Archangelsky 1997; Hansen & Richardson 1998; Valladares 1994). The use of any of the hypotheses mentioned above does not affect the chaetotaxic nomenclature developed in this paper.

Results

Primary chaetotaxy of *Hydrobius fuscipes*

CHAETOTAXY OF HEAD CAPSULE (Figs. 1–2)

Frontale: with 44 sensilla altogether. Central part with three pairs of sensilla divergent posteriad – FR1 short, trichoid, situated close to frontal sulci; FR2 pore-like, situated more anteriorly and more mesally; FR3 trichoid, short and rather stout, situated even more anteriorly and slightly more mesally than FR2, but behind imaginary line connecting antennal sockets. Two long setae (FR5 and FR6) and one pore-like sensillum (FR4) situated slightly posteromesally to antennal socket, forming a triangular group. Seta FR7 moderately long, trichoid, close to inner margin of antennal socket. Nasale with group of six equidistant, stout and short setae (gFR1), the most lateral seta on each side situated in groove between nasale and epistomal lobe. Each epistomal lobe with a group of 4 moderately long setae (gFR2), two mesal setae slightly shorter than outer setae.

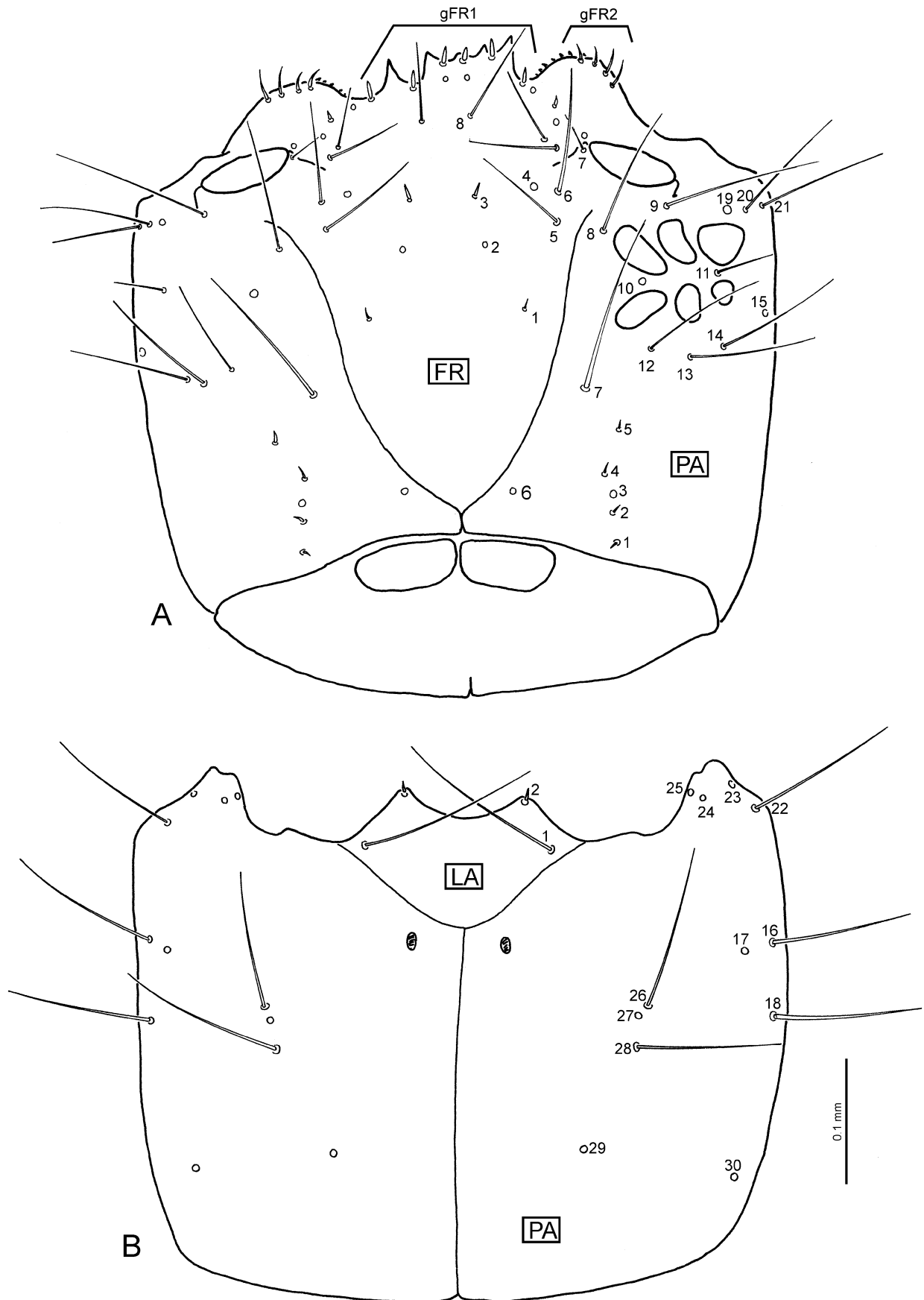


FIGURE 1. *Hydrobius fuscipes*, head capsule. (A) dorsal view; (B) ventral view.

