Zootaxa 3087: 1–55 (2011)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Notation of primary setae and pores on larvae of Dytiscinae (Coleoptera: Dytiscidae), with phylogenetic considerations

YVES ALARIE[1], MARIANO C. MICHAT[2] & KELLY B. MILLER[3]

[1]*Department of Biology, Laurentian University, Ransey Lake Road, Sudbury, Ontario, Canada. E-mail: yalarie@laurentian.ca*
[2]*CONICET, Laboratory of Entomology, DBBE, FCEyN, UBA, Buenos Aires, Argentina. E-mail: marianoide@gmail.com*
[3]*Department of Biology, University of New Mexico, Albuquerque, NM 87131-0001 USA. E-mail: kbmiller@unm.edu*

Abstract

An analysis of the primary setae and pores of first instars of 13 species of Dytiscinae was performed to deduce the ancestral system of primary setae and pores of the head capsule, head appendages, legs, last abdominal segment and urogomphus. One hundred and thirty-one setae, 69 pores and three setal groups have been assigned to the ground-plan pattern of the dytiscine larva, 27 setae and 20 pores on the head capsule; 30 setae, 25 pores and three setal groups on the cephalic appendages; 51 setae and 18 pores on the legs; 15 setae and three pores on the last abdominal segment; and eight setae and three pores on the urogomphus. A hypothesis of the phylogeny of the tribes of Dytiscinae is presented on a cladistic analysis of first instar chaetotaxy characters conducted using the program TNT. All tribes of Dytiscinae were included with larger tribes represented by multiple genera. Our concept of the subfamily Dytiscinae as defined on the basis of first instar chaetotaxy was found separated into three distinct clades: (1) Cybistrini, (2) Dytiscini + Hyderodini, and (3) Aubehydrini + Hydaticini + Eretini + Aciliini. The proposed relationships of the tribes of Dytiscinae are ((Cybistrini + (Hyderodini + Dytiscini)) + (Aubehydrini + (Hydaticini + (Eretini + Aciliini)))). Characters useful for phylogenetic analysis of the subfamily are described and illustrated.

Key words: Chaetotaxy, larval morphology, Adephaga, Dytiscinae, phylogeny.

Introduction

The adephagan beetle family Dytiscidae (predaceous water beetles), with some 4000 described species (Nilsson 2001, 2003, 2004; Nilsson & Fery 2006) represents one of the largest and most commonly encountered groups of aquatic insects. Both adults and larvae are predaceous, and will attack a wide variety of aquatic organisms. Dytiscids are found in virtually any aquatic freshwater ecosystem. In terms of classification, Dytiscidae is separated into 10 subfamilies including the Dytiscinae (Nilsson 2001), a group of 377 species subdivided into19 genera and seven tribes (Nilsson 2001).

Recent studies have demonstrated the taxonomic and phylogenetic value of chaetotaxy in studying larval Adephaga (e.g., Carabidae: Bousquet & Goulet 1984; Dytiscidae: cf. references below; Hygrobiidae: Alarie *et al.* 2004; Aspidytidae: Alarie & Bilton 2005; Meruidae: Alarie *et al.* 2011). There is an overall pattern of primary setae and pores (i.e., found in first instar), 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.

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 most dytiscid subfamilies except the Dytiscinae: Agabinae and Colymbetinae (Alarie 1995, 1998), Copelatinae (Michat & Torres 2009), Hydroporinae (Alarie *et al.* 1990; Alarie & Harper 1990; Alarie 1991; Alarie & Michat 2007), Laccophilinae (Alarie *et al.* 2000; Alarie, Spangler *et al.* 2002), Lancetinae (Alarie, Archangelsky *et al*. 2002), and Matinae (Alarie *et al.* 2001). Whereas most of the recent descriptions of larval Dytiscinae emphasized chaetotaxic analysis (e.g., *Notaticus* Zimmermann (Miller *et al.* 2007; Michat & Alarie 2009; *Megadytes* Sharp (Michat 2006, 2010), *Hydaticus* Leach (Michat & Torres

Accepted by P. Perkins: 30 Sep. 2011; published: 1 Nov. 2011

2006), *Thermonectus* Dejean (Michat & Torres 2005), these studies lack comparative precision and detail resulting from the absence of a unified system of nomenclature of the primary setae and pores for the entire subfamily Dytiscinae. Here we expand the chaetotaxic analysis of the Dytiscidae to include all major supra-generic groups and nearly sixty percent of the genera of the subfamily Dytiscinae. The aims of this paper therefore are: (i) to examine the primary chaetotaxy of the cephalic capsule, head appendages, legs, last abdominal segment and urogomphus of the Dytiscinae; (ii) to propose the ground plan pattern of primary setae and pores for this subfamily; and, (iii) to analyze the generic/tribal differences observed in a phylogenetic context based on larval primary chaetotaxy.

Material and methods

The taxonomy here follows the most recent world catalog of Dytiscidae (Nilsson 2001). All recognized tribes of Dytiscinae and 11 out of 19 currently recognized genera were included in the study (Table 1). The notation of primary setae and pores is based on the study of first-instar larvae of 13 species of Dytiscinae along with larvae of other dytiscid subfamilies and other Adephaga families for which the primary setae and pores have been studied in detail (cf. introduction for selected references). Voucher specimens are deposited in the research larval collection of Y. Alarie (Laurentian University, Department of Biology, Sudbury, Ontario, Canada) and M.C. Michat (Laboratory of Entomology, Buenos Aires University, Argentina).

TABLE 1. List of taxa studied to derive the ground plan pattern of primary setae and pores of the subfamily Dytiscinae.

Tribe	Species
Aciliini	
	Acilius semisulcatus Aubé
	Graphoderus occidentalis Horn
	Thermonectus succinctus (Aubé)
Aubehydrini	
	Notaticus fasciatus Zimmermann
Cybistrini	
	Cybister tripunctatus (Olivier)
	Megadytes (Megadytes) carcharias Griffini
	Megadytes (Paramegadytes) glaucus (Brullé)
	Megadytes (Trifurcitus) fallax (Aubé)
	Onychohydrus scutellaris (Germar)
Dytiscini	
	Dytiscus harrisii Kirby
Eretini	
	Eretes australis (Erichson)
Hydaticini	
	Hydaticus tuyuensis Trémouilles
Hyderodini	
	Hyderodes shuckardi Hope

The larvae studied were cleared in lactic acid. The cephalic capsule, head appendages, legs, last abdominal segment and urogomphus were removed and mounted in polyvinyl-lacto-glycerol. Observation (at magnifications up to 800x) was made using an Olympus BX50 compound microscope equipped with Nomarsky differential interference optics. Figures were prepared through use of a drawing tube attached to the microscope. Drawings were scanned and digitally edited.

The terminology used follows Bousquet & Goulet (1984), Alarie *et al.* (1990), Alarie & Harper (1990), Alarie (1991, 1995, 1998), Alarie *et al.* (2000), Alarie *et al.* (2001), Alarie, Spangler *et al.* (2002), Alarie, Archangelsky *et al.* (2002), Alarie *et al.*, (2004), Alarie & Bilton (2005), Alarie & Michat (2007), Michat & Torres (2009) and Alarie *et al.* (2011). "Sensillum" refers to all socketed chaetotaxal surface structures (setae and pores), whereas "spinula" refers to non-socketed cuticular structures. Each seta is coded by two upper case letters corresponding to the first two letters of the name of the structure on which it is located (e.g., AN, antenna; FR, frontoclypeus; LA, labium; MN, mandible; MX, maxilla; PA, parietale) and a number. Pores are coded in a similar manner, except that the number is replaced with a lower case letter. The position of sensilla is described by the addition of the following abbreviations: A, anterior; Ap, apical; D, dorsal; Di, distal, L, lateral; M, medial; P, posterior; Pr, proximal; V, ventral. Owing to their small size, number, and position, the sensilla found at the apex of the antenna and the labial and maxillary palpi are very difficult to determine. Accordingly, they were identified as setal groups and coded by two upper case letters (the same as those used for setae and pores) preceded by the lower case letter "g" (for group).

Hypotheses of homology stated in this paper are based mainly on the criterion of similarity in position (Wiley 1981). 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). Homology within the context of the systems proposed for other Adephaga (cf. references listed above) was attempted for each of the structures studied.

Cladistic analysis

The phylogenetic relationships of the Dytiscinae tribes were analyzed cladistically using the program TNT (Goloboff *et al.* 2008). The tree was rooted in *Lancetes* (Lancetinae), which is postulated to be closely related to Dytiscinae (Miller 2001; Alarie *et al*. 2002). Larvae of other subfamilies of Dytiscidae were not included in our analysis because a more comprehensive study of the entire family Dytiscidae including characters from all larval instars is in progress. Such study should allow to better define the groundplan of the Dytiscinae with respect to other related groups.

The distribution of character states among the terminal taxa are listed (Table 6). All characters were treated as unordered and equally weighted. Multistate characters were treated as non-additive. The small size of the matrix allowed for the implementation of an exact solution algorithm (implicit enumeration). Bremer support values were calculated using the commands 'hold 20000', 'sub n' and 'bsupport', where 'n' is the number of extra steps allowed. The process was repeated increasing the length of the suboptimal cladograms by one step, until all Bremer values were obtained (Kitching *et al.* 1998). Jackknife values were calculated with 2000 replicates and P (removal probability) = 36.

Results

The primary sensilla found and their locations are indicated in Tables 2–5 and illustrated in Figures 1–183.

Head capsule:

Except for five pores (FRe and FRf on the frontoclypeus and PAl, PAm and PAo on the ventral surface of the parietale), the ancestral pattern is remarkably consistent among the Dytiscinae. Forty-seven sensilla (27 setae and 20 pores) are coded. The sensilla observed are illustrated in Figures 1–26 and they are listed with their positions in Table 2.

Frontoclypeus. Nine setae (FR2, FR3, FR4, FR5, FR6, FR7, FR8, FR9, FR10) and five pores (FRb, FRc, FRd, FRe, FRf) comprise the ancestral number of primary sensilla on the frontoclypeus. These are invariable except in *Notaticus* and *Eretes* where pore FRf is absent and in *Dytiscus* and *Hyderodes*, which are the only dytiscine genera with the pore FRe. Larvae of *Dytiscus* and *Hyderodes* are also characterized by the presence of 4–6 additional pores over the anterior margin (Figs 7–8). Setae FR2, FR3, FR4, FR5, FR7, FR8 and FR10 are either unifid (Figs 1–4, 6–8) or multifid (Figs 3, 9–13). Seta FR3 is lanceolate within Aciliini and Eretini (Figs 1–4). Setae FR9 and FR10 were difficult to locate in *Eretes* owing to their position below the row of lamellae clypeales (cf. below). Larvae of Cybistrini are characterized by the presence of several additional setae (Figs 9–13).

TABLE 2. Position of ancestral setae and pores on the head capsule of first instars of Dytiscinae. Ap = apical, D = dorsal, FR = frontale, M = medial, L = lateral, PA= parietale, Pr = proximal, V = ventral, * = homologous with the setae and pores of the Carabidae.

Setae or pores	Position	Setae or pores	Position
FR2*	DLDi	PA13*	VLDi
FR3*	DLM	PA14*	VLDi
FR4*	DAp	PA16*	VM
FR5*	DAp	PA17*	VL
FR6*	DLAp	PA18*	VMDi
FR7*	DLAp	PA19*	VMAp
FR8*	DLAp	PA21	DLDi
FR9*	DLAp	PA22	DLDi
FR10*	DLAp	PAa*	DLPr/VLPr
FRb*	DLPr	PAb*	DLPr
FRc*	DML	PAc*	DL
FRd*	DAp	PAd*	DLDi
FRe*	DAp	PAe*	VLDi
FRf*	DLAp	PAf*	VLAp
PA1*	DLPr	PAg*	VLAp
PA2*	DLPr	PAh*	VLAp
PA3*	DLPr	PAi*	VLAp
PA6*	DL	PAj*	VLDi
PA7*	DLDi	PAk*	VLPr
PA8*	DLDi	PAl*	VMPr
PA9*	DLDi	PAm*	VM
PA10*	DLDi	PAo*	VMAp
PA11*	VLAp	PAp	DM
PA12*	VLAp		

The ventroapical margin of the frontoclypeus is also characterized by the presence of a row of typical sensilla [*lamellae clypeales* of Bertrand (1972)]. These sensilla have not been included in the ancestral pattern of the frontoclypeus owing to their great variability (both in number and shape) (Figs 1–13).

Parietale. Eighteen 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 4 pores dorsally (PAa, PAb, PAc, PAp), and three setae (PA14, PA16, PA17) and 5 pores (PAe, PAj, PAk, PAl, PAm) ventrally. The distal portion of the parietale bears five setae (PA8, PA9, PA10, PA21, PA22) and one pore (PAd) dorsally, and five setae (PA11, PA12, PA13, PA18, PA19) and five pores (PAf, PAg, PAh, PAi, PAo) ventrally. Pore PAa is generally inserted dorsolaterally (Figs 1–4, 6–7, 13) except in *Notaticus*, *Hyderodes*, *Cybister*, and *Megadytes* where it is located ventrolaterally (Figs 18, 21–25). Pores PAm and PAo lacking in *Thermonectus* and *Acilius* (Figs 14–15). Pore PAl absent within Aciliini (Figs 14–16). One additional seta was observed on the anteroventral margin in *Dytiscus*, *Notaticus*, *Hyderodes*, *Hydaticus* and *Eretes* (Figs 17–21). Larvae of Cybistrini are characterized by the presence of several additional setae both dorsally and ventrally (Figs 9–13, 22–26). Setae PA6–PA19 and PA21–PA22 multifid in Cybistrini (Figs 9–13, 22–26). Setae PA3 and PA16–PA19 multifid in Aubehydrini (Figs 5, 18). Setae PA16 and PA19 lanceolate in Aciliini and Eretini (Figs 14–17).

Head appendages:

Thirty setae, 25 pores and three setal groups are coded on the head appendages. The sensilla observed are illustrated in Figures 27–117 and their positions are listed in Table 3.

TABLE 3. Position of ancestral setae and pores on the head appendages of first instars of Dytiscinae. A = anterior, AN = antenna, Ap = apical, D = dorsal, Di = distal, L = lateral, LA = labium, M = medial, MN = mandible, MX = maxilla, Pr = proximal, V = ventral, * = homologous with the setae and pores of the Carabidae.

Setae or pores	Position	Setae or pores	Position
AN1*	DPr/DLDi	MN1*	LM/LDi
AN2*	VApL/DApL	MN2*	DAp
AN3*	VM/VAp	MNa*	DLPr/DLM
gAN1	Ap	MNb*	DPr
ANa*	DLPr	MNc*	LM/LDi
ANb*	DApL	MX1*	V
ANc*	DAp/DL	MX2*	LDi
ANd*	VApL	MX3*	LDi
ANe*	VApL	MX4*	LM
ANf*	DLM	MX5*	LM
ANg*	DLPr/DL	MX6*	LM
ANh	DLDi/DLM	MX7*	VDi
ANi	VAp/VLM	MX8*	Di/Ap
LA1*	VPr/VDi	MX9*	Di/Ap
LA2*	VDi	MX10*	V
LA3*	DAp	MX11*	VAp
LA4*	DAp	MX12*	VLAp
LA5*	DAp	MX13	DLPr
LA6*	VAp	MX14	LM
LA8	DAp	MXb*	VLDi
LA9	VPrL	MXc*	VDi/VPr
LA10	VL/VApL	MXd*	VPr
LA11	DLM/VLM	MXe*	VLAp
LA12	VApL	MXf*	VLAp
gLA2	Ap	MXg*	VLAp
LAa*	DAp/VAp	MXh	VLAp/VAp
LAb*	DLAp/VLAp	MXi	VLAp
LAc*	VLM	MXj	DM
LAd	VApL	gMX3	Ap

1, including setae AN4, AN5, AN6 described for the Hydroporinae (Alarie 1991); 2, including setae LA13, LA14, LA15 described for the Hydroporinae (Alarie 1991); 3, including setae MX12 and MX13 described for the Hydroporinae (Alarie 1991).

Antenna: the primary sensilla (three setae, nine pores and a sensillum group) observed on the antenna show an extremely consistent pattern among the species studied. The ancestral pattern of primary setae and pores of the antenna (Figs 27–52) 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 lateral pore (ANf) on antennomere III, and one lateral pore (ANg) and 2–3 small apical setae and possibly a pore (gAN) on antennomere IV. The position of several pores varies among the genera studied (see character analysis). Antennomere III is also characterized by the presence of a ventroapical spinula in every species studied (Figs 33–38, 46–52). Larvae of Cybistrini are characterized by the presence of several additional setae on antennomeres I–II (Figs 41–45, 48–52). Finally, larvae of *Onychohydrus scutellaris* are unique among the specimens studied by the presence of 3 additional pores on antennomere I (Fig. 45).

TABLE 4. Position of ancestral setae and pores on legs of first instar larvae of Dytiscinae. A = anterior, CO = coxa, D = dorsal, Di = distal, FE = femur, M = median, P = posterior, Pr = proximal; PT = pretarsus, TA = tarsus, TI = tibia, TR = trochanter, V = ventral, * = homologous with the setae and pores of the Carabidae.

Setae or pores	Position	Setae or pores	Position
CO1 *	DPr	FE4 *	PVDi
CO2 *	ADPr	FE5 *	PDi
CO3 *	ADPr	FE6 *	DDi
CO4 *	APr	FE7	AVDi
CO5 *	APr	FE8	AV
CO6 *	ADDi	FE9	AV
CO7 *	ADPr	FE10	AVPr
CO8 *	ADi	FEa *	PDDi
CO9 *	ADi	FEb *	APr
CO10 *	AVDi		
CO11 *	PVDi	TI1 *	DDi
CO12 *	PDDi	TI2 *	ADDi
CO13 *	PPr	TI3 *	ADi
CO14 *	PDPr	TI4 *	AVDi
CO15 *	PDPr	TI5 *	PVDi
CO16 *	DPr	TI6 *	PDDi
C017 *	VPr	TI7 *	PDDi
CO18	ADPr	TIa *	PM
COa *	APr		
COd *	PDDi	TA1 *	DDi
		TA2 *	ADDi
TR1 *	DPr	TA3 *	ADi
TR2 *	AVDi	TA4 *	AVDi
TR3 *	AVDi	TA5 *	PVDi
TR4 *	VDi	TA6 *	PDi
TR5 *	PVDi	TA7 *	PDDi
TR6 *	PDi	TAa *	DM
TR7 *	VDi	TAb *	DDi
TRa *	ADDi	TAc *	AVDi
TRb *	DM	TAd *	AVDi
TRc *	ADM	TAe *	PVDi
TRd *	AM	TAf *	PVDi
TRe *	AVM		
TRf *	PVM	PT1 *	AV
TRg *	PDM	PT2 *	PV
FE1 *	DPr		
FE2 *	ADDi		
FE3 *	ADi		

Mandible: Two setae (MN1, MN2) and three pores (MNa, MNb, MNc) are coded on the mandible of every species studied (Figs 53–65). The seta MN1 is more difficult to homologize in Cybistrini owing to the presence of several additional setae (Figs 61–65). Larvae of *Megadytes* and *Cybister* are characterized by the presence of a crown of elongate additional setae at distal third (Figs 61–62, 64).

TABLE 5. Position of ancestral setae and pores on the last abdominal segment and the urogomphus of Dytiscinae. A = anterior, AB = last abdominal segment, Ap = apical, D = dorsal, Di = distal, L = lateral, M = median, P = posterior, Pr = proximal, UR = urogomphus, V = ventral.

Setae and pores	Position	Setae and pores	Position
AB1	DAL	UR1	DPr
AB2	DPL/DML	UR2	DLPr
AB3	DPL	UR3	VLPr/DLM
AB4	DPAp	UR4	DM/DL
AB5	DMAp	UR5	Ap
AB6	DLAp	UR6	AP
AB7	DAp	UR7	Ap
AB8	VAp	UR8	AP
AB9	DPL	URa	DPr/DLPr
AB10	VPL	URb	DLM
AB11	VPL/VML	URc	DLDi/DMDi
AB12	VAL		
AB13	VAM		
AB14	VAp		
AB15	VPL/VML		
ABa	DAM		
ABb	DPM/DPL		
ABc	DPL		

Maxilla: the primary sensilla (14 setae, nine pores, and a setal group) observed on the maxilla show an extremely consistent pattern among the species studied (Figs 66–91). One seta (MX1) is found on the cardo. Six setae (MX2, MX3, MX4, MX5, MX6, MX7) and 2 pores (MXb, MXc) are the basal number of sensilla on the maxillary stipes. Seta MX6 is lacking in Aciliini and *Eretes* (Figs 66–69). Two setae (MX8, MX9) and 2 pores (MXd, MXh) appear on the galea (on the stipes in Cybistrini). 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. Larvae of Aciliini and *Eretes* are characterized by the presence of several elongate and spine-like setae along the inner margin of the stipes (Figs 66–69). Larvae of Aciliini, *Eretes*, *Dytiscus* and *Hyderodes* are characterized by the presence of 2–4 very small additional setae on palpomere III (Figs 66–73, 76–81) and larvae of Cybistrini are characterized by the presence of several additional setae on stipes, palpifer and palpomeres I and II (Figs 82–91). Setae MX1, MX2, MX3, MX11, MX12 and MX14 either multifid (Figs 78, 82–91) or unifid (Figs 66–77, 79–81). Larvae of *Eretes* are unique among Dytiscinae in that setae MX2 and MX3 are lanceolate (Fig. 73). Larvae of Aciliini and *Eretes* are characterized by the presence of spinulae on the stipes and the maxillary palpomeres (Figs 66–73).

Labium: Eleven setae, four pores and a setal group comprise the ancestral pattern of primary sensilla on the labium (Figs 92–117). The prementum is characterized by the presence of seven setae (LA1, LA2, LA3, LA4, LA5, LA6, LA8) and one pore (LAa). *Notaticus*, *Dytiscus* and *Megadytes carcharias* are distinguished from other Dytiscinae by the absence of seta LA8 (Figs 100–101, 104–105, 108–109). The prementum of Aciliini, *Eretes* and *Hyderodes* is characterized by the presence of 1–5 additional setae dorsally. 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 minute and very difficult to see. Larvae of Aciliini, *Eretes*, *Hyderodes* and *Hydaticus* (palpus only) characterize by the presence of numerous spinulae on the dorsal surface of prementum and over lateral margin of palpomeres I and II (Figs 92–99, 102–103, 106–107). Larvae of Cybistrini are unique among the Dytiscinae by presence of several additional setae on palpomere I as well as by the shape of setae LA2, LA6 and LA11, which are multifid (Figs 108–

117). *Eretes* differs from all other Dytiscinae studied in that here seta LA11 is lanceolate (Fig. 98). Larvae of Aciliini are characterized by the presence of an additional anterodorsal pore on the prementum (Figs 92, 94, 96). Finally, larvae of all species studied except those of Cybistrini and *Notaticus* (Figs 100–101, 108–117) are characterized by the presence of additional setae on palpomere II.

Legs:

Fifty-one setae and 18 pores are coded on the leg (Figs 118–143).

Coxa with 18 setae (CO1–CO18) and two pores (COa, COd); seta CO6 articulated more proximally in *Notaticus* (Fig. 126) and to a lesser extent, *Thermonectus* (Fig. 120); *Cybister, Megadytes*, *Onychohydrus* and *Hyderodes* with several additional setae on anterior (Figs 132, 134–143) and posterior surface (lacking in *Hyderodes* (Fig. 133)); *Cybister, Megadytes*, *Onychohydrus*, *Hyderodes* and *Dytiscus* with a variable number of additional pores (Figs 130–133, 135. 137, 139, 141, 143) on posterior surface and anterior surface (*Dytiscus* and *Hyderodes* only).

Trochanter with seven setae (TR1–TR7) and seven pores (TRa–TRg). Seta TR2 lacking in Aciliini and *Eretes* (Figs 118, 120, 122, 124); additional setae present in *Hyderodes* and Cybistrini (Figs 132, 134–143).

Femur with 10 setae (FE1–FE10) and two pores (FEa–FEb). Setae FE4 and FE5 lacking in *Notaticus*, *Acilius*, *Graphoderus*, *Hydaticus*, *Thermonectus*, *Eretes* and *Dytiscus* (except FE5 present) (Figs 119, 121, 123, 125, 127, 129, 131). Seta FE6 multifid in Cybistrini (Figs 135, 137, 139, 141, 143). All genera are characterized by the presence of a variable number of hair-like natatory setae along both anteroventral and posterodorsal margins (Figs 118–143).

Tibia with seven setae (TI1–TI7) and one pore (TIa); seta TI1 generally unifid except in Cybistrini multifid (Figs 135, 137, 139, 141). Seta TI4 generally short and spine-like except in *Acilius*, *Graphoderus*, *Notaticus*, *Hydaticus*, *Thermonectus* and *Eretes* elongate and hair-like (Figs 118, 120, 122, 124, 126, 128); seta TI5 spine-like in *Notaticus*, *Megadytes* and *Cybister* (Figs 127, 135, 137, 139, 141, 143), hair-like among other genera studied (Figs 118, 120, 122, 124, 128, 131, 133). Seta TI6 hair-like, elongate in most genera (Figs 119, 121, 123, 125, 127, 129, 131, 133), shorter in Cybistrini (Figs 135, 137, 139, 141, 143). All species characterized by the presence of a row of natatory setae on posterodorsal surface, and a row of additional setae on anteroventral surface. These anteroventral setae are stout and short to moderately elongate in Cybistrini (Figs, 134, 136, 138, 140, 142) or elongate and hair-like in other genera studied (Figs 118, 120, 122, 124, 126, 128,130, 132); *Dytiscus* and *Hyderodes* also characterize by the presence of a variable number of additional pores on the posterior surface (Figs 131, 133).

Tarsus with seven setae (TA1–TA7) and six pores (TAa–TAf); the individual pores of the pairs TAc/TAd and TAe/TAf are very difficult to distinguish owing to their small size and because they are positioned close together along the ventral margin of the tarsus; pore TAb is also difficult to locate because of presence of setae TA2 and TA7 apically. Pore TAa articulated more proximally (compared to medially in other Dytiscinae) and pores TAc, TAd, TAe and TAf lacking in Aciliini. Seta TA5 posterodistal in *Eretes* (Fig. 125). Spine-like and hair-like additional setae are present in Cybisrini (Figs 134–143). The species of Cybistrini are also characterized by a row of natatory setae on the posterodorsal surface (Figs 135, 137, 139, 141, 143).

Pretarsus with two short spiniform setae (PT1–PT2), lacking in Aciliini and *Eretes*.

Last abdominal segment:

The ancestral system of primary setae and pores on the last abdominal segment is illustrated in Figures 144–169. The sensilla observed and their positions are listed in Table 5. This ancestral pattern is remarkably consistent among the taxa studied, except for pore ABc, which is lacking in Aciliini and Eretini (Figs 144–147) and seta AB6, which is absent in the genus *Notaticus* (Fig. 148). Fifteen setae and three pores have been coded for the Dytiscinae. Three minute setae (AB1, AB12, AB13) and one pore (ABa) occur on the anterior portion of the segment. Seta AB13 is absent in *Eretes* (Fig. 160). The remaining twelve setae and two pores are inserted posteriorly. Setae AB2, AB3, AB4, AB5, AB6, AB7 and AB9 along with pores ABb and ABc are dorsal (Figs 144–156). Their relative distribution varies among taxa according to siphon shape. Setae AB8, AB10, AB11, AB14 and AB15 are ventral (Figs 157–169). Larvae of all Dytiscinae are characterized by the presence of several elongate hair-like setae along the lateral margin (Figs 144–156). Cybistrini differ by the presence of several additional setae on dorsal and ventral surface (Figs 152–156, 165–169). Additional setae are also observed in *Hyderodes* except that these are restricted to the dorsal surface (Fig. 151). Larvae of Cybistrini, *Graphoderus*, *Dytiscus* and *Hyderodes* have a variable number of additional pores dorsally (Figs 146, 150–156). Setae AB2, AB3, AB9, AB11 and AB15 are either unifid

(Figs 144–147, 149–151, 157–160, 162–164) or multifid (Figs 148, 152–156, 161, 165–169). Larvae of Aciliini and Eretini are unique amongst Dytiscinae in having seta AB9 lanceolate (Figs 144–147).

Urogomphi:

The primary sensilla observed on each dytiscine urogomphus are represented in Figures 170–183 and listed in Table 5. Overall eight setae and three pores were coded for most Dytiscinae except *Megadytes*, which is characterized by the presence of six (*M. carcharias*) and seven (*M. galucus*, *M. fallax*) primary setae respectively (Figs 178–180). Pores ABb and ABc are lacking within the Cybistrini (Figs 178–182). Homology was not attempted for the primary setae of *Cybister* and *Megadytes* owing to the very reduced condition of the urogomphus in these taxa, which makes the comparison impossible.

