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# Subgeneric classification, description of head structures, and world check list of *Hydraena* KUGELANN (Insecta: Coleoptera: Hydraenidae)

M.A. Jäch*, R.G. Beutel**, J.A. Díaz*** & J. Kodada****

## Abstract

A subgeneric classification of *Hydraena* KUGELANN (Insecta: Coleoptera: Hydraenidae) is proposed, following a cladistic analysis of 31 morphological characters of adults. The monophyly and the subgeneric status of *Hydraenopsis* are well supported by the analysis. An incomplete or absent longitudinal median genal suture, a very short or absent pregula, and structural details of the hypomeral antennal cleaner are autapomorphies of *Hydraenopsis*. Within *Hydraena* s.l. (excl. *Hydraenopsis*) the following branching pattern is suggested: *H. rugosa* + (*H. monikae* + (*H. circulata* + ('*Phothydraena*' + (*H. frondsicola* + (*H. cordata* + (((*H.* cf. *cirrata* + *H. grandis*) + *H. riparia*)) + (('*Haenydra*' + *H. armipalpis*) + (*H. minutissima* + *H. servilia*))))))). '*Haenydra*' and '*Phothydraena*' are well supported by apomorphies, but should not be credited subgeneric status as long as the phylogenetic relationships of the basal lineages within *Hydraena* s.l. (excl. *Hydraenopsis*) are more satisfactorily understood.

In addition to the cladistic analysis, head structures of two species (*Hydraena circulata* PERKINS and *H. isolinae* JÄCH & DÍAZ) are described in detail and compared to structures found in other adult Coleoptera. Additional characters of potential taxonomic/phylogenetic relevance are listed. The following morphological characters are reported for the first time for *Hydraena* s.l.: 1) genae with paired, small, paramesal protuberances on smooth area between submentum and anterior transverse genal ridge (*H. isolinae*); 2) pronotal membrane ('*Phothydraena*' lineage, *Hydraena frondsicola* PERKINS and *H. paeminosa* PERKINS); 3) glabrous (unpubescent) spots at middle of posterior margin of ventrites 1 - 4 (*H. vedrasi* d'ORCHYMONT); 4) anterior corners of ventrites modified, e.g. lacking pubescence (*H. cyclops* JÄCH & DÍAZ) or with elongate, densely set, squamose sclerotized structures (*H. isolinae*).

A world check list of the species of *Hydraena* assigned to subgenera is presented.

## Zusammenfassung

31 morphologische Merkmale von adulten Hydraeninae (Insecta: Coleoptera: Hydraenidae) werden kladistisch analysiert, um eine phylogenetisch fundierte Untergattungseinteilung zu erstellen. Die Monophylie und die Rechtfertigung des Untergattungs-Status von *Hydraenopsis* werden durch diese Analyse bestätigt. Innerhalb von *Hydraena* s.l. (excl. *Hydraenopsis*) werden die folgenden Verzweigungsmuster angenommen: *H. rugosa* + (*H. monikae* + (*H. circulata* + ('*Phothydraena*' + (*H. frondsicola* + (*H. cordata* + (((*H.* cf. *cirrata* + *H. grandis*) + *H. riparia*)) + (('*Haenydra*' + *H. armipalpis*) + (*H. minutissima* + *H. servilia*))))))). '*Haenydra*' und '*Phothydraena*' sind durch Autapomorphien gestützt, sollten aber nicht als Untergattungen geführt werden, solange die phylogenetischen Beziehungen der basalen Linien innerhalb von *Hydraena* s.l. (excl. *Hydraenopsis*) nicht restlos aufgeklärt sind.

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Zusätzlich zur phylogenetischen Analyse werden die Kopfstrukturen von *Hydraena circulata* PERKINS und *H. isolinae* JÄCH & DÍAZ detailliert beschrieben und mit entsprechenden Strukturen anderer Coleoptera verglichen. Weitere, nicht analysierte, morphologische Merkmale von potentieller phylogenetischer Bedeutung für *Hydraena* s.l. werden aufgelistet. Mehrere morphologische Merkmale (z.B.: Halschildmembran bei '*Phothydraena*', *Hydraena frondsicola* und *H. paeminosa*) werden erstmals für *Hydraena* s.l. nachgewiesen.

Eine Checklist aller bisher beschriebenen, nach Untergattungen geordneten Arten von *Hydraena* wird präsentiert.

**Key words**: Insecta, Coleoptera, Hydraenidae, *Hadrenya*, *Haenydra*, *Holcohydraena*, *Hoplydraena*, *Hydraena*, *Hydraenopsis*, *Phothydraena*, *Spanglerina*, *Taenhydraena*, subgenera, phylogeny.

## Introduction

*Hydraena* KUGELANN (type genus of Hydraenidae) is the world's most speciose water beetle genus. So far, 539 species have been described (see check list below); however, this number probably reflects only 50 % (or even less) of the total number of species actually dwelling on earth. The distribution of the genus is generally world-wide, although it has, for instance, not been recorded from southern South America, Alaska, and many remote islands (e.g. Hawaii, Galápagos, Azores, Iceland). Almost all species of *Hydraena* are True Water Beetles (sensu JÄCH 1998), living in streams, stagnant water and in hygropetric habitats; only a few species (undescribed ones) appear to be riparian or terrestrial in the adult stage.

*Hydraena* is a well defined genus within Hydraeninae. Its monophyly is well supported by a number of conspicuous autapomorphies: e.g. presence of a labral-mandibular interlocking device; mentum with acute median projection anteriorly; various complex sensilla; and specialized features of the secretion delivery system.

On the contrary, the subgeneric classification of *Hydraena* has repeatedly been subject of scholarly controversy. Various concepts have been proposed so far (see BERTHÉLEMY 1986, HANSEN 1991, PERKINS 1997); however, none of these concepts was based on modern cladistic methods. BERTHÉLEMY (1986) based his observations mainly on a single character, i.e. number of elytral striae, regarding 10 striae as groundplan feature. PERKINS (1997) partly followed the latter author by using a similarly limited character set (hypomeral antennal pocket structures and elytral striation) and, in addition, ignored fundamental phylogenetic principles, such as reversal and parallelism (instead regarding character evolution as strictly "mono-directional").

The following subgenera have so far been described (in alphabetical order, type species in square brackets): *Hadrenya* REY [*Hydraena minutissima* STEPHENS], *Haenydra* REY [*Hydraena gracilis* GERMAR], *Hydraena* s.str. [*Hydraena riparia* KUGELANN], *Holcohydraena* KUWERT [*Hydraena rugosa* MULSANT], *Hoplydraena* KUWERT [*Hydraena armipes* REY], *Hydraenopsis* JANSSENS [*Hydraena vietnamensis* JANSSENS], *Phothydraena* KUWERT [*Hydraena testacea* CURTIS], *Spanglerina* PERKINS [*Hydraena ingens* PERKINS], *Taenhydraena* KUWERT [*Hydraena exarata* KIESENWETTER]. *Grammhydraena* KUWERT and *Sphaenhydraena* KUWERT are junior objective synonyms of *Hadrenya* resp. *Haenydra*; therefore these two names need not be taken into further consideration taxonomically.

In this paper we present the results of a comprehensive cladistic analysis of the subgeneric classification of the genus *Hydraena* s.l., based primarily on 24 species of

*Hydraena* s.l. and four outgroup taxa (representatives of three other hydraenine genera). We have analysed a total of 31 morphological characters from all major body parts of the imago.