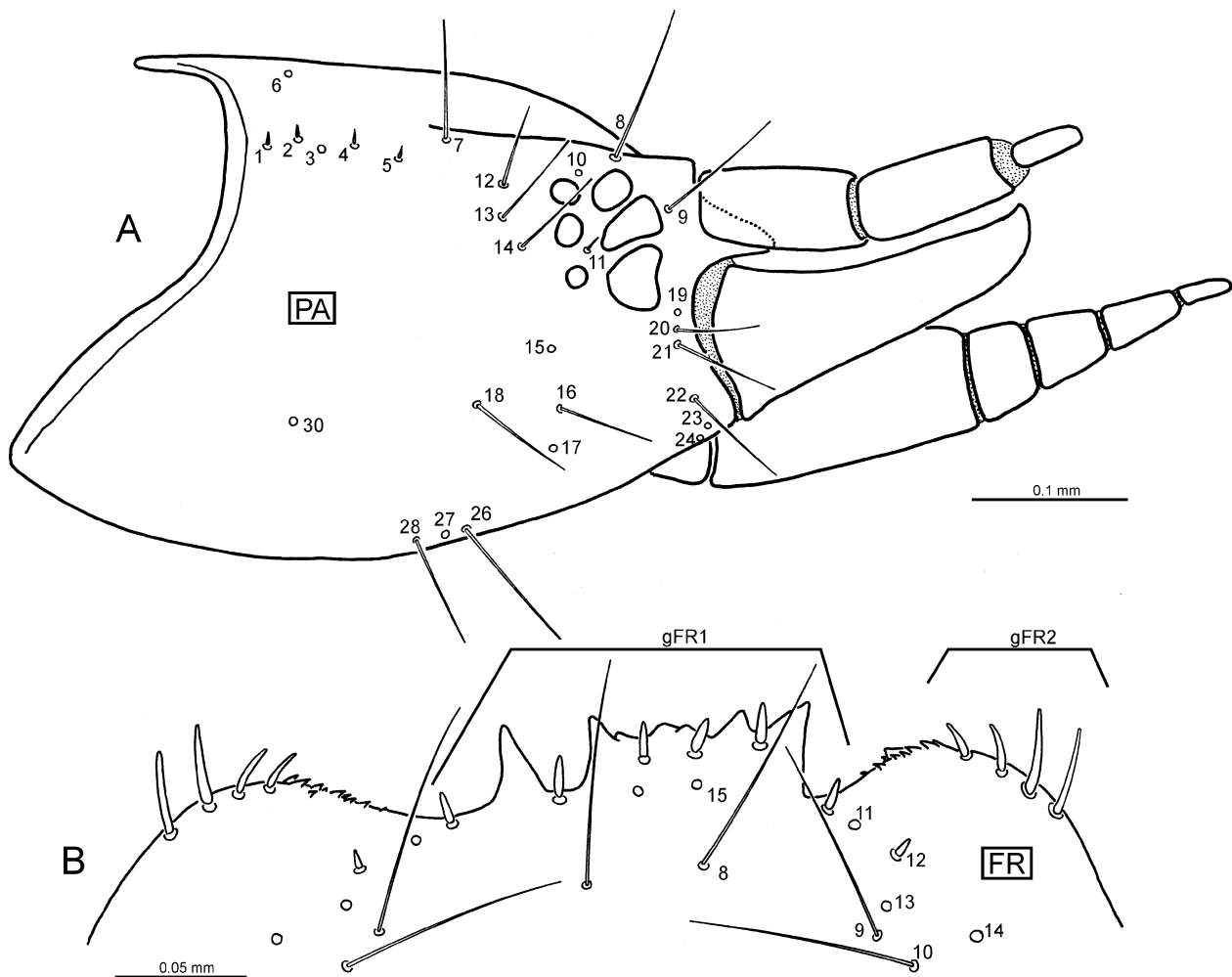


FIGURE 2. Head capsule of *Hydrobius fuscipes*. (A) lateral view; (B) detail of anterior margin of the head capsule.

Pore-like sensillum FR15 placed posterior to median setae of nasale; seta FR8 situated posteriorly to FR15. Two pairs of long trichoid setae (FR9 and FR10) situated between antennal socket and FR8. Epistomal lobes with four sensilla on each side – three equidistant pore-like sensilla (FR11, FR13 and FR14) and one short and stout seta (FR12) located outside of line connecting FR11 and FR13.

Parietale: with 30 sensilla each. Dorsal surface with a group of five sensilla (PA1–5) situated posteriorly on a longitudinal row at midwidth; PA3 pore-like, situated between PA2 and PA4; remaining sensilla short, trichoid. Sensillum PA6 pore-like, located posteromesally close to joint of epicranial and frontal sulci, more distant from posterior margin of head than PA1. Setae PA7 and PA8 long, trichoid, situated close to frontal sulcus; PA7 equidistant from PA8 and PA6, mesally of imaginary line connecting setae PA1 and PA5. Seta PA8 on anterior 0.25 of head. Seta PA9 long, trichoid, close to outer margin of antennal socket. Sensilla PA10 pore-like and PA11 trichoid, behind antennal socket; PA10 closer to frontal sulcus than PA11. Three long, trichoid setae (PA12–14) situated approximately at midlength of parietale, behind PA10-11. Anterolateral corner of epicranium with one pore-like sensillum (PA19) and three long trichoid setae (PA20–22); PA19 situated dorsally to the latter setae. Two pore-like sensilla (PA15 and PA17) and two long trichoid setae (PA16 and PA18) laterally on anterior third of parietale; PA15 situated dorsally, PA16-18 situated ventrally. Ventral surface with three pore-like sensilla (PA23–25) on anterior margin close to ventral mandibular acetabulum; PA23 more distant from PA24–25 than the latter from each other. Two long trichoid setae (PA26 and PA28) and one pore-like sensillum (PA27) situated at midlength of parietale on ventral surface; PA27 situated between the latter setae. Two pore-like sensilla (PA29–30) located ventrally on basal third of parietale, behind PA28.