The sensilla are subdivided into two groups. A proximal group is composed of a small spine-like seta (UR1), two pores (URa, URb) and three elongate setae (UR2, UR3, UR4) articulated on the upper half. These setae are variably present in the taxa studied. The distal group of sensilla is composed of four setae (UR5, UR6, UR7, UR8) and one pore (URc). These setae are contiguously positioned at the apex of the urogomphus. Lavae of *Dytiscus* and *Hyderodes* differ from other dytiscine studied by the presence of elongate hair-like setae along the outer margin and several additional pores on the dorsal surface (Figs 176–177). Seta UR4 in these two genera is incorporated into the row of natatory setae. *Onychohydrus* is characterized by the presence of several short additional setae ventroproximally (Fig. 183).

Character analysis

There now follows a list of larval chaetotaxy characters that could be used for phylogenetic analysis. The polarity rationale presented below is carried out individually for each character. The states are coded to reflect the hypothesized polarity, i.e. the presumptive plesiomorphic condition is scored as (0) and reflects the condition in the outgroup (i.e. *Lancetes*).

(00) *Medial projection of frontoclypeus*: (0) absent; (1) sharp apically, with few subapical setae; (2) truncate apically, with numerous apical setae directed forward

(01)Seta FR9: (0) inserted close to seta FR10; (1) inserted far from seta FR10

(02)Pore FRc: (0) separate from frontal suture by a short distance; (1) contiguous to frontal suture

(03)Pore FRe: (0) present; (1) absent

(04)Pore FRf: (0) present; (1) absent

(05)Additional setae on surface of frontoclypeus: (0) absent; (1) present

(06)Number of lamellae clypeales: (0) two; (1) many

(07)Lamellae clypeales: (0) digitiform to spatulate; (1) spiniform; (2) setiform; (3) bifid

(08)Additional pores on anterior margin of frontoclypeus: (0) absent; (1) present

(09)Setae FR3, PA16, PA19 and AB9: (0) not lanceolate; (1) lanceolate

(10)Pore PAa: (0) dorsal; (1) ventral

(11)Pore PAl: (0) present; (1) absent

(12)Pore PAm: (0) present; (1) absent

(13)Pore PAo: (0) present; (1) absent

(14)Dorsal surface of parietale: (0) lacking additional setae; (1) with several additional setae

(15)Ventral surface of parietale: (0) lacking additional setae; (1) with one VAp marginal additional seta; (2) with several additional setae

(16)Multifid setae on cephalic capsule and abdominal segment VIII: (0) absent; (1) present

(17)Multifid setae on head appendages: (0) absent; (1) present

(18)Seta AN1: (0) proximal to median; (1) distal

(19)Seta AN3: (0) articulated sub-distally; (1) articulated apically

(20)Pore ANc: (0) DLAp at about same level of pore ANb; (1) DLDi, somewhat proximal to pore ANb; (2) DLM, distinctly proximal to pore ANb

(21)Pore ANf: (0) median to proximal; (1) subdistal

(22)Pore ANg: (0) located basally; (1) located medially

(23)Pore ANi: (0) sub-median; (1) sub-distal to sub-apical
(24)Antennomere I: (0) lacking additional pores; (1) with 3 additional pores
(25)Antennomeres I–II: (0) lacking spinulae; (1) with spinulae along apical margin; (2) with spinulae over most surface
(26)Antennomeres I–II: (0) lacking additional setae; (1) with several additional setae
(27)Antennomere III: (0) lacking spinulae; (1) with spinulae over most surface
(28)Antennomere IV: (0) lacking a lateral spinula; (1) with a lateral spinula
(29)Seta MN1: (0) articulated more distally than pore MNc; (1) articulated more proximally than pore MNc
(30)Pore MNa: (0) inserted at approximately the same level as pore MNb; (1) inserted distally to pore MNb
(31)Additional setae on mandible: (0) absent; (1) present
(32)Distal third of mandible: (0) lacking a crown of multifid additional setae; (1) with a crown of multifid additional setae
(33)Spinulae on stipes: (0) absent; (1) present
(34)Spinulae on galea: (0) present; (1) absent
(35)Maxillary palpomeres: (0) lacking spinulae; (1) with spinulae on palpomeres I and II; (2) with spinulae on every palpomere
(36)Setae MX2, MX3 and LA11: (0) not lanceolate; (1) lanceolate
(37)Seta MX6: (0) present; (1) absent
(38)Setae MX8 and MX9 and pores MXd and MXh: (0) inserted on the galea; (1) inserted on the stipes
(39)Additional setae on the stipes: (0) absent; (1) one (contiguous to MX6); (2) dorsal row of elongate spine-like setae; (3) several hair-like setae
(40)Additional setae on palpifer and maxillary palpomere I: (0) absent; (1) present
(41)Additional setae on maxillary palpomere II: (0) absent; (1) present
(42)Additional setae on maxillary palpomere III: (0) absent; (1) present
(43)Dorsal surface of prementum: (0) lacking spinulae; (1) covered with numerous spinulae
(44)Seta LA8: (0) present; (1) absent
(45)Pore LAc: (0) articulated at about mid-length of palpomere II; (1) articulated proximally, near posterior margin of palpomere II
(46)Additional setae on anterodorsal surface of prementum: (0) present; (1) absent
(47)Prementum: (0) additional dorsal pore present; (1) additional dorsal pore lacking
(48)Lateral margin of labial palpomeres I and II: (0) lacking spinulae; (1) with several spinulae
(49)Additional setae on labial palpomere I: (0) absent; (1) present
(50)Additional setae on labial palpomere II: (0) absent; (1) present
(51)Ligula: (0) absent; (1) lacking setae; (2) with setae
(52)Seta CO6: (0) articulated distally, close to setae CO8 and CO9; (1) articulated more proximally
(53)Seta CO7 on meso- and metacoxa: (0) inserted proximally, at about level of seta CO18; (1) inserted distally, far from seta CO18
(54)Seta CO12: (0) PDDi; (1) PMDi
(55)Additional setae on coxa: (0) absent; (1) present on anterior surface only; (2) present on both anterior and posterior surfaces
(56)Natatory anterodorsal setae on coxa: (0) absent; (1) present
(57)Additional pores on anterior surface of coxa: (0) absent; (1) present
(58)Additional pores on posterior surface of coxa: (0) absent; (1) present
(59)Seta TR2: (0) present; (1) absent
(60)Additional setae on trochanter: (0) absent; (1) present
(61)Seta FE1: (0) inserted submedially; (1) inserted proximally
(62)Seta FE4: (0) present; (1) absent
(63)Seta FE5: (0) present; (1) absent
(64)Additional dorsal short spine-like setae on femur: (0) absent; (1) present
(65)Additional pores on femur: (0) absent; (1) present
(66)AV hair-like natatory setae on femur: (0) lacking (1) less than 9; (2) 10–20; (3) more than 20
(67)PD hair-like natatory setae on femur: (0) lacking; (1) less than 15; (2) more than 16

(68)Seta TI1: (0) inserted distally; (1) inserted more proximally
(69)Seta TI4: (0) short and spine-like; (1) elongate and hair-like
(70)Seta TI5: (0) distal; (1) proximal
(71)Seta TI5: (0) short and spine-like; (1) elongate and hair-like
(72)Seta TI7: (0) elongate, hair-like; (1) short, spine-like
(73)Additional anterodorsal short spine-like setae on tibia: (0) absent; (1) present
(74)Additional pores on tibia: (0) absent; (1) present
(75)Additional natatory posterodorsal setae on tibia: (0) absent; (1) present
(76)Row of additional anteroventral setae on tibia: (0) stout, subequal in length; (1) stout, unequal in length; (2) mostly elongate and hair-like
(77)Seta TA5: (0) posteroventrodistal; (1) posterodorsodistal
(78)Pore TAa: (0) articulated medioproximally to medially; (1) articulated proximally
(79)Pores TAc, TAd, TAe and TAf: (0) present; (1) absent
(80)Natatory posterodorsal setae on tarsus: (0) absent; (1) present
(81)Additional anteroventral setae on meso- and metatarsus: (0) absent; (1) short, stout and subequal in length; (2) short, stout and unequal in length
(82)Setae PT1 and PT2: (0) present; (1) absent
(83)Ventral margin of tarsal claw: (0) lacking spinulae; (1) with spinulae
(84)Seta AB6: (0) present; (1) absent
(85)Setae AB10, AB11 and AB15: (0) inserted in a longitudinal row; (1) inserted in a transversal row
(86)Setae AB11 and AB15: (0) spine-like; (1) hair-like; (2) multifid
(87)Seta AB13: (0) present; (1) absent
(88)Pore ABc: (0) close to seta AB3; (1) far from seta AB3; (2) absent
(89)Dorsal surface of LAS: (0) lacking additional setae; (1) with a variable number of short additional setae
(90)Ventral surface of LAS: (0) lacking additional setae; (1) with a variable number of short additional setae
(91)Dorsal surface of LAS: (0) lacking additional pores; (1) with a variable number of additional pores
(92)Additional natatory setae on lateral margin of abdominal segment VIII: (0) absent; (1) present
(93)Pores URb and URc: (0) present; (1) absent
(94)Urogomphus: (0) with eight primary setae; (1) with seven primary setae; (2) with six primary setae
(95)Ventroproximal surface of urogomphus: (0) lacking additional setae; (1) with a variable number of short spine-like additional setae
(96)Additional pores on urogomphus: (0) absent; (1) present
(97)Natatory setae on outer margin of urogomphus: (0) absent; (1) present

Phylogenetic analysis

The final data matrix included 14 taxa and 98 characters (62 binary and 16 multistate) (Table 6). The parsimony analysis with TNT yields a single most parsimonious cladogram of length 162 (CI = 72; RI = 83). Whereas the only parsimony tree had low support for the two deep nodes (Jackknife values < 50%; Bremer values = 1) there were very good branch support for three clades: (1) Eretini + Aciliini; (2) Hyderodini + Dytiscini; and, (3) Cybistrini (Fig. 184). A sister group relationship of Aubehydrini with Hydaticini + (Eretini + Aciliini) and Hyderodini + Dytiscini with Cybistrini was resolved in this analysis albeit less well supported as indicated by both Jacknife and Bremer support values.

TABLE 6. Character matrix of 98 larval chaetotaxy characters of selected genera of Dytiscinae. The 98 columns correspond to the character numbers given in the text.

	Character																	
Genus	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
Lancetes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acilius	0	0	0	1	0	0	1	0	0	1	0	1	1	1	0	0	0	0
Graphoderus	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0
Thermonectus	0	0	0	1	0	0	1	0	0	1	0	1	1	1	0	0	0	0
Notaticus	0	1	0	1	1	0	1	0	0	0	1	0	0	0	0	1	1	0
Cybister	2	1	0	1	0	1	1	1	0	0	1	0	0	0	1	2	1	1
Megadytes (Megadytes)	2	1	0	1	0	1	1	1	0	0	1	0	0	0	1	2	1	1
Megadytes (Paramegadytes)	2	1	0	1	0	1	1	1	0	0	1	0	0	0	1	2	1	1
Megadytes (Trifurcitus)	1	1	0	1	0	1	1	1	0	0	1	0	0	0	1	2	1	1
Onychohydrus	2	1	0	1	0	1	1	1	0	0	0	0	0	0	1	2	1	1
Dytiscus	0	1	1	0	0	0	1	2	1	0	0	0	0	0	0	1	0	0
Eretes	0	?	0	1	1	0	1	3	0	1	0	0	0	0	0	1	0	0
Hydaticus	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Hyderodes	0	1	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0

continued.

	Character																	
Genus	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3
	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
Lancetes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acilius	0	0	1	0	0	1	2	2	0	1	1	0	0	0	0	1	1	2
Graphoderus	0	0	1	0	0	1	1	1	0	0	1	0	1	0	0	1	0	0
Thermonectus	0	0	1	0	0	1	2	2	0	0	1	0	1	0	0	1	0	1
Notaticus	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Cybister	0	0	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0
Megadytes (Megadytes)	0	0	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0
Megadytes (Paramegadytes)	0	1	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0
Megadytes (Trifurcitus)	0	1	1	0	0	0	0	0	1	0	0	?	1	1	0	0	0	0
Onychohydrus	0	0	1	0	0	0	0	0	1	0	0	?	1	1	0	0	0	0
Dytiscus	0	1	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Eretes	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	1	1	0
Hydaticus	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Hyderodes	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

continued.

Genus	Character																	
	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Lancetes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acilius	0	1	0	2	0	0	1	1	0	0	0	0	1	0	1	2	0	1
Graphoderus	0	1	0	2	0	0	1	1	0	0	0	0	1	0	1	2	0	1
Thermonectus	0	1	0	2	0	0	1	1	0	0	1	0	1	0	1	2	1	0
Notaticus	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0
Cybister	0	0	1	3	1	1	0	0	0	0	1	1	0	1	0	1	0	?
Megadytes (Megadytes)	0	0	1	3	1	1	0	0	1	0	1	1	0	1	0	1	0	?
Megadytes (Paramegadytes)	0	0	1	3	1	1	0	0	0	0	1	1	0	1	0	1	0	?
Megadytes (Trifurcitus)	0	0	1	3	1	1	0	0	0	0	1	1	0	1	0	1	0	?
Onychohydrus	0	0	1	3	1	1	0	0	0	0	1	1	0	1	0	1	0	?
Dytiscus	0	0	0	1	0	0	1	0	1	0	1	1	0	0	1	0	0	0
Eretes	1	1	0	2	0	0	1	1	0	0	0	1	1	0	1	2	1	0
Hydaticus	0	0	0	1	0	0	1	0	0	0	1	1	1	0	1	2	0	1
Hyderodes	0	0	0	1	0	0	1	1	0	0	0	1	1	0	1	0	0	0

continued.

Genus	Character															
	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69
Lancetes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acilius	1	0	0	0	0	1	0	1	1	1	0	0	2	1	0	1
Graphoderus	0	0	0	0	0	1	0	1	1	1	0	0	2	1	0	1
Thermonectus	1	0	0	0	0	1	0	1	1	1	0	0	1	1	0	1
Notaticus	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1
Cybister	0	2	0	0	1	0	1	1	0	0	1	0	3	2	0	0
Megadytes (Megadytes)	0	2	0	0	1	0	1	1	0	0	1	0	3	1	0	0
Megadytes (Paramegadytes)	0	2	0	0	1	0	1	1	0	0	1	0	3	1	0	0
Megadytes (Trifurcitus)	0	2	0	0	1	0	1	1	0	0	1	0	3	1	0	0
Onychohydrus	0	2	0	0	1	0	1	1	0	0	1	0	3	2	0	0
Dytiscus	0	0	0	1	1	0	0	1	1	0	1	1	3	2	0	0
Eretes	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	1
Hydaticus	0	0	0	0	0	0	0	1	1	1	0	0	2	1	0	1
Hyderodes	0	1	1	1	1	0	1	1	0	0	1	1	3	1	0	0

continued.

	Character																
Genus	7 0	7 1	7 2	7 3	7 4	7 5	7 6	7 7	7 8	7 9	8 0	8 1	8 2	8 3	8 4	8 5	8 6
Lancetes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acilius	1	1	0	0	0	1	2	0	1	1	0	0	1	0	0	1	1
Graphoderus	1	1	0	0	0	1	2	0	1	1	0	0	1	0	0	1	1
Thermonectus	1	1	0	0	0	1	2	0	1	1	0	0	1	0	0	1	1
Notaticus	0	0	0	0	0	1	2	0	0	0	0	0	0	0	1	1	2
Cybister	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	2
Megadytes (Megadytes)	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	2
Megadytes (Paramegadytes)	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	2
Megadytes (Trifurcitus)	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	1	2
Onychohydrus	0	1	1	1	0	1	1	0	0	0	1	2	0	0	0	1	2
Dytiscus	0	1	0	1	1	1	2	0	0	0	0	0	0	0	0	0	1
Eretes	1	1	0	0	0	1	2	1	1	0	0	0	1	0	0	1	1
Hydaticus	0	1	0	0	0	1	2	0	0	0	0	0	0	1	0	1	1
Hyderodes	0	1	0	1	1	1	2	0	0	0	0	0	0	1	0	0	1

continued.

	Character										
Genus	8 7	8 8	8 9	9 0	9 1	9 2	9 3	9 4	9 5	9 6	9 7
Lancetes	0	0	0	0	0	0	0	0	0	0	0
Acilius	0	2	0	0	0	1	0	0	0	0	0
Graphoderus	0	2	0	0	1	1	0	0	0	0	0
Thermonectus	0	2	0	0	0	1	0	0	0	0	0
Notaticus	0	0	0	0	0	1	0	0	0	0	0
Cybister	0	0	1	1	1	1	1	0	0	0	0
Megadytes (Megadytes)	0	0	1	1	1	1	1	2	0	0	0
Megadytes (Paramegadytes)	0	0	1	1	1	1	1	1	0	0	0
Megadytes (Trifurcitus)	0	0	1	1	1	1	1	1	0	0	0
Onychohydrus	0	1	1	1	1	1	1	0	1	0	0
Dytiscus	0	0	0	0	1	1	0	0	0	1	1
Eretes	1	2	0	0	0	1	0	0	0	0	0
Hydaticus	0	0	0	0	0	1	0	0	0	0	0
Hyderodes	0	0	1	0	1	1	0	0	0	1	1

Discussion

There are few good cladistic analyses of the Dytiscidae. In the first relatively comprehensive phylogenetic analyses of the family, Burmeister (1976) provided evidence that the subfamily Dytiscinae is monophyletic based on characters of female genitalia, a hypothesis corroborated by Miller (2000, 2001, 2003), Miller *et al.* (2007) and Michat (2006, 2010) but not in Ribera *et al.* (2008). Whereas our study does not represent the proper context within which this hypothesis should be tested, it provides arguments in support of the idea that the Dytiscinae is a natural group based on the following three synapomorphies (Fig. 185): (1) presence of numerous lamellae clypeales (character

06) (Figs 1–13) and presence of several additional natatory setae both (2) on the posterodorsal margin of tibia (character 75) (Figs 119, 121, 123, 125, 127, 129, 131, 133, 135, 137, 139, 141, 143) and (3) along the lateral margin of the last abdominal segment (character 92) (Figs 144–156). Perhaps the most striking features of the first instar larva of Dytiscinae are the development of several elongate hair-like sensilla, which are deemed to represent devices helpful at enhancing swimming propensity. Indeed hair-bearing appendages may have a direct functional relationship to swimming ability (Loudon *et al.* 1994; Vogel 1994). A non-monophyletic Dytiscinae, therefore, would imply the independent origin of the most spectacular modifications of the dytiscine larvae, usually interpreted as adaptations to high-speed swimming.

An examination of the Cybistrini taxa studied suggests that members of this tribe are very different from other Dytiscinae, which corraborates previous results based on various data sets (Miller 2001, 2003; Miller *et al.* 2006; Ribera *et al.* 2002; 2008). Indeed, all genera studied are unambiguously grouped (Jackknife value = 100; Bremer value = 16) by an exceptional number of 20 apomorphies including (Fig. 185) the presence of a large number of additional setae on selected body structures (characters 5, 14, 15, 26, 31, 39, 40, 41, 49, 55, 58, 64, 66, 73, 80, 90) (e.g., Figs 9–13), the presence of multifid setae on head appendages (character 17) (Figs 41–45, 61–65, 87–91, 108–117), the presence of spiniform lamellae clypeales (character 7) (Figs 9–13), the articulation of the primary setae MX8 and MX9 and pores MXd and MXh on the stipes (most likely resulting from the reduction/absence of the galea) (character 38) (Figs 87–91), and the disappearance of the primary pores URb and URc (character 93) (Figs 178–182). It is worth noting that larvae of Cybistrini represent the only Dytiscinae with additional natatory setae on the tarsus (character 80) (Figs 135, 137, 139, 141, 143), which in addition to a significantly larger number of natatory setae (character 66) suggest that Cybistrini are the most highly evolved swimmers within the Dytiscinae.

In our analysis the Australian element *Onychohydrus* is resolved as sister to *Megadytes* and *Cybister* (Jackknife value = 61; Bremer value = 2), which is in agreement with previous studies based on molecular data sets (Miller *et al.* 2007; Ribera *et al.* 2008). *Onychohydrus* larvae exhibit a large number of unique morphological apomorphies (Fig. 185) including (1) the presence of three additional pores on antennomere I (character 24) (Fig. 45); (2) a short and spine-like seta TI7 (character 72) (Fig. 143); (3) the presence of a row of stout anteroventral setae on tibia (character 76.1) and meso- and metatarsus (character 81.2), which are unequal in length (Fig. 142); (4) the articulation of pore ABc far from the articulation of seta AB3 (Character 88) (Fig. 156); and the presence of several short and spine-like setae over the ventroproximal surface of urogomphus (character 95) (Fig. 183). A monophyletic *Megadytes* + *Cybister* on the other hand is supported by the presence of a row of stout anteroventral setae on tibia (character 76.0) and meso- and metatarsus (character 81.1), which are subequal in length (Figs 134, 136, 138, 140). Whereas fully resolved in this study, the hypothesis of a monophyletic origin of *Megadytes* is not supported by any convincing synapomorphies.

Previous cladistic analyses (Miller 2000, 2001; Ribera *et al*. 2008 and Miller *et al*. 2009) indicated that *Eretes* is phylogenetically placed well within the Dytiscinae with Aciliini as its sister tribe. This is also suppported from larval characters (Jackknife value = 99; Bremer value = 10) (Fig. 184). Members of Aciliini and Eretini share the following putative larval synapomorphies (Fig. 185): (1) the lanceolate shape of setae FR3, PA16, PA19 and AB9 (character 9) (Figs 1–4, 14–17, 144–147); (2) the more distad position of pore ANi (character 23) (Figs 33–36); (3) the presence of spinulae on stipes (character 33) (Figs 66–69); (4) the absence of seta MX6 (character 37) (Figs 66–69); (5) the presence of a row of spiniform additional setae on dorsal surface of stipes (character 39.2) (Figs 66–69); (6) the absence of seta TR2 (character 59) (Figs 118, 120, 122, 124); the more proximad articulation of (7) seta TI5 (character 70) and (8) pore TAa (character 78) (Figs 118, 120, 122, 124); (9) the absence of setae PT1 and PT2 (character 82) (Figs 118–125); and (10) the absence of pore ABc (character 88.2) (Figs 144–147). Larval morphology would suggest also that Aciliini are natural (Jackniffe value = 94; Bremer value = 4) and supported by convincing synapomorphies (Fig. 185): (1) the absence of pore PAl (character 11) (Figs 14–16); (2) the absence of additional setae on ventral surface of parietale (character 15) (Figs 14–16); (3) the presence of an additional pore on dorsal surface of prementum (character 47) (Figs 92, 94, 96); (4) the absence of pores TAc, TAd, TAe and TAf (character 79) (Figs 118–123). Compared to Aciliini, larvae of Eretini have diversified extensively in morphological design. Indeed larvae of *Eretes* evolved (1) bifid lamellae clypeales (character 7.3) (Fig. 4); (2) pore ANc positioned dorsolateroapically at about same level as pore ANb (character 20) (Fig. 30); a more distad position of pores (3) ANf (character 21) and (4) ANg (character 22) (Fig. 30); (5) lancealoate setae MX2, MX3 and LA11 (character 36) (Figs 73, 98); (6) seta TA5 articulated posterodorsodistally (character 77) (Fig. 125); (7) and loss of seta AB13 (character 87) (Fig. 160).

The Dytiscini + Hyderodini is another well supported clade in this analysis (Jackknife value = 99; Bremer value = 8) (Figs 184–185). This group is supported by (1) the postion of pore FRc, which is contiguous to frontal suture (character 02) (Figs 7–8), (2) the presence of pore FRe (character 03) (Figures 7–8), the presence of several additional pores on (3) anterior margin of the frontoclypeus (character 08) (Figs 7–8) (4) on femur (character 65), (5) on tibia (character 74) (Figs 130–133) and (6) on urogomphus (character 96) (Figs 176–177), (7) the articulation of setae AB10, AB11 and AB15 in a transversal row (character 85) (Figs 163–164) and (8) the presence of natatory setae along outer margin of the urogomphus (character 97) (Figs 176–177). In a previous analysis Ribera et al. (2002) placed *Hyderodes* (Hyderodini) within a clade comprised of Aubehydrini + Hydaticini + Eretini + Aciliini. The position of *Hyderodes* within the group, however, was deemed weakly supported by the authors. *Hyderodes* is most certainly not member of Hydaticini + Eretini + Aciliini since it lacks all the structural apomorphies of that clade and has several unique character states (e.g., the presence of urogomphal natatory setae) that suggest a much closer relationship with *Dytiscus*, a conclusion supported by several previous analyses (Miller 2000, 2001, 2003; Miller *et al*. 2009).

The tribe Hydaticini was found to be closely related to the clade Eretini + Aciliini in this study, though relationships among these groups are not firmly established (Jackknife value = 49; Bremer value = 2) (Fig. 184). In a previous analysis (Miller 2003), Hydaticini was found to be paraphyletic with respect to a group including Eretini and Aciliini. In absence of unambiguous synapomorphies, the relative position of Hydaticini as resolved in our study sounds contentious. First instar larvae of *Hydaticus*, however, share with those of *Notaticus* (Aubehydrini) and Eretini + Aciliini three striking features that would support a monophyletic origin of these taxa (Fig. 185): (1) the presence of a lateral spinula on antennomere IV (character 28) (Figs 33–38), (2) the absence of seta FE5 (character 63) (Figs 119, 121, 123, 125, 127, 129) and (3) the elongate and hair-like aspect of seta TI4 (character 69) (Figs 118, 120, 122, 124, 126, 128). Moreover, inclusion of *Notaticus* in a group comprised of Hydaticini, Eretini and Aciliini represents a hypothesis that has been supported both by molecules and morphology (Miller 2000, 2001; Ribera *et al*. 2002; Miller *et al.* 2007; Michat and Alarie 2009).

In spite of the low resolution among the deeper nodes of the most parsimonious tree elaborated in our study (Fig. 184), our concept of the subfamily Dytiscinae as defined on the basis of first instar chaetotaxy was found separated into three distinct clades: (1) Cybistrini, (2) Dytiscini + Hederodini and (3) Aubehydrini + Hydaticini + Eretini + Aciliini. Interestingly, Sharp (1882) also divided the current Dytiscinae into three lineages (Cybistrini, Dytiscini and Hydaticides) with *Hyderodes* being included in Dytiscini. Whereas Dytiscini + Hyderodini resolved as sister to the Cybistrini in this study, the relatively weak support of that node suggests this hypothesis is contentious. The idea that Cybistrini is the sister-group to a clade containing the rest of the Dytiscinae, which was suggested in some recent analyses (Miller 2000, 2003; Miller *et al*. 2007) must therefore still be seen as a valid option.

Acknowledgements

Financial support was provided by the Natural Sciences and Engineering Research Council of Canada in the form of a Discovery research grant to Y.A. M.C.M. was supported by an external scholarship from CONICET. Special thanks to C.H.S. Watts (Adelaide, Australia) who kindly donated first instar specimens of *Eretes.*

References

Alarie, Y. (1991) Primary setae and pores on the cephalic capsule and head appendages of larval Hydroporinae (Coleoptera: Dytiscidae). *Canadian Journal of Zoology,* 69, 2255–2265.

Alarie, Y. (1995) Primary setae and pores on the legs, the last abdominal segment, and the urogomphi of larvae of Nearctic Colymbetinae (Coleoptera: Adephaga: Dytiscidae) with an analysis of their phylogenetic relationships. *The Canadian Entomologist*, 127, 913–943.

Alarie, Y. (1998) Primary setae and pores on the cephalic capsule and head appendages of larvae of Nearctic Colymbetinae (Coleoptera: Adephaga: Dytiscidae) with an analysis of their phylogenetic relationships. *The Canadian Entomologist,* 130,803–824.

Alarie, Y., Archangelsky, M., Nilsson, A.N. & Watts, C.H.S. (2002). Larval morphology of the genus *Lancetes* Sharp (Coleoptera: Adephaga: Dytiscidae) descriptions of six species and phylogenetic relationships. *The Canadian Entomologist,* 134, 467–501.

Alarie, Y., Beutel, R.G. & Watts, C.H.S. (2004) Larval morphology of three species of Hygrobiidae (Coleoptera: Adephaga, Dytiscoidea) with phylogenetic considerations. *European Journal of Entomology,* 101, 293–311.

Alarie, Y. & Bilton, D.T. (2005) Larval morphology of Aspidytidae (Coleoptera: Adephaga) and its phylogenetic implications. *Annals of the Entomological Society of America,* 98, 417–430.

