Chapter 2
Larval Chaetotaxy of World Dytiscidae (Coleoptera: Adephaga) and Implications for the Study of Hydradephaga

Yves Alarie and Mariano C. Michat

Abstract Although the Dytiscidae (Coleoptera) are among the most common insect inhabitants of freshwaters, knowledge of their larval morphology is scanty throughout the World. The identification of larvae is a continuing problem because the literature available to accomplish this is scattered, limited to certain groups, outdated, difficult to use or non-existent. Recent studies have demonstrated the taxonomic and phylogenetic value of chaetotaxy in studying larval Dytiscidae. The study of body sensilla (setae and pores) was shown to be useful and important both for diagnosis and study of phylogenetic relationships among taxa. The fact that all these studies were conducted separately over a period of more or less 30 years, however, does not facilitate comparison among taxa. This chapter synthesizes these studies into a more comprehensive approach, which should facilitate comparison among the dytiscid subfamilies. Although this framework is useful for the study of larval morphology of the Dytiscidae, it has also recently contributed to the study of larvae of other families of Hydradephaga, namely Aspidytidae, Gyrinidae, Haliplidae, Hygrobiidae, Meruidae and Noteridae. A corollary objective of this chapter therefore is to illustrate the power of larval chaetotaxy for testing hypotheses of phylogenetic relationships of Hydradephaga.

Keywords Larval morphology · Chaetotaxy · Meruidae · Aspidytidae · Gyrinidae · Haliplidae · Hygrobiidae · Noteridae · Dytiscidae

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2.1 Introduction

Coleoptera is the largest order of the Kingdom Animalia, comprising a quarter of all known animal species (Gullan and Cranston 2010). The order is represented in almost every non-marine habitat on Earth. It includes many of the most beneficial and destructive insects known, yet an enormous amount of basic taxonomy and biological study is necessary to raise our understanding of this group to the level attained in most other insect orders. The current state of coleopteran taxonomy is uneven in several ways, with many large geographical, developmental and taxonomic gaps (Stehr 1991).

While the state of knowledge of adult beetle taxonomy varies widely across taxa, our knowledge of coleopteran larvae is generally poor. Most beetle larvae are unidentifiable to species, even though the larval stage typically lasts longer than the adult stage and often has the greatest impacts on humans and the environment. As Holometabola, beetle larvae are under differing selection pressures compared to adults and as such show quite different morphological features. As a different expression of the same genotype, each larval instar represents an ontogenetic stage with its own characters, each being important in determining taxa, reconstructing phylogenies, and building classifications.

With over 4600 described species (Nilsson and Hájek 2022), the beetle family Dytiscidae represents one of the largest and most commonly encountered groups of aquatic insects. Up until recently, however, the identification of their larvae was a regular and continuing problem for many because the literature available to accomplish this was widely scattered, limited to certain groups, outdated, difficult to use, or non-existent (Larson et al. 2000). Moreover, larval descriptions were usually lacking or, where present, inadequate because of lack of comparative precision and detail. In part because of this, and also to develop a system useful for phylogenetic analysis, a system of nomenclature of larval chaetotaxy was devised for most Dytiscidae subfamilies but the Hydrodytinae: Agabinae (Alarie 1995, 1998; Alarie et al. 2019; Hájek et al. 2019; Okada et al. 2019; Alarie and Michat 2020), Colymbetinae (Alarie 1995, 1998; Michat 2005; Alarie and Hughes 2006; Alarie et al. 2009), Copelatinae (Michat and Torres 2009), Coptotominae (Michat and Alarie 2013), Dytiscinae (Miller et al. 2007; Alarie et al. 2011a; Michat et al. 2015, 2019), Hydroporinae (Alarie et al. 1990; Alarie and Harper 1990; Alarie 1991; Alarie and Michat 2007a), Laccophilinae (Alarie et al. 2000, 2002b; Michat and Toledo 2015), Lancetinae (Alarie et al. 2002a), and Matinae (Alarie et al. 2001). The fact that all these studies were conducted separately over a period of more or less 30 years does not facilitate comparison among taxa. The main purpose of this chapter therefore is to synthesize these studies into a more comprehensive approach, which should facilitate comparison among the dytiscid subfamilies. Whereas such framework was particularly useful in studies of larval morphology of the Dytiscidae, it has also contributed more recently towards the reconstruction of the larval ground plan of other Hydradephaga families, namely Aspidytidae (Alarie and Bilton 2005), Gyrinidae (Archangelsky and Michat 2007; Michat et al. 2010, 2016, 2017b; Michat and

Gustafson 2016; Colpani et al. 2018, 2020), Haliplidae (Michat et al. 2020), Hygrobiidae (Alarie et al. 2004), Meruidae (Alarie et al. 2011b), and Noteridae (Urcola et al. 2019, 2019a, b, 2020, 2021). A corollary objective of this chapter therefore is to illustrate the power of larval chaetotaxy as a tool for testing hypotheses of phylogenetic relationships of the Hydradephaga families by comparing in particular the generalized leg chaetotaxy pattern derived from that of the Dytiscidae.

2.2 General Morphology of Dytiscidae Larvae

Like other Adephaga, dytiscid larvae are campodeiform with a strongly sclerotized head capsule and prognathous mouthparts. The body is variously shaped, usually elongate and fusiform, generally widest at level of metathorax or middle abdomen (Figs. 2.1a–c, 2.2a–c and 2.3a–l). The dorsal surface of the body is usually distinctly sclerotized, whereas the ventral surface is mostly membranous with sclerotized plates, if present, restricted to the most posterior segments. Sclerites are usually

Fig. 2.1 Dorsal habitus of selected Dytiscidae: (**a**) *Agabus/Ilybius* sp.; (**b**) *Cybister fimbriolatus* (Say, 1823); (**c**) *Dytiscus* sp. Courtesy of Dr. Steve Marshall, University of Guelph, ON, Canada

Fig. 2.2 Dorsal habitus of selected Dytiscidae: (**a**) *Hydrovatus pustulatus* (E.F. Melsheimer, 1844); (**b**) *Laccophilus* sp.; (**c**) *Neoporus undulatus* (Say, 1823). Courtesy of Dr. Steve Marshall, University of Guelph, ON, Canada

more pigmented than the rest of the body. Colour patterns occur on the head capsule and terga of most taxa.

The head capsule is strongly sclerotized and variable in shape (triangular, subquadrate, subrectangular, subtrapezoidal, rounded or pyriform (Fig. 2.4a–f). It is divided above by a Y-shaped epicranial suture, which delimits a frontoclypeal region and two lateral epicranial plates (= parietals). An occipital suture may be present, which crosses the back of the head capsule, intersecting the stem of the epicranial suture (Fig. 2.4a). The anterior margin of the frontoclypeus is usually moderately arcuate, but in some groups (e.g., the Hydroporinae) it extends anteriorly, forming a median projecting lobe called the nasale (Fig. 2.4e and f). The first instar of most taxa possesses a pair of spine-like tubercules or egg-bursters (*ruptor ovi* of Bertrand (1972)), usually located on the posterior half of the frontoclypeus (Fig. 2.4a, c and e). Each parietal bears an antennal fossa and six stemmata (absent in subterranean taxa). The antennae are elongated and are comprised of four antennomeres (Fig. 2.5a–d). The antennomere III apically bears a sensory process, which may be short and non-apparent (Fig. 2.5b) or elongate, sometimes as long as the antennomere IV (Fig. 2.5d). The mandibles are well developed, narrow and falcate and in most taxa are grooved mesally as an adaptation for a liquid mode of

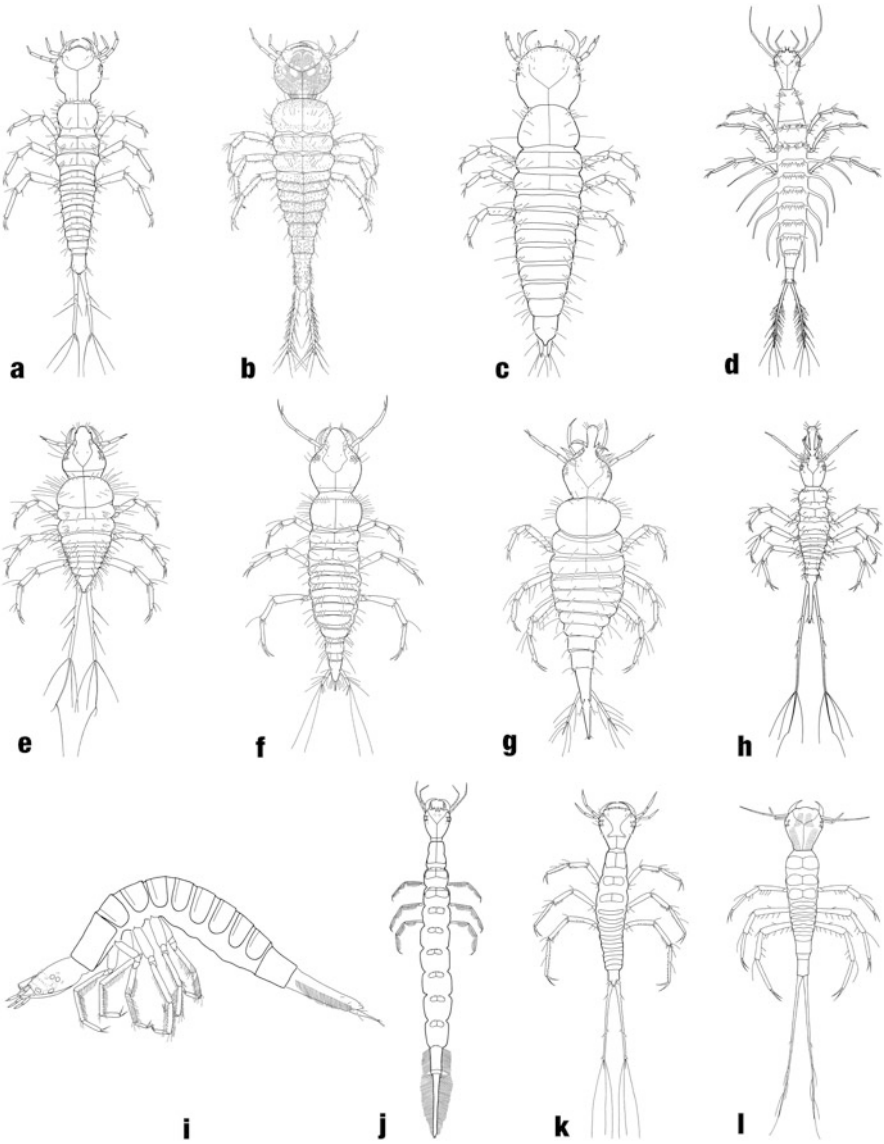

Fig. 2.3 First instars of selected species of Dytiscidae, dorsal view: (**a**) *Platynectes curtulus* (Régimbart, 1899); (**b**) *Bunites distigma* (Brullé, 1838); (**c**) *Copelatus longicornis* Sharp, 1882; (**d**) *Coptotomus longulus lenticus* Hilsenhoff, 1980; (**e**) *Amarodytes duponti* (Aubé, 1838); (**f**) *Celina parallela* (Babington, 1842); (**g**) *Pachydrus obesus* Sharp, 1882; (**h**) *Derovatellus lentus* (Wehncke, 1876); (**i**) *Thermonectus succinctus* (Aubé, 1838); (**j**) *Megadytes glaucus* (Brullé, 1838); (**k**) *Laccophilus obliquatus* Regimbart, 1899; (**l**) *Lancetes marginatus* (Steinheil, 1869)