In addition to the phylogenetic analysis we present detailed descriptions of the head structures of two species (*Hydraena circulata* PERKINS and *H. isolinae* JÄCH & DÍAZ) and present numerous additional characters of putative taxonomic/phylogenetic relevance.

## Material and methods

**Taxa examined**: A total of four outgroup taxa and 24 species of *Hydraena* s.l. were selected for the data matrix. As for *Hydraena* s.l. we have included representatives of almost all hitherto recognized subgenera and species groups.

In the list below, these 24 species are tentatively grouped in four subgenera (*Haenydra*, *Hydraena* s.str., *Hydraenopsis*, and *Phothydraena*), which we initially had presumed to be justified phylogenetically (before carrying out our analysis). *Hadrenya* (including *Hydraena minutissima* and *H. pygmaea* WATERHOUSE) was recently regarded as a good subgenus by BERTHÉLEMY (1986), HANSEN (1991), and PERKINS (1997) only on account of the number of elytral striae and aedeagal characters. However, due to the overall conformity (e.g. morphology of aedeagal distal lobe; setal pattern of aedeagal main piece: 3 + 1; secondary sexual characters) of *H. minutissima* with some species closely related to the type species of *Hydraena*, and due to obvious contradictions[1] in the strial theory we found it absolutely justified to regard *Hadrenya* as a synonym of *Hydraena* s.str.

1. *Davidraena boukali* JÄCH
2. *Laeliaena sichuanensis* JÄCH
3. *Limnebius atomus* (DUFTSCHMID)
4. *L. truncatellus* (THUNBERG)

*Haenydra* REY:

5. *H. gracilis* GERMAR [type species of *Haenydra*]
6. *H. scitula* d'ORCHYMONT

*Hydraena* s.str.:

7. *H. armipalpis* JÄCH & DÍAZ
8. *H. circulata* PERKINS
9. *H.* cf. *cirrata* CHAMPION
10. *H. cordata* SCHAUFUSS
11. *H. frondsicola* SPANGLER [closely related with *H. ingens* (type species of *Spanglerina*)]
12. *H. grandis* REITTER [closely related with *H. armipes* (type species of *Hoplydraena*)]
13. *H. minutissima* STEPHENS [type species of *Hadrenya*]
14. *H. monikae* JÄCH & DÍAZ
15. *H. riparia* KUGELANN [type species of *Hydraena*]
16. *H. rugosa* MULSANT [type species of *Holcohydraena*]
17. *H. servilia* d'ORCHYMONT

*Hydraenopsis* JANSSENS:

18. *H. cordiformis* JÄCH & DÍAZ
19. *H. cristatigena* JÄCH & DÍAZ
20. *H. cyclops* JÄCH & DÍAZ
21. *H. isolinae* JÄCH & DÍAZ
22. *H. leechi* PERKINS
23. *H. paeminosa* PERKINS
24. *H. paucistriata* JÄCH & DÍAZ
25. *H. tubuliphallis* JÄCH
26. *H. vulgaris* JÄCH & DÍAZ

*Phothydraena* KUWERT:

27. *H. hernandoi* FRESNEDA & LAGAR [closely related with *H. testacea* (type species of *Phothydraena*)]
28. *H. putearius* JÄCH & DÍAZ

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[1] BERTHÉLEMY (1986), when postulating a separate subgeneric status for *H. minutissima*, depicted the elytra of 16 species of *Hydraena* s.l. (incl. *H. minutissima*). Remarkably, the elytral striation of one of the species (*H. pulchella* GERMAR), which the author placed in *Hydraena* s.str. appears to be practically identical with the elytral striation of *H. minutissima* (see BERTHÉLEMY 1986: Figs. 5, 16)!

In addition to the genera and species listed above, which we used for the data matrix (table 1) we have thoroughly examined several other hydraenine genera (*Coelometopon* JANSSENS, *Discozantaena* PERKINS & BALFOUR-BROWNE, *Gondraena* JÄCH, *Hydraenida* GERMAIN, *Parhydraena* d'ORCHYMONT) and numerous other species of *Hydraena* s.l.: e.g. *H. anisonycha* PERKINS, *H.* cf. *armipalpis* (undescribed), *H. audisioi* JÄCH, *H. cornelli* JÄCH & DÍAZ, *H. exarata* KIESENWETTER, *H. palustris* ERICHSON, *H. quadricollis* WOLLASTON, *H. serricollis* WOLLASTON, *H. speciosa* d'ORCHYMONT, *H. testacea*, *H. unca* VALLADARES, *H. vedrasi* d'ORCHYMONT, *H. vietnamensis*, *H. yoshitomii* JÄCH & DÍAZ.

We have not included *Hydraena vietnamensis* in the data matrix, because we had no specimens other than the types available. However, several species included in the data matrix (e.g. *H. isolinae*, *H. vulgaris*) are undoubtedly closely related with *H. vietnamensis*.

Due to its aedeagal resemblance to *H. rugosa* (type species of *Holcohydraena*) we have not included *Hydraena exarata* (type species of *Taenhydraena*) in the data matrix.

We have originally planned to include *Adelphydraena orchymonti* in the data matrix; however, since we were unable to thoroughly examine any specimen and data taken from the literature were found to be incomplete we removed *Adelphydraena* from the outgroup.

We have examined only the holotype and one paratype of *H. frondsicola*. The following three species were not examined by scanning electron microscopy: *Hydraena frondsicola*, *H. paeminosa* and *H. putearius*.

Specimens of *Ochthebius exsculptus* (GERMAR), *Meropathus zelandicus* (ORDISH) (Hydraenidae), *Neopelatops edwardsi* JEANNEL (Leiodidae), *Helophorus aquaticus* (L.), and *H. grandis* ILLIGER (Helophoridae) were examined for comparison of head structures.

**Histological sections**: Specimens of *Hydraena circulata*, *H. isolinae*, *Ochthebius exsculptus*, *Meropathus zelandicus*, and *Helophorus aquaticus* were preserved in 70% ethanol, imbedded in Historesin, cut at 3 µm, and stained with methylene-blue and acid fuchsine. Muscular nomenclature follows KÉLER (1963).

**Terminology of thoracic ventrites**: For simply pragmatic reasons, the "incorrect" terms "pro-" "meso-" and "meta**sternum**" are here used instead of the more correct (neutral) terms "pro-" "meso-" and "meta**ventrite**". In all endopterygotous insects the sclerites in question are mainly composed of pleural components and only a minor part is of true sternal origin (CAMPAU 1940, FERRIS 1940).

**Cladistic analysis**: Computer software (PAUP version 3.1) was used to calculate phylogenetic relationships between species of *Hydraena* s.l. Analysis of character evolution was conducted in MacClade (version 3; MADDISON & MADDISON 1992). Additional analyses were carried out after successive reweighting (FARRIS 1988, SWOFFORD 1991).

Most parsimonious trees were sought using heuristic search (stepwise addition random, 100 replicates, branch swapping algorithm tree bisection-reconnection). All characters were weighted equally and not ordered. All question marks in the matrix refer (table 1) to missing data, (-) refers to inapplicable data. The outgroup taxa were treated as all other groups in the analysis (simultaneous analysis; NIXON & CARPENTER 1993).