Alarie, Y. & Harper, P.-P. (1990) Primary setae and pores on the last abdominal segment and the urogomphi of larval

Hydroporinae (Coleoptera: Adephaga: Dytiscidae), with notes on other dytiscid larvae. *Canadian Journal of Zoology*, 68, 368–374.

Alarie, Y., Harper, P.-P & Maire, A. (1990) Primary setae and pores on legs of larvae of Nearctic Hydroporinae (Coleoptera: Dytiscidae). *Quaestiones Entomologicae*, 26, 199–210.

Alarie, Y. & Michat, M.C. (2007) Primary setae and pores on the maxilla of larvae of the subfamily Hydroporinae (Coleoptera: Adephaga: Dytiscidae): ground plan pattern reconsidered. *The Coleopterists Bulletin*, 61, 310–317.

Alarie, Y., Nilsson, A.N., Hendrich, L., Watts, C.H.S. & Balke, M. (2000) Larval morphology of four genera of Laccophilinae (Coleoptera: Dytiscidae) with an analysis of their phylogenetic relationships. *Insect Systematics and Evolution*, 31, 121–164.

Alarie, Y., Short, A.E.Z., Garcia, M. & Joly, L. (2011) Larval morphology of Meruidae (Coleoptera: Adephaga) and its phylogenetic implication. *Annals of the Entomological Socity of America*, 104, 25–36.

Alarie, Y., Spangler, P.J. & Steiner, W.E. (2002) Larval morphology of *Agabetes* Crotch (Coleoptera: Adephaga: Dytiscidae): the hypothesis of sister-group relationship with the subfamily Laccophilinae revisited. *The Coleopterists Bulletin* 56(4), 547–567.

Alarie, Y., Watts, C.H.S. & Nilsson, A.N. (2001) Larval morphology of the tribe Matini (Coleoptera: Dytiscidae, Colymbetinae): descriptions of *Batrachomatus daemeli*, *Matus bicarinatus*, and *Allomatus nannup* and phylogenetic relationships. *The Canadian Entomologist*, 133, 165–196.

Bousquet, Y. & Goulet, H. (1984) Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). *Canadian Journal of Zoology* 62, 573–588.

Burmeister, E.G. (1976) Der Ovipositor der Hydradephaga (Coleoptera) und seine phylogenetische Bedeutung unter besonderer Berückschtigung der Dytiscidae. *Zoomorphologie*, 85, 165–257.

Goloboff, P., Farris, J. & Nixon, K. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 774–786.

Kitching, I.J., Forey, P.L., Humphries, C.J. & Williams, D.M. (1998) *Cladistics, Second Edition. The theory and practice of parsimony analysis*. Systematic Association publications, 11. New York, Oxford University Press, New York. 228 pp.

Loudon, C., Best, B.A. & Koehl, M.A.R. (1994) When does motion relative to neighboring surfaces alter the flow through arrays of hairs? *Journal of Experimental Biology*, 193, 233–254.

Michat, M.C. (2006) Descriptions of larvae of *Megadytes* (Coleoptera: Dytiscidae: Dytiscinae): the hypothesis of monophyletic origin revisited. *European Journal of Entomology* 103, 831–842.

Michat, M.C. (2010) Descriptions of larvae of *Megadytes* (Coleoptera: Dytiscidae: Dytiscinae): the subgenera *Trifurcitus* and *Megadytes* s. str., ground plan of chaetotaxy of the genus and phylogenetic analysis. *European Journal of Entomology*, 107, 377–390.

Michat, M.C. & Alarie, Y. (2009) Phylogenetic relationships of *Notaticus* Zimmermann (Coleoptera: Dytiscidae) based on larval morphology. *Annals of the Entomological Society of America*, 102, 797–808.

Michat, M.C. & Torres, P.L.M. (2005) Larval morphology of *Thermonectus succinctus* (Aubé 1838) (Coleoptera: Dytiscidae: Dytiscinae), with biological notes and chaetotaxic analysis. *Aquatic Insects*, 27, 281–292.

Michat, M.C. & Torres, P.L.M. (2006) *Hydaticus tuyuensis* Trémouilles (Coleoptera: Dytiscidae): larval morphology and phylogenetic relationships within Dytiscinae. *Hydrobiologia*, 563, 479–492.

Michat, M.C. & Torres, P.L.M. (2009) A preliminary study on the phylogenetic relationships of *Copelatus* Erichson (Coleoptera: Dytiscidae: Copelatinae) based on larval chaetotaxy and morphology. *Hydrobiologia*, 632, 309–327.

Miller, K.B. (2000) Cladistics analysis of the tribes of Dytiscinae and the phylogenetic position of the genus *Notaticus* Zimmermann (Coleoptera: Dytiscidae). *Insect Systematics and Evolution*, 31, 165–177.

Miller, K.B. (2001) On the phylogeny of the Dytiscidae (Insecta: Coleoptera) with emphasis on the morphology of the female reproductive system. *Insect Systematics and Evolution*, 32, 45–92.

Miller, KB. (2003) The phylogeny of diving beetles (Coleoptera: Dytiscidae) and the evolution of sexual conflict. *Biological Journal of the Linnaean Society*, 79, 359–388.

Miller, K.B., Alarie, Y. & Whiting, M.F. (2007) Description of the larva of *Notaticus fasciatus* Zimmermann (Coleoptera: Dytiscidae) associated with adults using DNA sequence data. *Annals of the Entomological Society of America* 100: 787–797.

Miller, K.B., Bergsten, J. & Whiting, M.F. (2007) Phylogeny and classification of diving beetles in the tribe Cybistrini (Coleoptera: Dytiscidae: Dytiscinae). *Zoologica Scripta*, 36, 41–59.

Miller, K.B., Bergsten, J. & Whiting, M.F. (2009) Phylogeny and classification of the tribe Hydaticini (Coleoptera: Dytiscidae): partition choice for Bayesian analysis with multiple nuclear and mitochondrial protein-coding genes. *Zoologica Scripta*, 38, 591–615.

Nilsson, A.N. (2001) Dytiscidae (Coleoptera). World Catalogue of Insects 3. Apollo Books. Stenstrup, Denmark, 395 pp.

Nilsson, A.N. (2003) World Catalogue of Dytiscidae – corrections and additions, 1. (Coleoptera: Dytiscidae) *Koleopterologische Rundschau*. 73, 65–74.

Nilsson, A.N. (2004) World Catalogue of Dytiscidae – corrections and additions, 2. (Coleoptera: Dytiscidae). *Koleopterologische Rundschau*, 74,157–174.

Nilsson, A.N.& Fery, H. (2006) World Catalogue of Dytiscidae – corrections and additions, 3. *Koleopterologische Rundschau*. 76, 55–74.

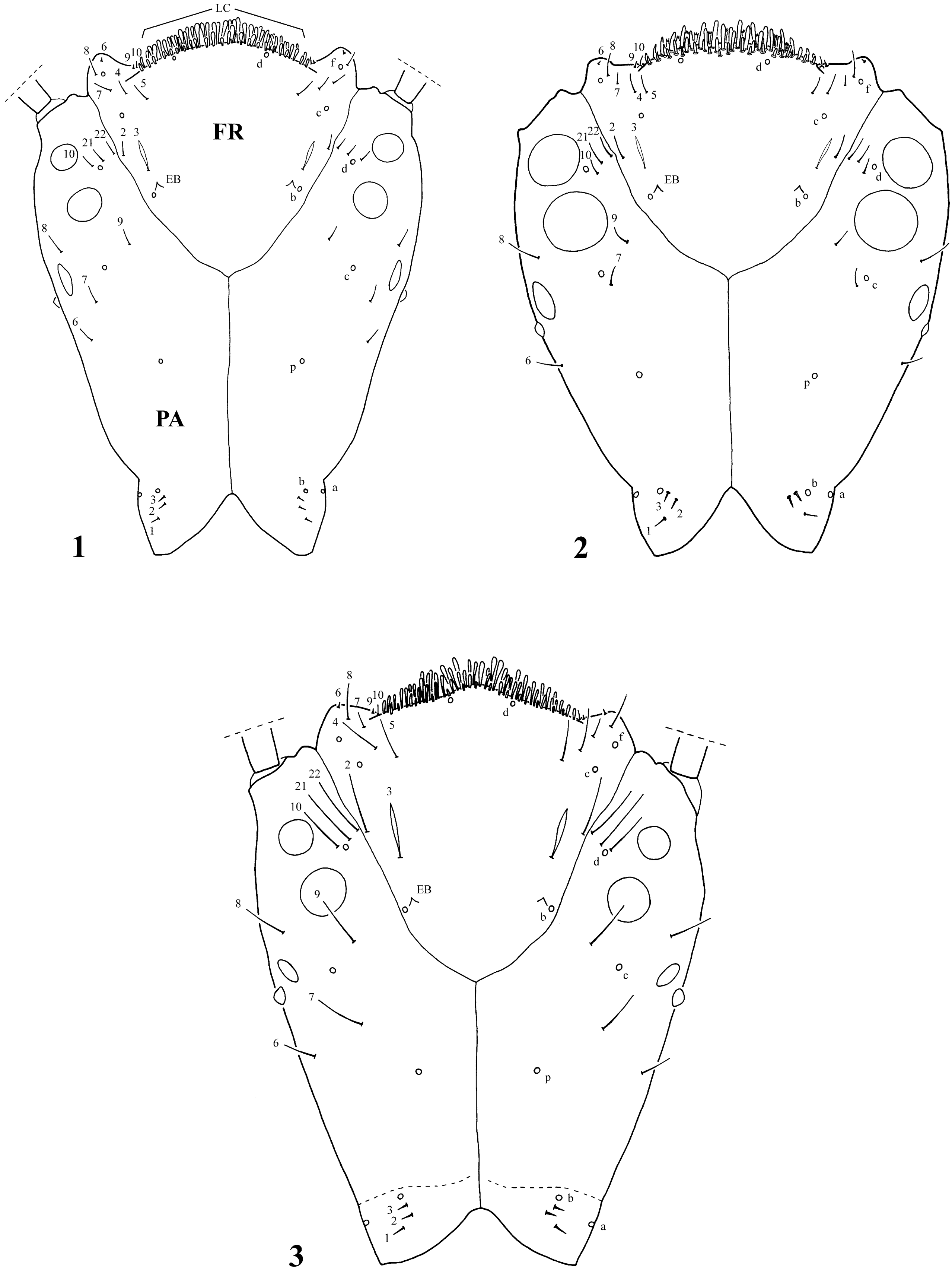
Ribera, I., Hogan, J.E. & Vogler, A.P. (2002) Phylogeny of Hydradephagan water beetles inferred from 18S rRNA sequences. *Molecular Phylogenetics and Evolution*, 23, 43–62.

Ribera, I., Vogler, A.P. & Balke, M. (2008) Phylogeny and diversification of diving beetles (Coleoptera: Dytiscidae). *Cladistics*, 24, 563–590.

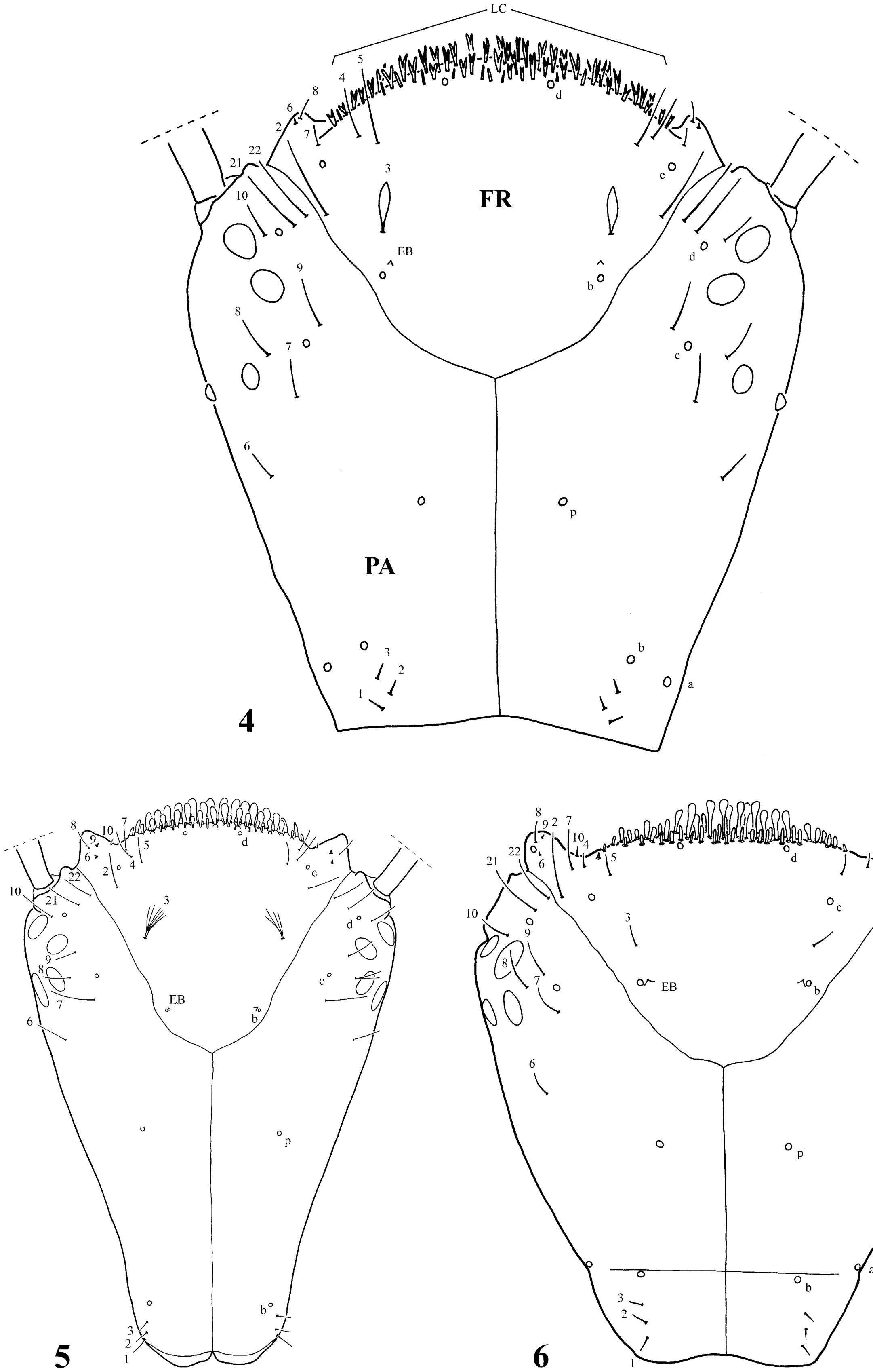
Sharp. D. (1882) On aquatic carnivorous Coleoptera or Dytiscidae. *Scientific Transactions of the Royal Dublin Society*, 2, 179–1003.

Vogel, S. (1994) Life in moving fluids. The physical biology of flow. Willard Grant Press, Boston. 467 pp.

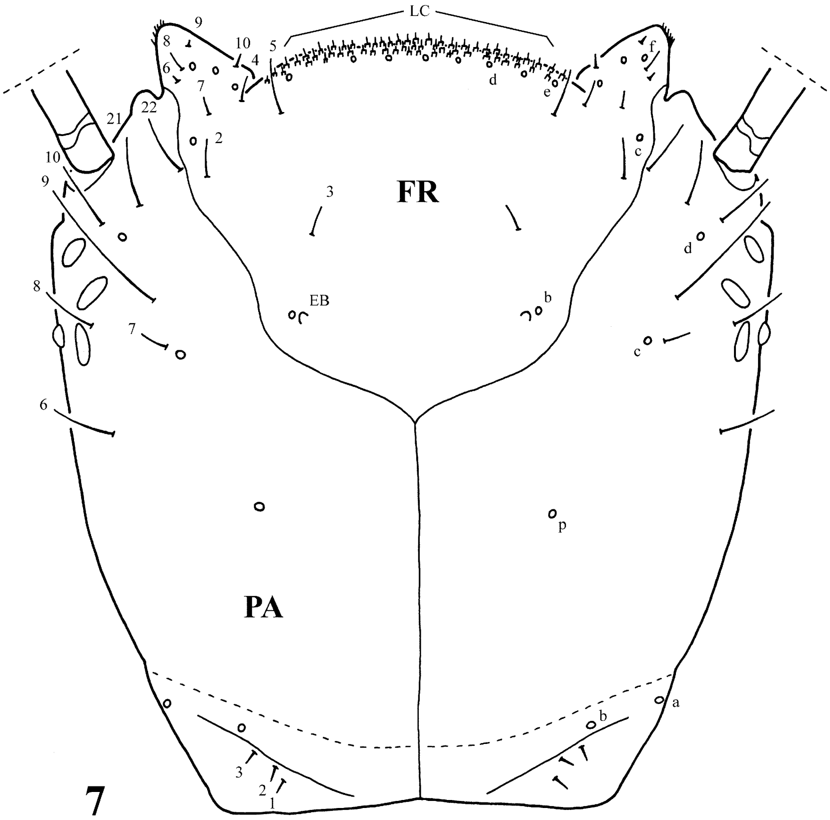
Wiley, E.O. (1981) Phylogenetics. The theory and practice of phylogenetic systematics. John Wiley & Sons, New York, 439 pp.

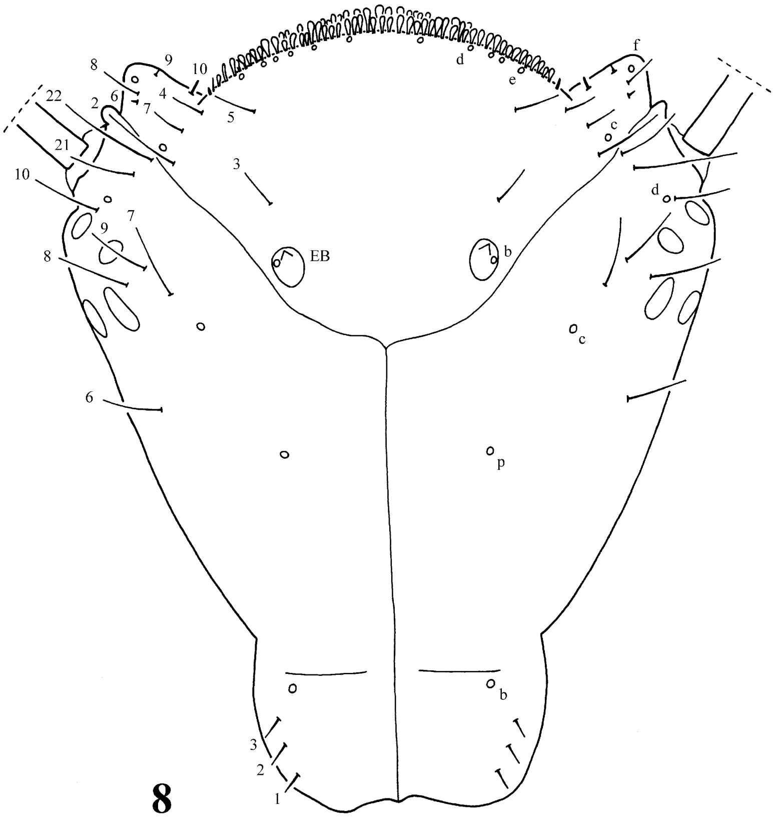


FIGURES 1–3. Distribution of ancestral setae and pores on dorsal surface of head capsule of first instar of selected species of Dytiscinae; (1) *Acilius semisulcatus*; (2) *Thermonectus succinctus*; (3) *Graphoderus occidentalis*; EB, egg bursters, FR, fronto-clypeus; LC, lamellae clypeales; PA, parietale; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2 for list of setae and pores).

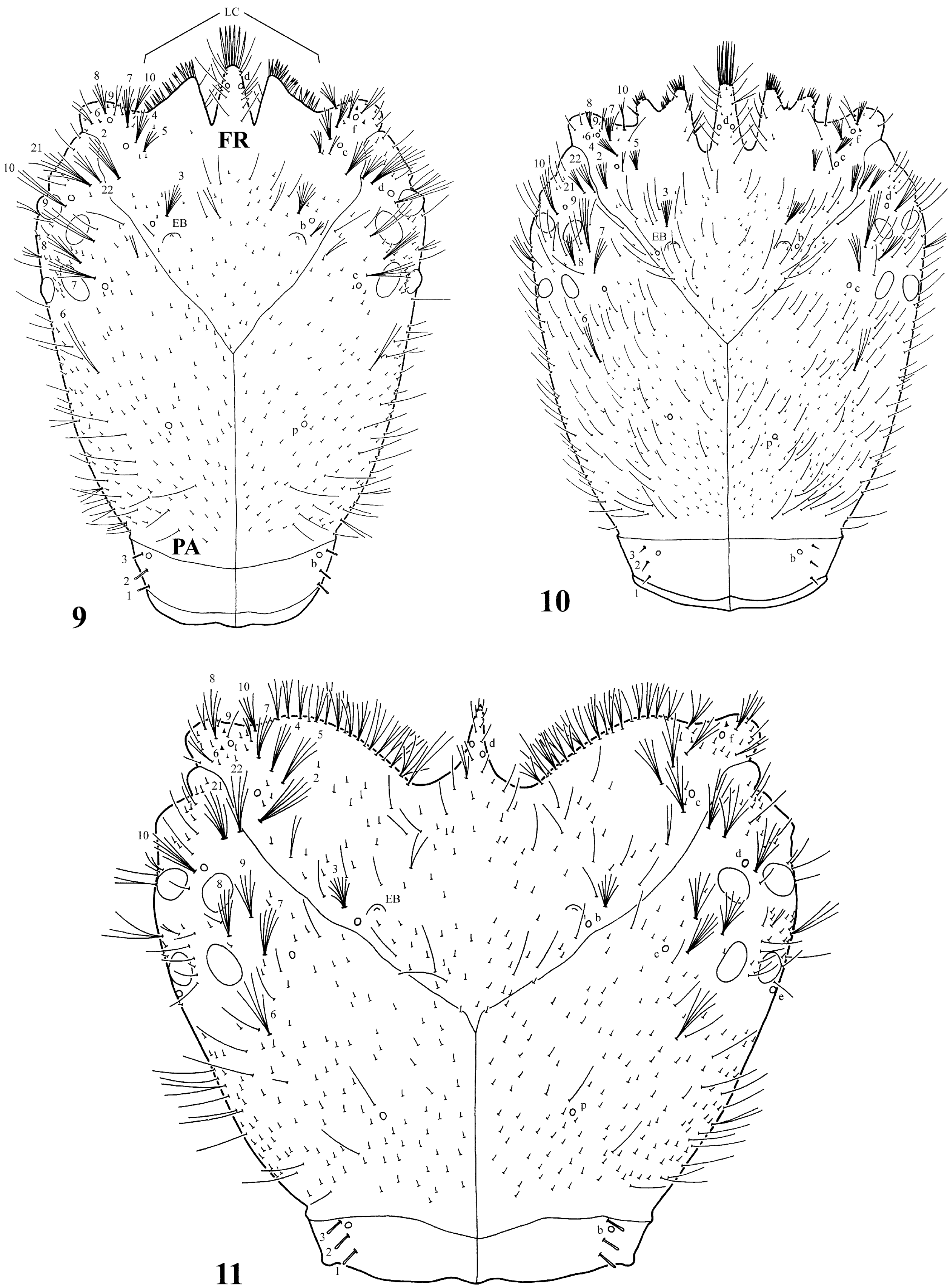


FIGURES 4–6. Distribution of ancestral setae and pores on dorsal surface of head capsule of first instar of selected species of Dytiscinae; (4) *Eretes australis*; (5) *Notaticus fasciatus*; (6) *Hydaticus tuyuensis*; EB, egg bursters, FR, frontoclypeus; LC, lamellae clypeales; PA, parietale; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2 for list of setae and pores).

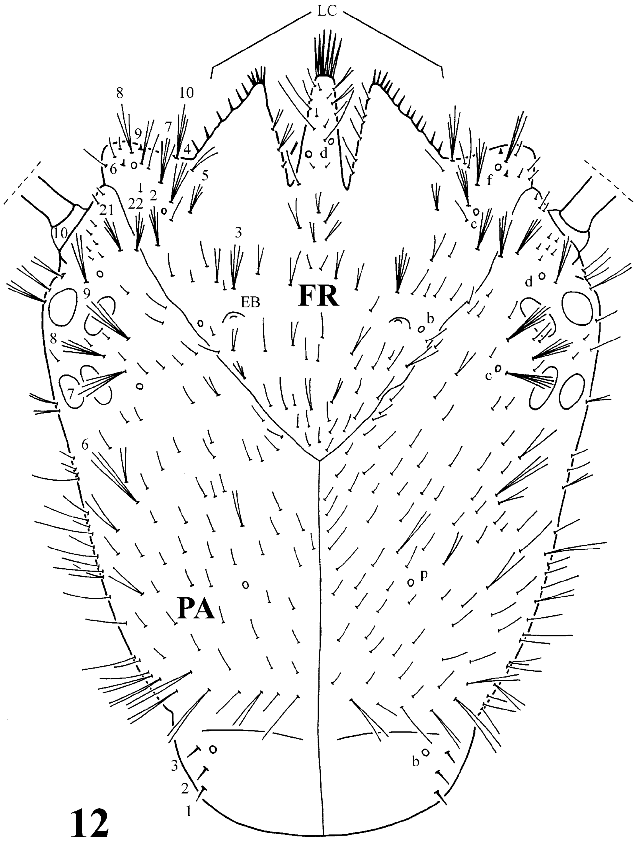




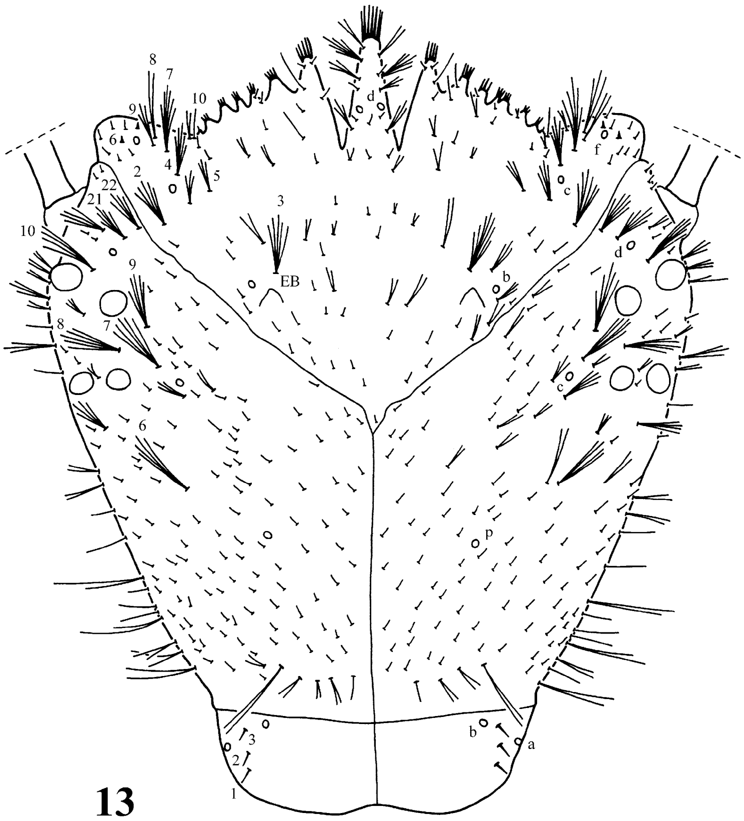
FIGURES 7–8. Distribution of ancestral setae and pores on dorsal surface of head capsule of first instar of selected species of Dytiscinae; (7) *Dytiscus harrisii*; (8) *Hyderodes shuckardi*; EB, egg bursters, FR, frontoclypeus; LC, lamellae clypeales; PA, parietale; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2 for list of setae and pores).



FIGURES 9–11. Distribution of ancestral setae and pores on dorsal surface of head capsule of first instar of selected species of Dytiscinae; (9) *Megadytes (Megadytes) carcharias*; (10) *Megadytes (Paramegadytes) glaucus*; (11) *Megadytes (Trifurcitus) fallax;* EB, egg bursters, FR, frontoclypeus; LC, lamellae clypeales; PA, parietale; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2 for list of setae and pores).