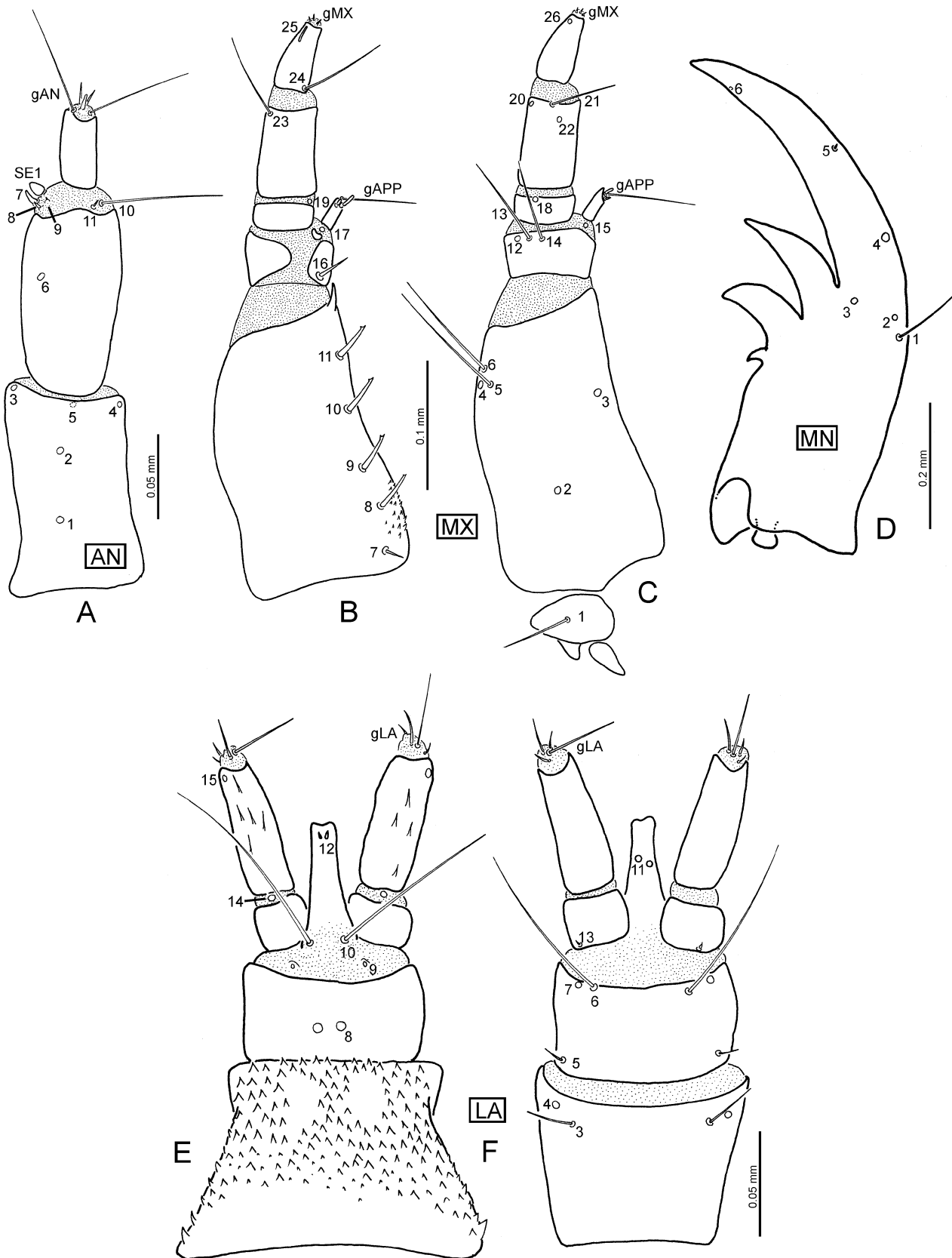


FIGURE 3. Head appendages of *Hydrobius fuscipes*. (A) left antenna, dorsal view; (B) left maxilla, dorsal view; (C) left maxilla, ventral view; (D) right mandible, dorsal view; (E) labium, dorsal view; (F) labium, ventral view.