**Scanning electron micrographs**: For scanning electron microscopy, specimens were dehydrated in graded ethanol series and air-dried from absolute ethanol, mounted on stubs with Tempfix, sputter coated with gold and then viewed in a Jeol 840 at 5, 10 or 15 kv.

**Abbreviations**: **ac**: antennal cleaner; **amo**: anatomical mouth; **ap**: apex; **ata**: anterior tentorial arms; **atgr**: anterior transverse genal ridge; **bst**: basistipes; **c**: cardo; **ce**: compound eye; **cer**: cerebrum; **cl**: clypeus; **co**: condyle of primary mandibular joint; **coes**: circumoesophageal connective; **cor**: circumocular ridge; **cu**: antennal cupule; **dp**: dorsolateral mandibular process; **dta**: dorsal tentorial arms; **ep**: exocrine pores; **ga**: galea; **gag**: genal antennal groove; **gags**: genal antennal groove setae; **gc**: gonocoxite; **gl**: glands; **gs**: glabrous spot; **gp**: gular pit; **gu**: gula; **haps**: hypomeral antennal pocket setae; **hc**: hypomeral carina; **hf**: hypomeral fovea; **hy**: hypopharynx; **ic**: intercoxal cavity; **is**: intercoxal sternite; **itgr**: intermediate transverse genal ridge; **la**: lacinia; **lam**: lower antennal muscles; **lbr**: labrum; **lcar**: longitudinal internal carina; **lgcar**: lateral internal gular carina; **lmgs**: longitudinal median genal suture; **ma**: mesosternal angle; **md**: mandible; **mo**: mola; **mp**: maxillary palp; **mst**: mediostipes; **mt**: mentum; **mx**: maxillary muscle with unclear homology; **mxg**: maxillary groove; **nrec**: nervus recurrens; **ocar**: oblique carina; **opo**: oblique hypopharyngeal pouch; **p**: prostheca; **pf**: palpifer; **pgu**: pregula; **ph**: pharynx; **pm**: pronotal membrane; **pph**: prepharynx; **ps**: postocular setae; **pst**: pseudostylus; **ptgr**: posterior transverse genal ridge; **ptp**: posterior tentorial pit; **rm**: ring muscle; **sga**: spiculate genal area; **sag**: subocular antennal groove; **sl**: semimembranous lobe; **sm**: submentum; **soes**: suboesophageal ganglion; **sr**: subocular ridge; **ss**: secretion sulcus; **sX**: sternite X; **tb**: tentorial bridge; **tbo**: tentorial body; **tgcar**: transverse internal gular carina; **tlb**: transverse labial bar; **tX**: tergite X; **uam**: upper antennal muscles.

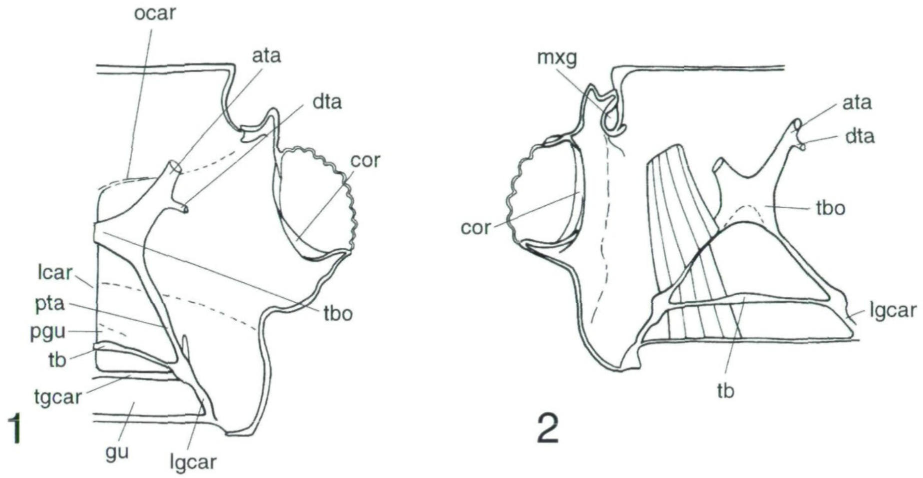
## Descriptions of head structures

### *Hydraena circulata*:

**General appearence of head capsule, external features** (Figs. 177, 178, 180, 188 - 194). The head is prognathous and the posteriormost part is retracted into the prothorax. The clypeolabral suture is straight. The frontoclypeal suture is distinct and slightly arcuate. The clypeus is twice as long as the frontal margin anterior to the compound eye. The lateral margins are almost straight and converging anteriorly. The surface structure of an extensive part of the clypeus is reticulate and covered with scattered setae. A small anteromedian area is almost smooth and the narrow posterolateral margin is covered with very small tubercles (Fig. 178). The frontal area (Fig. 180) lacks distinct impressions (foveae?) or tuberculi (ocelli?). A fairly long anterior part is covered with densely arranged, large and fairly shallow pores (punctures) with a characteristic flower-like internal microscultpure. It is separated from a short, reticulate posterior section by a slightly arcuate edge and from the vertex by a distinct, smooth and arcuate transverse ridge, which laterally demarcates the compound eyes from a postocular, triangular temporal extension. The posterior part of the head is distinctly narrowed, thus forming a neck region. It is dorsally covered with a fine, posteriorly directed pubescence. A median longitudinal concentration of hairs is hardly recognizable. The compound eyes are distinctly protruding. Small fascicular sensilla are inserted in pores between the ommatidia dorsally and laterally (Figs. 177, 188). The antennae (Figs. 181, 182, 188) insert below the anterolateral frontal margin. The articulation is not visible from above. Fairly indistinct antennal grooves (Fig. 191) are present ventromesally to the compound eye (subocular antennal groove) and the temporal extension (genal antennal groove). The subocular antennal groove is mesally limited by the subocular ridge. The maxillary grooves are fairly distinct and inserted between the lateral submental margin and the subocular antennal groove. The submentum (Figs. 188, 189) is almost parallel-sided and slightly concave laterally. It is separated from the mentum (Fig. 188) by an almost straight transverse suture. It is completely fused with the head capsule posteriorly, but separated from the posteroventral part of the head by slightly elevated transverse bulges, which are clearly separated from each other medially, and demarcated anteriorly and posteriorly by medially converging sulci, the anterior and posterior transverse genal ridges (Figs. 189, 190). An additonal, fairly indistinct intermediate transverse (Figs. 189, 190) genal ridge is only recognizable laterally. The transverse area between submentum and gula is probably derived from confluent genae. The longitudinal median genal suture (Figs. 188, 189) is deeply impressed between the bulges but faintly developed posteriorly. The genal area which is posteriorly adjacent with the posterior transverse genal ridge is smooth. The posterior, pubescent genal area is covered with a moderately dense layer of setae. This is laterally continuous with a row of longer setae, which borders the genal antennal groove posteriorly. The gula (Figs. 188, 189) is approximately trapezoid, with an obtuse angle anteromedially. The gular sutures diverge posteriorly. They are posterolaterally continuous with the postoccipital suture. The posterior tentorial pits at the anterolateral gular margin are very distinct. The anteriormost part of the gula (here termed pregula) is smooth. The rest is covered with a transversely reticulate microsculpture. The gular pits demarcate the origin of the postoccipital ridge on both sides of the head capsule. The surface structure of the temporal area lateral to the gula is reticulate or almost scale-like.