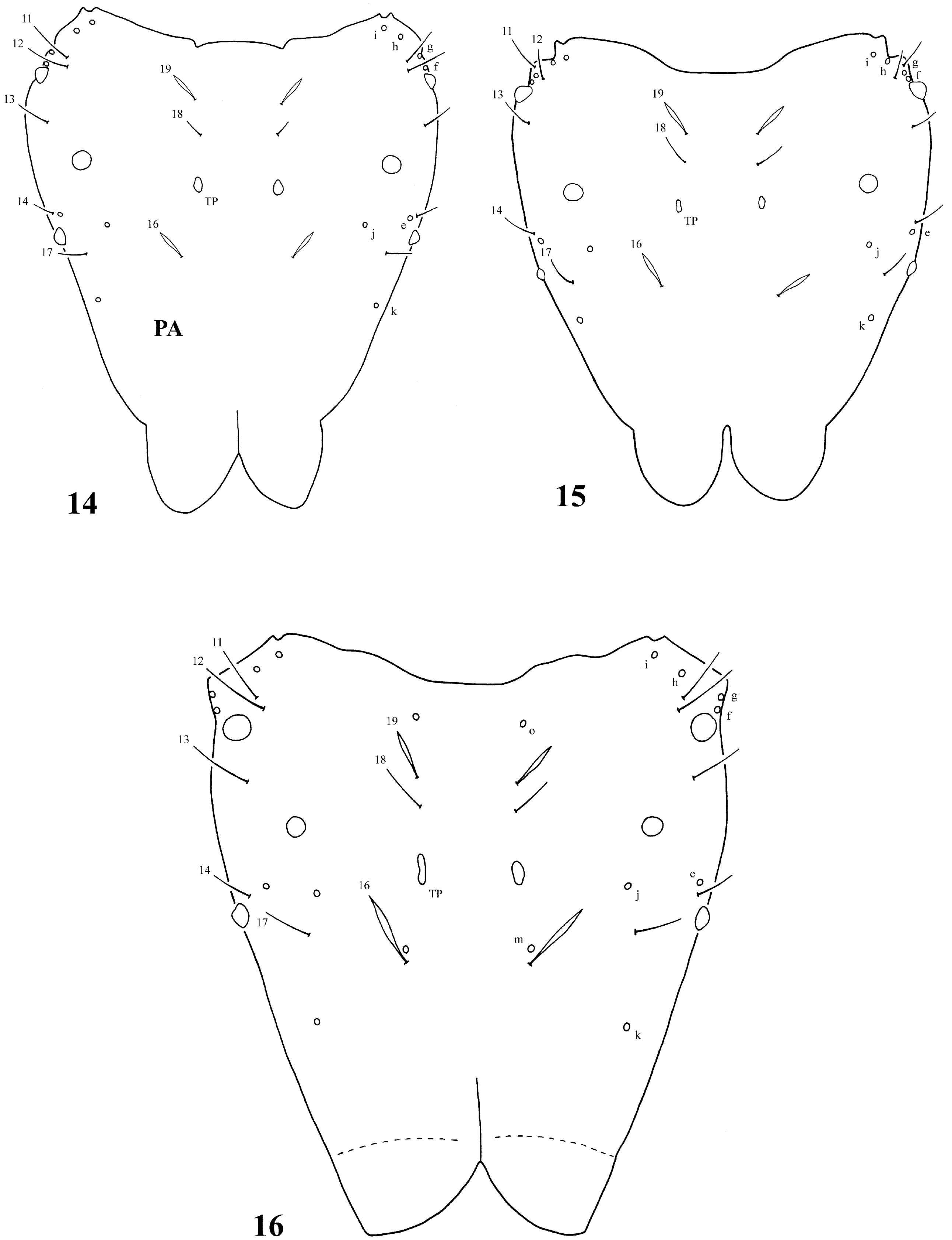


12

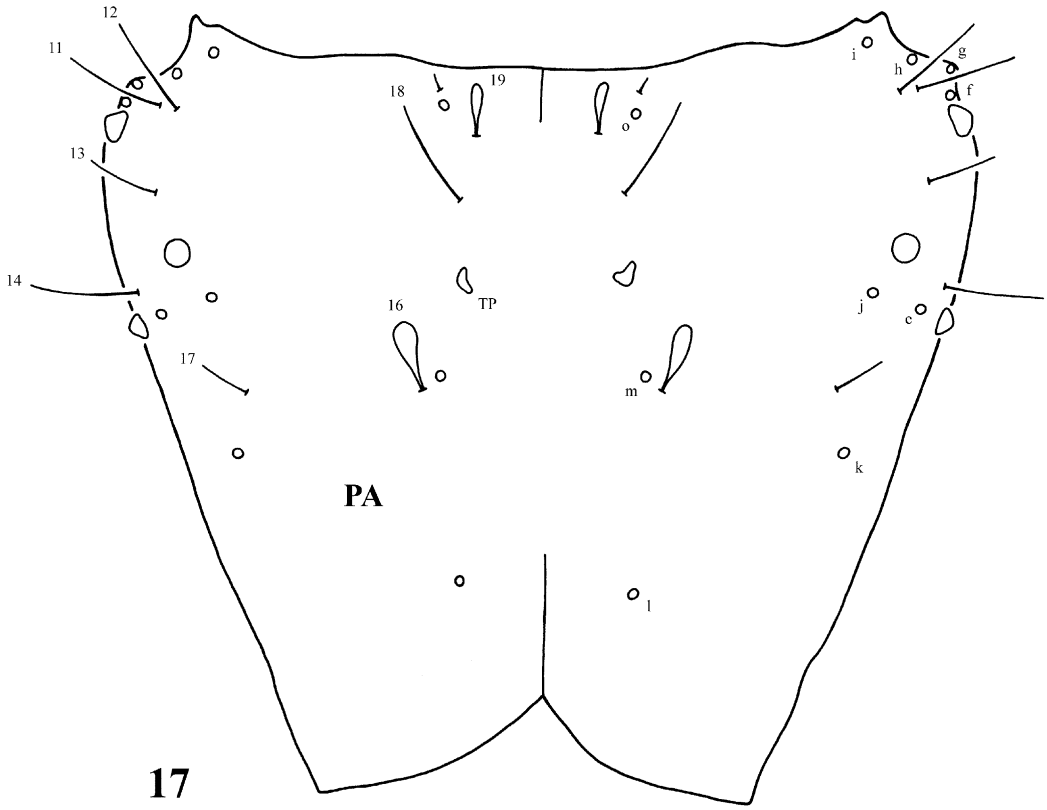


13

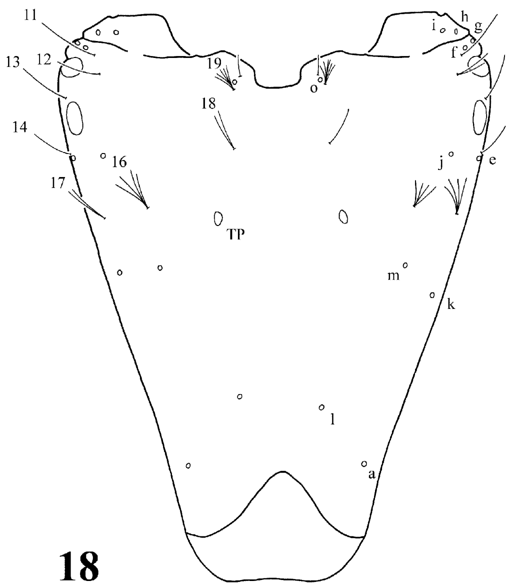
FIGURES 12–13. Distribution of ancestral setae and pores on dorsal surface of head capsule of first instar of selected species of Dytiscinae; (12) *Cybister tripunctatus*; (13) *Onychohydrus scutellaris*; EB, egg bursters, FR, frontoclypeus; LC, lamellae clypeales; PA, parietale; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2 for list of setae and pores).



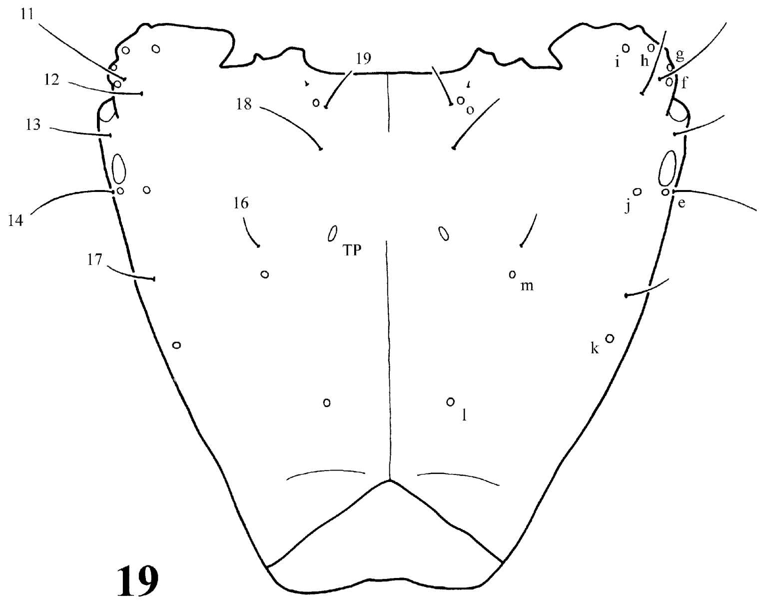
FIGURES 14–16. Distribution of ancestral setae and pores on ventral surface of head capsule of first instar of selected species of Dytiscinae; (14) *Acilius semisulcatus*; (15) *Thermonectus succinctus*; (16) *Graphoderus occidentalis*; PA, parietale; TP, tentorial pits; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2 for list of setae and pores).



17

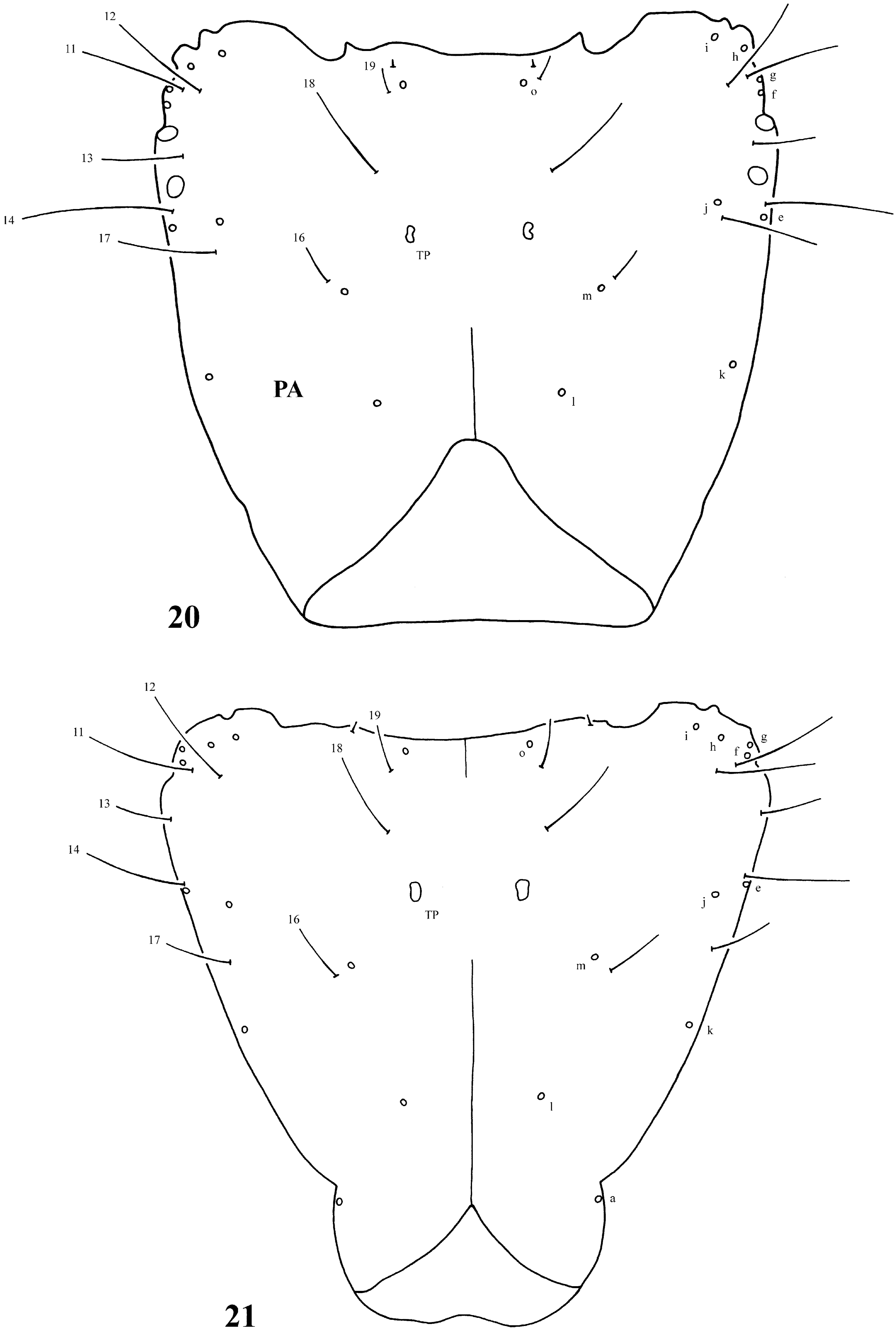


18

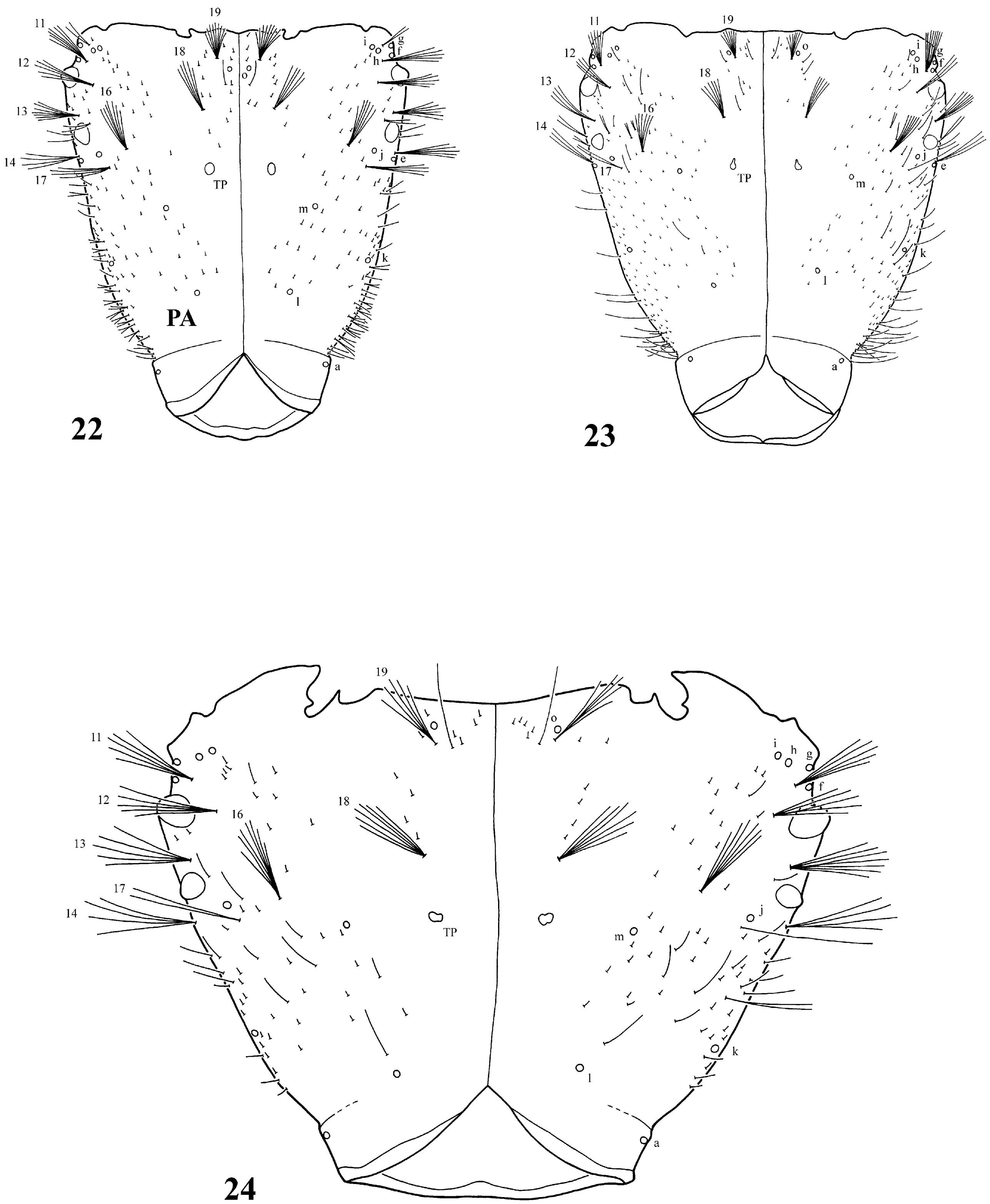


19

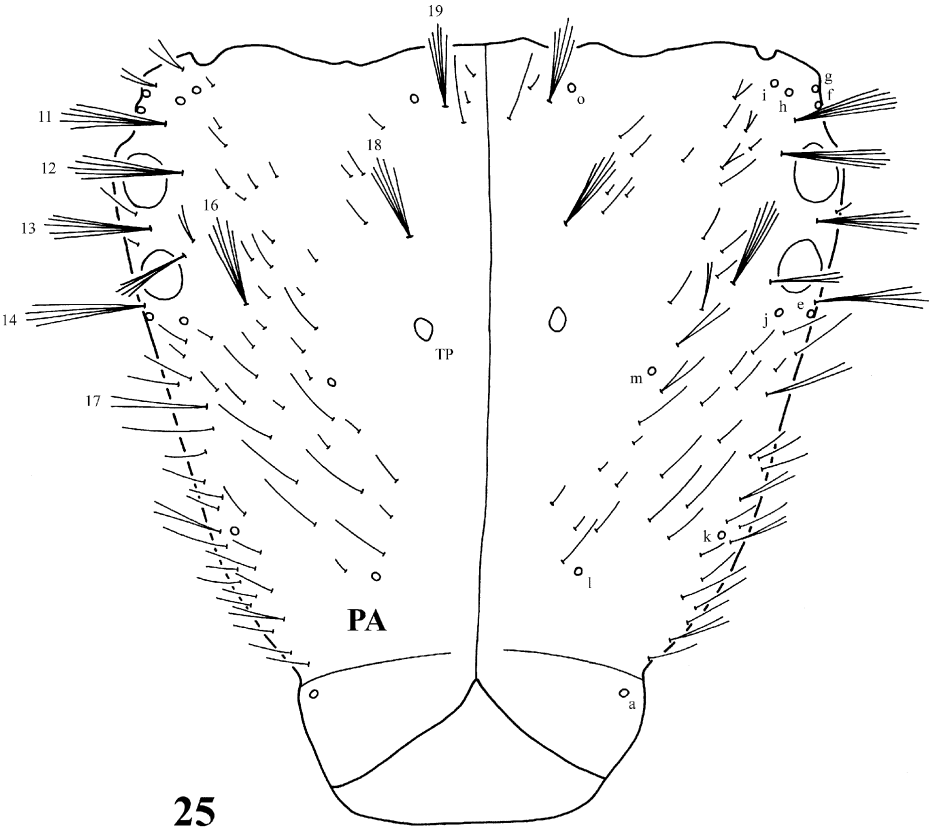
FIGURES 17–19. Distribution of ancestral setae and pores on ventral surface of head capsule of first instar of selected species of Dytiscinae; (17) *Eretes australis*; (18) *Notaticus fasciatus*; (19) *Hydaticus tuyuensis*; PA, parietale; TP, tentorial pits; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2 for list of setae and pores).

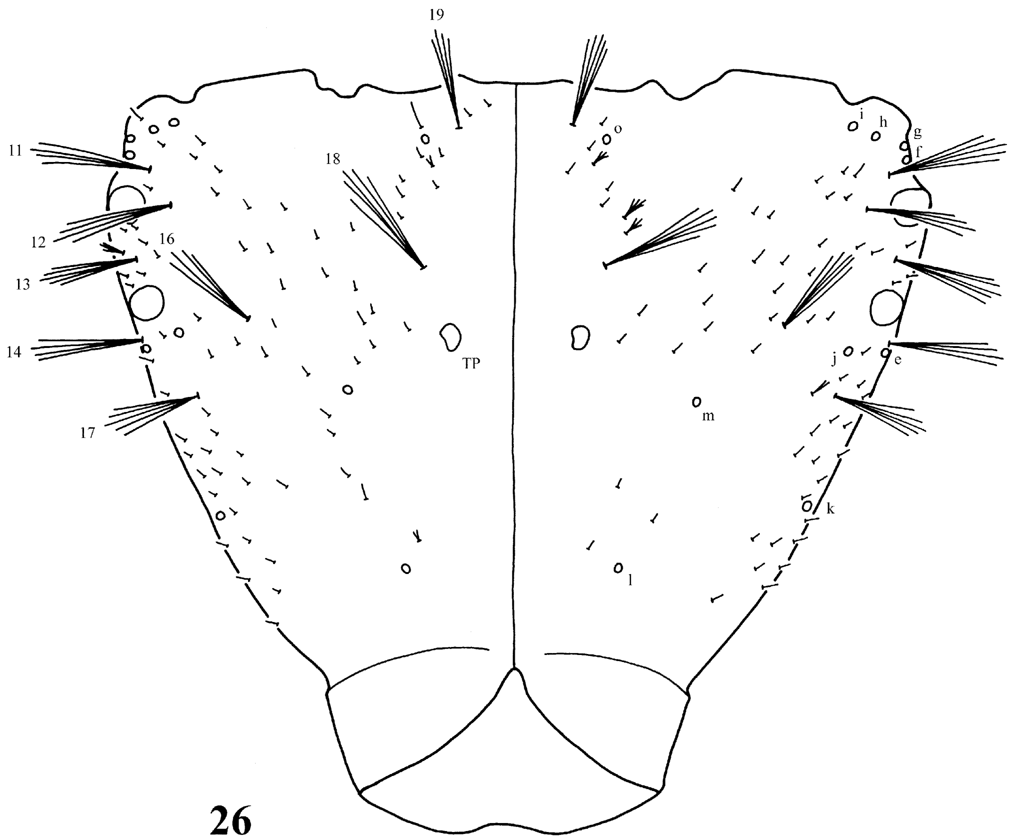


FIGURES 20–21. Distribution of ancestral setae and pores on ventral surface of head capsule of first instar of selected species of Dytiscinae; (20) *Dytiscus harrisii*; (21) *Hyderodes shuckardi*; PA, parietale; TP, tentorial pits; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2 for list of setae and pores).

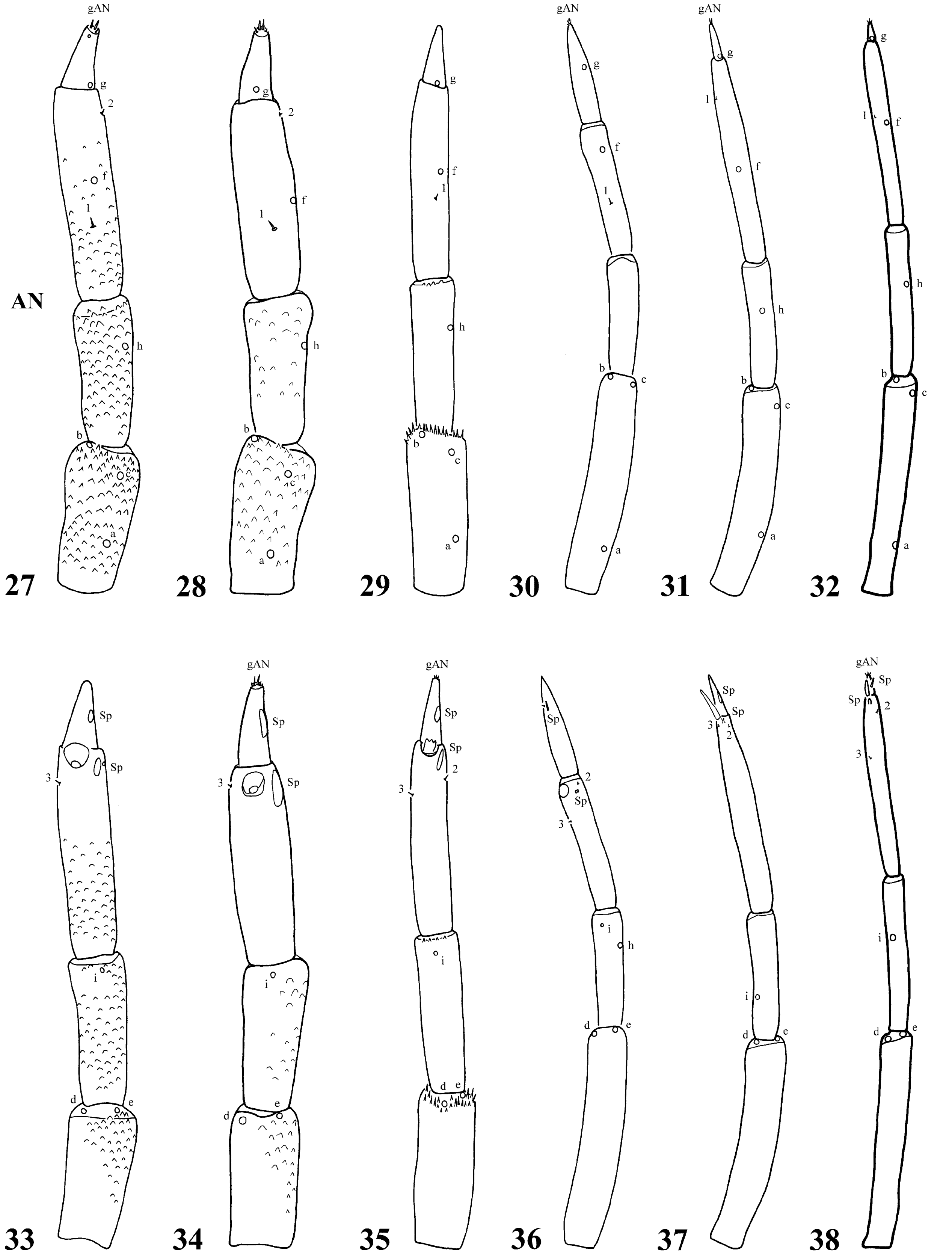


FIGURES 22–24. Distribution of ancestral setae and pores on ventral surface of head capsule of first instar of selected species of Dytiscinae; (22) *Megadytes (Megadytes) carcharias*; (23) *Megadytes (Paramegadytes) glaucus*; (24) *Megadytes (Trifurcitus) fallax;* PA, parietale; TP, tentorial pits; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 2 for list of setae and pores).