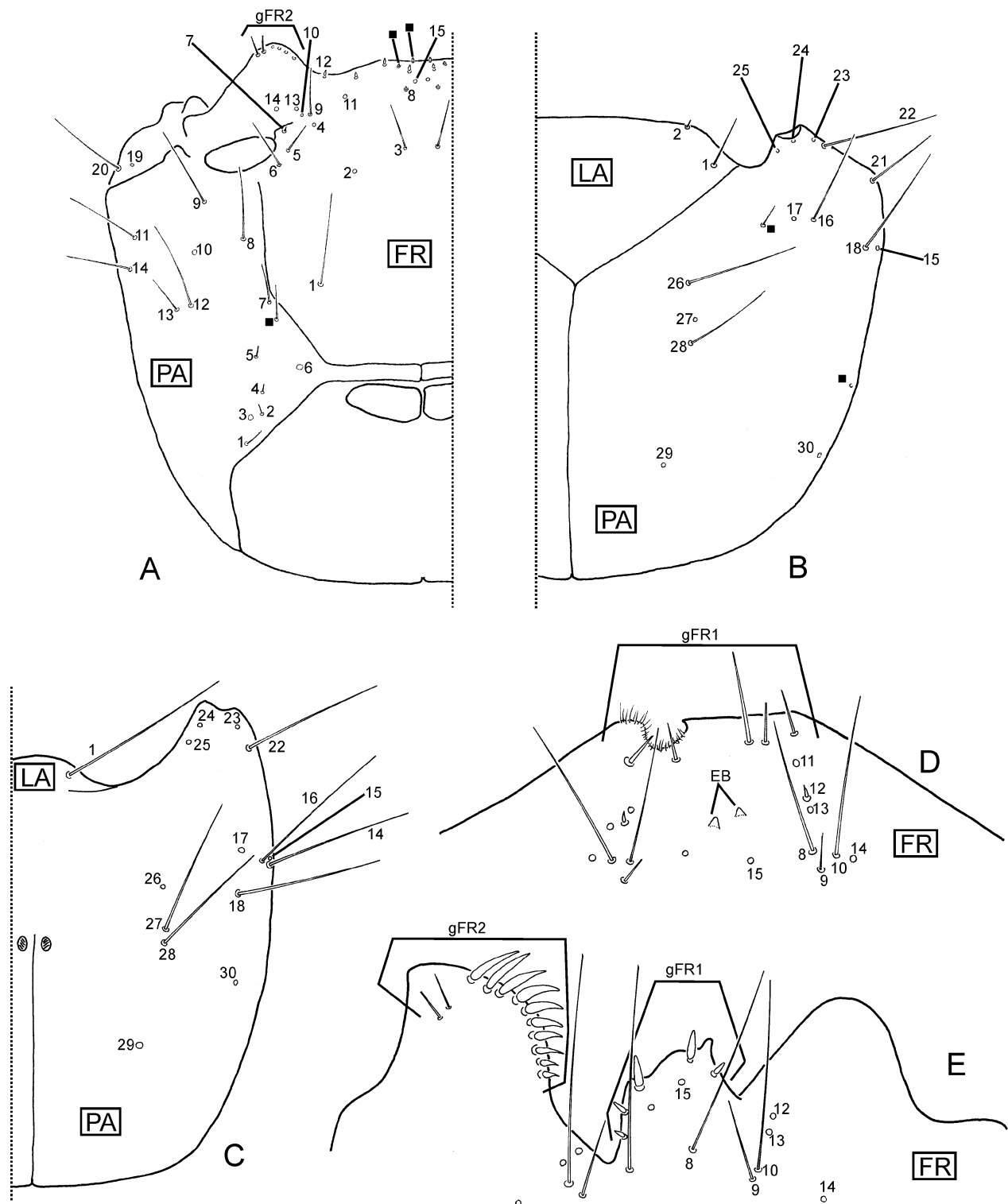


FIGURE 4. Head capsule of *Hydrophilus piceus* (A, B), *Laccobius striatulus* (C, E) and *Cercyon convexiusculus* (D). (A) head capsule, dorsal view; (B, C) head capsule, ventral view; (D, E) detail of anterior margin of head capsule. EB: egg bursters.

CHAETOTAXY OF HEAD APPENDAGES (Fig. 3)

Antenna: Antennomere I with five pore-like sensilla (AN1–5); AN1 situated in basal 0.5, AN2 in distal 0.25; AN3–5 on distal margin, AN3–4 dorsally, AN5 ventrally. Antennomere II with one pore-like sensillum (AN6) situated dorsally in distal 0.4, and five setae (AN7–11) situated on intersegmentary membrane between

antennomeres II and III; setae AN7–9 small, stout, situated on outer face of antenna next to sensorium (SE1); setae AN10–11 on inner face of antenna; AN10 long and trichoid, AN11 short, conical, both setae close to each other. SE1 small, much shorter than antennomere III, about as long as AN7. Antennomere III with five setae (gAN) situated in apical membranous area: two long trichoid setae, two short conical setae and one very short seta with highly projecting base.

Mandible: with 2 setae and 4 pore-like sensilla. Seta MN1 long, trichoid, on outer margin. Sensilla MN2–4 pore-like, forming a triangle at midlength on dorsal surface; MN2 more closely attached to MN1 than to MN3; MN4 situated at midlength between MN2 and MN5. Seta MN5 minute, situated on outer margin at midlength between retinacular base and mandibular apex. Pore-like sensillum MN6 situated subapically on inner face of mandible.

Maxilla: Cardo with one long, trichoid ventral seta (MX1). Stipes with a row of five moderately long, spiniform setae (MX7–11) situated dorsally along inner margin; all setae evenly spaced among themselves; MX7 shorter than MX8–11; MX8–11 with small subapical tooth. Ventral surface of stipes with two pore-like sensilla (MX2 and MX3) situated in basal and apical 0.33, respectively; outer margin of stipes with one pore-like sensillum (MX4) and two long, trichoid setae (MX5–6) situated in distal 0.2. Palpomere I with one moderately long spiniform seta (MX16) basally on inner face, and with pore-like sensillum (MX12) and two trichoid setae (MX13–14) ventrally along distal margin of sclerite; MX13 equidistant from MX12 and MX15. Two pore-like sensilla (MX15 and MX17) situated on membrane below inner appendage, MX17 dorsally, MX15 ventrally. Appendage with one long and four minute setae apically (gAPP). Palpomere II with two pore-like sensilla, one ventral (MX18) and one dorsal (MX19), on inner face on membrane between palpomeres II and III. Palpomere III with trichoid seta (MX21) and pore-like sensillum (MX22) ventrally at midwidth, and with pore-like sensillum (MX20) and moderately long seta (MX23) on outer face close to distal margin of sclerite. Palpomere IV with proximal long seta (MX24) on inner face of sclerite, and with digitiform sensillum (MX25) and pore-like sensillum (MX26) situated subapically. Apical membranous area of palpomere IV with 6 minute setae (gMX).

Labium: Submentum fused to head capsule, with two pairs of setae (LA1–2); LA1 long and trichoid on lateral corners, LA2 minute on anterior lobes. Mentum with 2 pairs of ventral sensilla, moderately long seta LA3 located more mesally than pore-like sensillum LA4; all sensilla situated close to distal margin of sclerite. Ventral surface of prementum with three pairs of sensilla; seta LA5 short, trichoid, situated proximo-laterally; LA6 long, trichoid; LA7 pore-like; LA6 and LA7 close to distal margin of sclerite, LA7 closer to lateral margin than LA6. Dorsal surface of prementum with a pair of pore-like sensilla (LA8) situated submesally close to midlength of sclerite. Membrane between prementum and palpi with one pair of long trichoid setae (LA10) at base of ligula, and a pair of small pore-like sensilla (LA9) more laterally between LA10 and distal margin of prementum. Ligula with two pairs of pore-like sensilla; LA12 subapical, situated dorsally; LA11 situated ventrally close to midlength of ligula (its position slightly variable among examined specimens). Labial palpomere I with a minute seta (LA13) ventrally on its base; pore-like sensillum LA14 dorsal, on membrane between palpomeres I and II; pore-like sensillum LA15 subapical, on outer face of palpomere II. Apical membranous area of palpomere II with 4 moderately long setae (gLA).