**Internal skeletal structures** (Figs. 1, 3 - 5). The posterior margin of the gula and the head capsule is developed as a very distinct transverse bulge. The gular carinae are high and connected by a fairly thin and almost straight tentorial bridge. The anterior gular margin is demarcated by a strong, sclerotized transverse bar (Figs. 1, 4: tgcar). The presumptive genal areas anterior to the gula are separated by a very distinct, long, median internal carina (Figs. 5, 7: lcar), which forks anteriorly into 2 fairly indistinct oblique carinae, which attain the maxillary groove laterally (Fig. 1). The posterior tentorial arms originate from the posterior tentorial pits. They are connected with the gular ridges posteriorly, converging anteriorly and broadly connected below the pharynx, thus forming a massive tentorial body with an anteromedian process above the suboesophageal ganglion (Figs. 1, 5: tbo). The dorsal arms are strong (Fig. 1) and attached to the head capsule. The anterior arms are fairly slender but strongly sclerotized (Fig. 6).

**Labrum** (Figs. 11 - 14, 177, 178). The labrum is connected with the clypeus by an internal membrane. It is bilobed anteriorly and symmetrical. The median emargination is V-shaped and ends distinctly posterior to the midlength of the labrum. It is equipped with very dense, mesally directed fringes of hairs, whereas the lateral and anterior margins of the anterior lobes bear a fairly sparse row of very long setae. The group of laterally directed stiff hairs close to the labral base is fairly indistinct. The dorsal surface, especially the posterior half is covered with oblique rugosities. The distribution of setae is shown in Fig. 178. The anterior epipharynx is covered with a dense, semicircular row of fairly short hairs lateral to the median emargination and with a dense oblique row of



Figs. 1 - 2: Head, horizontal section, ventral view, most or all muscles removed; 1) *Hydraena circulata*; 2) *H. isolinae*.

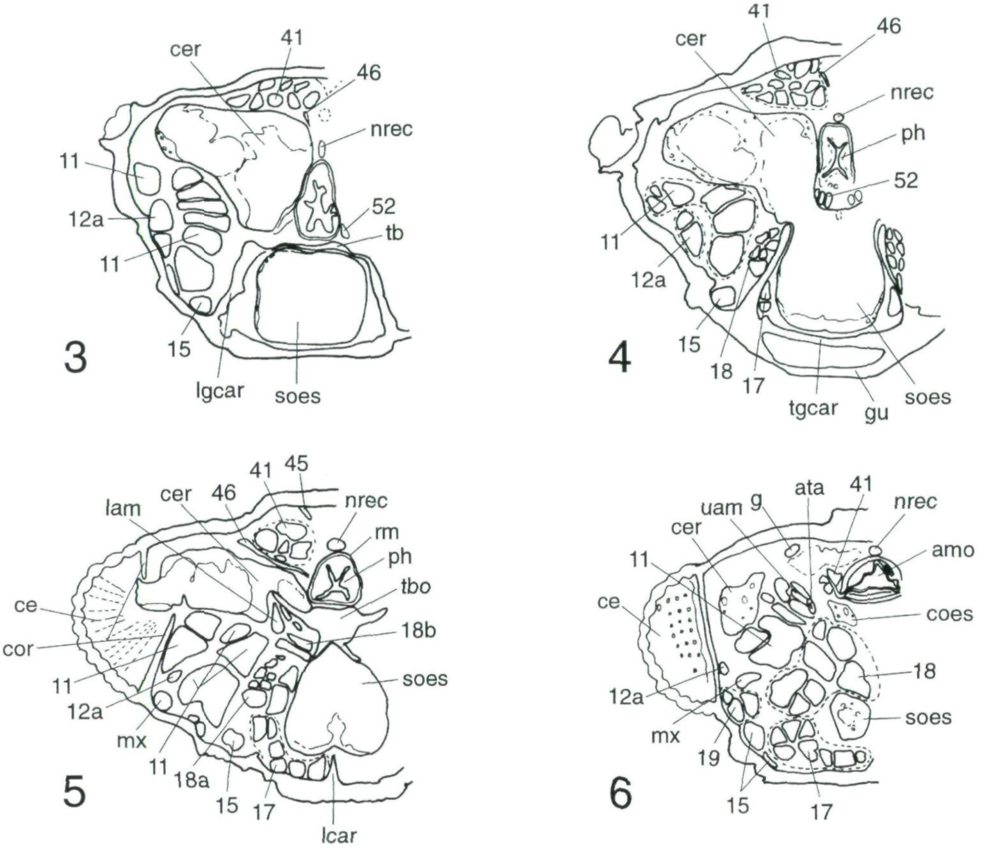
very long hairs. The epipharynx (Fig. 179) is largely smooth posteriorly, with a small posteromedian pubescent area anterior to the closed prepharyngeal tube. It is posterolaterally connected with strong hypopharyngeal suspensoria.

Musculature (Fig. 11): M 7: M. labroepipharyngalis, represented by two moderately sized bundles: Origin: dorsal wall of labrum; Insertion: anterior epipharynx; M 9: frontoepipharyngalis: Origin: anterolateral frons; Insertion: suspensorium.

**Antenna** (Figs. 181, 182, 188). The antenna is 9-segmented. The scapus is strongly elongated and curved, about 2.5 times as long as the pedicellus, which is fairly wide at its base, but narrowing towards the distal part. Antennomere III is extremely small. The cupule is well developed and pointed laterad. The antennomeres V - IX form a rather loose pubescent club. The sensorial hairs differ in length and thickness.

Musculature (Figs. 5, 6): Unusual arrangement, represented by a distinctly separated upper (Fig. 6: uam) and lower unit (Fig. 5: lam); upper group represented by 3 bundles; Origin: anterior tentorial arm; Insertion: anteriorly and dorsally on the base of the scapus; lower group, composed of several strong bundles; Origin: tentorial body; Insertion: dorsolaterally on the base of the scapus, by means of a tendon.