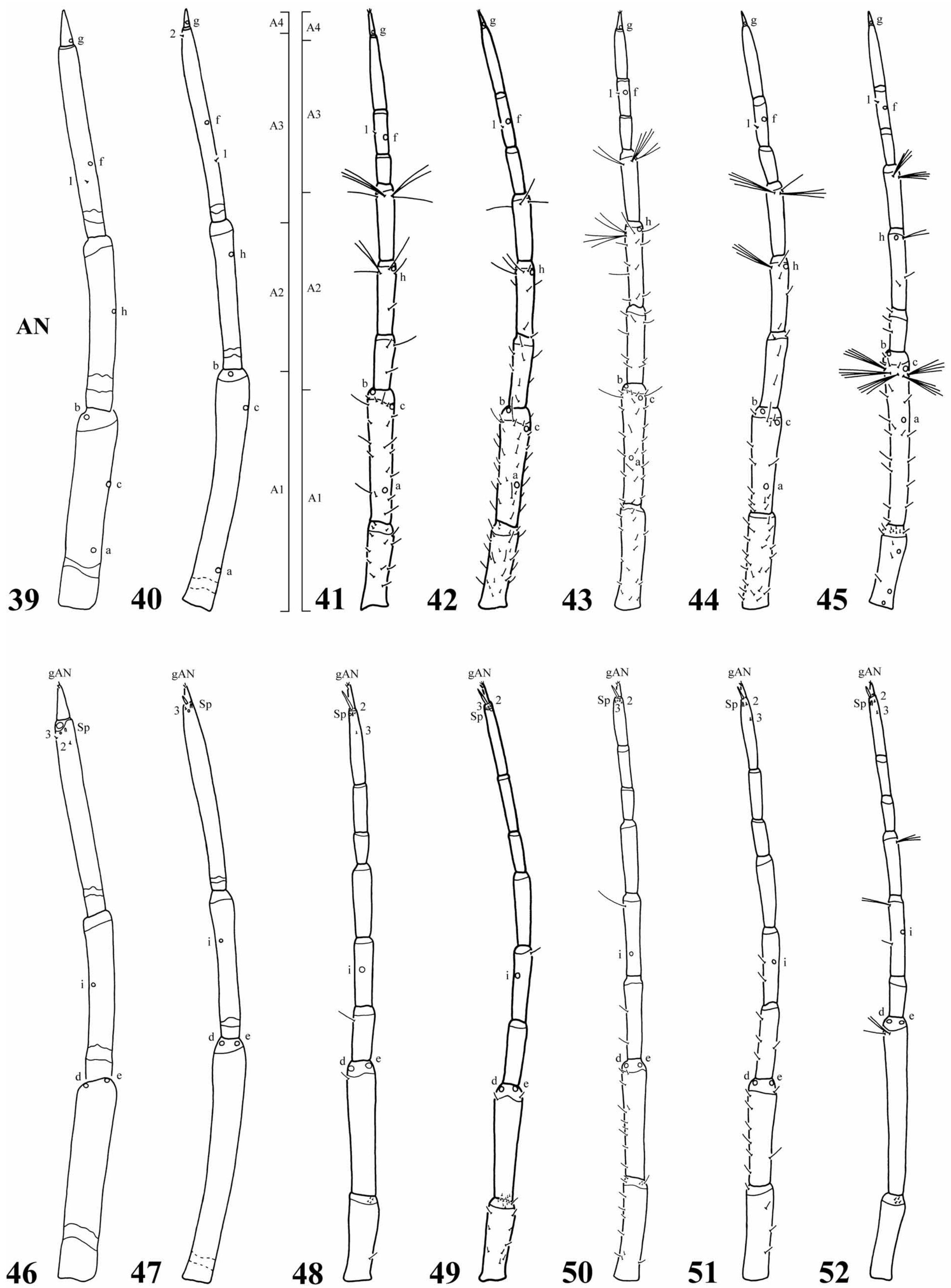




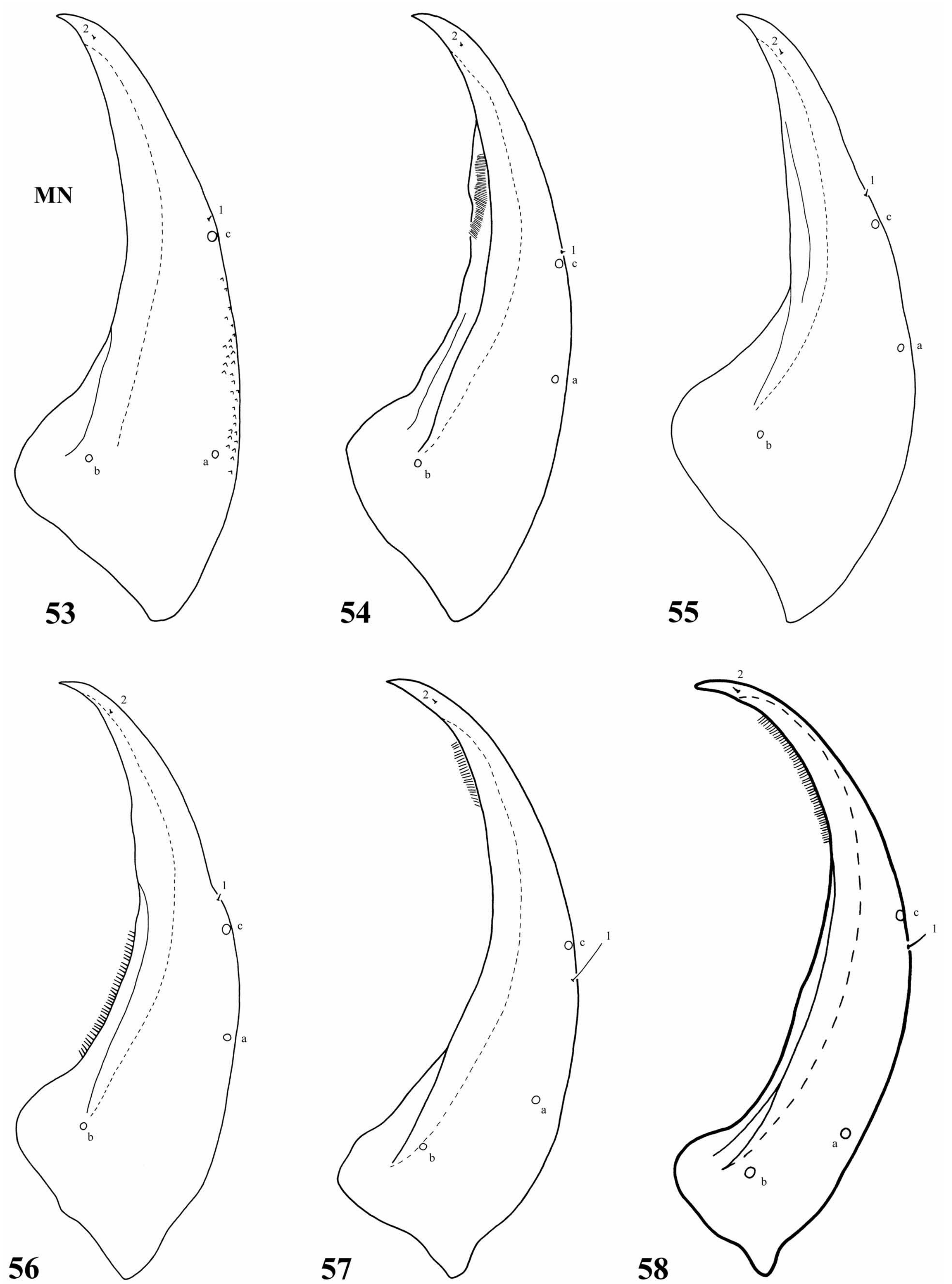
FIGURES 25–26. Distribution of ancestral setae and pores on ventral surface of head capsule of first instar of selected species of Dytiscinae; (25) *Cybister tripunctatus*; (26) *Onychohydrus scutellaris*; PA, parietale; TP, tentorial pits; numbers and lower-case letters refer to primary setae and pores, respectively (see Table 2 for list of setae and pores).



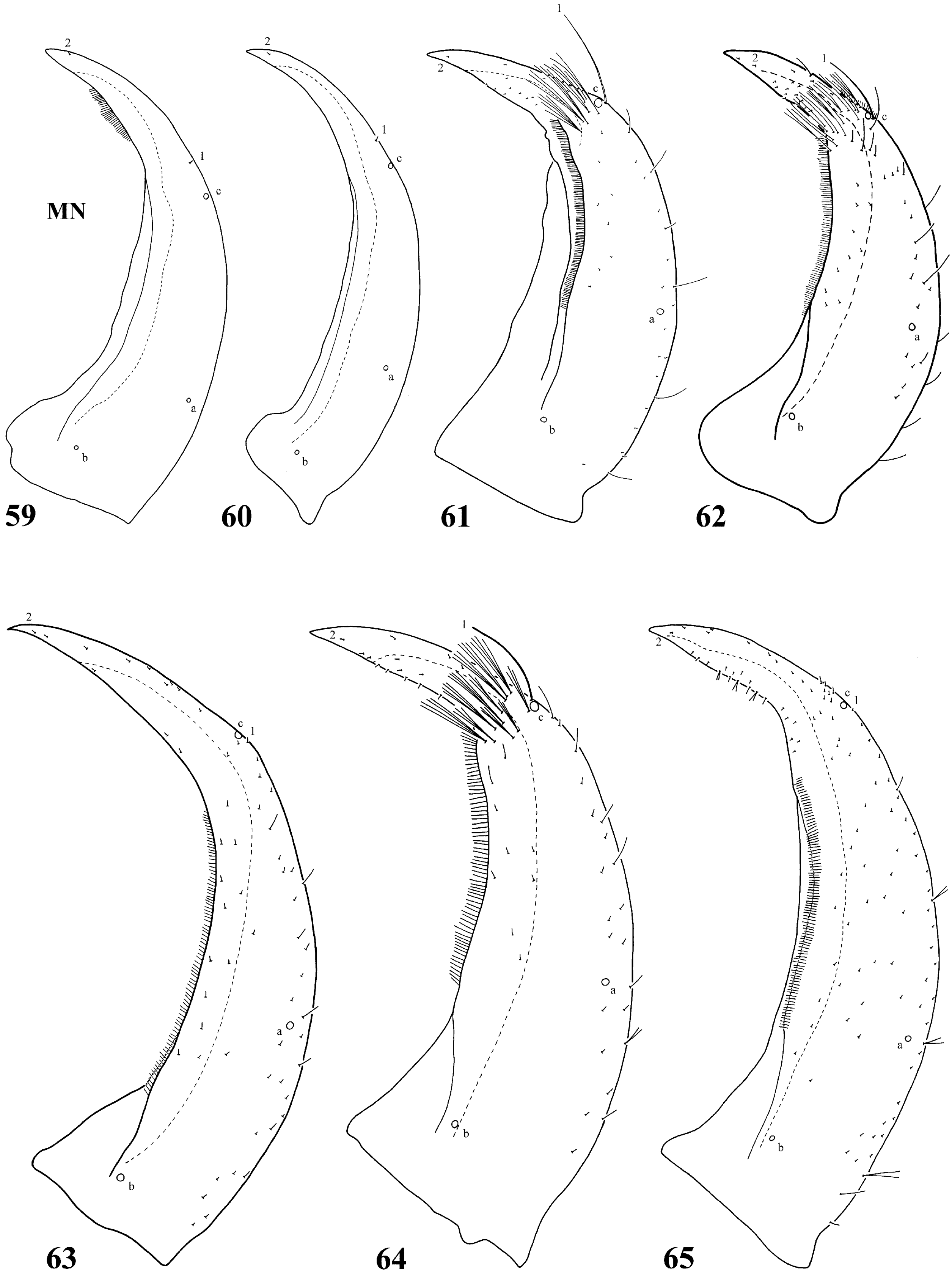
FIGURES 27–38. Distribution of ancestral setae and pores on antenna of first instar of selected species of Dytiscinae; (27–32) right antenna, dorsal surface; (33–38) left antenna, ventral surface; (27, 33) *Acilius semisulcatus*; (28, 34) *Thermonectus succinctus*; (29, 35) *Graphoderus occidentalis*; (30, 36) *Eretes australis*; (31, 37) *Notaticus fasciatus*; (32, 38) *Hydaticus tuyuensis*; AN, antenna; Sp, spinula; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



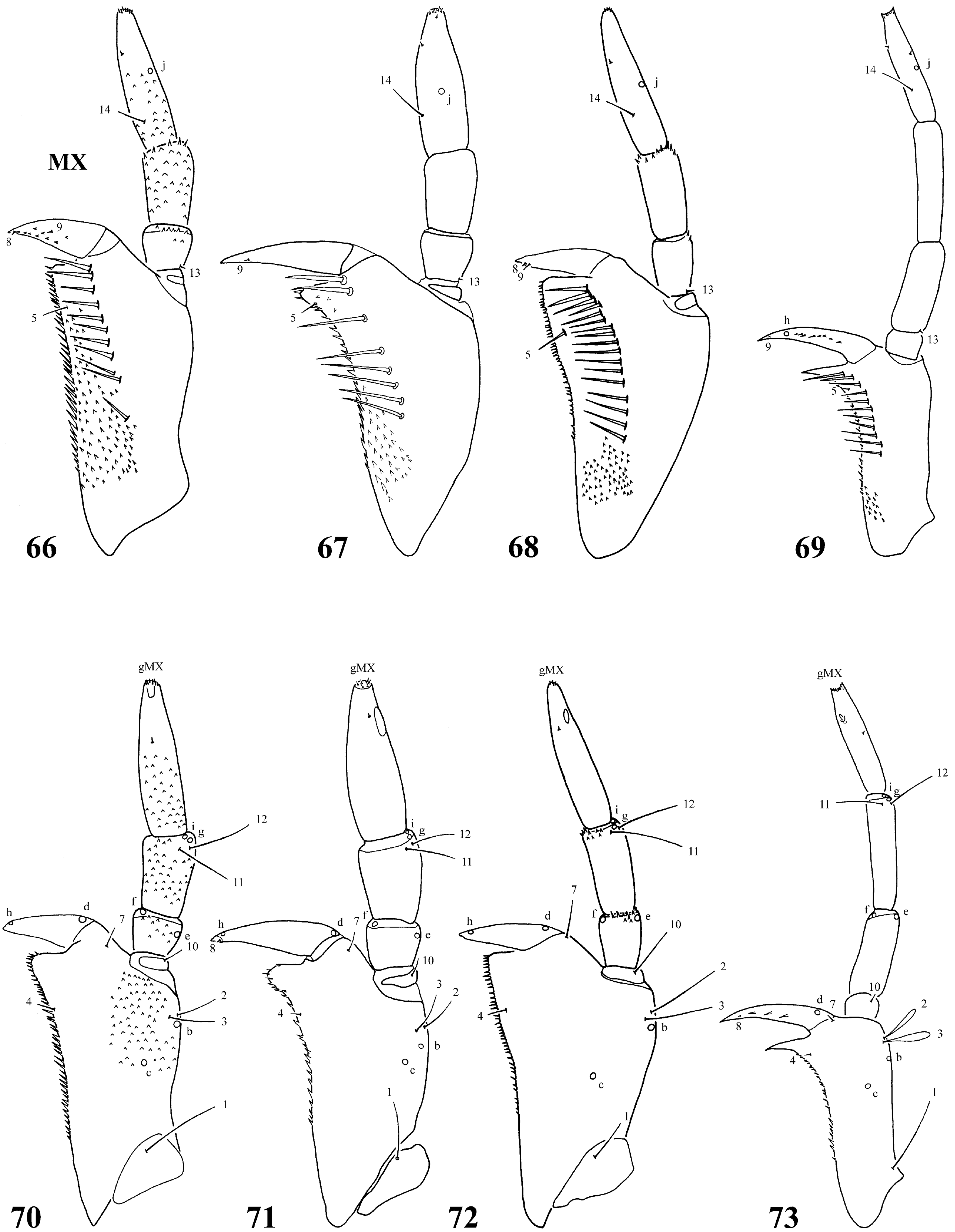
FIGURES 39–52. Distribution of ancestral setae and pores on antenna of first instar of selected species of Dytiscinae; (39–45) right antenna, dorsal surface; (46–52) left antenna, ventral surface; (39, 46) *Dytiscus harrisii*; (40, 47) *Hyderodes shuckardi*; (41, 48) *Megadytes (Megadytes) carcharias*; (42, 49) *Megadytes (Paramegadytes) glaucus*; (43, 50) *Megadytes (Trifurcitus) fallax*; (44, 51) *Cybister tripunctatus*; (45, 52) *Onychohydrus scutellaris*; A1–A4, antennomeres 1–4; AN, antenna; Sp, spinula; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



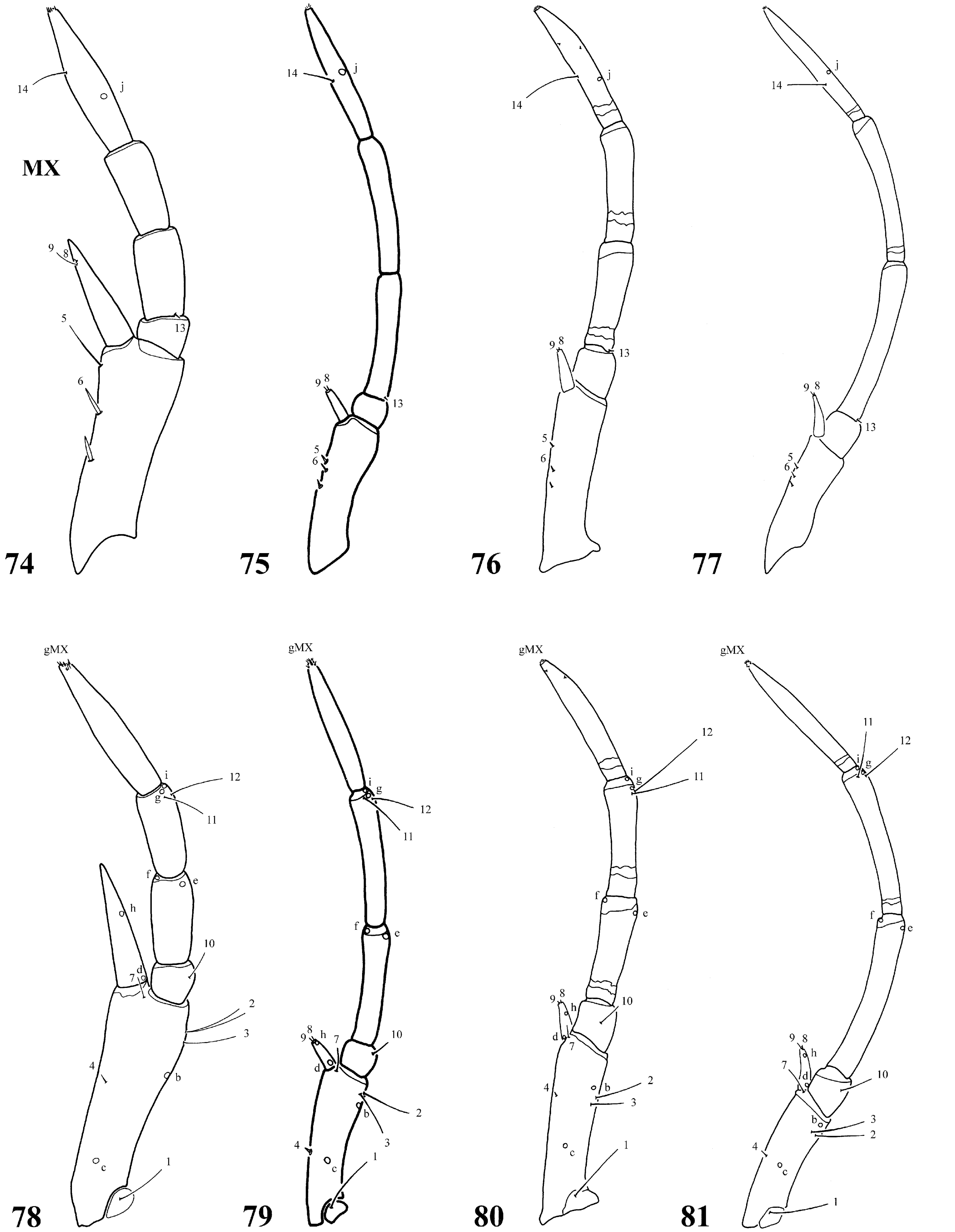
FIGURES 53–58. Distribution of ancestral setae and pores on right mandible of first instar of selected species of Dytiscinae, dorsal view; (53) *Acilius semisulcatus*; (54) *Thermonectus succinctus*; (55) *Graphoderus occidentalis*; (56) *Eretes australis*; (57) *Notaticus fasciatus*; (58) *Hydaticus tuyuensis*; MN. mandible; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



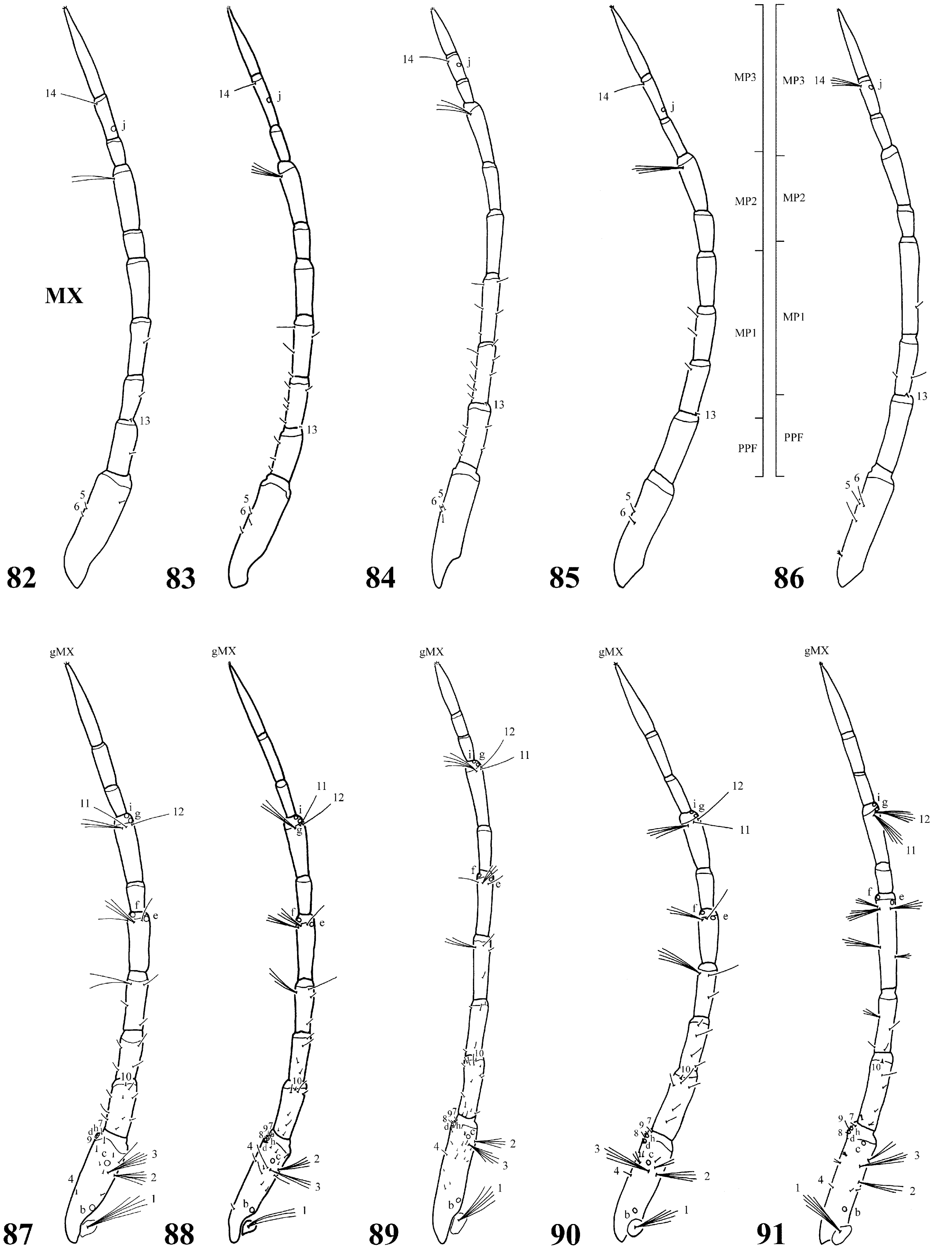
FIGURES 59–65. Distribution of ancestral setae and pores on right mandible of first instar of selected species of Dytiscinae, dorsal view; (59) *Dytiscus harrisii*; (60) *Hyderodes shuckardi*; (61) *Megadytes (Megadytes) carcharias*; (62) *Megadytes (Paramegadytes) glaucus*; (63) *Megadytes (Trifurcitus) fallax*; (64) *Cybister tripunctatus*; (65) *Onychohydrus scutellaris*; MN, mandible; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



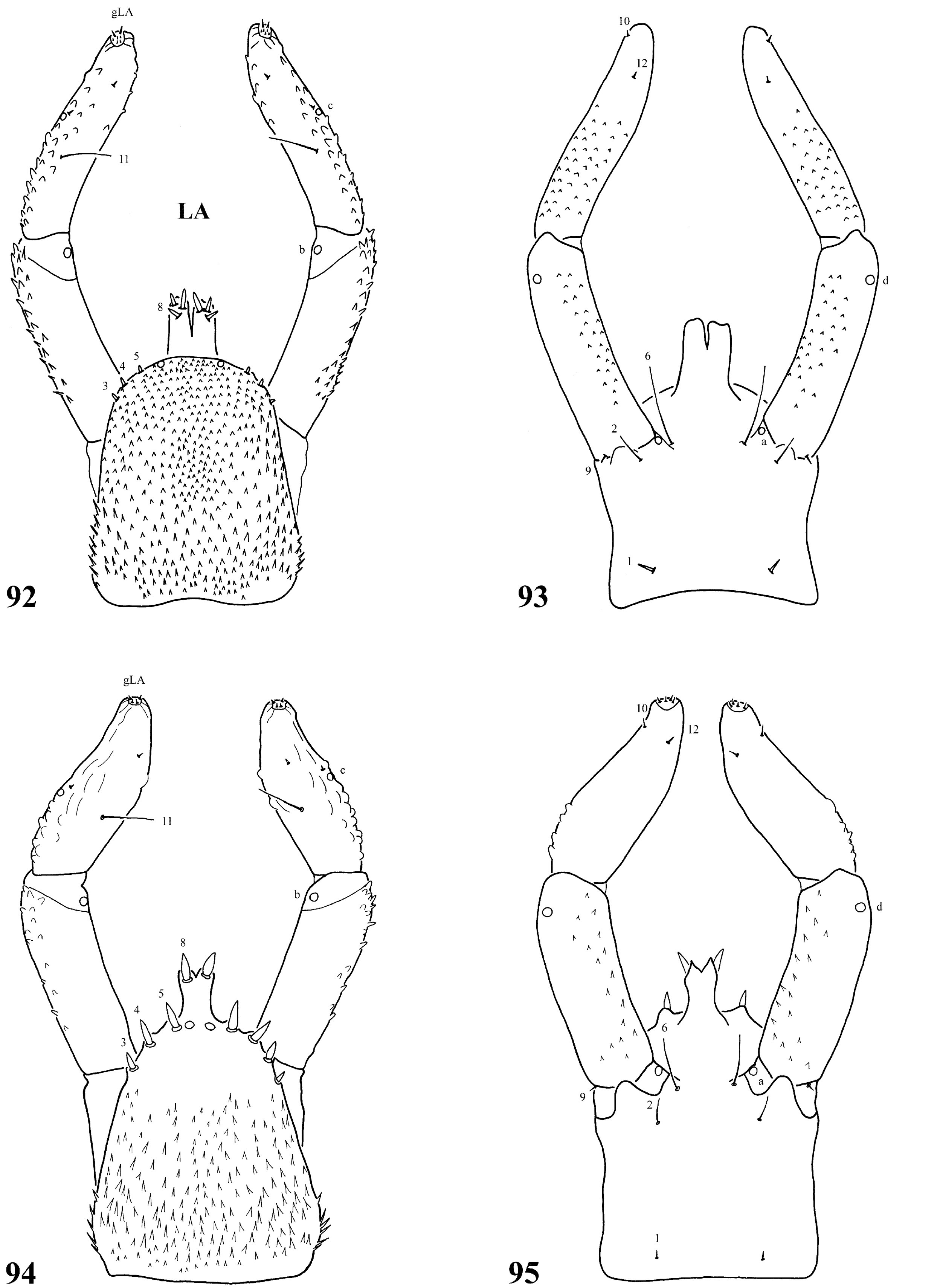
FIGURES 66–73. Distribution of ancestral setae and pores on maxilla of first instar of selected species of Dytiscinae; (66–69) right maxilla, dorsal surface; (70–73) left maxilla, ventral surface; (66, 70) *Acilius semisulcatus*; (67, 71) *Thermonectus succinctus*; (68, 72) *Graphoderus occidentalis*; (69, 73) *Eretes australis*; MX, maxilla; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