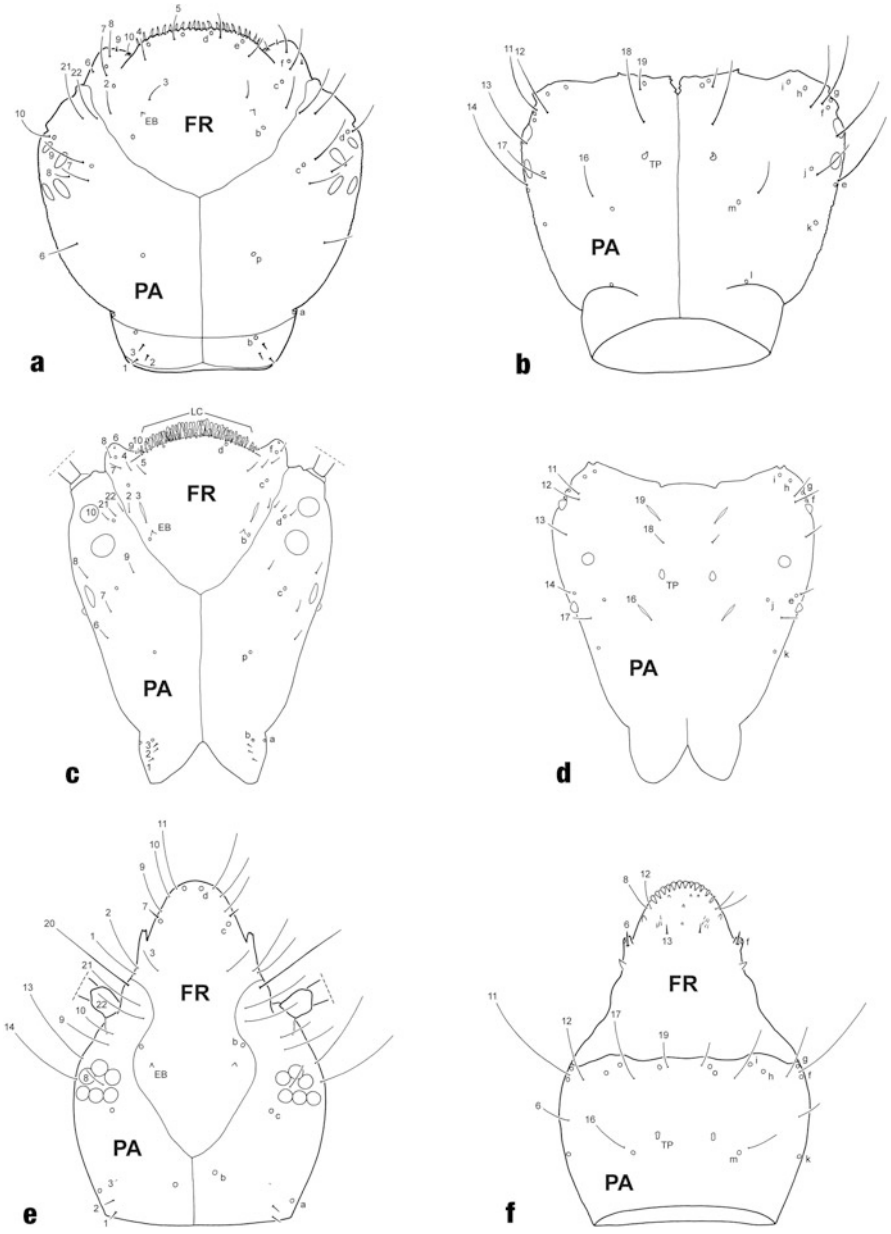

Fig. 2.4 Distribution of ancestral setae and pores on the cephalic capsule of first instars of selected species of Dytiscidae: (**a–b**) *Rhantus calileguai* Trémouilles, 1984, (**a**) dorsal surface, (**b**) ventral surface; (**c–d**) *Acilius semisulcatus* Aubé, 1838, (**c**) dorsal surface, (**d**) ventral surface; (**e–f**) *Anodocheilus maculatus* Babington, 1842, (**e**) dorsal surface, (**f**) ventral surface. *EB* egg burster, *FR* frontoclypeus; *LC* lamellae clypeales, *PA* parietale, *TP* tentorial pit; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2.1 for list of setae and pores)

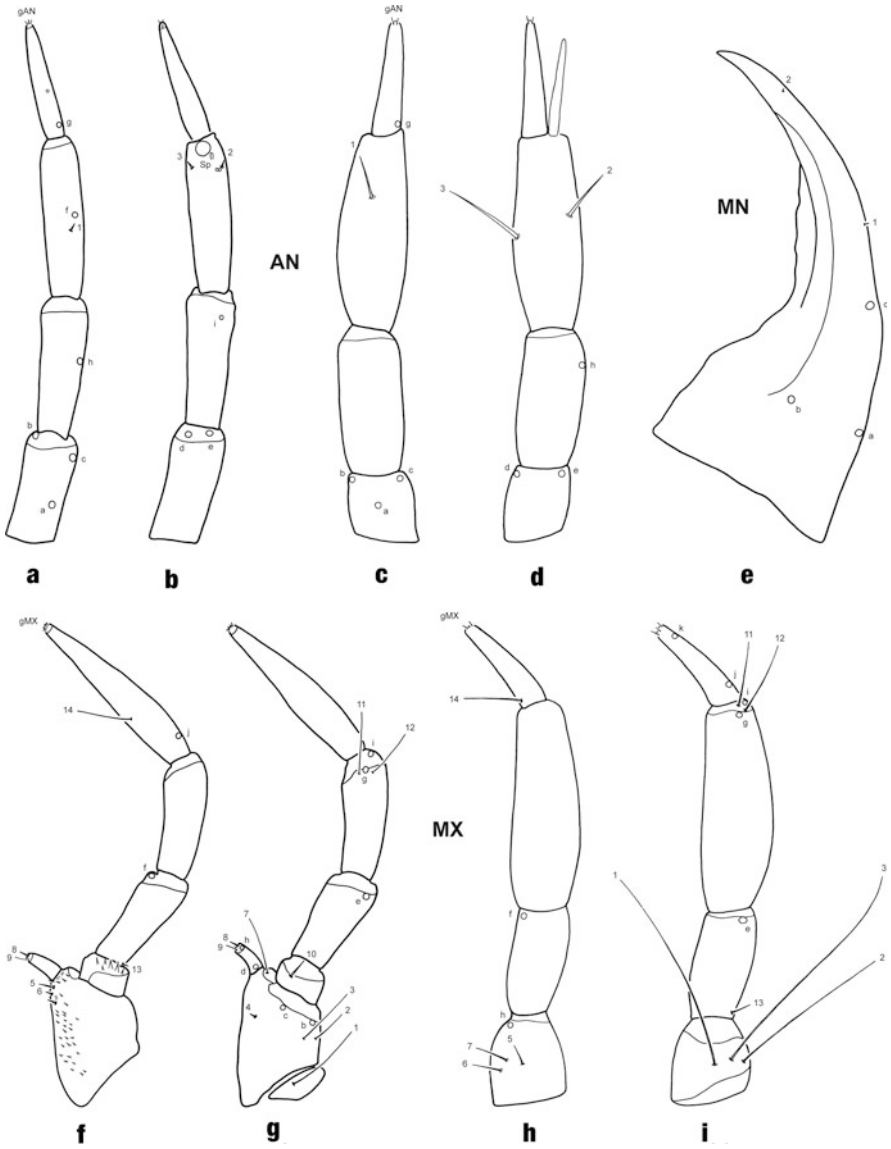

Fig. 2.5 Distribution of ancestral setae and pores on the head appendages of first instars of selected species of Dytiscidae: (**a–b**) *Platynectes curtulus* (Régimbart, 1899), (**a**) right antenna, dorsal surface, (**b**) left antenna, ventral surface; (**c–d**) *Liodessus flavofasciatus* (Steinheil, 1869), (**c**) right antenna, dorsal surface, (**d**) left antenna, ventral surface; (**e**) *Platynectes curtulus*, right mandible, dorsal surface; (**f–g**) *Platynectes curtulus*, (**f**) right maxilla, dorsal surface, (**g**) left maxilla, ventral surface; (**h–i**) *Liodessus flavofasciatus*, (**h**) right maxilla, dorsal surface, (**i**) left maxilla, ventral surface. *AN* antenna, *MN* mandible, *MX* maxilla, *Sp* spinula; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2.2 for list of setae and pores)

feeding (Fig. 2.5e). The maxilla usually consists of a small basal cardo, a larger stipes, a palp of three palpomeres borne on a palpifer, and a palpiform galea (Figs. 2.5f and g). The galea is reduced or lacking among the Hydroporinae (Fig. 2.5h and i) and Cybistrini. In some hydroporine larvae, the cardo is fused to the stipes (Fig. 2.5i). There has been considerable confusion about the number of maxillary palpomeres, the basic number of segments being three. However, the palpifer may appear to be a basal palpomere, and some Dytiscinae larvae have a secondary segmentation, which increases the apparent number of palpomeres (Fig. 2.6d). Finally, the labium consists of three major parts; the basal postmentum, the apical prementum (sometimes called the mentum), and a pair of labial palps attached to the prementum by a small palpiger (Fig. 2.6e and f). Basically, the labial palp is composed of two palpomeres except for some Hydroporinae (e.g., *Vatellus* Sharp, *Paroster* Sharp), which have one and three, respectively.

The thorax consists of three segments, the pro-, meso- and metathorax, each of which bears a pair of articulated legs (Figs. 2.1a–c, 2.2a–c and 2.3a–l). Each segment has a large tergite and, in most specimens, a pair of smaller laterotergites associated with each leg attachment. Each tergum is usually divided at the midline by a narrow ecdysal suture (e.g., Fig. 2.3a). The ventral region of the thorax is membranous except for a small sclerotized plate or presternum on the prothorax of some groups. One pair of spiracles is usually present on the lateral margin of the mesothorax in the third instar larva. The legs are usually long and slender, the prothoracic legs shortest, the meso- and metathoracic pairs progressively longer and are 6-segmented (sensu Lawrence 1991). The coxa and femur are the longest, and the trochanter is the smallest segment (Fig. 2.7a and b). The tarsal claws are usually unequal in length.

The abdomen is subcylindrical and consists of eight visible segments; segments 1–7 more or less similar in form, segment 8 variously modified for respiration (Figs. 2.1a–c, 2.2a–c and 2.3a–l). Each segment has the dorsum consisting of a large median plate, which extends laterally slightly over the pleura. The tergal plate of segment 8 is usually extending posteriorly well beyond the origin of the urogomphi forming a prolongation of the segment called the siphon (e.g., Fig. 2.3e–h). The ventral surface of the abdominal segments is variously sclerotized. Eight pairs of spiracles are present on the abdomen. The first seven pairs, which are present only in the third instar, are usually located laterodorsally on, or proximad to, the tergal plates. The spiracles on segment 8 are borne dorsally at the apex of the siphon, these being the only spiracles functional throughout the larval stage. The abdominal segment 8 bears a pair of terminal (or subterminal) articulated urogomphi (Figs. 2.1a–c, 2.2a–c and 2.3a–l). These consist of one (e.g., Fig. 2.3a and b) or two (e.g., Fig. 2.3e–h) segments.

2.3 Chaetotaxy Analysis: Methodological Approach

The term 'chaetotaxy' is derived from two Greek words: 'chatite' = long hairs; and 'taxis' = arrangement (Gordh and Headrick 2001) and refers to the arrangement, nomenclature or classification of setae distributed over the insect body (Nichols and Schuh 1989). As pointed out by Solodovnikov (2007), however, in the literature on beetle larvae, which considers chaetotaxy in sufficient detail (e.g., Thomas 1957; Ashe and Watrous 1984; Bousquet and Goulet 1984; Wheeler 1990; Lawrence 1991; Kovarik and Passoa 1993; Makarov 1996; Kilian 1998), the system of characters known as 'larval chaetotaxy' is sometimes understood more broadly to include a number of other structures such as cuticular extensions (e.g., microtrichia, setiferous tubercles, scales, spines). As defined in the context of this chapter, however, chaetotaxy is understood more narrowly as a system of setae and pores (sensilla placodea).

The larval chaetotaxy system of the Dytiscidae developed over the past 30 years is a complex of setae and pores demonstrating some patterns in their distribution, similar to the analogous systems of designations originally described for the Carabidae (Bousquet and Goulet 1984). All these systems are based on comparative examination of a certain sample of taxa for evaluating stable versus variable elements of chaetotaxy, finding homologous structures among them, and providing those with a system of designations. Hypotheses of homology were based mainly on the criterion of similarity in position (Wiley 1981) dealing with subsets (i.e., subfamilies). This was based mainly on the assumption that, at lower taxonomic levels, it is possible to determine homology with great precision using stable subpatterns of sensilla distribution.