Discussion

DEVELOPMENT OF THE CHAETOTAXIC SYSTEM

After reviewing the systems used in other groups of Coleoptera in detail (see the review above) we decided to create a different system because we did not agree completely with the other nomenclature systems for the following reasons:

Ashe & Watrous (1984) used third-instar larvae for their system. This was done on the premise that third instars had the most complete setal pattern. We consider that a system based on primary chaetotaxy is better

since it is not obscured by presence of secondary setae; other authors agree with this point of view (e.g., Alarie 1991; Wheeler 1990; Kovarik & Passoa 1993).

We have made no distinction between setae and pores for several reasons:

(1) The term “pore” may concern many types of structures (campaniform, conical or placoid sensilla) (Chapman 1998; Solodovnikov 2007).

(2) In many cases it is not possible to distinguish clearly between pores and setae because many setae are minute, and can be confused with pores using the magnifications of compound microscope.

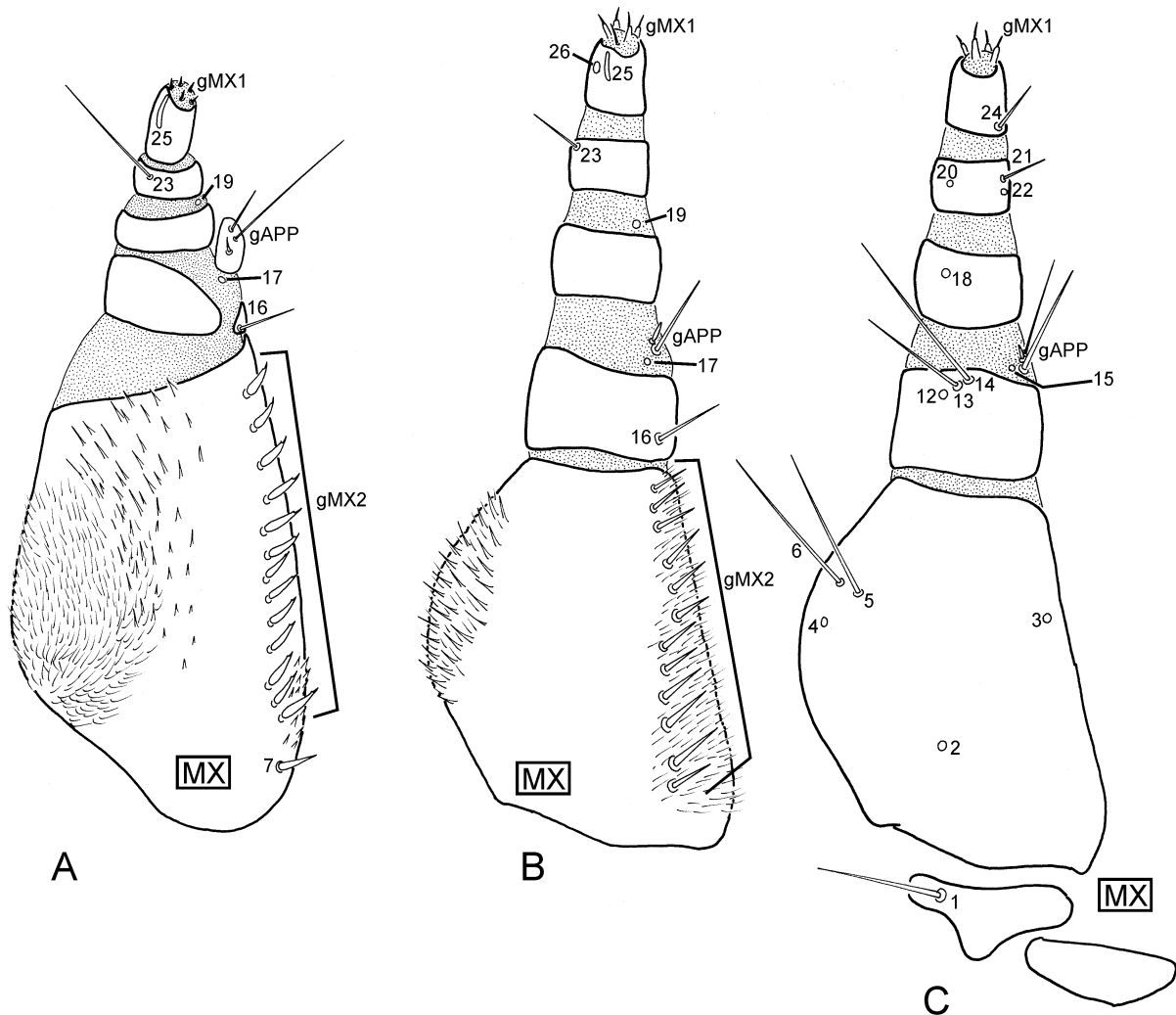


FIGURE 5. Left maxilla of *Coelostoma orbiculare* (A) and *Sphaeridium* sp. (B, C). (A, B) dorsal view; (C) ventral view.

(3) In some cases the external appearance of a particular sensillum is not constant among various hydrophilid taxa or even within the same specimen. The most striking example is sensillum MN5, which is pore-like on left mandible, but developed as small seta in right mandible of *Cercyon convexiusculus* and *Sphaeridium* sp. (Figs. 6B, C). Another example is the appearance of sensilla PA26 and PA27 in *Laccobius striatulus* (Fig. 4C) and *Coelostoma orbiculare*: PA26 is pore-like (developed as a seta in remaining taxa) and PA27 is developed as a long seta (pore-like in remaining taxa). A shift of the position of sensilla PA26 and PA27 could be an alternative explanation in this case and the homology of sensilla PA26–27 in *Laccobius* and *Coelostoma* with those of remaining taxa examined is therefore ambiguous. The position of sensilla PA26–28 is, however, very constant in all taxa examined (including the histerid *Teretrius fabricii*), forming a longitudinal or slightly oblique row (see Figs. 1B and 4B; Kovarik & Passoa 1993, Fig. 2). Taking into account the variable appear-

ance of sensillum MN5, we therefore consider the morphological modification of sensilla PA26 and PA27 of *Laccobius* and *Coelostoma* as a more parsimonious explanation than a shift in their position. Moreover, shifts in morphology of homologous sensilla (from pore-like sensillum to seta or vice-versa) are known also in other insect larvae (e.g., in Coleoptera: Cerambycidae (P. Švácha, pers. comm.) and Neuroptera: Mantispidae and Chrysopidae (Hoffman & Brushwein 1992)).