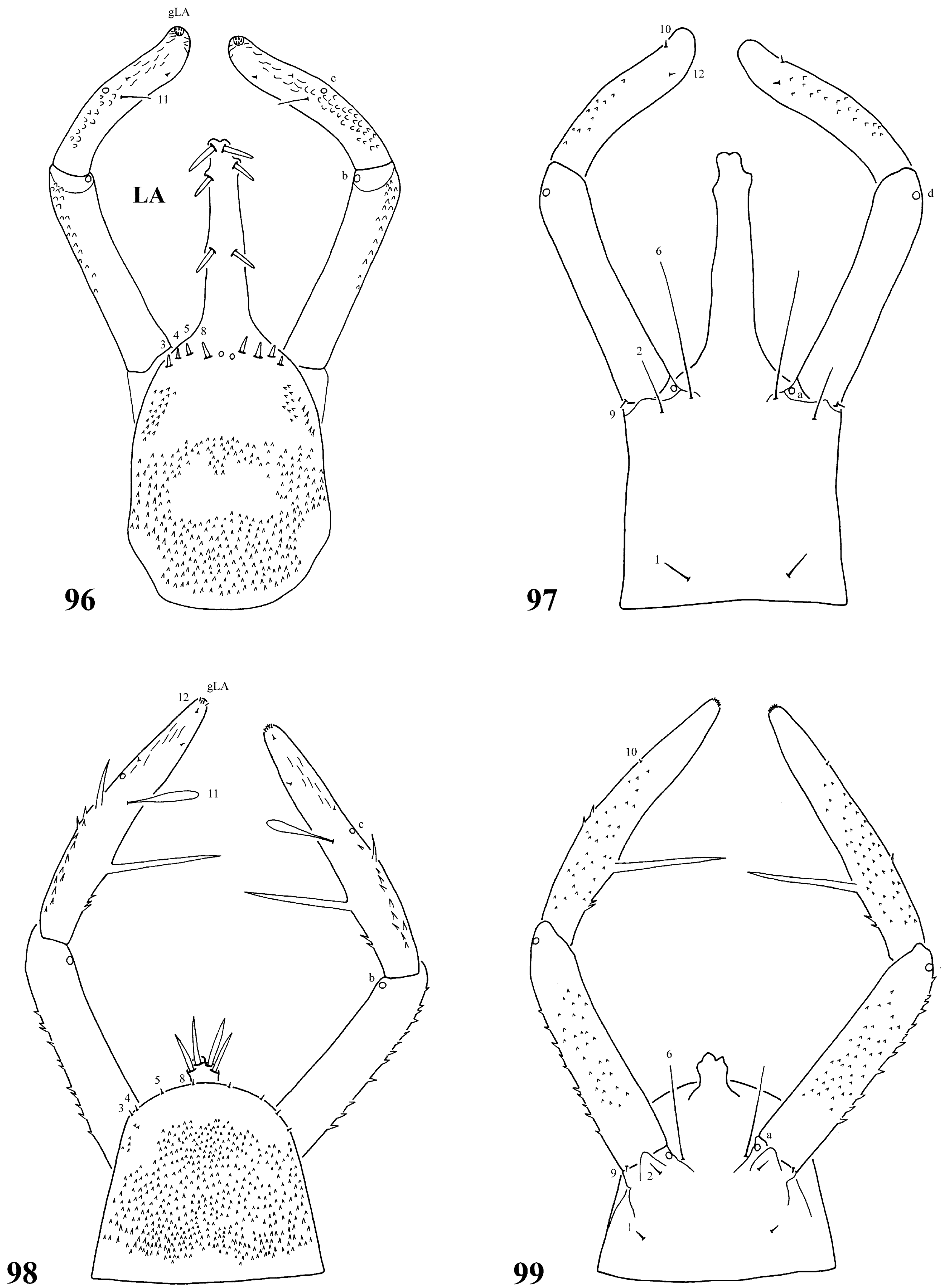
FIGURES 74–81. Distribution of ancestral setae and pores on maxilla of first instar of selected species of Dytiscinae; (74–77) right maxilla, dorsal surface; (78–81) left maxilla, ventral surface; (74, 78) *Notaticus fasciatus*; (75, 79) *Hydaticus tuyuensis*; (76, 80) *Dytiscus harrisii*; (77, 81) *Hyderodes shuckardi*; MX, maxilla; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



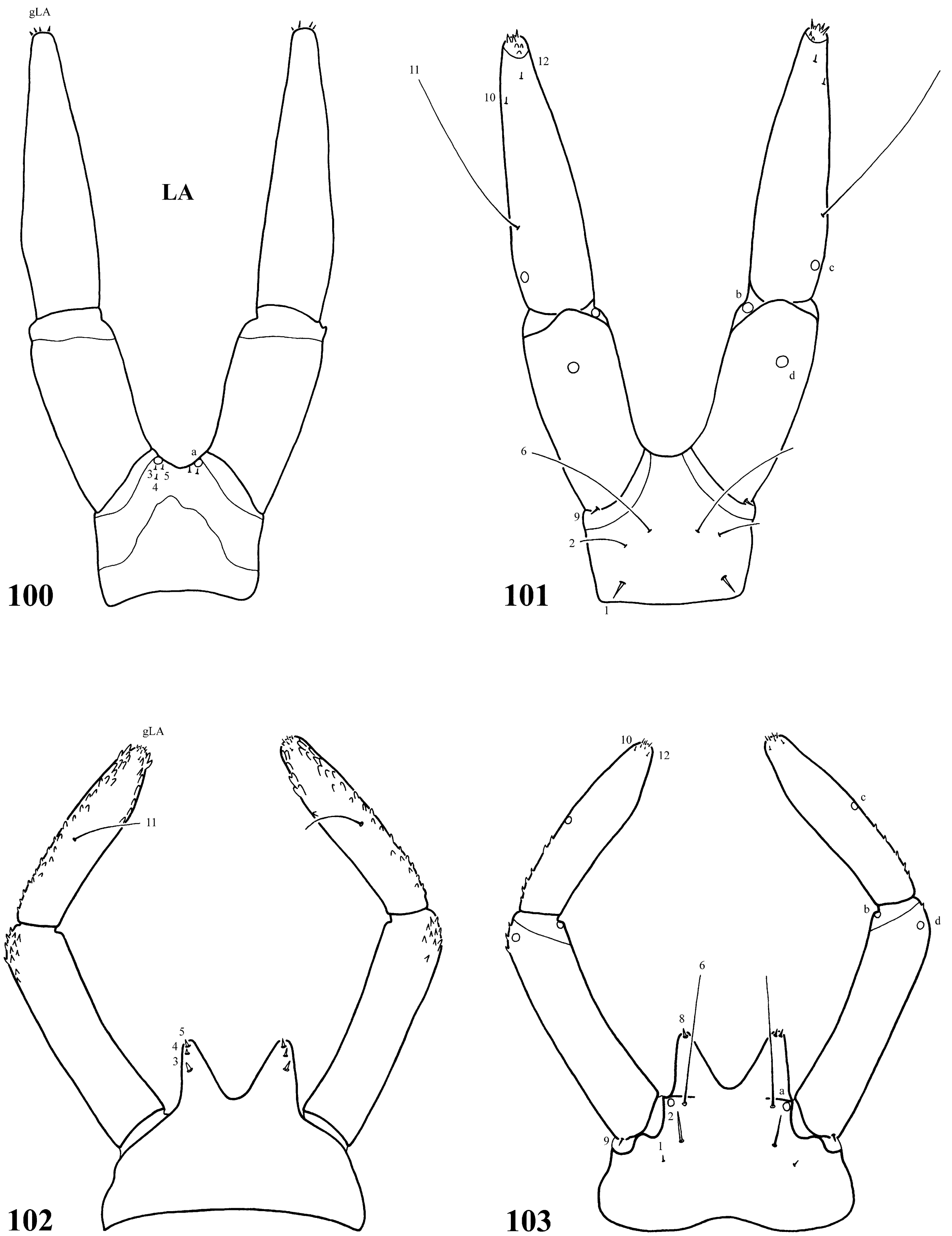
FIGURES 82–91. Distribution of ancestral setae and pores on maxilla of first instar of selected species of Dytiscinae; (82–86) right maxilla, dorsal surface; (87–91) left maxilla, ventral surface; (82, 87) *Megadytes (Megadytes) carcharias*; (83, 88) *Megadytes (Paramegadytes) glaucus*; (84, 89) *Megadytes (Trifurcitus) fallax*; (85, 90) *Cybister tripunctatus*; (86, 91) *Onychohydrus scutellaris*; MP1–MP3, maxillary palpomeres 1–3; MX, maxilla; PPF, palpifer; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



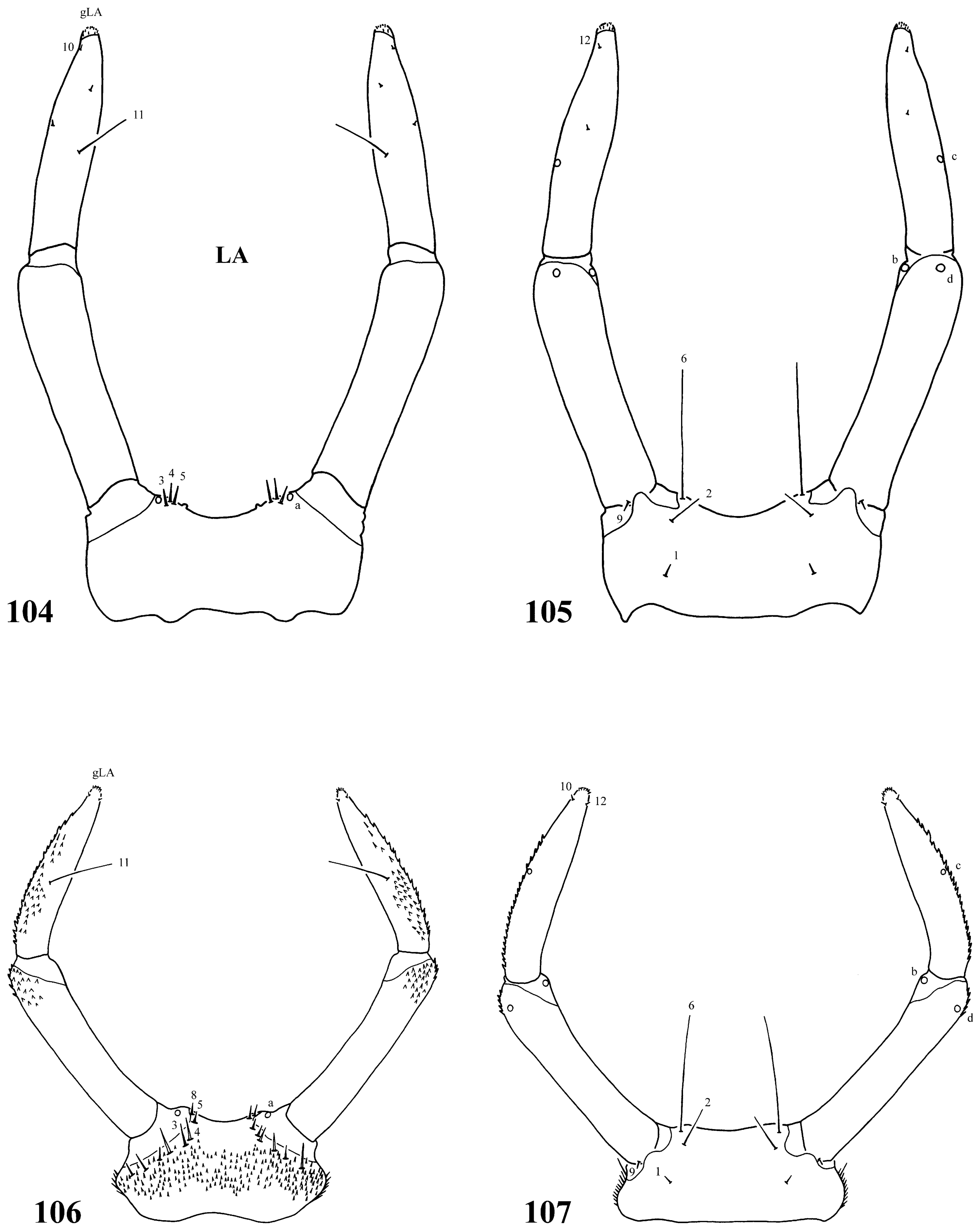
FIGURES 92–95. Distribution of ancestral setae and pores on labium of first instar of selected species of Dytiscinae; (92–93) *Acilius semisulcatus*, (92) dorsal surface, (93) ventral surface; (94–95) *Thermonectus succinctus*, (94) dorsal surface, (95) ventral surface; LA, labium; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



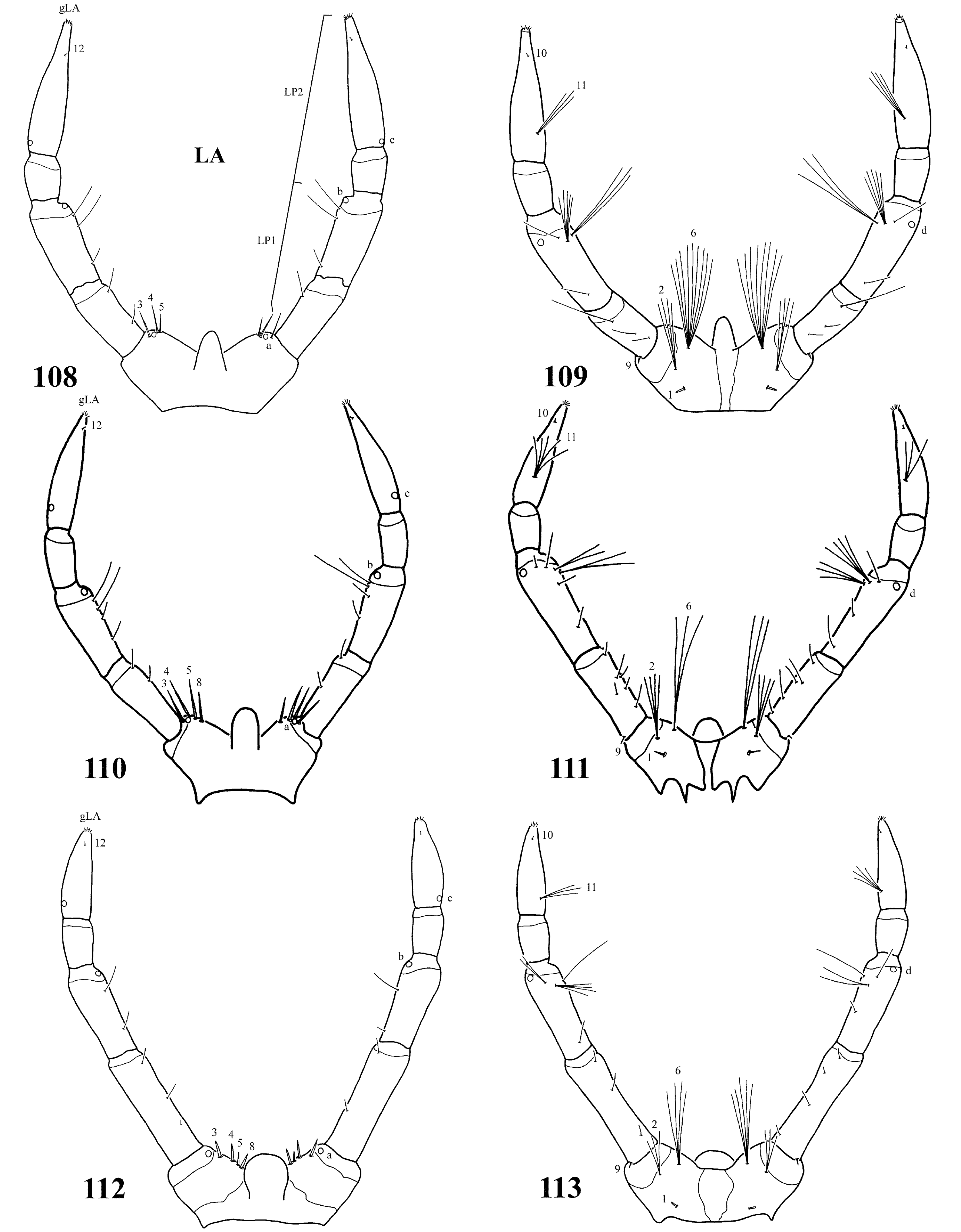
FIGURES 96–99. Distribution of ancestral setae and pores on labium of first instar of selected species of Dytiscinae; (96–97) *Graphoderus occidentalis*, (96) dorsal surface, (97) ventral surface; (98–99) *Eretes australis*, (98) dorsal surface, (99) ventral surface; LA, labium; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



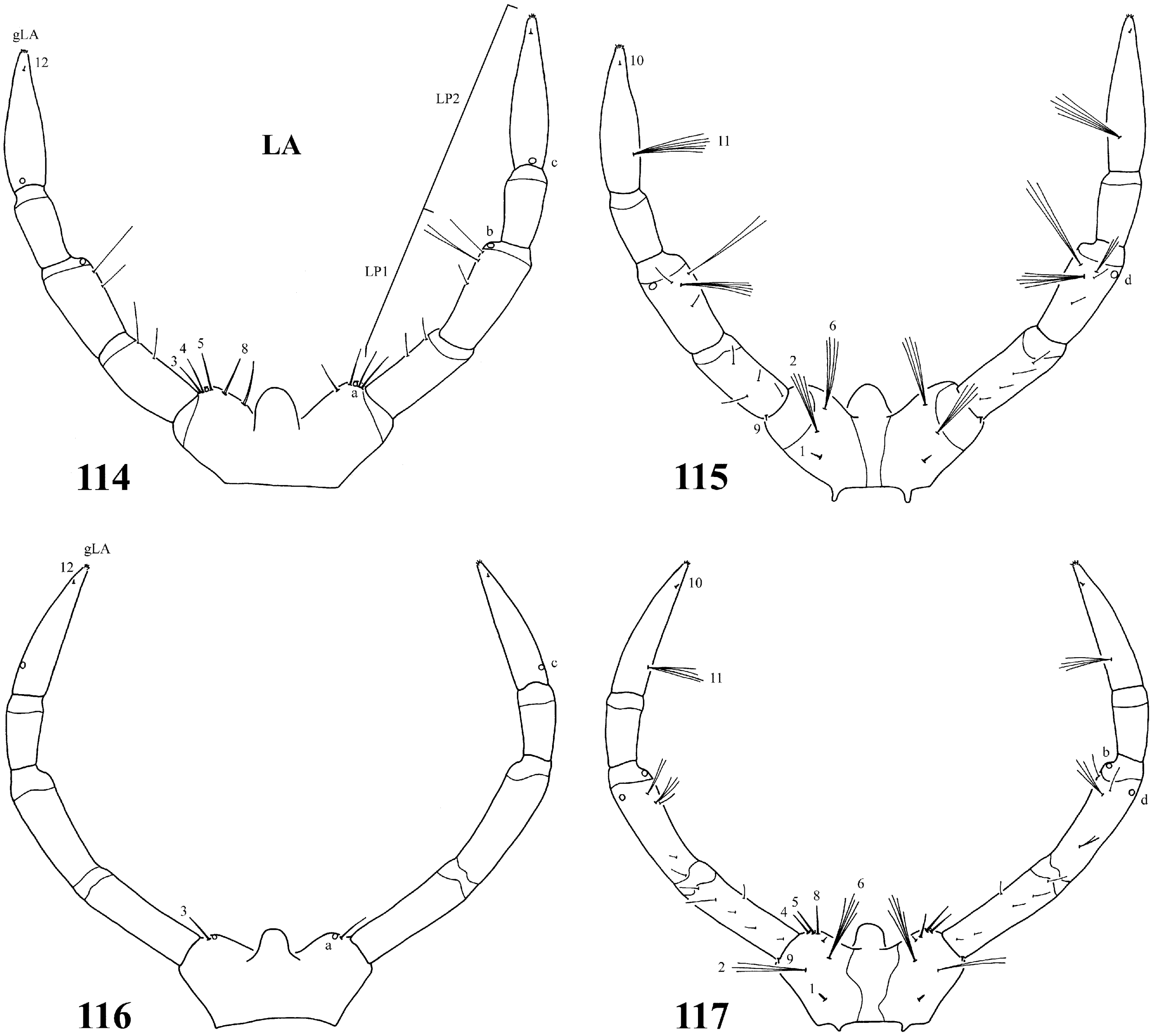
FIGURES 100–103. Distribution of ancestral setae and pores on labium of first instar of selected species of Dytiscinae; (100–101) *Notaticus fasciatus*, (100) dorsal surface, (101) ventral surface; (102–103) *Hydaticus tuyuensis*, (102) dorsal surface, (103) ventral surface; LA, labium; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



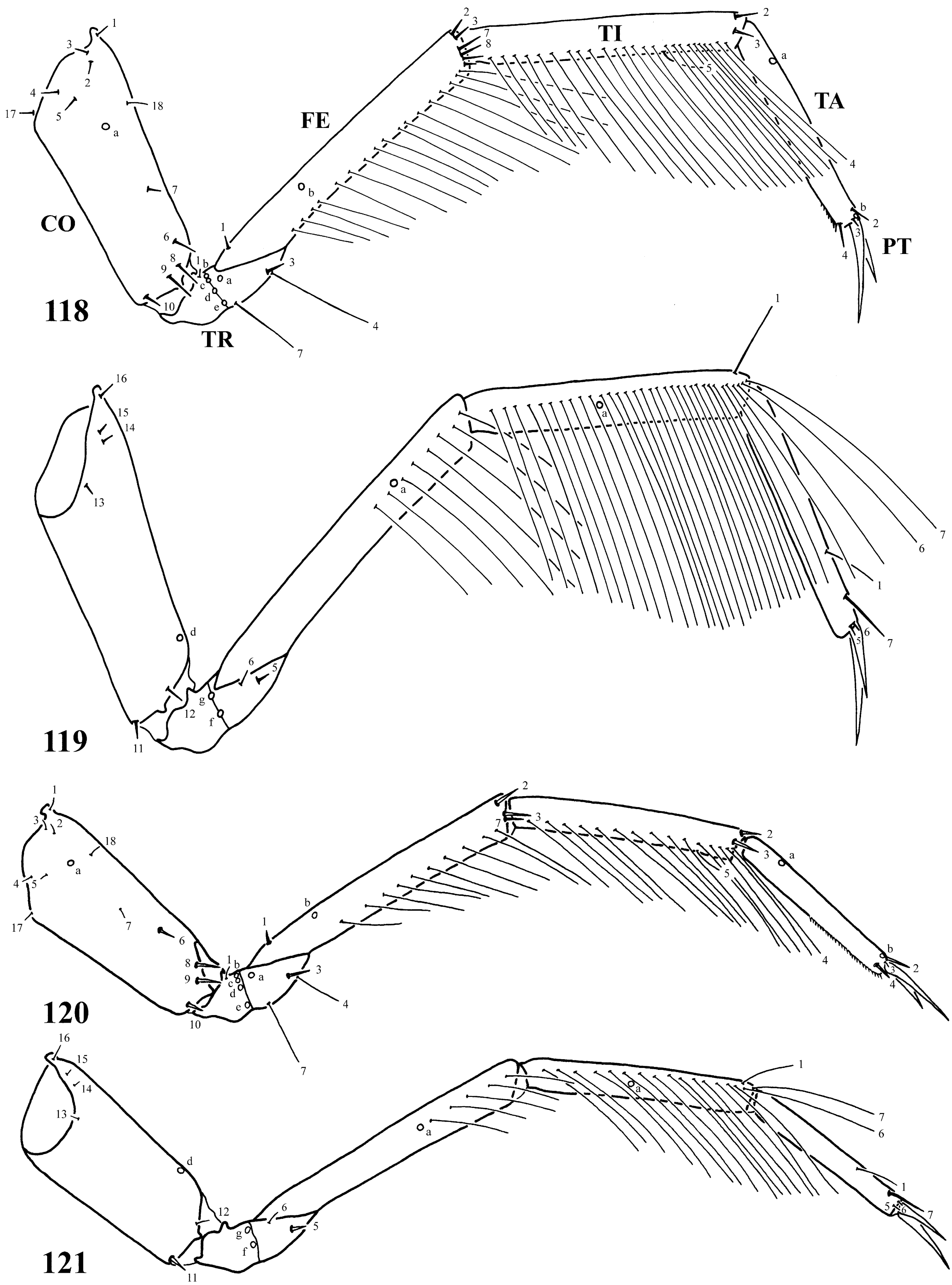
FIGURES 104–107. Distribution of ancestral setae and pores on labium of first instar of selected species of Dytiscinae; (104–105) *Dytiscus harrisii*, (104) dorsal surface, (105) ventral surface; (106–107) *Hyderodes shuckardi*, (106) dorsal surface, (107) ventral surface; LA, labium; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



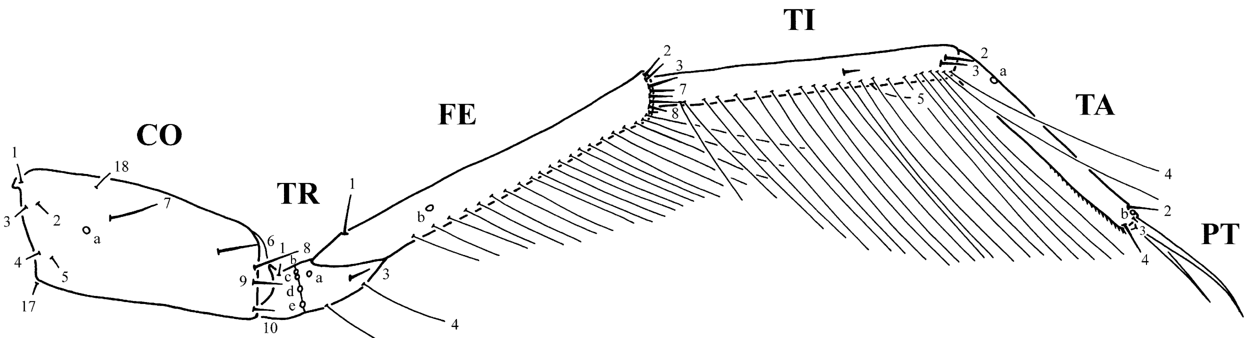
FIGURES 108–113. Distribution of ancestral setae and pores on labium of first instar of selected species of Dytiscinae; (108–109) *Megadytes (Megadytes) carcharias*, (108) dorsal surface, (109) ventral surface; (110–111) *Megadytes (Paramegadytes) glaucus*, (110) dorsal surface, (111) ventral surface; (112–113) *Megadytes (Trifurcitus) fallax*; (112) dorsal surface, (113) ventral surface; LA, labium; LP1 and LP2, labial palpomeres 1 and 2; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



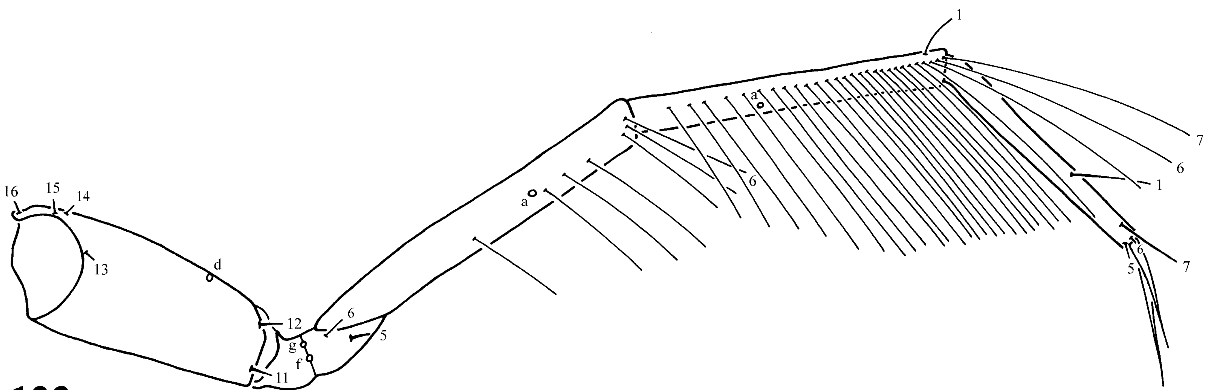
FIGURES 114–117. Distribution of ancestral setae and pores on labium of first instar of selected species of Dytiscinae; (114–115) *Cybister tripunctatus*, (114) dorsal surface, (115) ventral surface; (116–117) *Onychohydrus scutellaris*, (116) dorsal surface, (117) ventral surface; LA, labium; LP1 and LP2, labial palpomeres 1 and 2; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 3 for list of setae and pores).



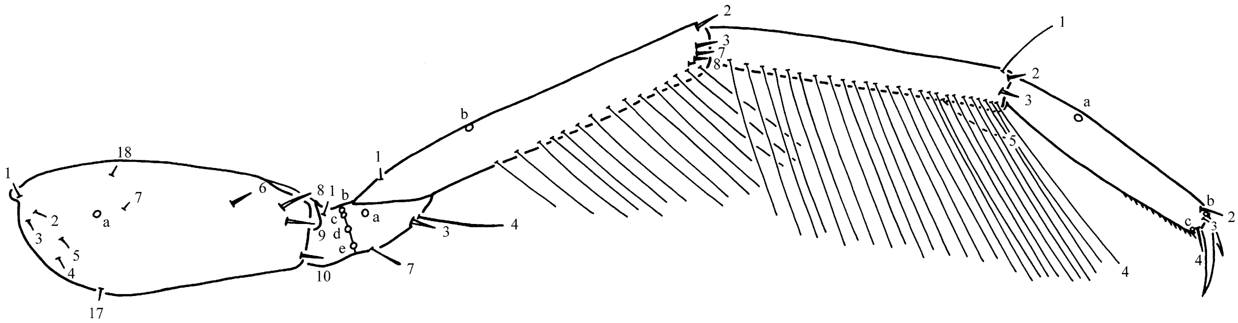
FIGURES 118–121. Distribution of ancestral setae and pores on metathoracic leg of selected species of Dytiscinae; (118–119) *Acilius semisulcatus*, (118) anterior surface, (119) posterior surface; (120–121) *Thermonectus succinctus*, (120) anterior surface, (121) posterior surface; CO, coxa, FE, femur; PT, pretarsus; TA, tarsus; TI, tibia, TR, trochanter; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 4 for list of setae and pores).