The value of the nomenclatural system of chaetotaxy that was derived for the Dytiscidae is enhanced because it differentiates the primary setae and pores (found in the first instar) from the secondary ones, which are added in later two instars. There is an overall primary pattern, which is widespread among taxa, though it is modified in a variety of groups. This generalized pattern is consistent enough to be used for phylogenetic analysis and yet sufficiently variable to allow for taxonomic distinction. In addition to this, secondary setae and pores added through the ontogenetic development of the larva often show specific variations in number, position and size that may also serve taxonomic and phylogenetic purposes.

The notation of primary setae and pores of larval Dytiscidae presented in this chapter was based on the study of the first instars of selected taxa belonging to different tribes and genera. Larvae of other adephagan families were also examined for any significant differences in distribution of primary setae and pores within this group of taxa to ensure that the ground plan pattern developed could be extrapolated to related taxa. Descriptions of larval structures were based on specimens cleared either in 10% KOH or lactic acid and mounted on standard glass slides with either Euparal or Hoyer's medium. Microscopic examination at magnifications of 40–1000X was done using an Olympus BX50 compound microscope equipped with Nomarsky differential interference optics. In these systems, each seta is

coded by two capital letters corresponding to the first two letters of the name of the structure on which it is located (e.g., AB, last abdominal segment; AN, antenna; CO, coxa; FR, frontoclypeus; LA, labium) and a number. Pores are coded in a similar manner, except that the number is replaced by a lower case letter.

In the larval chaetotaxy systems proposed for the Dytiscidae, the primary setae and pores were subdivided into two categories: **ancestral**, i.e., those associated with the ancestral pattern (recognized and homologized in most or all of examined taxa), and **additional**, i.e., those evolved secondarily in the first instar (generally restricted to a genus or tribe). Only the setae and pores associated with the ancestral pattern were coded here.

2.4 Ground Plan Pattern of Primary Setae and Pores of the Dytiscidae

Analyses of the primary setae and pores of larval structures such as the head capsule, head appendages, legs, last abdominal segment, and urogomphus have been provided for all dytiscid subfamilies but the Hydrodytinae (c.f., references above). Primary setae and pores are generally easily recognized for most species owing to their similar distribution pattern on the body parts. For some species, however, the homology of some setae and pores may be difficult owing to (1) the presence of additional setae and (or) pores, which could confuse their identification, (2) loss of setae and (or) pores, which disrupts the distribution pattern, and (3) the drastic change of position of setae and (or) pores caused in general by an important modification of the sclerite (e.g., the elongation of the frontoclypeus of the Hydroporinae into a nasale or the variability of the relative elongation of the last abdominal segment into a siphon). The system of primary setae and pores, as defined below for the family Dytiscidae, has a great potential as a source of significant systematic data. The vast number of coded setae (137) and pores (70) and their associated states provide a complex pattern of modification useful at recognizing taxa, at reconstructing phylogeny and at building classification. The characterization of the ground plan pattern of primary setae and pores on selected structures of the Dytiscidae is based on a reconstructed, or generalized, species bearing all primary setae and pores.

2.4.1 Cephalic Capsule

Fifty-two sensilla (32 setae and 20 pores) are coded on the cephalic capsule of the Dytiscidae. These sensilla are illustrated in Fig. 2.4a–f, and they are listed in Table 2.1.

Table 2.1 Ancestral setae and pores on the head capsule of first instars of Dytiscidae subfamilies: *AGA* Agabinae, *COL* Colymbetinae, *CPL* Copelatinae, *COP* Coptotominae, *DYT* Dytiscinae, *HYD* Hydroporinae, *LAC* Laccophilinae, *LAN* Lancetinae, *MAT* Matinae

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
FR1	0	0	0	0	0	1	0	0	0
FR2	1	1	1	1	1	1	1	1	1
FR3	1	1	1	1	1	1	1	1	1
FR4	1	1	1	1	1	0	1	1	1
FR5	1	1	1	1	1	0	1	1	1
FR6	1	1	1	1	1	1	1	1	1
FR7	1	1	1	1	1	1	1	1	1
FR8	1	1	1	1	1	1	1	1	1
FR9	1	1	1	1	1	1	1	1	1
FR10	1	1	1	1	1	1	1	1	1
FR11	0	0	0	0	0	1	0	0	0
FR12	0	0	0	0	0	1	0	0	0
FR13	0	0	0	0	0	0/1	0	0	0
FRb	1	1	1	1	1	0/1	1	1	1
FRc	1	1	1	1	1	1	1	1	1
FRd	1	1	1	1	1	1	1	1	1
FRe	0	1	0	0	0/1	0	0/1	1	0
FRf	1	1	1	1	0/1	1	1	1	1
PA1	1	1	1	1	1	1	1	1	1
PA2	1	1	1	1	1	1	1	1	1
PA3	1	1	1	1	1	1	1	1	1
PA6	1	1	1	1	1	1	1	1	1
PA7	1	1	1	1	1	0	1	1	1
PA8	1	1	1	1	1	1	1	1	1
PA9	1	1	1	1	1	1	1	1	1
PA10	1	1	1	1	1	1	1	1	1
PA11	1	1	1	1	1	1	1	1	1
PA12	1	1	1	1	1	1	1	1	1
PA13	1	1	1	1	1	1	1	1	1
PA14	1	1	1	1	1	1	1	1	1
PA16	1	1	1	1	1	1	1	1	1
PA17	1	1	1	1	1	1	1	1	1
PA18	1	1	1	1	1	0	1	1	1
PA19	1	1	1	1	1	1	1	1	1
PA20	0	0	0	0	0	1	0	0	0
PA21	1	1	1	1	1	1	1	1	1
PA22	1	1	1	1	1	1	1	1	1
PAa	1	1	1	1	1	1	1	1	1
PAb	1	1	1	1	1	1	1	1	1
PAc	1	1	1	1	1	1	0/1	1	1
PAd	1	1	1	1	1	0/1	1	1	1

(continued)

Table 2.1 (continued)

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
PAe	1	1	1	1	1	0/1	1	1	1
PAf	1	1	1	1	1	1	1	1	1
PAg	1	1	1	1	1	1	1	1	1
PAh	1	1	1	1	1	1	1	1	1
PAi	1	1	1	1	1	1	1	1	1
PAj	1	1	1	1	1	0/1	1	1	1
PAk	1	1	1	1	1	1	1	1	1
PAl	1	1	1	1	0/1	0	1	1	1
PAm	1	1	1	1	0/1	1	1	1	1
PAo	1	1	1	1	0/1	1	1	1	1
PAp	1	1	1	1	1	0	1	1	1

FR frontale, *PA* parietale, 0 = absent; 1 = present

Frontoclypeus Thirteen setae (FR1, FR2, FR3, FR4, FR5, FR6, FR7, FR8, FR9, FR10, FR11, FR12, FR13) and five pores (FRb, FRc, FRd, FRe, FRf) compose the basal number of primary sensilla on the frontoclypeus. Except for setae FR1, FR11, FR12 and FR13, which are restricted to the subfamily Hydroporinae (Fig. 2.4e and f), pore FRe, which is only found in the Colymbetinae (Fig. 2.4a), Lancetinae, and some Dytiscinae (*Dytiscus* L., 1758 and *Hyderodes* Hope, 1838) and Laccophilinae (*Neptosternus* Sharp, 1882), and setae FR4 and FR5, which are lacking in the Hydroporinae, all other setae (FR2, FR3, FR4, FR6, FR7, FR8, FR9, FR10) and pores (FRb, FRc, FRd, FRf) are generalized within the Dytiscidae with few exceptions (members of *Notaticus* Zimmermann, 1928 and *Eretes* Laporte, 1833 (Dytiscinae), *Laccornis* Gozis, 1914 (Hydroporinae) and Hyphydrini (Hydroporinae) are the only dytiscids where (1) pore FRf, (2) seta FR13, and (3) pore FRb are lacking, respectively). It is worth noting that the ventroapical margin of the frontoclypeus is also characterized by the presence of a row of typical sensilla [*lamellae clypeales* of Bertrand (1972)] (Fig. 2.4a, c and f). These sensilla have not been included in the ground plan pattern of the frontoclypeus owing to their great variability (both in number and shape).

Parietale 19 setae and 15 pores form the ancestral system of the parietale. The basal half of the sclerite bears five setae (PA1, PA2, PA3, PA6, PA7) and four pores dorsally (PAa, PAb, PAc, PAp), and three setae (PA14, PA16, PA17) and five pores (PAe, PAj, PAk, PAl, PAm) ventrally. The distal portion of the parietale bears six setae (PA8, PA9, PA10, PA20, PA21, PA22) and one pore (PAd) dorsally, and five setae (PA11, PA12, PA13, PA18, PA19) and five pores (PAf, PAg, PAh, PAi, PAo) ventrally. The primary sensilla found on this portion of the head capsule show an extremely consistent pattern within the Dytiscidae except for setae PA6 and PA18, and pores PAl and PAp, which are lacking within the Hydroporinae (Fig. 2.4e and f). Pores PAm, PAo and PAl are also lacking in some genera of the dytiscine tribe

Aciliini (Fig. 2.4f). Hydroporine larvae are also the only dytiscid in which seta PA20 is present, and pores PAd, PAe and PAj are either present or absent (Fig. 2.4e and f).

2.4.2 Head Appendages

Thirty-one setae, 26 pores and three setal groups are coded on the head appendages. The sensilla observed are illustrated in Figs. 2.5a–i and 2.6a–i and their positions are listed in Table 2.2.

Antenna The primary sensilla (three setae, nine pores and a sensillum group) observed on the dytiscid antenna show an extremely consistent pattern among the subfamilies studied (Fig. 2.5a and b). This system is composed of five pores on antennomere I (ANa, ANb, ANc, ANd, ANe), two pores on antennomere II (ANh, ANi), three setae (AN1, AN2, AN3) and one pore (ANf) on antennomere III, and one lateral pore (ANg) and a setal group composed of 2–3 small apical setae and possibly a pore (gAN) on antennomere IV. Antennomere III is also characterized by the presence/absence of a ventroapical spinula (Fig. 2.5b). Hydroporinae is distinctive within the Dytiscidae in that here, the pore ANi is lacking, and pores ANf and ANh are either present or absent (Fig. 2.5c–e). Pores ANe, ANh and ANi are also present or absent within the subfamily Laccophilinae.

Mandible Two setae (MN1, MN2) and three pores (MNa, MNb, MNc) are coded on the mandible of every dytiscid species known as larva (Fig. 2.5e). Seta MN1 is more difficult to homologize in Cybistrini (Dytiscinae) owing to the presence of several additional setae, whereas seta MN2 is minute and pore-like in most Hydroporinae.