Within this paper, we do not state any homologies of the hydrophilid larval sensilla with representatives of non-hydrophilid beetle families, even though sensillum abbreviations used by us may be similar or the same as in the chaetotaxic systems used for adepagan larvae and the Histeridae. We applied our chaetotaxic nomenclature to the larva of *Teretrius fabricii* (Histeridae), but this was done solely for comparative purposes (Table 2).

PRIMARY CHAETOTAXY OF THE LARVAL HEAD OF THE HYDROPHILIDAE

Primary sensilla on the larval head are rather constant regarding their presence/absence, size and shape in all hydrophilid taxa examined. All observed differences are summarized in Table 2, some of the most important ones are commented below. The variability is restricted to a few areas of the head capsule and head appendages, chaetotaxy of remaining parts is constant in number, size and shape of sensilla even in representatives of different tribes and subfamilies. Most of the observed differences concern the positions of the sensilla on the body part or its relative positions to adjacent sensilla. These “positional” differences are very distinct between representatives of different tribes/subtribes, but only a few differences were observed between closely related genera (*Helochares*, *Enochrus* and *Cymbiodyta* in our study). Comparison of European species of the genus *Enochrus* (M. Fikáček, unpublished data) revealed only minute differences between species of the genus. This stands in contrast with many other beetle groups with freely-living larvae (e.g., Carabidae, Dytiscidae, Staphylinidae, Leiodidae) in which rather high interspecific variability was observed and drastic changes in chaetotaxy often occur among groups on higher taxonomic levels (Makarov 1996, Alarie 1991, Solodovnikov & Newton 2005, Kilian 1998).

On the hydrophilid head capsule, the most considerable variability concerns the chaetotaxy of the nasale and epistomal lobes (groups gFR1 and gFR2). The nasale usually bears six setae (gFR1), but this number is reduced to five setae in *Laccobius* (Fig. 4D), *Cercyon convexiusculus* (Fig. 4E) and *Sphaeridium*, and to four setae in many Coelostomatini (*Coelostoma* in our study). Chaetotaxy of epistomal lobes (gFR2) is even more variable both in number, size and shape of the sensilla (Table 2) and is one of few chaetotaxic characters usable for distinguishing species of one genus in some taxa (e.g., see Table 2 for the differences in number of sensilla between *Hydrobius fuscipes* and *H. melaenus*). Larvae of *Berosus* and *Laccobius* differ most apparently from *Hydrobius fuscipes* in this aspect: the left epistomal lobe is enlarged and armed with strong setae directed mesally (gFR2), whereas the right lobe lacks sensilla (*Laccobius*, Fig. 4E) or is completely absent (*Berosus*). In *Sphaeridium* and representatives of the Megasternini, epistomal lobes including their sensilla are missing (Fig. 4D; Archangelsky 1997). Remaining sensilla of the head capsule do not vary much among taxa. The most considerable difference from the chaetotaxy of *Hydrobius fuscipes* is found in *Hydrophilus piceus*, possibly due to its large body size: two additional sensilla are present on the anterior part of the frontale (these same sensilla are present also in *Tropisternus*) and three additional sensilla are developed on each parietale (Figs. 4A, B). Appearance of ventral sensilla of parietale (PA26 and PA27) varies in larvae of *Laccobius* (Fig. 4C) and *Coelostoma* and was already discussed above.

Antennal chaetotaxy shows little variation among taxa, with larger differences found only in *Hydrophilus piceus*, in which inner face of antennomere I bears a group of long and stout additional setae and an additional pore-like sensillum is present on the antennomere III (Fig. 6D). Remaining taxa vary in number of small sensilla adjacent to sensorium 1, ranges from one in *Berosus* to three in many Hydrophilini taxa including *Hydrobius fuscipes*. An additional pore-like sensillum is present in distal part of antennomere I in *Berosus*.

TABLE 2. Comparison of head primary chaetotaxy (absence/presence of sensilla and their appearance) of taxa examined for this study. Abbreviations: + - present; - - absent; a - on anterior part of frons; asym. - asymmetrical; p - on posterior part of frons; sym. - symmetrical; * - symmetrical; # - different appearance on left and right mandible; (?) - ambiguously homologized sensillum. For taxa abbreviations see Table 1.