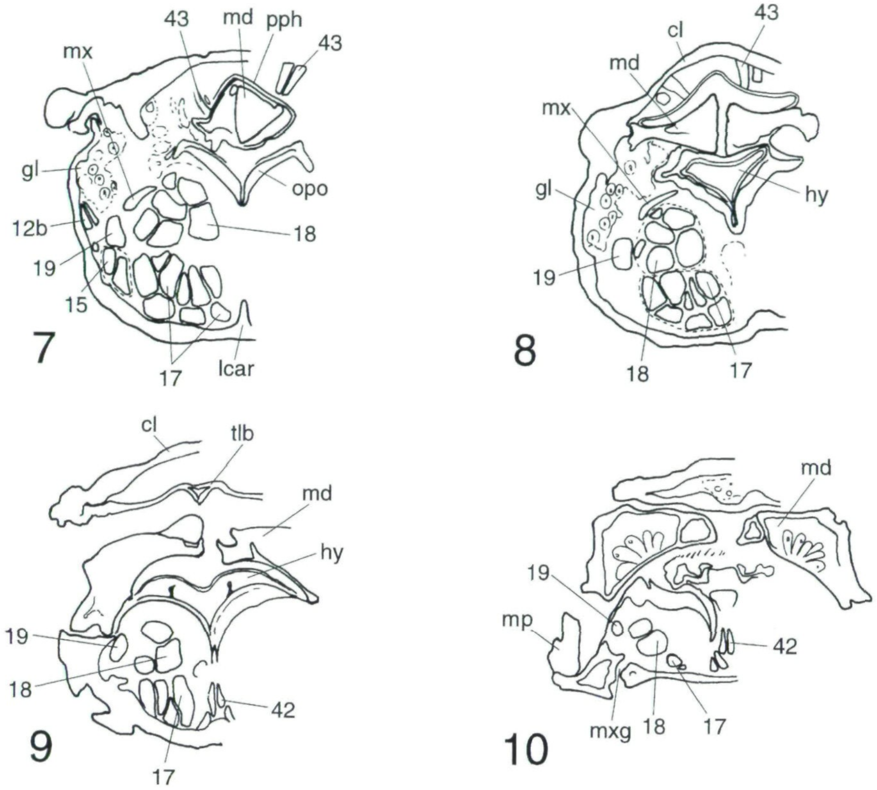
**Mandible** (Figs. 8 - 12, 183, 184). The mandibles are short and flat, and roughly triangular. They are distinctly asymmetrical, especially at the molar region. Both mandibles bear a strongly expressed, fairly broad process on the proximal outer edge. This process is separated from the mesal part by a deep furrow on the dorsal side. Both apices insert slightly proximal to the cranial mandibular margin. The right apex is rather broad and flat, whereas the left one is short and conical. A pointed prostheca and a rounded, semimembranous lobe densely covered with trichia is present subapically. The mola of the left mandible is rather blunt, whereas the right mola is flattened, strongly protruding and equipped with a mesally directed, pointed, conical process at its base. The molar surfaces show a pattern of short rows of asperities which is less dense on the right mandible. The right mola reaches deeply into the prepharynx posteriorly (Fig. 7).



Figs. 3 - 6: Cross sections, *Hydraena circulata*; 3) posterior cerebral region; 4) intermediate cerebral region; 5) anterior cerebral region; 6) anatomical mouth region. Muscles: 9: M. frontoepipharyngalis, 11: M. craniomandibularis internus, 12: M. craniomandibularis externus, 15: M. craniocardinalis, 17: M. tentoriocardinalis, 18: M. tentoriostipitalis, 19: M. craniolacinialis, 41: M. frontohypopharyngalis, 42: M. tentoriohypopharyngalis, 46: M. frontobuccalis posterior, 46: M. frontobuccalis posterior, 52: M. tentoriopharyngalis.

Musculature (Figs. 3 - 7): M 11: M. craniomandibularis internus, composed of several strong bundles; Origin: posterolateral area of the head capsule; Insertion: adductor tendon; M 12: M. craniomandibularis externus, composed of a posterior (12a) and a small and very short anterior component (12b); Origin: anteriormost bundle originates from anterior part of the circumocular ridge, posterior part originates from the posterolateral part of the head capsule, between attachment areas of M 11 (Figs. 3 - 5); Insertion: abductor tendon.

**Maxilla** (Figs. 185 - 187). The maxilla is internally connected with the labium and hypopharynx (Figs. 7 - 12). The dorsal membrane which limits the maxillolabial complex appears bilobed in cross sections. The deep median incision (Fig. 9) is connected with the narrow base of the posterior hypopharynx. The sclerotized external part of the cardo is small and approximately semicircular. It is connected with the triangular



Figs. 7 - 10: Cross sections, *Hydraena circulata*; 7) posterior prepharyngeal region; 8) anterior prepharyngeal region; 9) posterior cibarial region; 10) anterior cibarial region. Muscles: 9: M. frontoepipharyngalis, 11: M. craniomandibularis internus, 12: M. craniomandibularis externus, 17: M. tentoriocardinalis, 18: M. tentoriostipitalis, 19: M. craniolacinialis, 41: M. frontohypopharyngalis, 42: M. tentoriohypopharyngalis, 43: M. clypeopalatalis.

basistipes, which is laterally connected with the large palpifer. Both parts have a reticulate surface structure and several setae as shown in Figs. 186, 187. The palp is 4-segmented and strongly elongated. Palpomere I is very small and curved. Palpomere II is slightly sinuate and as long as the head capsule from the foramen occipitale to the anterior submental margin. It is slightly extended apically. Palpomere III is about half as long as II and also widened distally. Palpomere IV is slightly longer than III and spindle-shaped. The galea is inserted between the palpomere and the lateral margin of the lacinia. The base is fairly broad. It bears six regular rows of fimbriate lamellae. The lacinia is fused with the mediostipes. It is equipped with an apicolateral group of fimbriate lamellae, one or two apical pediculate spines, four apicomesal toothed lamellae, and a mesal row of straight and pointed hairs.

Maxillary musculature (Figs. 3 - 12): M 15: M. craniocardinalis; Origin: ventrolaterally from the head capsule; Insertion: posterolateral margin of cardo. M 17: M. tentoriocardinalis, divided in a ventromesal and a lateral component; Origin: ventromesally from the head capsule and from the posterior tentorial arm; Insertion: mesally on the cardo (Fig. 11); M 18: M. tentoriostipitalis, divided into two components; Origin: laterally on the posterior tentorial arm (18a) and tentorial body (18b); Insertion: mesally, on a membrane attached to the stipes; M 19: M. craniolacinialis; Origin: ventrolaterally from the head capsule, above attachment of M 15; Insertion: dorsally on the base of the lacinia; M 21: M. stipitogalealis; Origin: mediostipes; Insertion: medially on the base of the galea; the homology of a muscle which arises mesally from the mediostipes and is attached to the lateral base of the galea remains unlcear; Mm 22/23: M. stipitopalpalis externus and internus, well developed; Origin: base of palpifer; Insertion: base of maxillary palp.

The homology of one bundle (mx) which arises posterolaterally from the head capsule and is attached to the dorsal maxillolabial membrane could not be clarified (Figs. 5 - 8).

**Labium** (Figs. 10 - 14, 188, 189). The submentum has a reticulate surface structure posteriorly and is almost smooth along anterior margin. The mentum is represented by a large, sclerotized plate, which is slightly converging anteriorly and slightly concave laterally. The anterior margin forms a distinct angle with a conspicuous, spiniform, apicomedian projection. The surface structure is indistinctly reticulate posteriorly and irregular and faintly developed anteriorly. The prementum is obsolete and completely covered by the mentum. It appears at least partly fused with the mental surface, and is dorsally not clearly separated from the anterior hypopharynx (Figs. 10 - 12). The labial palp is 3-segmented and short. The basal palpomere is distinctly widened distally. Palpomere II is shorter than I, almost globular. Palpomere III is about as long as I, parallel-sided and cylindrical, and evenly rounded apically.

Musculature (Figs. 11 - 13): strongly derived; M 28: M. submentopraementalis; Origin: anteromedially on the mental plate; Insertion: medially on the prementum; Mm 29/30: M. tentoriopraementalis inferior/superior; Origin: lateral to M 28; Insertion: not clearly identified, probably on a transverse apodeme of the prementum (Fig. 15). M 34: Mm. praementopalpalis ext.: present, area of attachment not clearly identified.