Maxilla Fourteen primary setae, ten primary pores and one setal group are coded on the maxilla of the Dytiscidae (Fig. 2.5f and g). One seta (MX1) is either found on the cardo (where present) or the stipes. Six setae (MX2, MX3, MX4, MX5, MX6, MX7) and two pores (MXb, MXc) are the basal number of sensilla on the maxillary stipes. Two setae (MX8, MX9) and two pores (MXd, MXh) appear on the galea (except in Laccophilinae, Hydroporinae and Cybistrini, where some or all of them are either absent (Fig. 2.5h) or located on the stipes (Fig. 2.6d). Five setae, five pores, and a setal group occur on the palpus: one seta (MX10) on palpifer; one seta (MX13) and two pores (MXe, MXf) on palpolmere I; two setae (MX11, MX12) and two pores (MXg, MXi) on palpomere II; one seta (MX14), one pore (MXj) and a setal group (gMX) on palpomere III. This generalized pattern is fairly consistent within the family except for the subfamily Hydroporinae and members of the subfamilies Dytiscinae and Laccophilinae. Indeed the primary pores MXb, MXc, and MXd and to a lesser extent setae MX4 and MX10 are lacking within the Hydroporinae, which is likely correlated with the absence or reduction of the galea, an unsual feature within the Dytiscidae (Alarie and Michat 2007a) (Fig. 2.5h and i). Seta LA9 and pores MXb, MXd, MXf and MXi are either present or absent within

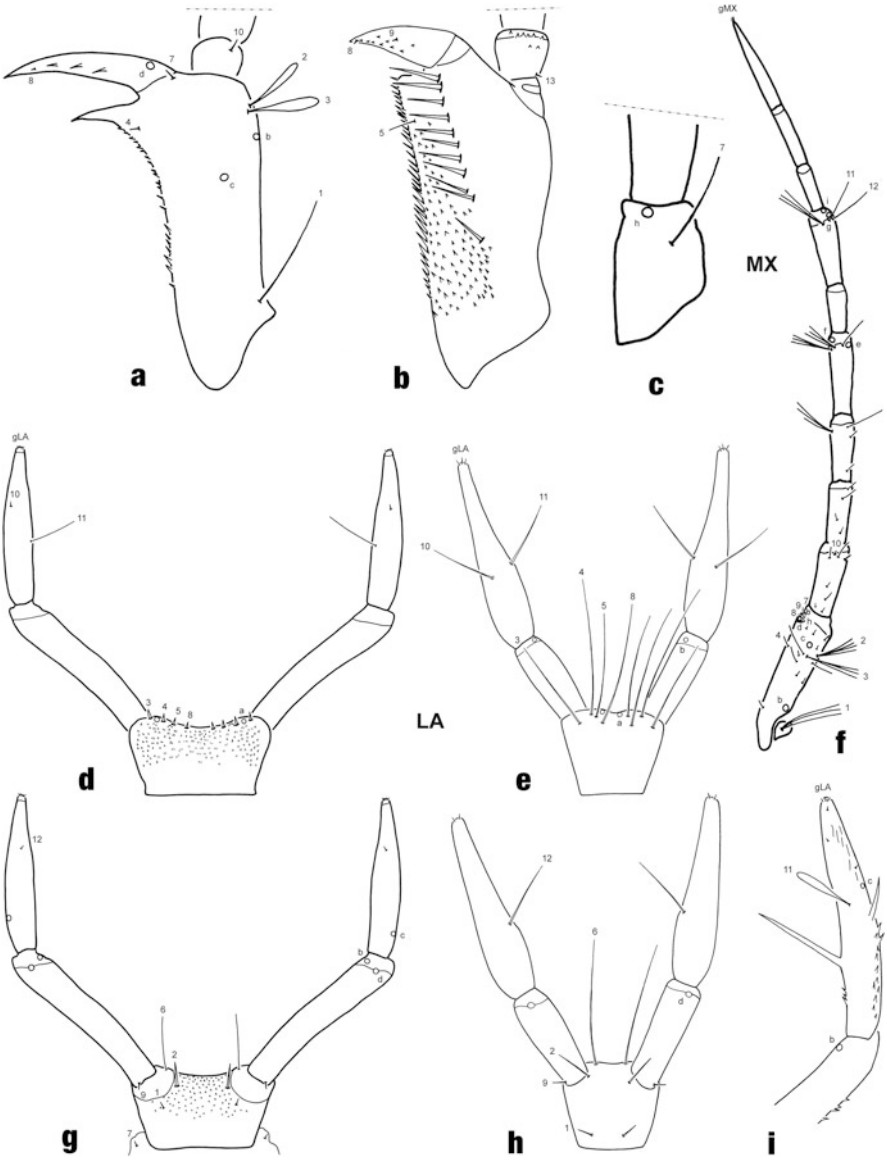

Fig. 2.6 Distribution of ancestral setae and pores on the head appendages of first instars of selected species of Dytiscidae: (**a**) *Eretes australis* (Erichson, 1842), stipes, ventral surface; (**b**) *Acilius semisulcatus* Aubé, 1838, stipes, dorsal surface; (**c**) *Desmopachria concolor* Sharp, 1882, stipes, dorsal surface; (**d**) *Megadytes glaucus* (Brullé, 1837), left maxilla, ventral surface; (**e–f**) *Platynectes curtulus* (Régimbart, 1899), labium, (**e**) dorsal surface, (**f**) ventral surface; (**g–h**) *Liodessus flavofasciatus* (Steinheil, 1869), labium, (**g**) dorsal surface, (**h**) ventral surface; (**i**) *Eretes australis*, labial palpomere 2, dorsal surface. *LA* labium, *MX* maxilla; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2.2 for list of setae and pores)

Table 2.2 Ancestral setae and pores on the head appendages of first instars of Dytiscidae subfamilies: *AGA* Agabinae, *COL* Colymbetinae, *CPL* Copelatinae, *COP* Coptotominae, *DYT* Dytiscinae, *HYD* Hydroporinae, *LAC* Laccophilinae, *LAN* Lancetinae, *MAT* Matinae

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
AN1	1	1	1	1	1	1	1	1	1
AN2	1	1	1	1	1	1	1	1	1
AN3	1	1	1	1	1	1	1	1	1
ANa	1	1	1	1	1	1	1	1	1
ANb	1	1	1	1	1	1	1	1	1
ANc	1	1	1	1	1	1	1	1	1
ANd	1	1	1	1	1	1	1	1	1
ANe	1	1	1	1	1	1	1	1	1
ANf	1	1	1	1	1	0/1	0/1	1	1
ANg	1	1	1	1	1	1	1	1	1
ANh	1	1	1	1	1	0/1	1	1	1
ANi	1	1	1	1	1	0	0	1	1
MN1	1	1	1	1	1	1	1	1	1
MN2	1	1	1	1	1	1[a]	1	1	1
MNa	1	1	1	1	1	1	1	1	1
MNb	1	1	1	1	1	1	1	1	1
MNc	1	1	1	1	1	1	1	1	1
MX1	1	1	1	1	1	1	1	1	1
MX2	1	1	1	1	1	1	1	1	1
MX3	1	1	1	1	1	1	1	1	1
MX4	1	1	1	1	1	0/1	1	1	1
MX5	1	1	1	1	1	0/1	0/1	1	1
MX6	1	1	0	1	0/1	0/1	0/1	1	1
MX7	1	1	1	1	1	1	1	1	1
MX8	1	1	1	1	1	0/1	1	1	1
MX9	1	1	1	1	1	0/1	1	1	1
MX10	1	1	1	1	1	0/1	1	1	1
MX11	1	1	1	1	1	1	1	1	1
MX12	1	1	1	1	1	1	1	1	1
MX13	1	1	1	1	1	1	1	1	1
MX14	1	1	1	1	1	1	1	1	1
MXb	1	1	1	1	1	0	1	1	1
MXc	1	1	1	1	1	0	1	1	1
MXd	1	1	1	1	1	0	1	1	1
MXe	1	1	1	1	1	1	1	1	1
MXf	1	1	1	1	1	1	1	1	1
MXg	1	1	1	1	1	1	1	1	1
MXh	1	1	1	1	1	1	1	1	1
MXi	1	1	1	1	1	1	1	1	1
MXj	1	1	1	1	1	1	1	1	1
MXk	0	0	0	0	0	1	0	0	0

(continued)

Table 2.2 (continued)

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
LA1	1	1	1	1	1	1	1	1	1
LA2	1	1	1	1	1	1	1	1	1
LA3	1	1	1	1	1	0/1	0/1	1	1
LA4	1	1	1	1	1	1	1	1	1
LA5	1	1	1	1	1	1	1	1	1
LA6	1	1	1	1	1	1	1	1	1
LA7	1	1	1	1	0	1	1	1	1
LA8	1	1	1	1	0/1	1	1	1	1
LA9	1	1	1	1	1	1	1	1	1
LA10	1	1	1	0	1	0/1	0	1	1
LA11	1	1	1	1	1	1	1	1	1
LA12	1	1	1	0	1	0/1	0	1	1
LAa	1	1	1	1	1	1	1	1	1
LAb	1	1	1	1	1	0/1	1	1	1
LAc	1	1	1	1	1	0	1	1	1
LAd	1	1	1	1	1	0/1	1	1	1

[a] Coded as MNd in Alarie (1991)
AN antenna, *LA* labium, *MN* mandible, *MX* maxilla; 0 = absent; 1 = present

the subfamily Laccophilinae. Unique features observed in some Dytiscinae are: (1) the presence of several elongate and spine-like setae along the dorsal margin of the stipes (Aciliini and Eretini) (Fig. 2.6b); (2) the presence of several additional setae on the stipes, palpifer and palpi in the Cybistrini (Fig. 2.6d); (3) setae either multifid (Cybistrini) (Fig. 2.6d) or lanceolate (Eretini) (Fig. 2.6a). It is worth noting that either of setae MX5 and MX6 or both are sometimes lacking (e,g, Dytiscinae (Aciliini and Eretini), Copelatinae, Laccophilinae (*Neptosternus*) and Hyphydrini (Fig. 2.6c)). The primary pore MXk is restricted to the Hydroporinae (Fig. 2.5i).

Labium Twelve primary setae, four primary pores and one setal group are coded on the labium (Fig. 2.6e and f). The prementum is characterized by the presence of seven setae (LA1, LA2, LA3, LA4, LA5, LA6, LA8) and one pore (LAa). Four setae, three pores and a setal group appear on the labial palpus: one small seta (LA9) and two pores (LAb, LAd) on palpomere I; three setae (LA10, LA11, LA12), a setal group (gLA), and one pore (LAc) on palpomere II. Setae LA10 and LA12 are lacking in the Coptotominae, Laccophilinae and Vatellini and are most often minute and very difficult to see in the Agabinae, Colymbetinae, Copelatinae, Dytiscinae and Lancetinae (Fig. 2.6e and f). Pore LAc is consistently lacking within the Hydroporinae (Fig. 2.6g and h) and sometimes within the Laccophilinae. Some laccophilines may also lack pore LAb. Larvae of Eretini and members of the tribe Cybistrini (Dytiscinae) differ from all other Dytiscidae in that here, the seta LA11 is lanceolate (Fig. 2.6i), and the setae LA2, LA6 and LA11 are multifid, respectively. It is worth stressing that the seta LA8 is sometimes absent within some members if the

subfamily Dytiscinae (*Notaticus*, *Dytiscus* and *Megadytes carcharias* Griffini, 1895) and that the seta LA3 is absent in some Hydroporinae (Hydrovatini, Methlini) and Laccophilinae (Laccophilini). The pores LAb and LAd are absent in members of the hydroporine tribes Hyphydrini and Vatellini, respectively.

2.4.3 Legs

Sixty-nine sensilla (51 setae and 18 pores) are coded on the leg of the Dytiscidae. These sensilla are illustrated in Fig. 2.7a–j and they are listed in Table 2.3.

Coxa Eighteen setae and two pores compose the basal number of primary sensilla on the coxa (Fig. 2.7a and b). Eleven small setae (CO1, CO2, CO3, CO4, CO5, CO13, CO14, CO15, CO16, CO17, CO18) and one pore (COa) appear on the proximal portion of the segment. Seven setae (CO6, CO7, CO8, CO9, CO10, CO11, CO12) and one pore (COd) appear on the distal portion. This pattern is quite uniform within the taxa studied. The only differences observed are the absence of pore COa in Pachydrini (Hydroporinae), and the relative positions of setae CO6 and CO7 and pore COd.

Trochanter Seven setae and seven pores are coded on the Dytiscidae trochanter (Fig. 2.7a and b). One seta (TR1) and one pore (TRb), and two hair-like setae (TR4, TR7) appear on the dorsal and ventral margin, respectively. The anterior surface is composed of two setae (TR2, TR3) and four pores (TRa, TRc, TRd, TRe) whilst the posterior surface is characterized by the presence of two setae (TR5, TR6) and two pores (TRf, TRg). The seta TR3 is lacking within the Hydroporinae and some Laccophilinae, whilst the seta TR2 is either present or absent amongst the Dytiscinae and the Hydroporinae.