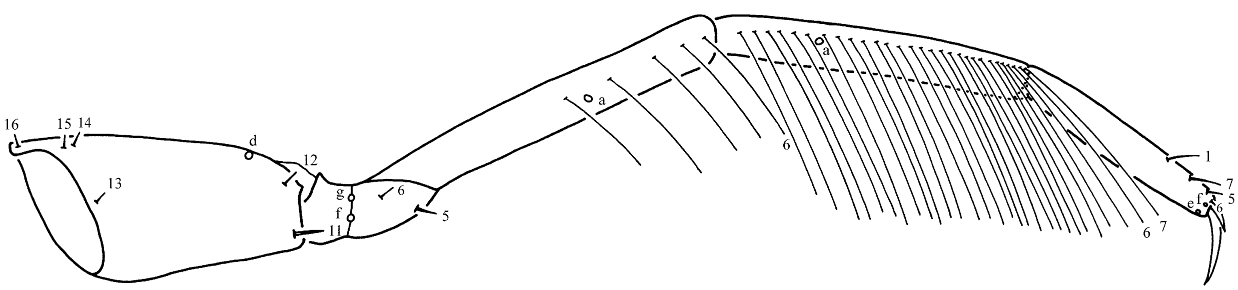
122



123

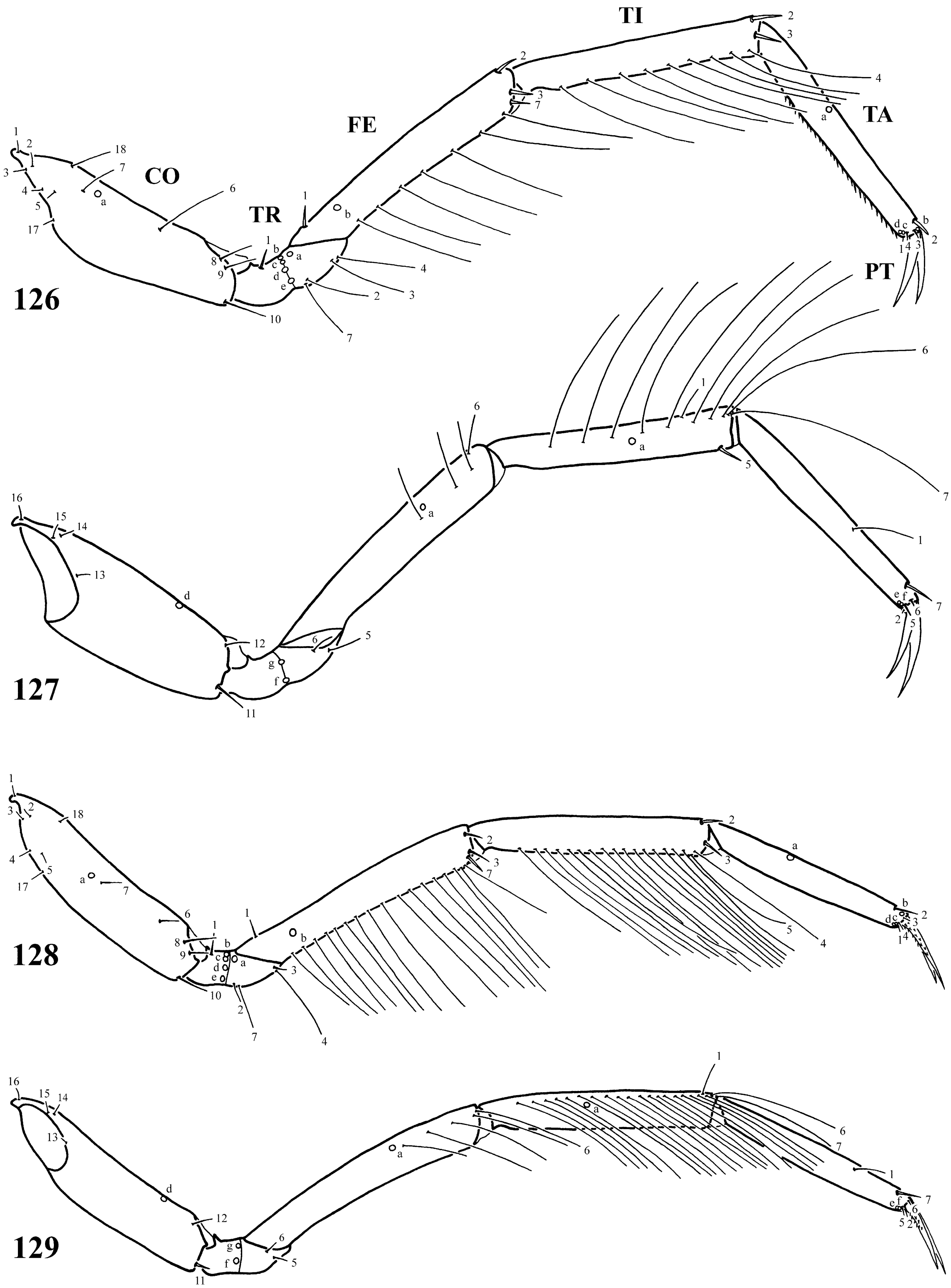


124

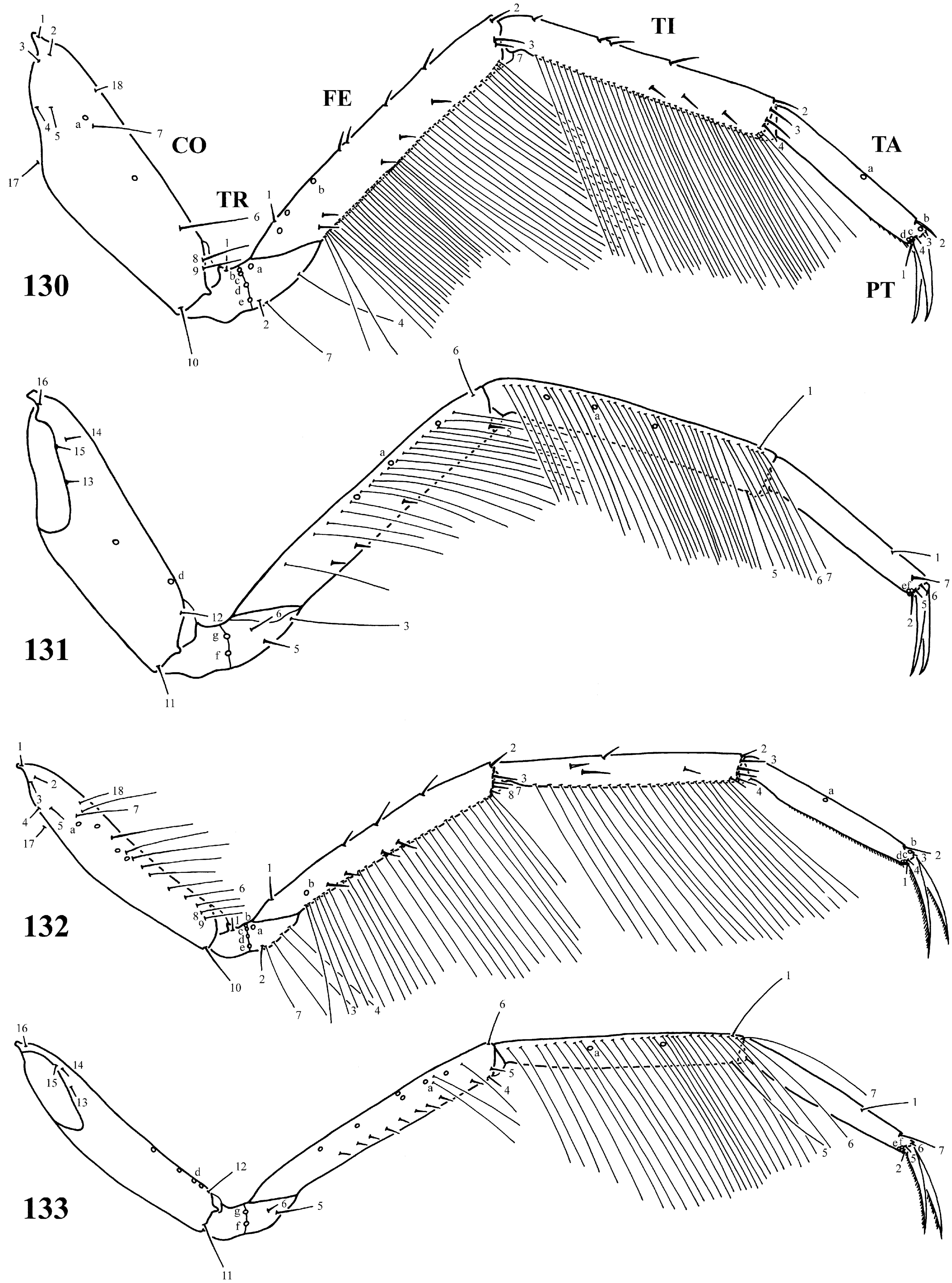


125

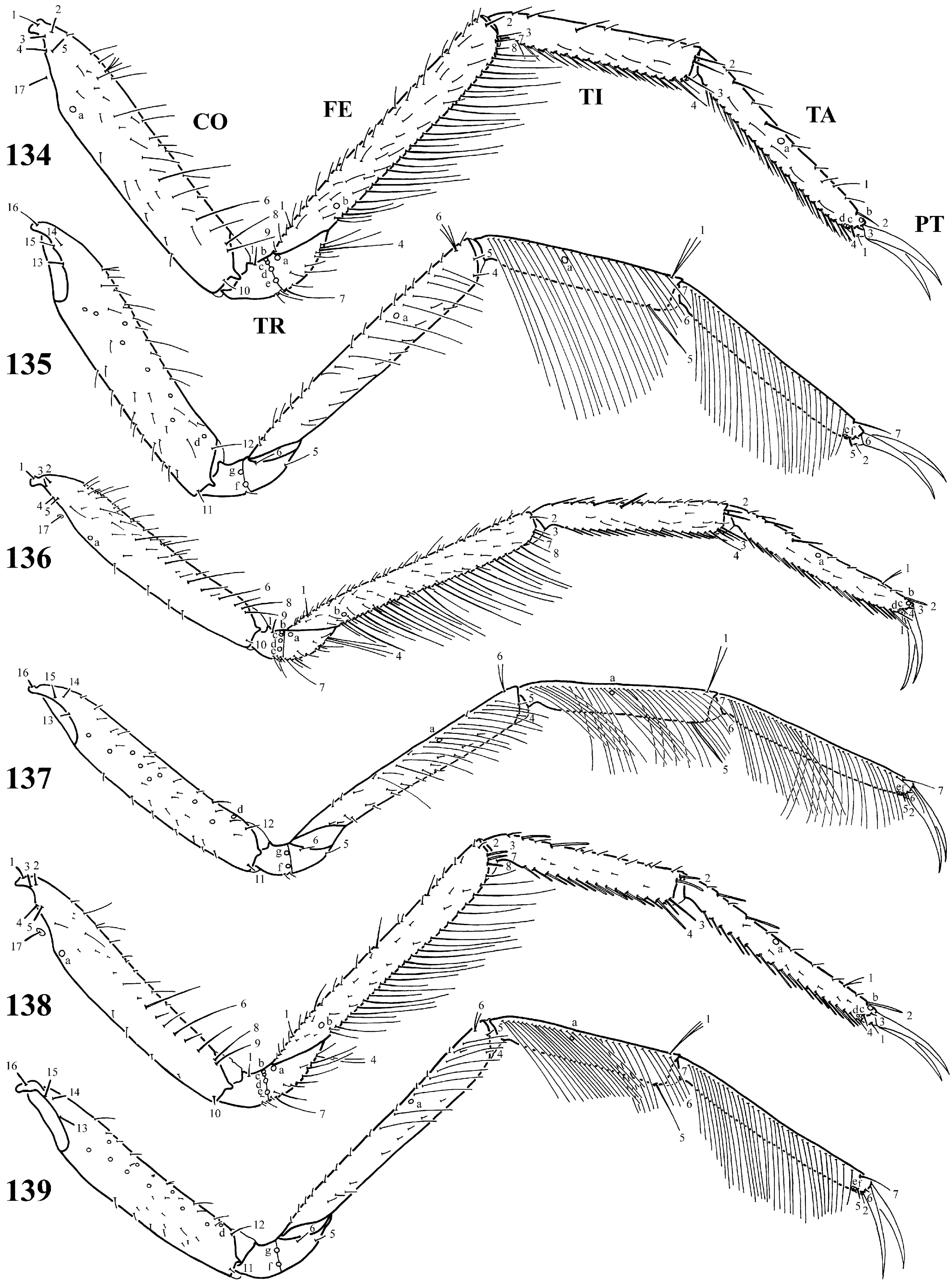
FIGURES 122–125. Distribution of ancestral setae and pores on metathoracic leg of selected species of Dytiscinae; (122–123) *Graphoderus occidentalis*, (122) anterior surface, (123) posterior surface; (124–125) *Eretes australis*, (124) anterior surface, (125) posterior surface; CO, coxa, FE, femur; PT, pretarsus; TA, tarsus; TI, tibia, TR, trochanter; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 4 for list of setae and pores).



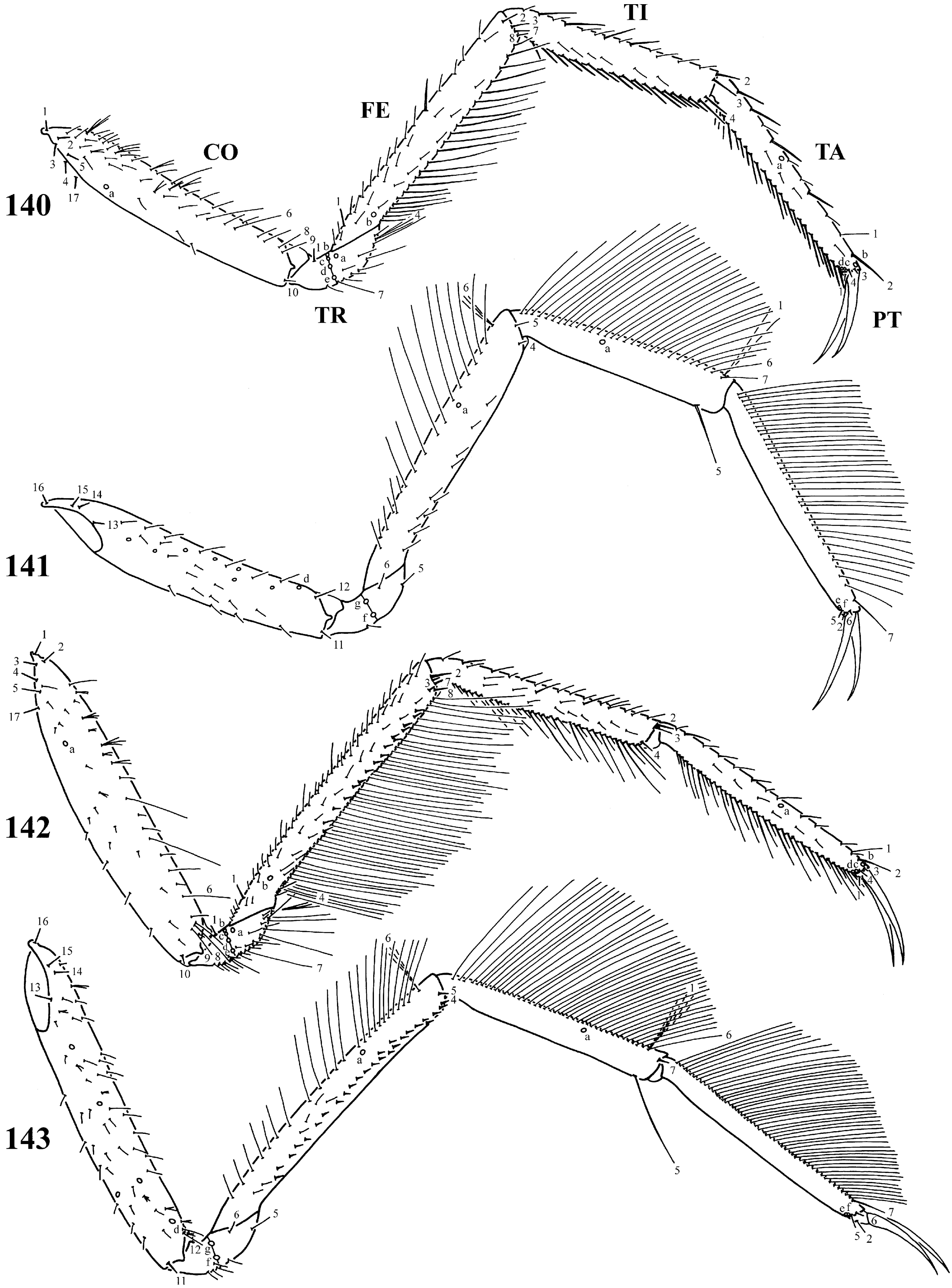
FIGURES 126–129. Distribution of ancestral setae and pores on metathoracic leg of selected species of Dytiscinae; (126–127) *Notaticus fasciatus*, (126) anterior surface, (127) posterior surface; (128–129) *Hydaticus tuyuensis*, (128) anterior surface, (129) posterior surface; CO, coxa, FE, femur; PT, pretarsus; TA, tarsus; TI, tibia, TR, trochanter; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 4 for list of setae and pores).



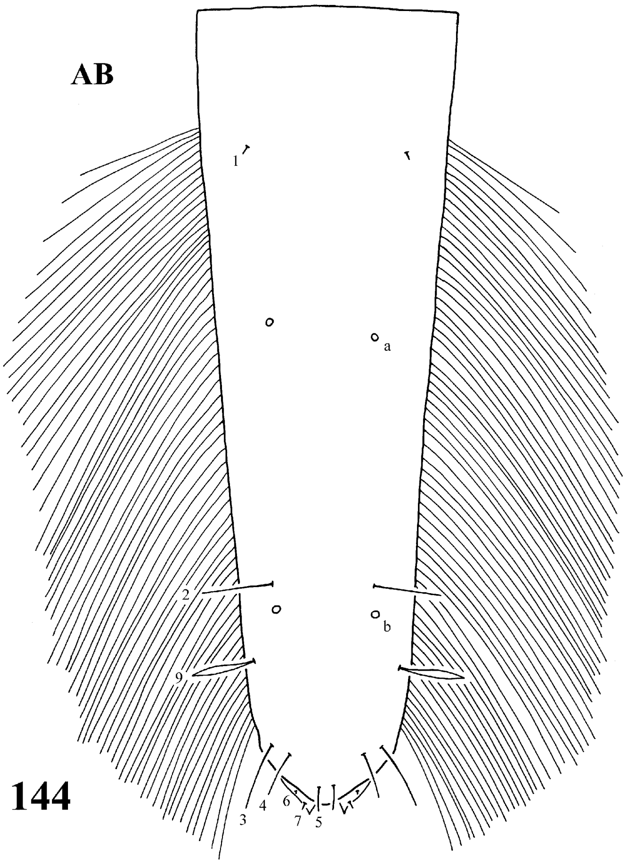
FIGURES 130–133. Distribution of ancestral setae and pores on metathoracic leg of selected species of Dytiscinae; (130–131) *Dytiscus harrisii*, (130) anterior surface, (131) posterior surface; (132–133) *Hyderodes shuckardi*, (132) anterior surface, (133) posterior surface; CO, coxa, FE, femur; PT, pretarsus; TA, tarsus; TI, tibia, TR, trochanter; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 4 for list of setae and pores).



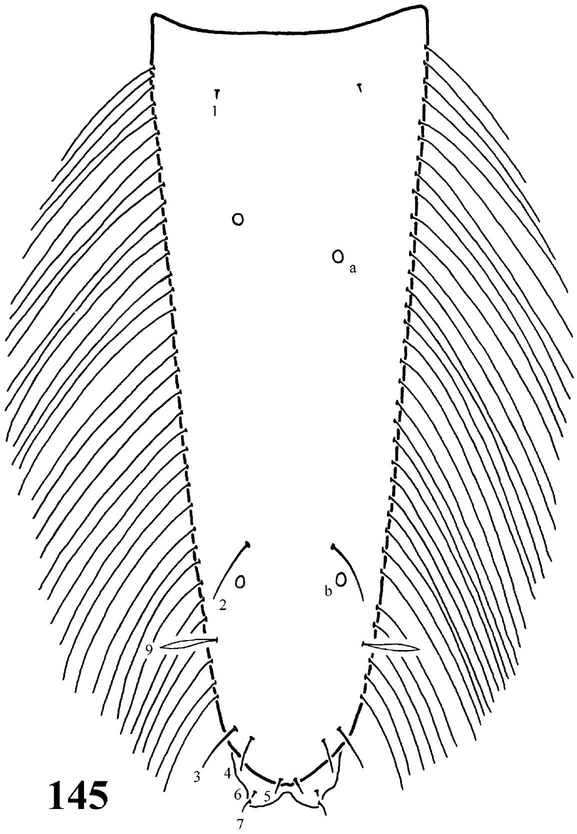
FIGURES 134–139. Distribution of ancestral setae and pores on metathoracic leg of selected species of Dytiscinae; (134–135) *Megadytes (Megadytes) carcharias*, (134) anterior surface, (135) posterior surface; (136–137) *Megadytes (Paramegadytes) glaucus*, (136) anterior surface, (137) posterior surface; (138–139) *Megadytes (Trifurcitus) fallax*, (138) anterior surface, (139) posterior surface; CO, coxa, FE, femur; PT, pretarsus; TA, tarsus; TI, tibia, TR, trochanter; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 4 for list of setae and pores).



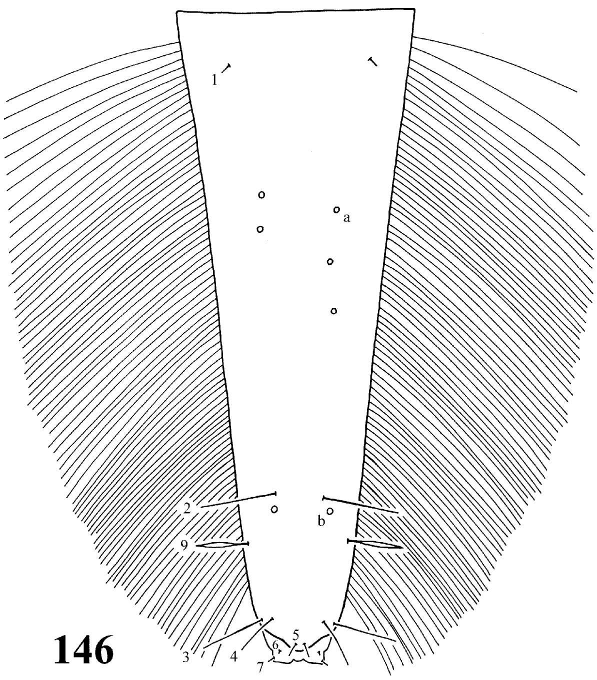
FIGURES 140–143. Distribution of ancestral setae and pores on metathoracic leg of selected species of Dytiscinae; (140–141) *Cybister tripunctatus*, (140) anterior surface, (141) posterior surface; (142–143) *Onychohydrus scutellaris*, (142) anterior surface, (143) posterior surface; CO, coxa, FE, femur; PT, pretarsus; TA, tarsus; TI, tibia, TR, trochanter; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 4 for list of setae and pores).