	Tef	HeL	SpE	HcM	BeS	LaS	PaS	ChS	CyM	EnC	HcO	HbF	HbM	HaA	HrC	HYP	TrL	CoO	CeC	Sph
Number of setae in gFR1	2	2	6	0	6	5	6	6	6	6	6	6	6	6	6	6	6	4	5	5
Chaetotaxy of epistomal lobes	sym.	sym.	?	sym.	asym.	asym.	sym.	sym.	sym.	sym.	sym.	sym.	sym.	sym.	sym.	sym.	sym.	sym.	?	?
Number of setae/pores in gFR2	6/1	5/3	0/0	6/0	11/0	12/0	2/0	4/0	2/1	0/2	4/1	4/0	8/0	7/0	4/2	2/4	4/0	2/0	0/0	0/0
Sensilla FR2	pore	pore	seta (?)	pore	pore	pore	-	pore	pore	pore	pore	pore	pore	pore	pore	pore	pore	pore	pore	pore
Setae FR3	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Setae FR7	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-
Sensilla FR11	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Additional sensilla on FR	4p	2p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4a	2a	-	-
Seta PA22	-	-	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sensillum PA26	seta	seta	seta	seta	seta	pore	seta	seta	seta	seta	seta	seta	seta	seta	seta	seta	seta	pore	seta	seta
Sensillum PA27	pore	pore	pore	pore	pore	seta	pore	pore	pore	pore	pore	pore	pore	pore	pore	pore	pore	pore	seta	pore
Additional sensilla on PA	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	1
Group of setae on inner face of antennomere I	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
Additional pore on antennomere I	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SE2 of antennomere II	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Number of sensilla adjacent to SE1 (and SE2 if this is present)	3	2	1	1	1	2	2	2	3	3	3	3	2	3	2	2	2	2	2	3
Number of sensilla on antennomere III (without gAN)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Sensillum MN5	seta	seta	seta	seta	seta	pore	seta	pore	seta	seta	seta	seta	seta	seta	pore	seta	seta	pore	pore/ seta*	pore/ seta*
Pore MN6	-	-(?)	-	-(?)	+	-	+	+	+	+	+	+	+	+	+	-	+	+	+	+
Additional minute pores on mandibular apex	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Number of setae on inner face of stipes	>7	5	5	5	5	5	5	5	5	5	5	5	5	7	5	6	5	5	>7	>7
Additional sensilla on palpomere I	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sensilla MX15 and MX17 gAPP	-	pores	pores	setae	pores	pores	pores	pores	pores	pores	pores	pores	pores	pores	pores	pores	pores	pores	pores	pores
Setae LA2	+	+	-	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sensilla LA4	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Setae LA5	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sensilla LA9	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Setae LA10	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Sensilla LA11	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Digitiform sensillum on labial palpomere 2	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pore LA14	+	+	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pore LA15	+	+	+	-	-	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Additional setae on mentum / prementum	-	-	1/0	1/0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

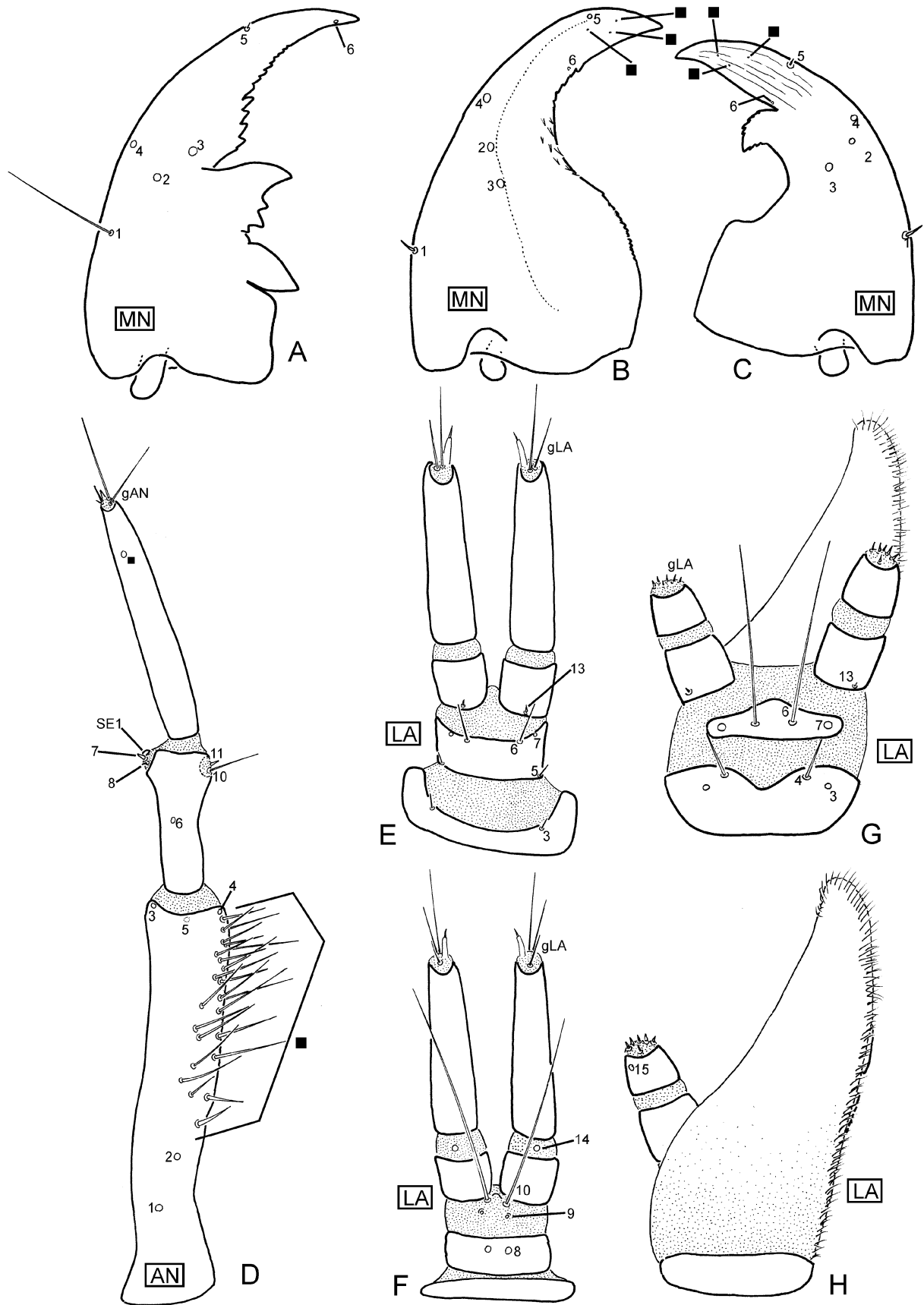


FIGURE 6. Head appendages of *Enochrus coarctatus* (A), *Cercyon convexiusculus* (B, C, G, H), *Hydrophilus piceus* (D) and *Berosus signaticollis* (E, F). (A, B) left mandible, dorsal view; (C) right mandible, dorsal view; (D) left antenna, dorsal view; (E, G) labium, ventral view; (F, H) labium, dorsal view.