Femur Ten setae and two pores characterize this segment (Fig. 2.7a and b). Seven setae (FE1, FE2, FE3, FE7, FE8, FE9, FE10) and one pore (FEb) appear on the anterior surface of the segment. Three setae (FE4, FE5, FE6) and one pore (FEa) are coded on the posterior surface. Setae FE4 and/or FE5 are lacking in some Dytiscinae (Aciliini, Aubehydrini, Dytiscini and Hydaticini) (Fig. 2.7d), whilst pore FEa is absent in some tribes of Hydroporinae (e.g., Bidessini, Hydrovatini, Hyphydrini, Laccornini and some Hydroporini) (Fig. 2.7f). It is interesting to note that the Dytiscinae larvae are characterized by the presence of a variable number of additional hair-like natatory setae along both the anteroventral and posterodorsal margins of the femur (Fig. 2.7c and d) and that seta FE6 is multifid within the tribe Cybistrini (Fig. 2.7e).

Tibia Seven setae and one pore are coded on the tibia (Fig. 2.7a and b). Three setae (TI2, TI3, TI4) are on the anterior surface and four setae (TI1, TI5, TI6, TI7) and one pore (TIa) are on the posterior surface. Setae TI2 and/or TI6 are absent in some Matinae (Fig. 2.7i and j). The ventral margin of the tibia is characterized by the presence of spinulae, which are generally more strongly developed on the protibia.

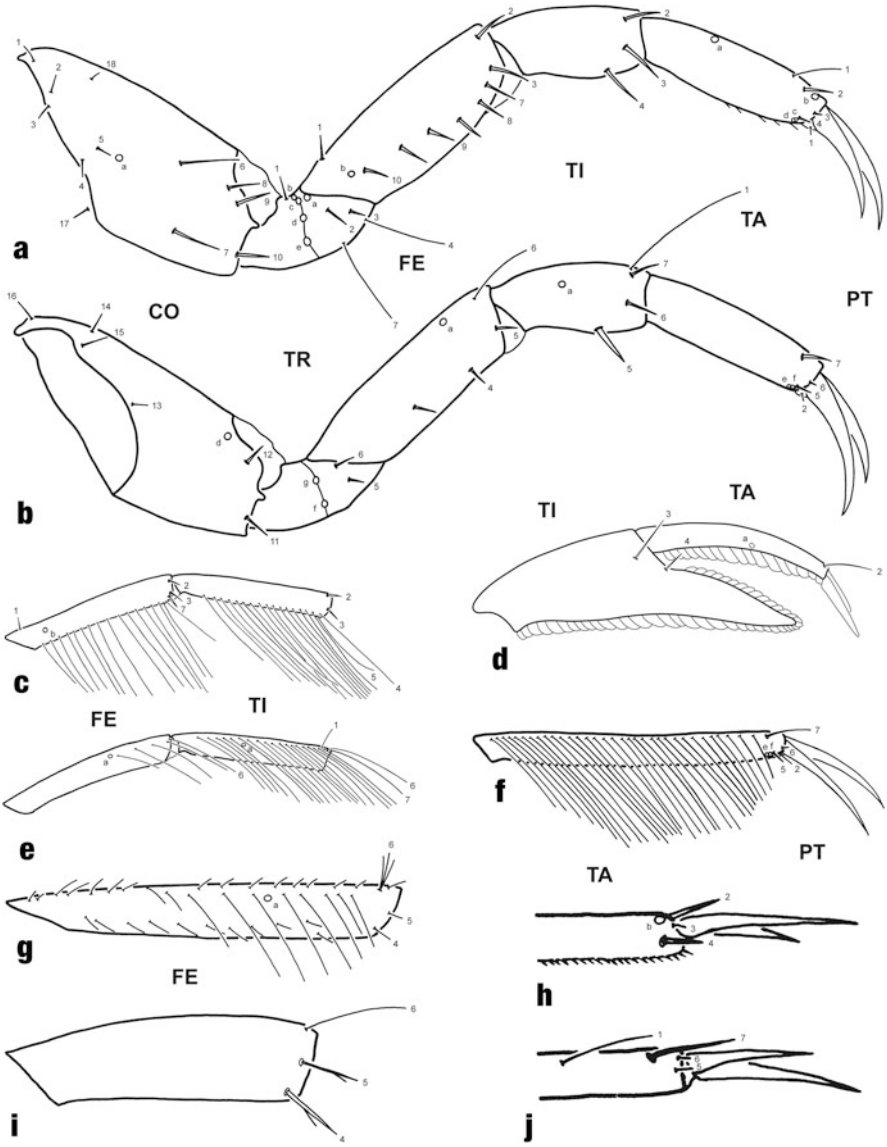

Fig. 2.7 Distribution of ancestral setae and pores on the legs of first instars of selected species of Dytiscidae: (**a–b**) *Copelatus longicornis* Sharp, 1882, metathoracic leg, (**a**) anterior surface, (**b**) posterior surface; (**c–d**) *Hydaticus tuyuensis* Trémouilles, 1996, metafemur and metatibia, (**c**) anterior surface, (**d**) posterior surface; (**e**) *Megadytes carcharias* Griffini, 1895, metafemur, posterior surface; (**f**) *Hydrovatus caraibus* Sharp, 1882, metafemur, posterior surface; (**g**) *Matus bicarinatus* (Say, 1823), protibia and protarsus, anterior surface; (**h**) *Megadytes fallax* (Aubé, 1838), metatarsus, posterior surface; (**i–j**) *Thermonectus succinctus* (Aubé, 1838), apex of metatarsus, (**i**) anterior surface; (**j**) posterior surface. *CO* coxa, *FE* femur, *PT* pretarsus, *TA* tarsus, *TI* tibia,

Larvae of *Matus* Aubé, 1836 (Matinae) are unique in that regard by the presence of characteristic feather-like spinulae on pro- and mesotibiae (Fig. 2.7g). Larvae of the Dytiscinae are characterized by the presence of a row of additional natatory setae on posterodorsal and anteroventral surfaces (Fig. 2.7c and d).

Tarsus Seven setae and six pores are coded on the tarsus (Fig. 2.7a and b). Three setae (TA2, TA3, TA4) and two pores (TAc,TAd) occur on the anterior surface and four setae (TA1, TA5, TA6, TA7) and two pores (TAe, TAf) are found posteriorly. Two other pores (TAa, TAb) are inserted dorsally. The individual pores of the pairs TAc/TAd and TAe/TAf are generally present (except within the tribe Aciliini (Dytiscinae) (Fig. 2.7i and j)) but very difficult to distinguish in some taxa because they are positioned close together and because the ventral margin of the tarsus is generally marked by a pronounced thickening of the marginal spinulae. The pore TAb is also very difficult to locate because of both its apical position and the presence of setae TA2 and TA7. The seta TA1 is generally inserted dorso-apically, and is extremely short and hair-like in some taxa. Members of the tribe Cybistrini (Dytiscinae) are characterized by a row of additional natatory setae on the posterodorsal surface (Fig. 2.7h).

Pretarsus Two short spiniform setae are located basally on the ventral surface of the pretarsus (Fig. 2.7a and b), except within the tribe Aciliini (Dytiscinae) (Fig. 2.7i and j). These may be overlooked easily and incorporated into the row of spinulae of the tarsus.

2.4.4 Last Abdominal Segment

The ground plan pattern of primary setae and pores on the last abdominal segment of the Dytiscidae is illustrated in Fig. 2.8a and b and the sensilla observed are listed in Table 2.4. Fifteen setae and three pores have been coded. Three minute setae (AB1, AB12, AB13) and one pore (ABa) occur on the anterior portion of the segment. The remaining twelve setae and two pores are inserted posteriorly. Setae AB2, AB3, AB4, AB5, AB6 and AB7 along with pores ABb and ABc are dorsal. Their relative distribution varies among taxa more than likely in correlation to the relative elongation of the segment posteriorly (i.e., siphon). Setae AB8, AB9, AB10, AB11, AB14 and AB15 are ventral, although seta AB9 may be more dorsally articulated in some taxa. Because of their small size, marginal position, and spine-like appearance, setae AB7, AB8 and AB14 (= pore ABd within the Hydroporinae) are often extremely difficult to distinguish from the spine-like microsculpture of the siphon. The primary setae AB2, AB6, AB7, AB8, AB13, AB14 and AB15, and the primary

Fig. 2.7 (continued) TR trochanter; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2.3 for list of setae and pores)

Table 2.3 Ancestral setae and pores on the legs of first instars of Dytiscidae subfamilies: *AGA* Agabinae, *COL* Colymbetinae, *CPL* Copelatinae, *COP* Coptotominae, *DYT* Dytiscinae, *HYD* Hydroporinae, *LAC* Laccophilinae, *LAN* Lancetinae, *MAT* Matinae

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
CO1	1	1	1	1	1	1	1	1	1
CO2	1	1	1	1	1	1	1	1	1
CO3	1	1	1	1	1	1	1	1	1
CO4	1	1	1	1	1	1	1	1	1
CO5	1	1	1	1	1	1	1	1	1
CO6	1	1	1	1	1	1	1	1	1
CO7	1	1	1	1	1	1	1	1	1
CO8	1	1	1	1	1	1	1	1	1
CO9	1	1	1	1	1	1	1	1	1
CO10	1	1	1	1	1	1	1	1	1
CO11	1	1	1	1	1	1	1	1	1
CO12	1	1	1	1	1	1	1	1	1
CO13	1	1	1	1	1	1	1	1	1
CO14	1	1	1	1	1	1	1	1	1
CO15	1	1	1	1	1	1	1	1	1
CO16	1	1	1	1	1	1	1	1	1
CO17	1	1	1	1	1	1	1	1	1
C018	1	1	1	1	1	1	1	1	1
COa	1	1	1	1	1	0/1	1	1	1
COd	1	1	1	1	1	1	1	1	1
TR1	1	1	1	1	1	1	1	1	1
TR2	1	1	1	1	0/1	0/1	1	1	1
TR3	1	1	1	1	1	0	1	1	1
TR4	1	1	1	1	1	1	1	1	1
TR5	1	1	1	1	1	1	1	1	1
TR6	1	1	1	1	1	1	1	1	1
TR7	1	1	1	1	1	1	1	1	1
TRa	1	1	1	1	1	1	1	1	1
TRb	1	1	1	1	1	1	1	1	1
TRc	1	1	1	1	1	1	1	1	1
TRd	1	1	1	1	1	1	1	1	1
TRe	1	1	1	1	1	1	1	1	1
TRf	1	1	1	1	1	1	1	1	1
TRg	1	1	1	1	1	1	1	1	1
FE1	1	1	1	1	1	1	1	1	1
FE2	1	1	1	1	1	1	1	1	1
FE3	1	1	1	1	1	1	1	1	1
FE4	1	1	1	1	0/1	1	1	1	1
FE5	1	1	1	1	0/1	1	1	1	1
FE6	1	1	1	1	1	1	1	1	1
FE7	1	1	1	1	1	1	1	1	1

(continued)

Table 2.3 (continued)

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
FE8	1	1	1	1	1	1	1	1	1
FE9	1	1	1	1	1	1	1	1	1
FE10	1	1	1	1	1	1	1	1	1
FEa	1	1	1	1	1	0/1	1	1	1
FEb	1	1	1	1	1	1	1	1	1
TI1	1	1	1	1	1	1	1	1	1
TI2	1	1	1	1	1	1	1	1	0/1
TI3	1	1	1	1	1	1	1	1	1
TI4	1	1	1	1	1	1	1	1	1
TI5	1	1	1	1	1	1	1	1	1
TI6	1	1	1	1	1	1	1	1	0/1
TI7	1	1	1	1	1	1	1	1	1
TIa	1	1	1	1	1	1	1	1	1
TA1	1	1	1	1	1	1	1	1	1
TA2	1	1	1	1	1	1	1	1	1
TA3	1	1	1	1	1	1	1	1	1
TA4	1	1	1	1	1	1	1	1	1
TA5	1	1	1	1	1	1	1	1	1
TA6	1	1	1	1	1	1	1	1	1
TA7	1	1	1	1	1	1	1	1	1
TAa	1	1	1	1	1	1	1	1	1
TAb	1	1	1	1	1	1	1	1	1
TAc	1	1	1	1	0/1	1	1	1	1
TAd	1	1	1	1	0/1	1	1	1	1
TAe	1	1	1	1	0/1	1	1	1	1
TAf	1	1	1	1	0/1	1	1	1	1
PT1	1	1	1	1	0/1	1	1	1	1
PT2	1	1	1	1	0/1	1	1	1	1

CO coxa, *FE* femur, *PT* pretarsus, *TA* tarsus, *TI* tibia, *TR* trochanter; 0 = absent; 1 = present

pores ABa and ABc are either present or absent amongst the Dytiscinae, Coptotominae, Hydroporinae and Laccophilinae (Fig. 2.8d and e). Larvae of all Dytiscinae are characterized by the presence of several additional elongate hair-like (natatory) setae along the lateral margin (Fig. 2.8d). Larvae of Aciliini and Eretini (Dytiscinae) are unique amongst the Dytiscidae in having the seta AB9 lanceolate (Fig. 2.8d). Larvae of Matinae, Cybistrini and some Colymbetinae (*Bunites* Spangler, 1972, *Meladema* Laporte, 1845, *Neoscutopterus* J. Balfour-Browne, 1943) are characterized by the presence of numerous additional setae (Fig. 2.8c).