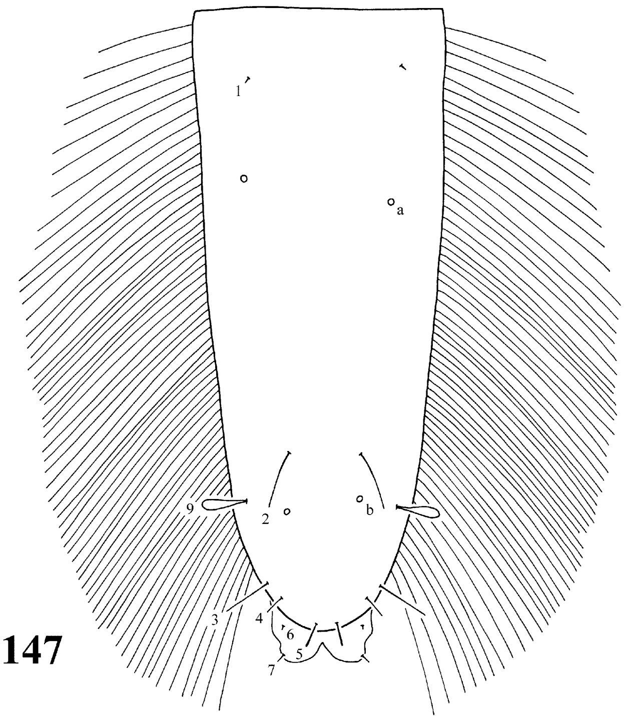
144



145

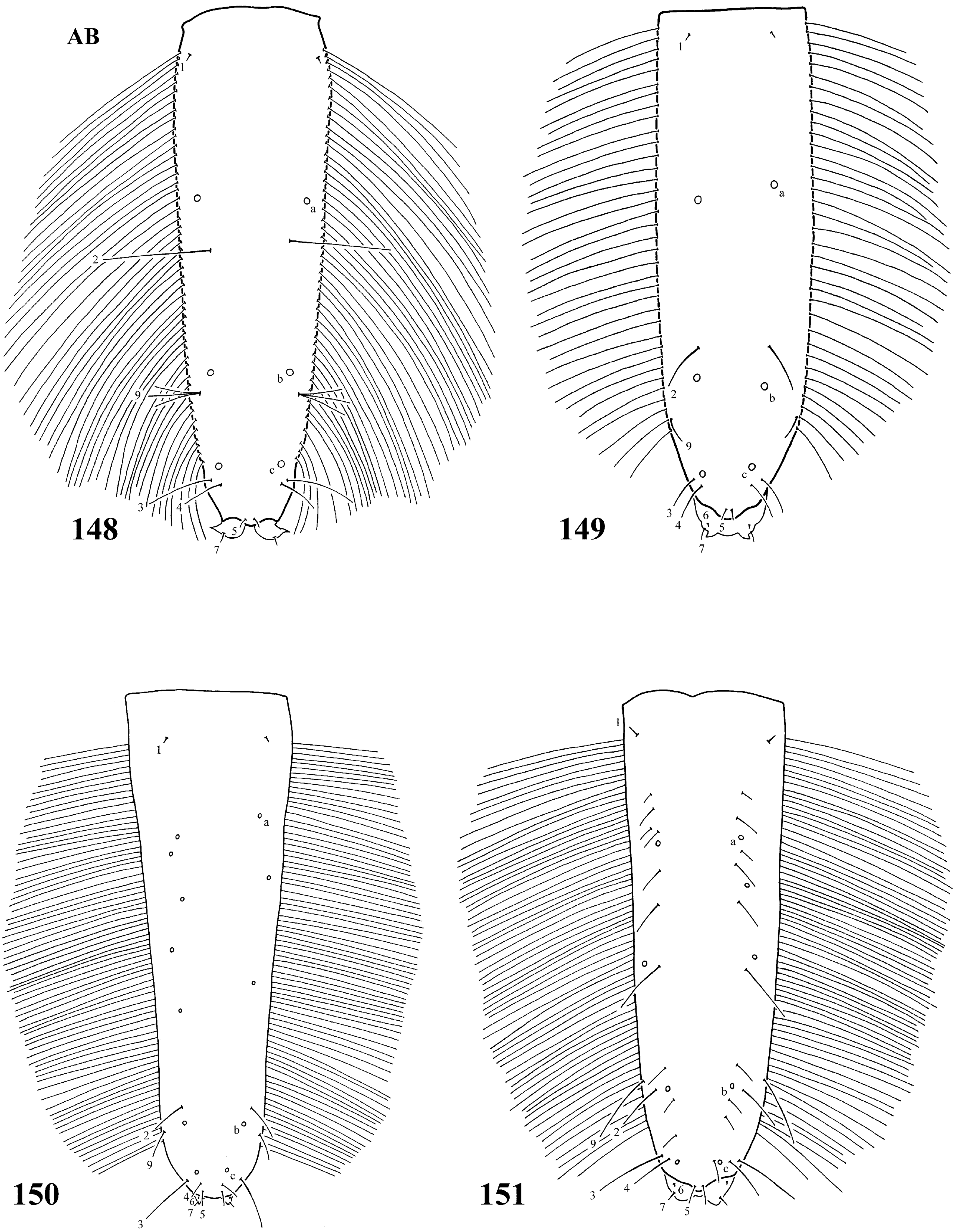


146

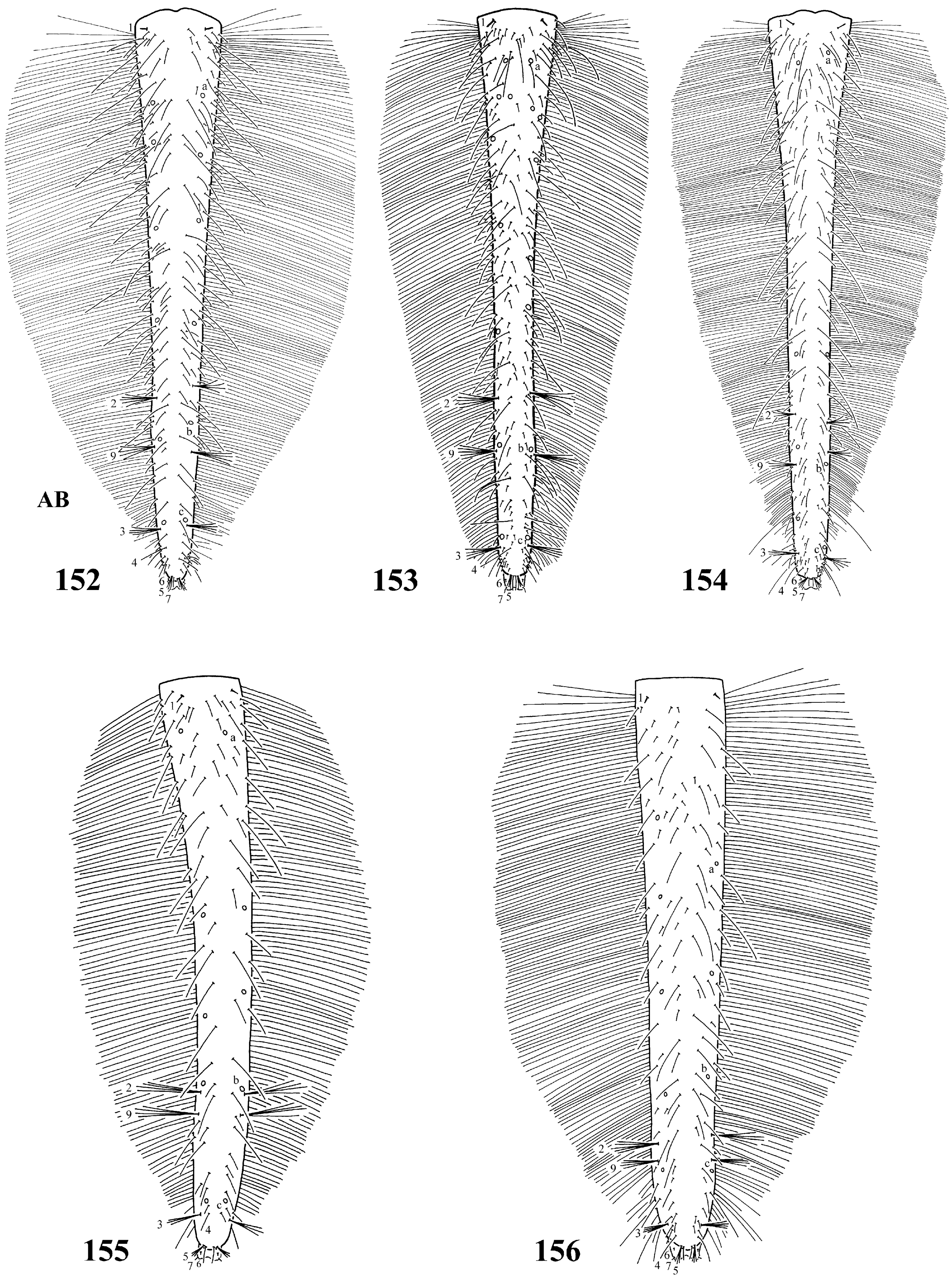


147

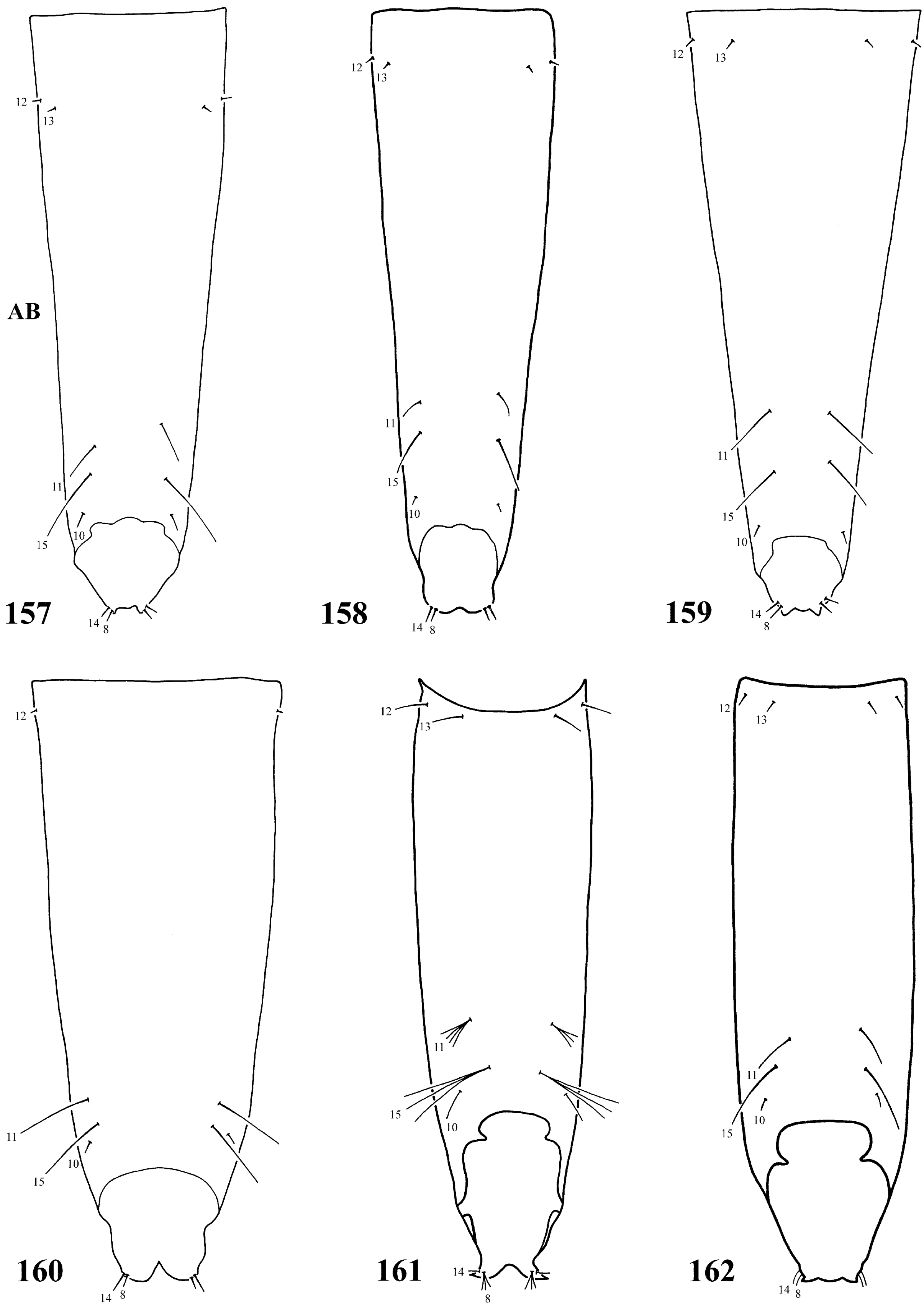
FIGURES 144–147. Distribution of ancestral setae and pores on dorsal surface of last abdominal segment of first instar of selected species of Dytiscinae; (144) *Acilius semisulcatus*; (145) *Thermonectus succinctus*; (146) *Graphoderus occidentalis*; (147) *Eretes australis*; AB, last abdominal segment; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 5 for list of setae and pores).



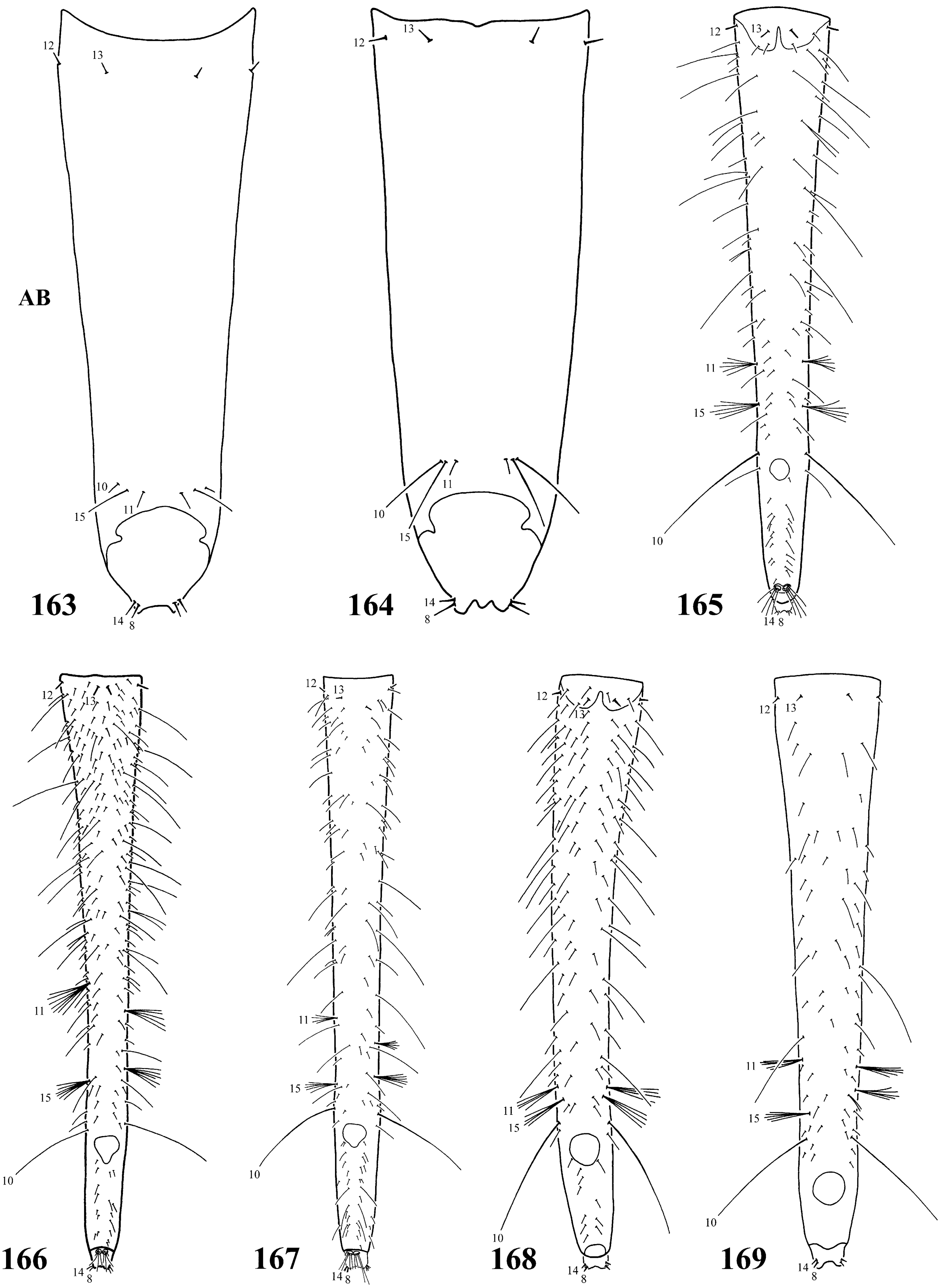
FIGURES 148–151. Distribution of ancestral setae and pores on dorsal surface of last abdominal segment of first instar of selected species of Dytiscinae; (148) *Notaticus fasciatus*; (149) *Hydaticus tuyuensis*; (150) *Dytiscus harrisii*; (151) *Hyderodes shuckardi*; AB, last abdominal segment; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 5 for list of setae and pores).



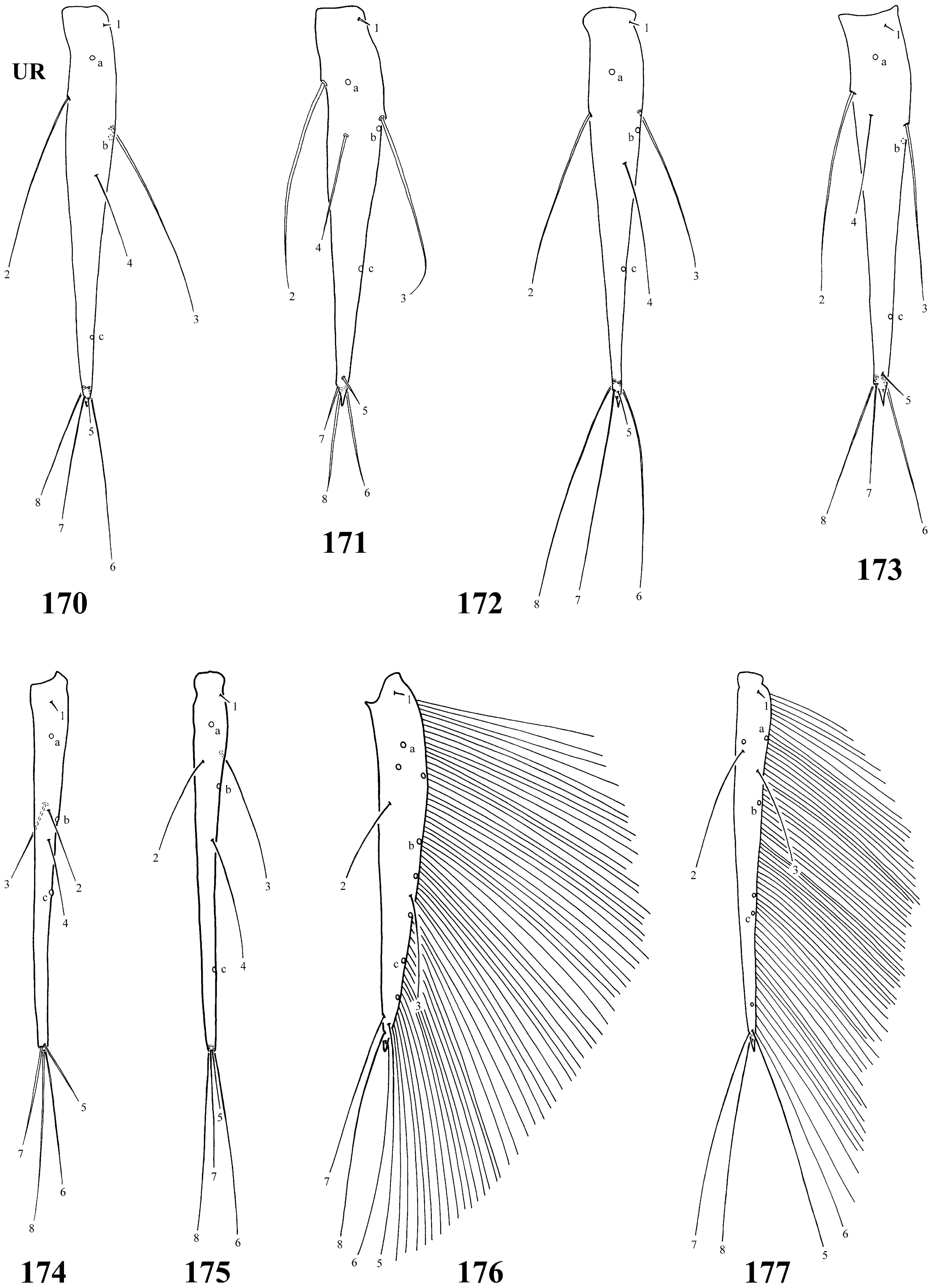
FIGURES 152–156. Distribution of ancestral setae and pores on dorsal surface of last abdominal segment of first instar of selected species of Dytiscinae; (152) *Megadytes (Megadytes) carcharias*; (153) *Megadytes (Paramegadytes) glaucus*; (154) *Megadytes (Trifurcitus) fallax*; (155) *Cybister tripunctatus*; (156) *Onychohydrus scutellaris*; AB, last abdominal segment; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 5 for list of setae and pores).



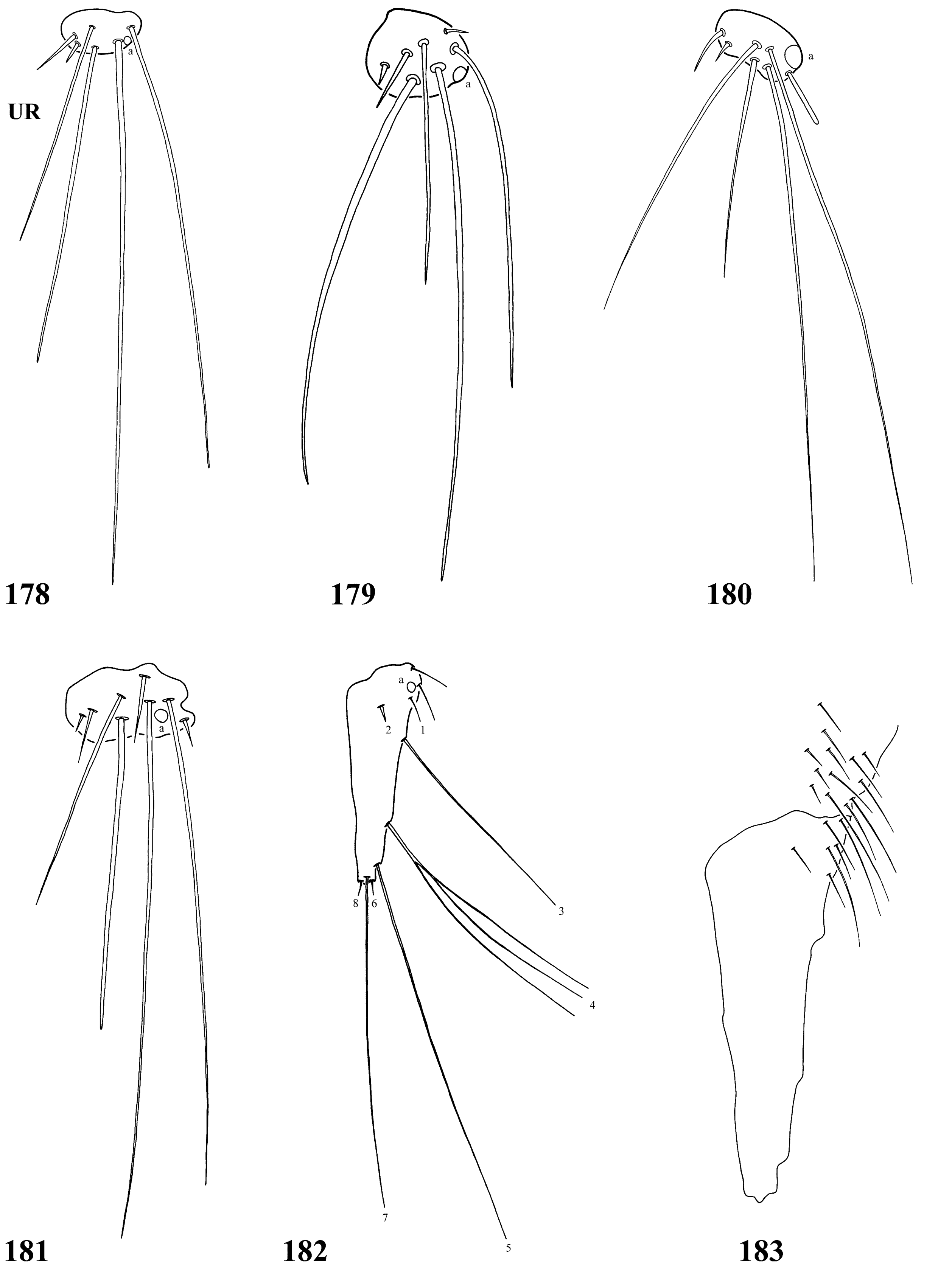
FIGURES 157–162. Distribution of ancestral setae and pores on ventral surface of last abdominal segment of first instar of selected species of Dytiscinae; (157) *Acilius semisulcatus*; (158) *Thermonectus succinctus*; (159) *Graphoderus occidentalis*; (160) *Eretes australis*; (161) *Notaticus fasciatus*; (162) *Hydaticus tuyuensis*; AB, last abdominal segment; numbers and lower-case letters refer to primary setae and pores, respectively (see Table 5 for list of setae and pores).



FIGURES 163–169. Distribution of ancestral setae and pores on ventral surface of last abdominal segment of first instar of selected species of Dytiscinae; (163) *Dytiscus harrisii*; (164) *Hyderodes shuckardi*; (165) *Megadytes (Megadytes) carcharias*; (166) *Megadytes (Paramegadytes) glaucus*; (167) *Megadytes (Trifurcitus) fallax*; (168) *Cybister tripunctatus*; (169) *Onychohydrus scutellaris*; AB, last abdominal segment; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 5 for list of setae and pores).



FIGURES 170–177. Distribution of ancestral setae and pores on right urogomphus of first instar of selected species of Dytiscinae, dorsal surface; (170) *Acilius semisulcatus*; (171) *Thermonectus succinctus*; (172) *Graphoderus occidentalis*; (173) *Eretes australis*; (174) *Notaticus fasciatus*; (175) *Hydaticus tuyuensis*; (176) *Dytiscus harrisii*; (177) *Hyderodes shuckardi*; UR, urogomphus; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 5 for list of setae and pores).



FIGURES 178–183. Distribution of ancestral setae and pores on left urogomphus of first instar of selected species of Dytiscinae, ventral surface (except 182 right urogomphus, dorsal surface); (178) *Megadytes (Megadytes) carcharias*; (179) *Megadytes (Paramegadytes) glaucus*; (180) *Megadytes (Trifurcitus) fallax*; (181) *Cybister tripunctatus*; (182–183) *Onychohydrus scutellaris*, (182) dorsal surface; (183) ventral surface; UR, urogomphus; numbers and lowercase letters refer to primary setae and pores, respectively (see Table 5 for list of setae and pores).

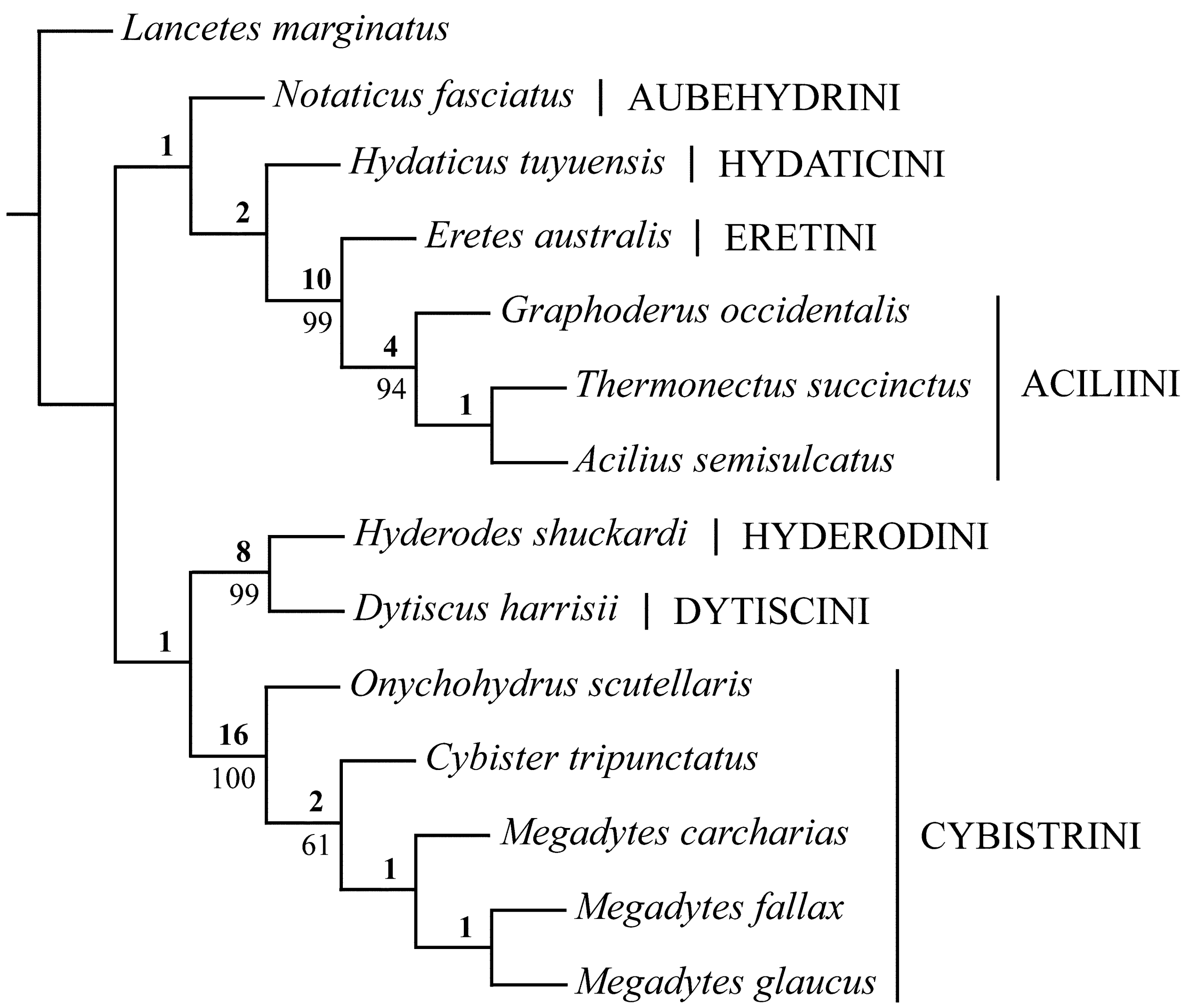


FIGURE 184. Single most parsimonious cladogram of 13 terminal taxa of Dytiscinae (length = 162, CI = 77, RI = 83), with Bremer support values indicated above branches and jackknife values above 50 indicated below branches.

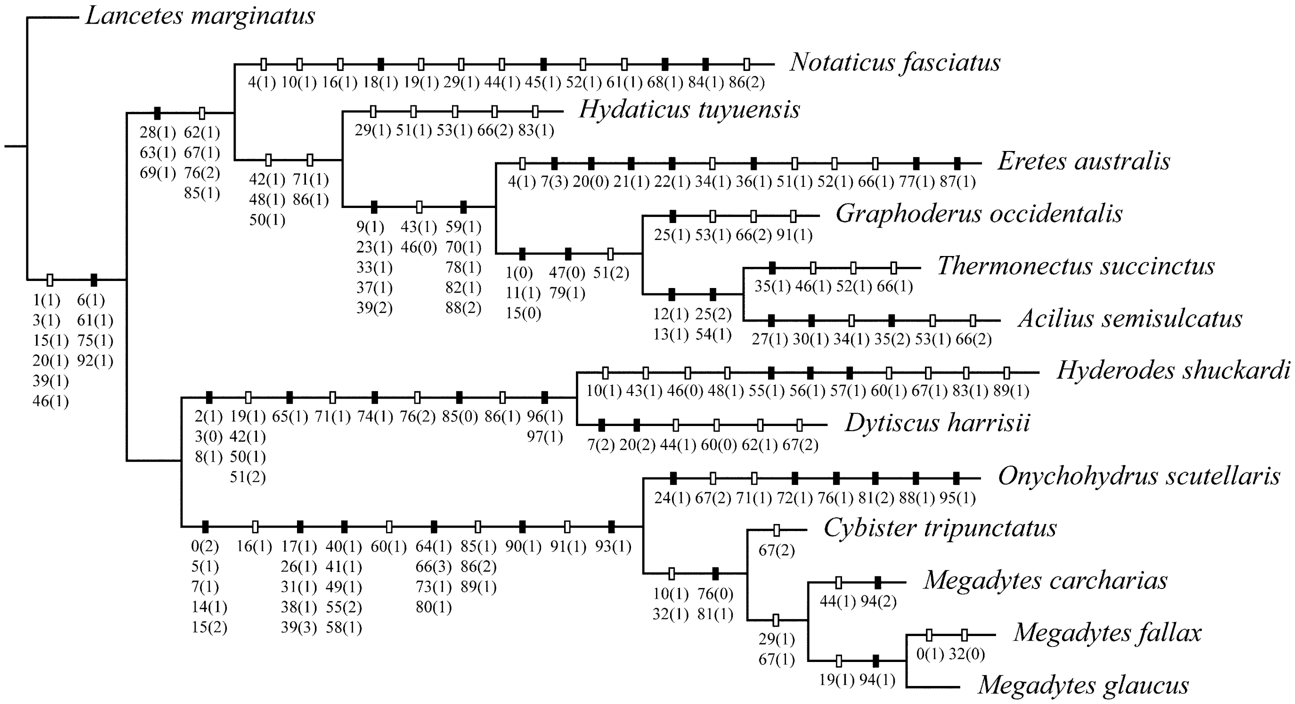


FIGURE 185. Single most parsimonious cladogram of 13 terminal taxa of Dytiscinae with character changes mapped for each clade. Solid rectangles indicate unique character state transformations; open rectangles indicate homoplastic character state transformations.