Mandibles are most conservative concerning their chaetotaxy, even though the relative position of sensilla varies considerably among taxa. Sensilla MN5 are developed as setae in most taxa, but pore-like sensilla were found in *Laccobius*, *Hydrochara* and *Tropisternus*. In *Cercyon* and *Sphaeridium*, the appearance of this sensillum on left mandible (pore-like sensillum) differs from that on right mandible (small seta) (Figs. 6B, C). Sub-apical pore-like sensillum MN6 is usually very small, and is absent in *Laccobius* and *Hydrophilus piceus*. Three additional minute pore-like sensilla are present on mandibular apices in *Coelostoma orbiculare* and *Cercyon convexiusculus* (Fig. 6B, C).

The maxilla varies especially in chaetotaxy of inner face of stipes. Most hydrophilid taxa bear five stout setae in this area (MX7–11) (Fig. 3B), but the number of setae increases and forms a group (gMX2) in all sphaeridiine taxa examined (Figs. 5A, C) and in *Hydracara argentina*. In all these taxa except of *Sphaeridium* (Fig. 5B), sensillum MX7 is still recognizable from this group by its shape and basal position (Fig. 5A) and gMX2 therefore seems to be homologous to setae MX8–11. In *Hydrophilus piceus*, one additional spiniform seta is present close to seta MX11 on distal part of stipes, but sensilla MX7–MX11 are easily recognizable. In Megasternini and *Sphaeridium*, the inner appendage of maxilla is reduced in size, but its sensilla (gAPP) are still present on distal part of maxillary palpomere 1 (Figs. 5B, C).

Chaetotaxy of labium varies considerably among taxa, but this variability is caused mainly by reduction of some labial structures. This concerns reduction of the ligula and its sensilla (LA11 and LA12) in *Berosus* (Fig. 6F) and *Cercyon* (Fig. 6H) (ligula is reduced also in *Laccobius*, in which LA11 are still present), and the partial reduction of mentum and prementum in *Laccobius*, *Berosus* (Figs. 6E, F) and all Megasternini (Figs. 6G, H). Representatives of the Megasternini and *Sphaeridium* bear a large hypopharyngeal lobe reaching or overlapping apices of labial palps distally (Figs. 6G, H). This lobe largely covers the prementum and may be the reason why many premental sensilla are reduced even in *Sphaeridium* in which the labium is generally not reduced. Except of this, the anterior pair of submental sensilla (LA2) is absent in *Berosus* and *Laccobius* (Fig. 4C).

Besides the low variability in the presence/absence, size, and shape of the sensilla, there is a rather high variability in the position of sensilla in various taxa (e.g., compare mandibular sensilla MN2–4 of *Hydrobius fuscipes* (Fig. 3D), *Enochrus coarctatus* (Fig. 5A) and *Cercyon convexiusculus* (Figs. 5B, C)). These “positional” differences provide enough characters for identification purposes and phylogenetic studies (Fikáček 2006), but are not so drastic as to disable the homologization of the sensilla among taxa. Because these differences are present mainly between higher taxa, chaetotaxic characters seem to be useful mainly as additional characters for reconstructing the intertribal and intergeneric phylogenetic relationships within the Hydrophilidae. A phylogenetic analysis using chaetotaxic larval characters is in preparation by the authors, using a wider taxon sampling than the one presented in this study.

PRIMARY CHAETOTAXY OF LARVAL HEAD IN OTHER HYDROPHILOID FAMILIES

Larvae of three other hydrophiloid families, Helophoridae, Hydrochidae and Spercheidae, were examined for this study, with each family represented by one species only (see Table 1). Head chaetotaxy of *Helophorus liguricus* was found to be rather similar to the Hydrophilidae, but resembling in several aspects the chaetotaxy of *Teretrius fabricii* (Histeridae) (Table 2). In contrast, the chaetotaxy of *Hydrochus megaphallus* and *Spercheus emarginatus* is highly modified in comparison with the Hydrophilidae and Helophoridae and seems to be correlated with the modified head morphology of these two families (see e.g. Archangelsky (1997) and Beutel (1999) for details on morphology). In all three families, head sensilla are however rather easily homologizable with those of the Hydrophilidae, and surprisingly few differences in presence/absence, size and shape of sensilla were observed (Table 2). This is true also for *Spercheus*, which head sensilla were considered as “irregularly distributed” by Beutel (1999). The chaetotaxic nomenclature developed above for the Hydrophilidae seems to be therefore easily applicable even for these hydrophiloid families.

Studies comprising more taxa of the above mentioned families and also representatives of the remaining two families (Georissidae and Epimetopidae) are needed for a better understanding the primary chaetotaxy of small hydrophiloid families. For that reason, we do not address the chaetotaxy of these families in detail in this study and use it only for comparative purposes.

Acknowledgements

We are indebted to P. Švácha and J. Klečka (both Institute of Entomology, Czech Academy of Science, České Budějovice) for providing us with some larval material used for this study. We are grateful to A. Solodnikov (Natural History Museum of Denmark), Y. Alarie (Laurentian University, Canada), M. Michat (University of Buenos Aires), and A. Short (University of Kansas, USA) who provided us with their notes and comments on an earlier version of this manuscript, and to V. Grebennikov (Canadian Food Inspection Agency) for a detailed review and valuable comments on the final manuscript. The preparation of the study was partly supported by the following grants: Charles University Grant Agency (GAUK) 18307/2007/B-Bio/PrF, Ministry of Education of the Czech Republic (MŠMT ČR) 0021620828 and Ministry of Culture of the Czech Republic (MK ČR) 00002327201, University of Buenos Aires PIB X846. This is contribution number 18 from LIESA.

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