**Epipharynx** (Figs. 8 - 14, 179). The anterior epipharynx is semimembranous. A distinct median carina is present posterior to the flat ventral wall of the labrum. It is strengthened by a transverse endoskeletal bar (Fig. 9: tlb) and flanked by rather shallow parasagital grooves. The posterior part forms the roof of a short, closed prepharyngeal tube which has a triangular shape in cross section immediately anterior to the anatomical mouth (Figs. 6 - 7).

Musculature (Figs. 7, 8): M. clypeopalatalis, M 43: a series of bundles which originate from the clypeus and are attached to the posterior epipharynx and to the epipharyngeal roof of the prepharyngeal tube.

**Hypopharynx** (Figs. 7 - 12). The anterior hypopharynx is not clearly separated from the prementum. Both parts form a functional unit. The dorsal surface is partly covered by extremely short spines (Figs. 10 - 12). The posterior hypopharynx is dorsolaterally supported by sclerotized internal ridges (Fig. 9). It is triangular in cross section with an extremely narrowed ventral part between the maxillae, and deeply invaginated in a preoral chamber below the mandibles, thus creating deep, oblique internal pouches (Fig. 7: opo). The posteriormost part forms the ventral wall of the prepharyngeal tube.

Musculature (Figs. 3 - 6, 10 - 12): M 41: M. frontohypopharyngalis, a very strong muscle composed of many bundles; Origin: posterodorsal part of the head capsule (vertex), posterior components arise close to foramen occipitale; Insertion: hypopharyngeal suspensorium; M 42: M. tentoriohypopharyngalis, tentorial component absent, possibly represented by one median, almost vertical bundle with unusual origin; Origin: mental plate, posterior to premental muscles (Mm 28-30); Insertion: medially on hypopharynx.

**Pharynx** (Figs. 3 - 5). The anterior pharynx is x-shaped in cross sections, with narrow dorsolateral and ventrolateral folds. (Figs. 4, 5). The folds are more irregular posteriorly and the lumen is less strongly narrowed (Fig. 3).

Musculature (Figs. 4, 5): M 45: M. frontobuccalis anterior, two thin parallel bundles; Origin: anteromesal frons; Insertion: dorsolateral folds of the pharynx, immediately posterior to the frontal connective; M 46: M. frontobuccalis posterior, composed of three very thin bundles; Origin: anterolateral frons, posterior to M 45 and posteromesal frons; Insertion: laterally and dorsolaterally on the anterior and posterior pharynx; M 51: M. verticopharyngalis: absent; M 52: M. tentoriopharyngalis, three fairly strong bundles; Origin: tentorial bridge; Insertion: ventrolaterally on the posterior pharynx.

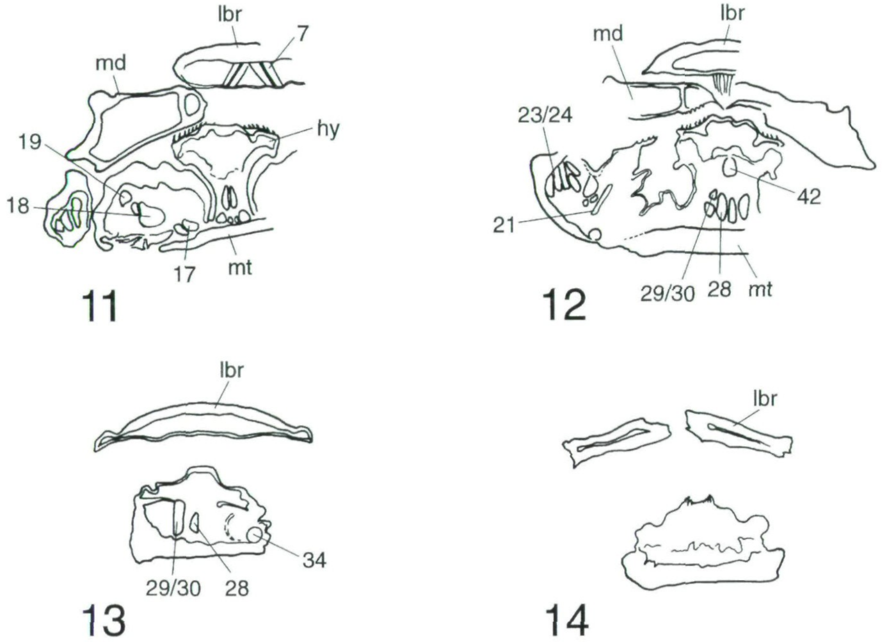
A well developed ring musculature is present over the entire length of the pharynx.

**Cerebrum, suboesophageal ganglion** (Figs. 3 - 6). The brain is located in the posterior part of the head capsule. Only the posteriormost part reaches the prothorax. It is large in relation to the head size. The suboesophageal ganglion is also large and laterally enclosed by the posterior tentorial arms and gular carinae.

**Fat body.** Fat body tissue is present in the anterior head region.

### *Hydraena isolinae*:

**General appearence of head capsule, external features** (Figs. 308 - 312, 320 - 325). General shape similar as in *H. circulata*. The clypeolabral suture is slightly arcuate. The frontoclypeal suture is less distinct and almost straight. The lateral margins of the long clypeus are very slightly rounded laterally and converging anteriorly. The surface of the clypeus is smooth except for a small posterolateral area. The distribution of setae is shown in Figs. 309. Impressions and tuberculi or ocelli are absent from the frontal area. The surface of the extensive anterior frontal region is smooth. The punctures are small and widely separated. The surface of the posterior section with scale-like reticulation. A distinct edge which separates both areas is absent. The posterior margin of the frons is demarcated by a broad, smooth ridge. It is biarcuated and separates the compound eyes from the postocular temporal extension laterally. A distinct emargination (genal antennal groove) with a group of strong setae posteriorly and a fringe of fine hairs anteriorly is developed at the lateral margin of the neck region. The vertex has a scale-like surface structure. Most parts are densely covered with hairs. A distinct median longitudinal concentration of longer setae is clearly recognizable (Fig. 312). The interspaces between the ommatidia of the compound eyes bear two types of fascicular sensilla (Fig. 311). The longer branched sensilla seem to be restricted to the posterior margin. The subocular antennal grooves are rather narrow and mesally limited by a moderately distinct subocular ridge. The submentum is distinctly concave laterally. It is separated from the posteriorly adjacent genal area by faint transversely arranged lines posterior of which there are conspicuous, paired, small, paramesal protuberances on smooth area between submentum and anterior transverse genal ridge. Anterior transverse genal ridge and posterior transverse genal ridge are gently convex, not ridged, glabrous, mesally broadly



Figs. 11 - 14: Cross sections, *Hydraena circulata*; 11) posterior labral region; 12) intermediate labral region; 13) anterior labral region; 14) cranialmost labral region. Muscles: 7: M. labroepipharyngalis, 17: M. tentoriocardinalis, 18: M. tentoriostipitalis, 19: M. craniolacinialis, 21: M. stipitogalealis, 23/24: Mm. stipitopalpalis internus/externus, 28: M. submentopraementalis, 29/30: Mm. tentoriopraementalis inferior/superior, 34: M. submentopalpalis, 42: M. tentoriohypopharyngalis.

confluent. A median line or suture is absent. The additonal, intermediate transverse genal ridge is very indistinct but recognizable laterally. The posterior genal area is densely covered with moderately long setae; anteriormost setae conspicuously longer than remaining setae. The surface structure is grooved or almost scale-like. A lateral group of longer setae borders the posterior margin of the genal antennal groove. The shape of the gula is trapezoid, with a straight anterior margin; pregula absent. An anteromedian angle is only very faintly indicated by the absence of a few setae. The posterior tentorial pits are very distinct. The surface structure of the gula is scale-like, with minute, anteriorly directed spines. The gular pits are distinct and bordered by a distinct egde medially. The surface structure of the temporal area lateral to the gula is distinctly scale-like.