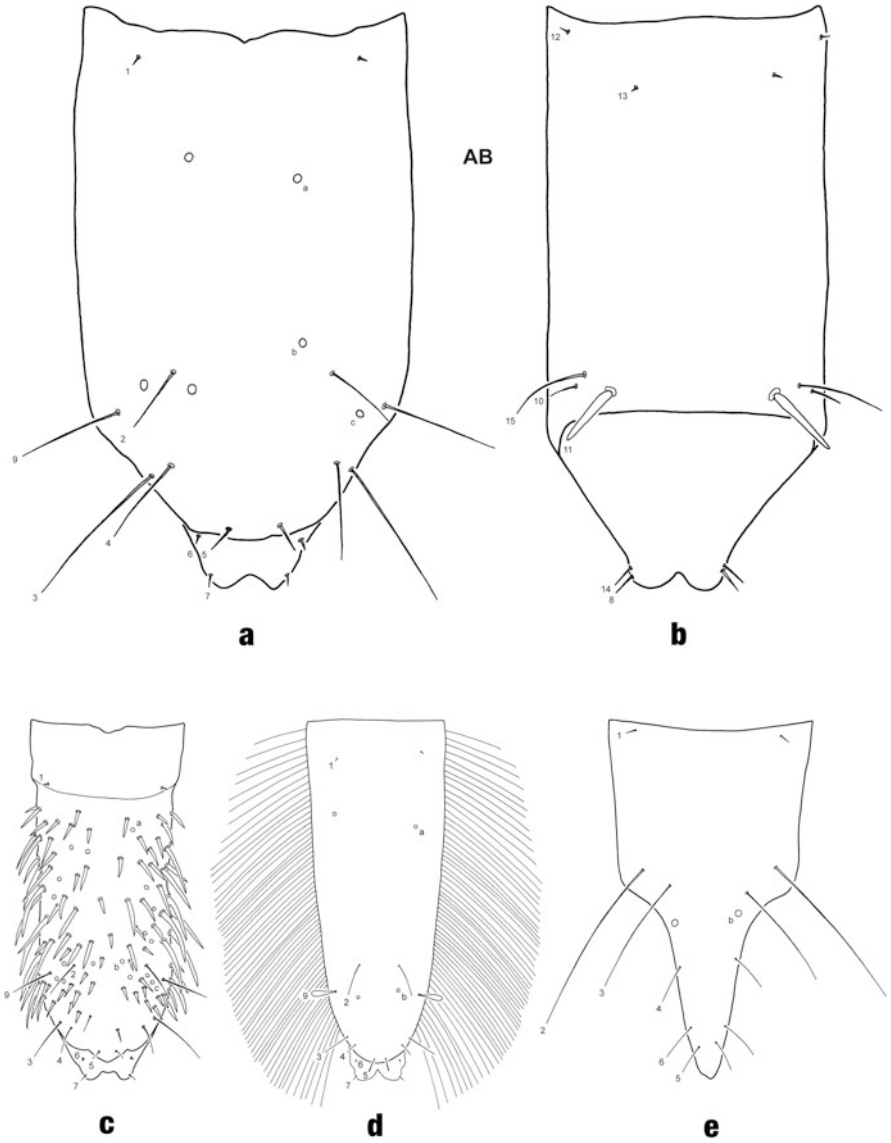

Fig. 2.8 Distribution of ancestral setae and pores on the last abdominal segment of first instars of selected species of Dytiscidae: (**a–b**) *Rhantus calileguai* Trémouilles, 1984, (**a**) dorsal surface, (**b**) ventral surface; (**c**) *Bunites distigma* (Brullé, 1837), dorsal surface; (**d**) *Eretes australis* (Erichson, 1832), dorsal surface; (**e**) *Anodocheilus maculatus* Babington, 1842, dorsal surface. *AB* abdominal segment 8; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2.4 for list of setae and pores)

Table 2.4 Ancestral setae and pores on the last abdominal segment and the urogomphus of first instars of Dytiscidae subfamilies: *AGA* Agabinae, *COL* Colymbetinae, *CPL* Copelatinae, *COP* Coptotominae, *DYT* Dytiscinae, *HYD* Hydroporinae, *LAC* Laccophilinae, *LAN* Lancetinae, *MAT* Matinae

Setae/pores	AGA	COL	CPL	COP	DYT	HYD	LAC	LAN	MAT
AB1	1	1	1	1	1	1	1	1	1
AB2	1	1	1	1	1	0/1	1	1	1
AB3	1	1	1	1	1	1	1	1	1
AB4	1	1	1	1	1	1	1	1	1
AB5	1	1	1	1	1	1	1	1	1
AB6	1	1	1	1	0/1	1	1	1	1
AB7	1	1	1	1	1	0/1	1	1	1
AB8	1	1	1	1	1	0/1	1	1	1
AB9	1	1	1	1	1	1	1	1	1
AB10	1	1	1	1	1	1	1	1	1
AB11	1	1	1	1	1	1	1	1	1
AB12	1	1	1	1	1	1	1	1	1
AB13	1	1	1	0	0/1	1	1	1	1
AB14	1	1	0	1	1	1[a]	0/1	1	1
AB15	1	1	1	1	1	0/1	0/1	1	1
ABa	1	1	1	1	1	0/1	1	1	1
ABb	1	1	1	1	1	1	1	1	1
ABc	1	1	1	0	0/1	0/1	0/1	1	1
UR1	1	1	1	1	1	1	1	1	1
UR2	1	1	1	1	1	1	1	1	1
UR3	1	1	1	1	1	1	1	1	1
UR4	1	1	1	1	1	1	1	1	1
UR5	1	1	1	1	1	1	1	1	1
UR6	1	1	1	1	1	1	1	1	1
UR7	1	1	1	1	1	1	1	1	1
UR8	1	1	1	1	1	0/1	1	1	1
URa	1	1	1	1	1	1	1	1	1
URb	1	1	1	1	0/1	0/1	1	1	1
URc	1	1	1	1	0/1	1	1	1	1

[a] Pore AB4 in Hydroporinae

AB last abdominal segment, *UR* urogomphus; 0 = absent; 1 = present

2.4.5 Urogomphus

The primary sensilla (eight setae and three pores) observed on the urogomphus also show an extremely consistent pattern within the family Dytiscidae. They are represented in Fig. 2.9a–i and listed in Table 2.4. Their relative distribution relies upon the shape of the urogomphus, which is either one- (e.g., Fig. 2.9a, g–i) or two-segmented (e.g., Fig. 2.9b–f). These sensilla are subdivided into three groups. A

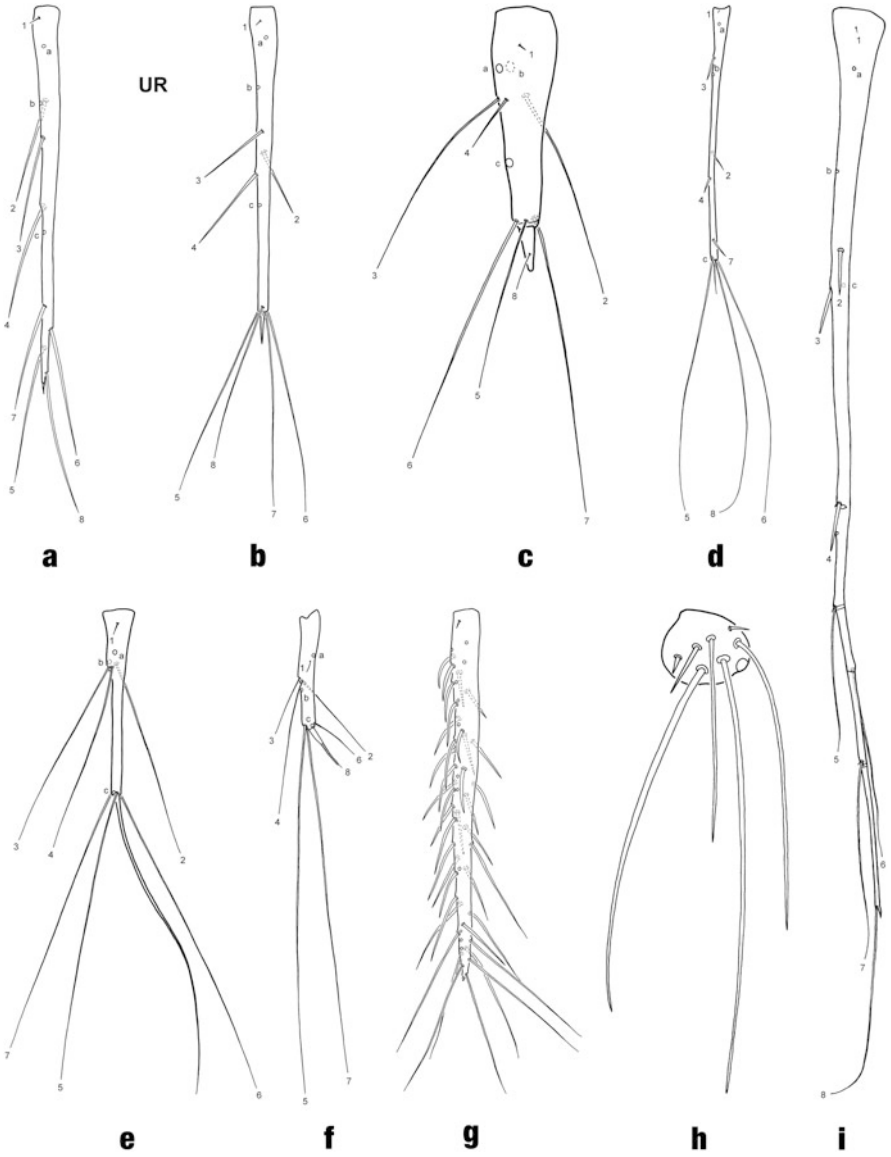

Fig. 2.9 Distribution of ancestral setae and pores on the left urogomphus of first instars of selected species of Dytiscidae: (**a**) *Meridirorhanthus antarcticus nahueli* (Trémouilles, 1984), dorsal surface; (**b**) *Platynectes curtulus* (Régimbart, 1899), dorsal surface; (**c**) *Copelatus longicornis* Sharp, 1882, dorsal surface; (**d**) *Laccophilus obliquatus* Regimbart, 1889, dorsal surface; (**e**) *Laccornellus lugubris* (Aubé, 1838), dorsal surface; (**f**) *Celina parallela* (Babington, 1842), dorsal surface; (**g**) *Bunites distigma* (Brullé, 1837), dorsal surface; (**h**) *Megadytes glaucus* (Brullé, 1837), ventral surface; (**i**) *Lancetes marginatus* (Steinheil, 1869), dorsal surface. *UR* urogomphus; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2.4 for list of setae and pores)

proximal group is composed of a small spine-like seta (UR1) and a pore (URa) near the base of the urogomphus. Both may be overlooked depending upon the shape of the siphon. The median group is composed of three spine-like setae (UR2, UR3, UR4) and one pore (URb). These setae are variably articulated among taxa. The distal group of primary urogomphal sensilla is composed of four setae (UR5, UR6, UR7, UR8) and one pore (URc). Seta UR8 is inserted on the urogomphomere 2 in Copelatinae (Fig. 2.9c) and Hydroporinae (Fig. 2.9e and f). In some hydroporines (*Canthyporus* Zimmermann, 1919, *Laccornellus* Roughley & Wolfe, 1987, *Hydrovatus* Motschulsky, 1853), it is absent (Fig. 2.9e). Pores URb and/or URc are lacking within the Cybistrini (Fig. 2.9h) and some Hydroporinae (URb in *Desmopachria* Babington, 1841). Larvae of some Dytiscinae (Dytiscini, Hyderodini) differ from other Dytiscidae by the presence of elongate hair-like (natatory) setae along the outer margin. Several Colymbetinae are characterized by the presence of numerous additional spine-like setae (Fig. 2.9g).