**Internal skeletal structures** (Fig. 2). The tranverse bulge at the posterior margin of the gula and head capsule is fairly narrow. The gular carinae are high. The connecting tentorial bridge is straight and fairly narrow. The sclerotized transverse bar of the anterior gular margin and the median internal carina are absent (Fig. 2). The oblique carinae are only recognizable laterally, close to the maxillary fossa. The posterior tentorial arms originate from the posterior tentorial pits. The tentorial body is present but less strongly developed than in *H. circulata*. The dorsal arms are flat. The anterior arms are slender but strongly sclerotized.

**Labrum** (Figs. 309). The median emargination ends at midlength of the labrum and is equipped with a very dense, mesally directed fringe of hairs. The group of laterally directed stiff hairs close to the labral base is conspicuous. The dorsal side has an irregular surface structure. The distribution of setae is shown on Fig. 309. Dense oblique fields of long hairs are present anterolaterally on the epipharyngeal surface. Parts of the posterior epipharynx are covered with extremely small microtrichia. A small posteromedian pubescent area is present. Strongly developed suspensoria are posterolaterally connected with the labrum.

Musculature: similar to *H. circulata.*

**Antenna** (Figs. 313 - 315). The scapus is slightly longer than in *H circulata.* The cupule is strongly pointed. Two distinctly different types of sensorial setae are present on the antennomeres V - IX, one of them fine, the other thick but rather short.

Musculature: similar to *H. circulata*, but less strongly developed, especially the lower component.

**Mandible** (Figs. 318, 319). The general shape of the mandibles is similar to that of *H. circulata.* However, both mandibles bear a characteristic, broad and bidentate apical part. A sclerotized, bidentate prostheca and a rounded, semimembranous lobe covered with trichia is present proximal to the apex of the left mandible. The right mandible bears a less strongly sclerotized prostheca which appears fimbriate at the apex, but the semimembranous rounded lobe seems to be lacking. The mola of the left mandible is rounded, bilobed, and the asperite surface structure is distinct. The opposite mola is strongly extended mesally, almost blade-like, apically pointed, and it reaches deep into the prepharynx as in *H. circulata.* The asperite surface structure is less distinctly expressed.

Musculature: similar to *M. circulata.*

**Maxilla** (Figs. 316, 317). Similar to the maxilla of *H. circulata.* The base of the galea and the lacinia are slightly shorter and broader.

Maxillary musculature: The non-tentorial part of M 17 arises from the gular part of the hind margin of the head capsule. Otherwise very similar to *H. circulata.*

**Labium** (Figs. 320, 321). The general arrangement is very similar to what is found in *H. circulata.* The submentum is largely smooth but has a central field with a shallow, reticulate surface structure. The lateral margin of the mentum is distinctly emarginated and the anterolateral edges are rounded. The anterior margin is densely set with unusually thick setae. It forms a shallow angle medially but is devoid of a tooth or projection. The anterior and lateral surface is reticulate to scale-like. The posteromedian part is more or less smooth, with some long and thin setae inserted in fairly deep pores.

Musculature: similar to *H. circulata.*

**Epipharynx**. A strongly pronounced longitudinal pubescent ridge is present posterior to the median protuberance of the ventral wall of the labrum. Its walls are connected by a transverse bar (as in *H. circulata*) and paramedian furrows are also present. The posterior part of the epipharynx forms the roof of the short prepharyngeal tube. It is rather flat anteriorly but strongly arched anterior to the anatomical mouth.

Musculature: similar to *H. circulata.*

**Hypopharynx.** The general shape and the connection with the labium are similar to the condition found in *H. circulata.* The dorsal surface of the anterior hypopharynx is very densely covered with fairly long microtrichia. A distinct median keel and lateral lobes are present. The dorsal surface of the posterior hypopharynx is flat or slighly concave. The internalized part is very similar to *H. circulata.*

Musculature: M 41: M. frontohypopharyngalis, less strongly developed than in *H. circulata*; Origin: posterior frons; Insertion: hypopharyngeal suspensorium; M 42: similar to *H. circulata.*

**Pharynx.** The lumen is fairly wide anteriorly and x-shaped in cross section. Dorsolateral and ventrolateral folds are present but quite indistinct. The lumen of the posterior pharynx is strongly narrowed.

Musculature: similar to *H. circulata.*

**Cerebrum, suboesophageal ganglion.** Very similar to *H. circulata.*

**Fat body.** Fat body tissue is present in the anterior head region.

## List of characters entered in data matrix

### Head:

**1. Labrum: lateral margin (0) straight or evenly arched; (1) abruptly constricted posteriorly.**

The shape of the labrum is remarkably variable in *Hydraena* s.l., also within subgenera. However, it is generally more abruptly constricted posteriorly in *Hydraena* s.str., *Haenydra* and *Phothydraena* than in *Hydraenopsis.*

**2. Labial palp: subapical setae of penultimate segment (0) widely separated from each other, located on outer and ventral margin respectively; (1) widely separated from each other, located on outer and inner edge respectively; (2) closely set (both on outer margin).**

The penultimate segment of the labial palp bears a pair of subapical setae. These are rather widely spaced in the outgroup and in *Phothydraena* whereas they are more closely set in the remaining lineages of *Hydraena* s.l.

**3. Mentum: anterior margin (0) without median projection; (1) with acute median projection.**

Although there is some variability in the shape of the median projection of the anterior margin of the mentum we were not able to find significant subgeneric differences.

**4. Gena: posterior transverse genal ridge (0) flat or slightly convex; (1) prominently crested.**

The posterior transverse genal ridge is always crested in *Hydraena* s.str., *Haenydra* and *Phothydraena*, whereas it is usually flat or slightly convex in *Hydraenopsis* (Figs. 55, 62, 73, 94, 101, 102, 114, 115, 127, 141, 144, 145, 154, 156, 157, 188 - 190, 221, 225, 226, 230, 231, 234, 235, 244 - 246, 248, 263 - 266, 288, 320, 321, 341, 347).

**5. Gena: longitudinal median genal suture (0) complete; (1) incomplete or absent.**

In *Hydraena* s.str. and *Haenydra* the longitudinal median genal suture extends from the posterior margin of the submentum to the anterior margin of the glabrous pregula; the genal ridges (especially the posterior one) are distinctly incised medially and the pubescent area of the gena is either sulcate or the pubescence is narrowly interrupted medially.

In *Hydraenopsis* and *Phothydraena* faint traces of the longitudinal median genal suture may be detectable (genal ridges very superficially impressed medially); pubescent area rarely narrowly interrupted (in which case the ridge is always uninterrupted). See Figs. 55, 62, 73, 94, 101, 102, 114, 115, 127, 141, 145, 157, 188, 189, 221, 225, 230, 231, 234, 235, 244, 247, 263, 265, 288, 320, 321, 341.