2.5 Making the Wealth of the Dytiscidae Chaetotaxy Pattern Available for Study Other Hydradephaga Larvae

The branching pattern of the Hydradephaga families [Aspidytidae, Dytiscidae, Hygrobiidae, Noteridae, Amphizoidae, Meruidae, Gyrinidae, Haliplidae] has received significant attention over the past decade, although no strong consensus on interfamilial relationships has yet emerged. In addition to the paraphyly of Hydradephaga, another long-standing area of phylogenetic uncertainty within Adephaga involves the families of Dytiscoidea: Aspidytidae, Amphizoidae, Hygrobiidae and Dytiscidae (Cai et al. 2020; Gustafson et al. 2021). A way to test these preliminary classifications, however, is to study larval morphology as each larval instar represents an ontogenetic stage with its own characters, each being important in determining taxa, reconstructing phylogenies, and building classifications.

Although little known until very recently the study of larvae of Hydradephaga families other than Dytiscidae has experienced remarkable progress in recent years largely due to the application of the chaetotaxy system developed for the Dytiscidae: Aspidytidae (Alarie and Bilton 2005; Michat et al. 2014b), Gyrinidae (Archangelsky and Michat 2007; Michat et al. 2010, 2016, 2017b; Michat and Gustafson 2016; Colpani et al. 2018, 2020), Haliplidae (Michat et al. 2020), Hygrobiidae (Alarie et al. 2004; Michat et al. 2014a), Meruidae (Alarie et al. 2011b), and Noteridae (Urcola et al. 2019, 2019a, b, 2020, 2021). As demonstrated in these papers, characteristics of setae and pores reveal to be useful and important both for diagnosis and study of the phylogenetic relationships of these taxa and have contributed towards the formulation of several hypotheses of phylogeny.

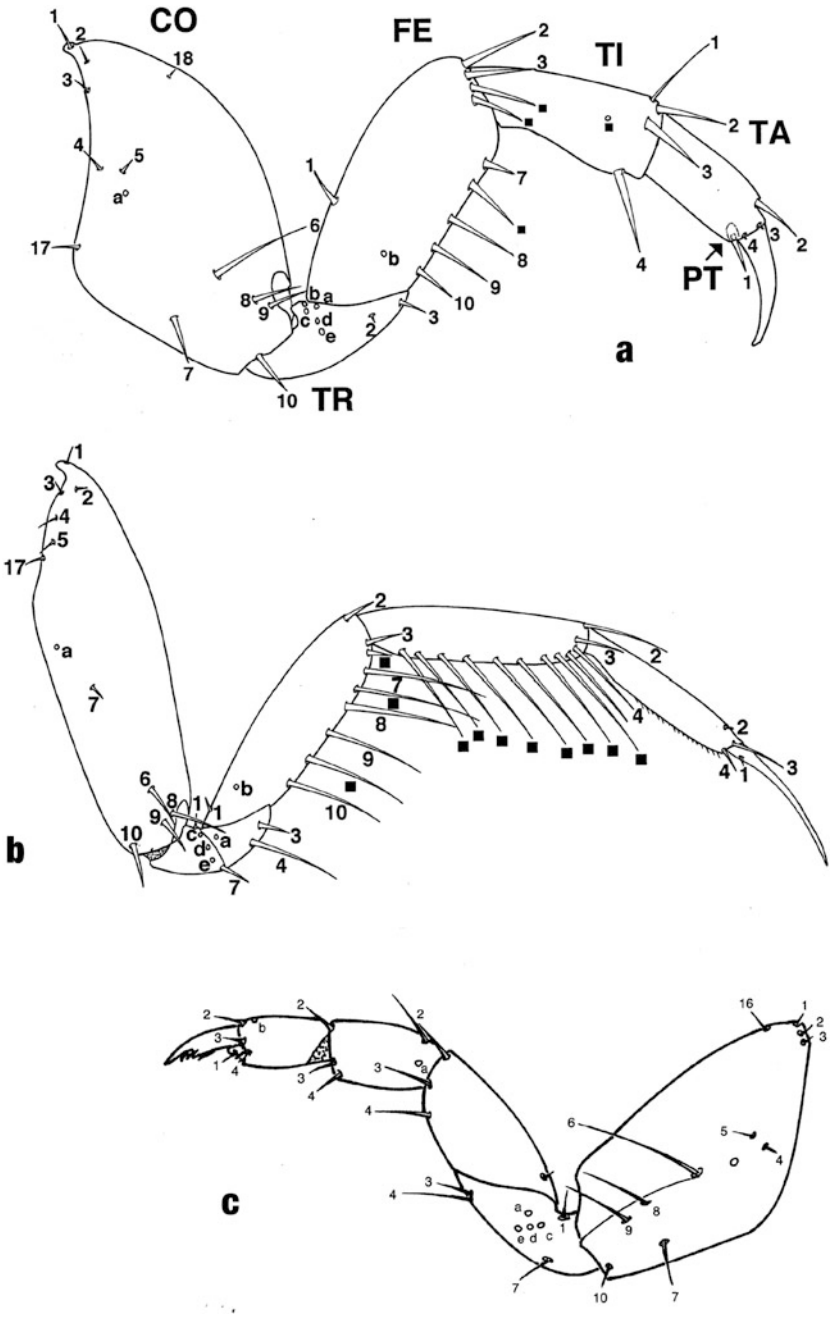

Fig. 2.10 Distribution of ancestral setae and pores on the anterior surface of the metathoracic leg of first instars of selected Hydradephaga families: (**a**) Aspidytidae: *Aspidytes niobe* Ribera, Beutel, Balke & Vogler, 2002; (**b**) Hygrobiidae: *Hygrobia hermani* (Fabricius, 1775); (**c**) Meruidae: *Meru phyllisae* Spangler & Steiner, 2005. *CO* coxa, *FE* femur, *PT* pretarsus, *TA* tarsus, *TI* tibia, *TR* trochanter; numbers and lowercase letters refer to primary setae and pores, respectively; filled

The study of the pattern of primary setae and pores observed on the leg of the larva of selected species belonging to each of the families of Hydradephaga (with the exception of Amphizoidae, whose larva remains to be studied) allows us to illustrate our point. These sensilla are illustrated in Figs. 2.7a–j, 2.10a–c and 2.11a–c and they are listed in Table 2.5. A quick glance at Table 2.5 shows the great similarity in the number of primary setae and pores observed amongst Hydradephaga larvae, although notable differences can be found there. Among these, we note the presence of the setae FE7-FE10 inserted along the ventral margin of the femur of Aspidytidae, Hygrobiidae and Dytiscidae (Figs. 2.7a and 2.10a and b). These setae are lacking in every other adephagan families (Figs. 2.10c and 2.11a–c), which clearly represent a putative strong synapomorphy supporting the monophyletic origin of the Dytiscoidea (Aspidytidae, Hygrobiidae, Dytiscidae, and Amphizoidae). Some families also have unique characteristics (Table 2.5). The larvae of Haliplidae, for one, share a unique character state in the absence of seta CO6 on the coxa (Fig. 2.11b); similarly, all known Noteridae larvae differ from those of other Hydradephaga by the presence of the primary pore COc located along the posteroventral margin of the coxa; finally the larvae of Meruidae are deemed to miss several primary setae and pores generally observed amongst other Hydradephaga (Fig. 2.11c).

In the past recent years, detailed studies of the primary chaetotaxy of other hydradephagan larval structures (e.g., head capsule, head appendages, last abdominal segment and urogomphi) have developed, in combination with more traditional morphological treatments. As evidenced by the example provided above the utility of exploring the character set provided by chaetotaxy relies not only in presence/absence but also in variations in position, size, and shape of sensilla, which have proven to provide a large number of characters useful to distinguish taxa at different taxonomic levels, and to study the phylogenetic relationships amongst these taxa.

2.6 Larval Chaetotaxy and Ontogeny

The value of the nomenclatural system of chaetotaxy that was derived for the Dytiscidae and other Hydradephaga families over the past 30 years is enhanced because it differentiates the primary setae and pores from the secondary ones that are added through the ontogenetic development of the larva. Secondary setae often show specific variation in number, position and size that may also serve taxonomic and phylogenetic purposes. This is best illustrated by comparing the secondary chaetotaxy of the legs of selected species of the subfamily Hydroporinae.

The Hydroporinae is a large, heterogeneous grouping of minute to small dytiscid species (adult length 1.00–7.10 mm) comprised of ca. 131 genera worldwide

Fig. 2.10 (continued) squares = additional setae or pore, i.e., not included in the ground plan pattern of Hydradephaga (see Table 2.5 for list of setae and pores)

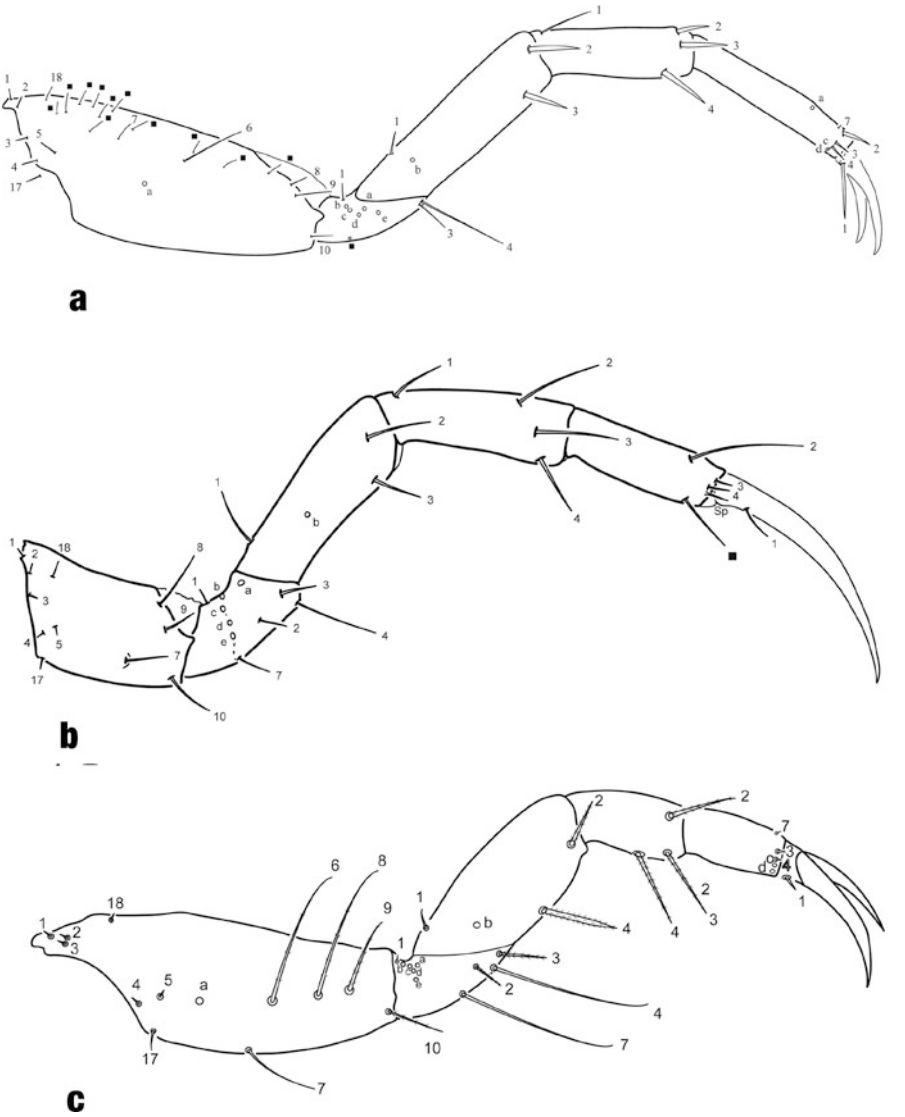

Fig. 2.11 Distribution of ancestral setae and pores on the anterior surface of the metathoracic leg of first instars of selected Hydradephaga families: (**a**) Gyrinidae: *Enhydrus sulcatus* (Wiedemann, 1821); (**b**) Haliplidae: *Haliplus indistinctus* Zimmermann, 1928; (**c**) Noteridae: *Suphisellus nigrinus* (Aubé, 1838). *CO* coxa, *FE* femur, *PT* pretarsus, *TA* tarsus, *TI* tibia, *TR* trochanter; numbers and lowercase letters refer to primary setae and pores, respectively; filled squares = additional setae or pore, i.e., not included in the ground plan pattern of Hydradephaga (see Table 2.5 for list of setae and pores)

Table 2.5 Ancestral setae and pores on the legs of first instars of Hydradephaga families: *ASP* Aspidytidae, *DYT* Dytiscidae, *GYR* Gyrinidae, *HAL* Haliplidae, *HYG* Hygrobiidae, *MER* Meruidae, *NOT* Noteridae

Setae/pores	DYT	ASP	GYR	HAL	HYG	MER	NOT
CO1	1	1	1	1	1	1	1
CO2	1	1	1	1	1	1	1
CO3	1	1	1	1	1	1	1
CO4	1	1	1	1	1	1	1
CO5	1	1	1	1	1	1	1
CO6	1	1	1	0	1	1	1
CO7	1	1	1	1	1	1	1
CO8	1	1	1	1	1	1	1
CO9	1	1	1	1	1	1	1
CO10	1	1	1	1	1	1	1
CO11	1	1	1	1	1	1	1
CO12	1	1	1	1	1	0	1
CO13	1	1	1	1	1	1	1
CO14	1	1	1	1	1	1	1
CO15	1	1	1	1	1	1	1
CO16	1	1	1	1	1	1	1
CO17	1	1	1	1	1	1	1
C018	1	1	1	1	0	1	1
COa	0/1	1	1	0	1	1	1
COc	0	0	0	0	0	0	1
COd	1	1	1	1	1	0	1
TR1	1	1	1	1	1	1	1
TR2	0/1	1	0/1	1	0	1	1
TR3	0/1	1	1	1	1	1	1
TR4	1	1	1	1	1	1	1
TR5	1	1	1	1	1	1	1
TR6	1	1	1	1	1	1	1
TR7	1	1	1	1	1	1	1
TRa	1	1	1	1	1	1	1
TRb	1	1	1	1	1	0	1
TRc	1	1	1	1	1	1	1
TRd	1	1	1	1	1	1	1
TRe	1	1	1	1	1	1	1
TRf	1	1	1	1	1	1	1
TRg	1	1	1	1	1	1	1
FE1	1	1	1	1	1	1	1
FE2	1	1	1	1	1	1	1
FE3	1	1	1	1	1	1	1
FE4	0/1	1	1	1	1	1	1
FE5	0/1	1	1	1	1	1	1
FE6	1	1	1	1	1	1	1

(continued)

Table 2.5 (continued)

Setae/pores	DYT	ASP	GYR	HAL	HYG	MER	NOT
FE7	1	1	0	0	1	0	0
FE8	1	1	0	0	1	0	0
FE9	1	1	0	0	1	0	0
FE10	1	1	0	0	1	0	0
FEa	0/1	1	0	0	1	0	0
FEb	1	1	1	1	1	0	1
TI1	1	1	1	1	1	1	1
TI2	0/1	1	1	1	1	1	1
TI3	1	1	1	1	1	1	1
TI4	1	1	1	1	1	1	1
TI5	1	1	1	1	1	1	1
TI6	0/1	1	1	1	1	1	1
TI7	1	1	1	1	1	1	1
TIa	1	1	1	1	1	1	1
TA1	1	0/1	1	1	1	0	1
TA2	1	1	1	1	1	1	1
TA3	1	1	1	1	1	1	1
TA4	1	1	1	1	1	1	1
TA5	1	1	1	1	1	1	1
TA6	1	1	1	1	1	1	1
TA7	1	1	1	1	1	1	1
TAa	1	1	1	1	1	0	1
TAb	1	1	1	1	1	1	0/1
TAc	0/1	1	1	0	1	0	1
TAd	0/1	1	1	0	1	0	1
TAe	0/1	1	1	0	1	0	1
TAf	0/1	1	1	0	1	0	1
PT1	0/1	1	1	1	1	1	1
PT2	0/1	1	1	1	1	1	1

CO coxa, *FE* femur, *PT* pretarsus, *TA* tarsus, *TI* tibia, *TR* trochanter; 0 = absent; 1 = present

(Nilsson and Hájek 2022). In term of primary setae and pores, the Hydroporinae legs show a pretty consistent pattern, including 50 setae and 18 pores (Table 2.3). Larvae of Hydroporinae, however, are quite variable in regard to both the number and the shape of secondary setae. Indeed, some species (e.g., *Heterosternuta sulphuria* (Matta & Wolfe, 1979) (Alarie and Longing 2010) and *Paroster couragei* Watts, 1978 (Alarie et al. 2009) are characterized by the presence of secondary spine-like setae, which may vary both in position and number (Fig. 2.12a and b). Other species, such as *Antiporus uncifer* Sharp, 1882 (Alarie and Watts 2004), differ from those species in that here a variable number of elongate and hair-like setae (which are deemed to play a role at enhancing the swimming ability and as such are called 'natatory setae') are added in addition to the secondary spine-like setae (Fig. 2.12c).

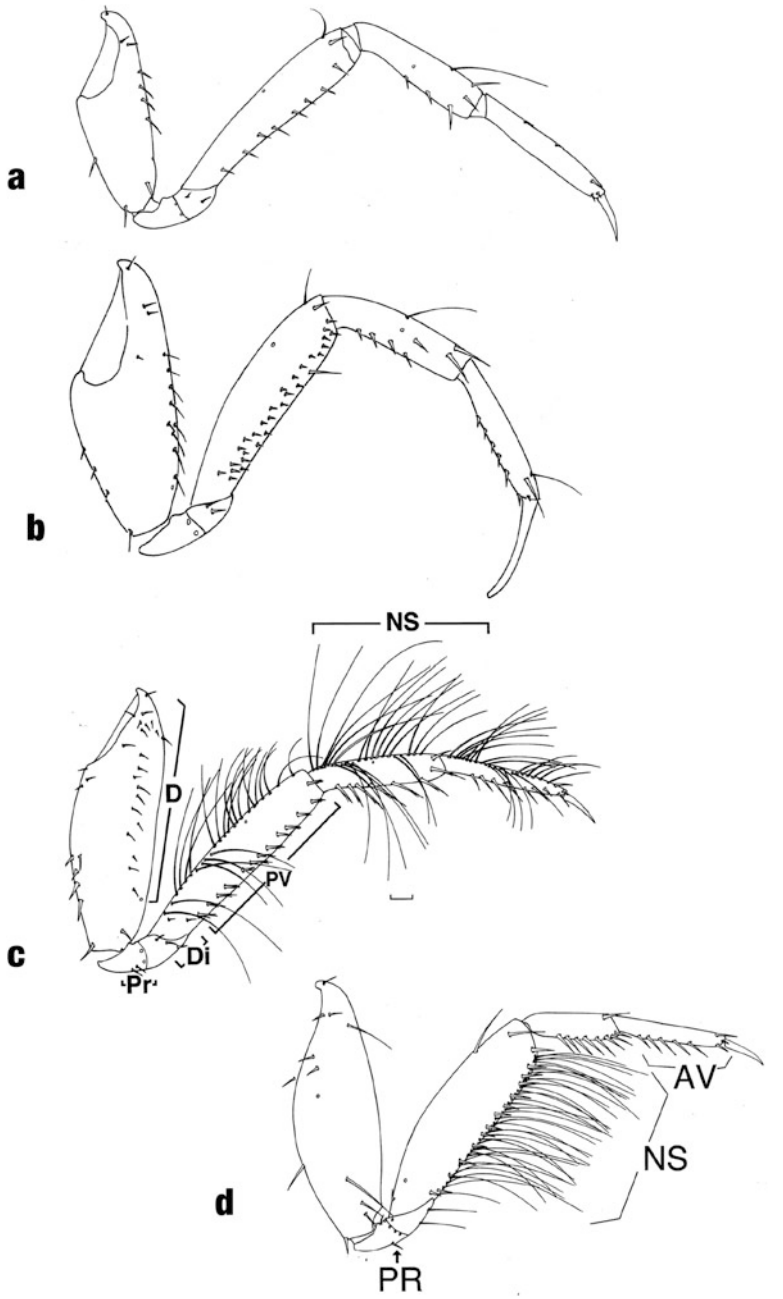

Fig. 2.12 Secondary setae on posterior surface of metathroracic legs of selected species of Hydroporinae: (**a**) *Heterosternuta sulphuria* (Matta & Wolfe, 1979); (**b**) *Paroster couragei* Watts, 1978; (**c**) *Antiporus uncifer* Sharp, 1882; (**d**) *Pachydrus obniger* (Chevrolat, 1863). *D* dorsal, *Di* distal, *NS* natatory setae, *Pr* proximal, *PV* posteroventral, *V* ventral

We stress that these natatory setae may also vary both in number and position, some species being readily distinguished from others in that the natatory setae are restricted to the tibiae and tarsi only compared to the femora, tibiae and tarsi. One of the most intriguing character states in regards to the secondary leg chaetotaxy of the Hydroporinae, however, can be found within the tribe Pachydrini. Indeed, larvae of the genus *Pachydrus* Sharp, 1882 (Alarie and Megna 2006) differ from any other member of the Hydroporinae in that here, the secondary natatory setae are all articulated along the ventral margin of the femora (Fig. 2.12d).

2.7 Summary: Prospective Ideas

The study of the larval morphology of the Dytiscidae over the past 30 years demonstrated a combination of careful attention to detail, thorough consideration of understudied character sets, and appropriate application of phylogenetic theory and methodology can lead to significant advances in our understanding of biodiversity. Such research has demonstrated the power of larval morphology, with its inherent chaetotaxic analysis, as a tool for testing hypotheses of phylogenetic relationships not only of the Dytiscidae but also of other Hydradephaga. Such studies demonstrated that larval structures could be used in phylogenetic reconstruction as a surrogate to adult structures, which have been the traditional cornerstone of systematic biology and subsequent classifications. It is generally held that the more characters support a clade, the more plausible is the hypothesis that the clade represents a natural group (DeSalle and Brower 1997). A more rigorous and stable classification will result from combining different characters from many life stages (Williamson 1992; Wiley 1981). When a phylogenetic hypothesis is supported by several independent lines of evidence, we gain confidence in it as an estimate of phylogenetic history. There is a relative increase in the probability of a tree being true if separate hypotheses of phylogeny from various data sets are congruent with one another. It is an analogue to an increase in statistical power (Lanyon 1993). Thus far, many established views concerning the taxonomic structure of the Dytiscidae have been challenged (e.g., Alarie and Michat 2007b; Michat et al. 2007, 2017a). The continued analyses of larvae of these taxa and those of related groups may possibly lead to a revision of our views on how they are taxonomically organized.

One item of practical significance in studying larval morphology is that association of aquatic beetle larvae with adults has the potential to make the wealth of characters present in the larval stage available for ecological and evolutionary study (e.g., Arnott et al. 2006; Belzile et al. 2006). From an applied viewpoint, the many aquatic ecologists who employ dytiscid beetles in their studies are now in a position to interpret their results from an evolutionary perspective A central tenet emerging from historical analyses of the evolution of morphology is that hypotheses about how these general patterns are generated may only be tested within an explicit phylogenetic framework, which has been the main output of the research conducted

on the larval morphology of the beetle family Dytiscidae and other Hydradephaga over the past recent years.

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