**6. Gena: longitudinal inner genal carina (0) complete; (1) incomplete; (2) absent.**

In *Hydraena* s.str. (with very few exceptions, e.g. *H. cordata*, *H. unca* and probably some other species related with *H. palustris*), *Phothydraena* and *Haenydra* the longitudinal inner genal carina extends from the posterior margin of the submentum to the anterior inner gular carina with which it is connected.

In *Hydraenopsis* the longitudinal inner genal carina is never complete (extending from the posterior margin of the submentum to approximately the posterior transverse genal ridge) or often absent.

**7. Gula: pregula (0) (sub)triangular; (1) absent or very short, not triangular.**

The gula is delimited laterally by the gular pit and the posterior tentorial pit (which are usually connected with each other by an inner ridge (lateral gular ridge)) and anteriorly by the transverse anterior inner gular carina (or a hypothetical line between the posterior tentorial pits). The gula is usually transversally microreticulate, rarely glabrous (*Limnebius*), never pubescent. The pregula is here defined as an area immediately anterior to the gula proper, being usually distinguished from the gula by the distinctly more glabrous surface. A distinctly triangular pregula is discernible in *Davidraena*, *Limnebius*, *Hydraena* s.str., *Haenydra* and *Phothydraena*. The pregula of *Davidraena* is not glabrous; in *Limnebius* gula and pregula are glabrous, the pregula being semicircular. In a few species of *Hydraenopsis* the pregula is very short and not triangular. There is no pregula in *Laeliaena* and most species of *Hydraenopsis*. See Figs. 22, 45, 46, 54, 55, 61, 62, 73, 93, 94, 100 - 102, 114, 115, 127, 141, 144, 145, 154, 157, 188, 189, 221, 225, 231, 234, 235, 244, 247, 248, 265, 288, 320, 321, 341.

**8. Gula: transverse anterior inner gular carina (0) present; (1) absent.**

The transverse anterior inner gular carina is present in *Davidraena*, *Hydraena* s.str., *Haenydra*, *Phothydraena*, and a few presumably basal species of *Hydraenopsis*; it is absent in *Limnebius*, *Laeliaena* and most species of *Hydraenopsis*.

**Prothorax:**

**9. Hypomeron: antennal pocket (0) widely open; (1) closed ventrolaterally, closure formed mainly by lateral (glabrous) hypomeron; (2) closed laterally (closure formed by lateral (glabrous) hypomeron) and partly closed ventrally (by mesial (pubescent) hypomeron).**

The hypomeral antennal pocket is widely open (a shallow cavity formed by the anterior, glabrous part of the mesial hypomeron) in *Laeliaena*, *Limnebius* and several other hydraenine genera (e.g. *Parhydraena, Discozantaena*); in *Hydraenopsis* and *Phothydraena* (except: *H. putearius*) it is closed laterally, but always open ventrally; in *Haenydra* it is always closed laterally and partly closed ventrally; and in *Hydraena* s.str. the degree of the closure is inconstant, the "open" condition being generally found in few presumably basal species (related with *H. rugosa*, *H. circulata* etc.). The situation in *Haenydra* differs from those species of *H.* s.str and *Phothydraena* with a similar degree of closure by their closure being almost exclusively formed by the mesial hypomeron. The antennal pocket of *Adelphydraena* is quite exceptional within Hydraeninae, being completely closed ventrally (closure formed mainly by mesial hypomeron); the question of the homology of its modified (widened, smooth) anterior margin is not solved (this conspicuous margin is probably homologous with the anterior margin of the mesial (pubescent) hypomeron, which is thickened in certain species of *Haenydra* and *H.* s.str.); in any case, the condition in *Adelphydraena* appears to be rather derived. See Figs. 30, 31, 49 - 51, 57, 58, 64, 65, 83, 96, 97, 106, 107, 117 - 119, 131, 132, 142, 143, 147, 148, 160, 162, 198, 201, 222, 223, 227 - 229, 232, 233, 237, 238, 252, 254, 268, 269, 293, 294, 328, 342, 343, 348.

**10. Hypomeron: antennal pocket setae (0) along ridge (hypomeral carina) between unmodified lateral (glabrous) hypomeron and mesial (pubescent) hypomeron; (1) along mesial margin of ventrolateral wall of antennal pocket; (2) immediately behind anterior margin of ventrolateral wall of antennal pocket; (3) on anterior apex of modified (widened, often smooth) longitudinal hypomeral carina (usually with one or more additional setae on adjacent anterior margin of hypomeral antennal pocket); (4) absent.**

Hypomeral antennal pocket setae are usually distributed along the border between the lateral hypomeron and the mesial hypomeron. According to the evolutionary modification of the hypomera (development of the antennal pocket) the position of these setae varies between genera. In *Laeliaena* and *Limnebius* the pocket setae are distributed along the unmodified longitudinal carina separating the lateral and mesial hypomeron. In *Parhydraena* they are also found along the posterior margin of the pocket (along the border of the anterior, glabrous part and posterior, pubescent part of the mesial hypomeron). In *Davidraena*, these setae are distributed along the mesial margin of the lateral hypomeron which has become strongly modified to form a conspicuous lamella (ventrolateral wall of antennal pocket). In *Phothydraena*, the pocket setae are found immediately behind the anterior margin of the ventrolateral wall of the antennal pocket. In the remaining subgenera of *Hydraena*, these setae are either absent (most *Haenydra*) or placed on anterior apex of modified (widened, often smooth) longitudinal hypomeral carina (usually with one or more additional setae found adjacently behind the anterior margin of the ventrolateral wall of the antennal pocket). In *Adelphydraena* there are two pocket setae at the antero-mesial margin of the antennal pocket. See Figs. 30, 50, 51, 58, 65, 84, 97, 108, 118, 119, 132, 143, 148, 162, 199, 224, 228, 233, 238, 254, 270, 294, 330, 343, 344, 348.

**11. Hypomeron: number of antennal pocket setae: (0) five or more; (1) two to four; (2) one or none.**

Within Hydraeninae the number of pocket setae varies from zero to more than ten. We were not able to confirm the observation made by PERKINS (1997: 109) who stated that they are usually "seven in number". In *Davidraena*, *Laeliaena*, *Limnebius*, *Parhydraena* and *Hydraenopsis*, the number of pocket setae is usually much higher than in *Hydraena* s.str. and *Haenydra*.

It must be noted that the number of antennal pocket setae can vary slightly within the same species, even between left and right body side on the same individual: in *Hydraena riparia* there are usually 3-4 setae, but occasionally five may be observed. See Figs. 30, 50, 51, 58, 65, 84, 97, 108, 118, 119, 132, 143, 148, 162, 199, 224, 228, 233, 238, 254, 270, 294, 330, 343, 344, 348.

### 12. Hypomeron: antennal cleaner (0) without squamose setae; (1) with squamose setae distributed along anterior part of longitudinal ridge; (2) squamose setae distributed on oblique process.

In most genera of Hydraeninae there is a remarkable structure, the hypomeral antennal cleaner, located in the posteromesial part of the hypomeral antennal pocket. It can be composed of hairs, squamose setae, various sensilla, asperites and longitudinal ridges. In *Davidraena* the antennal cleaner is indicated by a long reticulate ridge. In *Laeliaena* it forms a rather short reticulate ridge with some short scattered hairs and in *Limnebius* it is vaguely indicated by a very short ridge. In *Hydraena* s.l. the antennal cleaner is usually very complexly structured along a prominent longitudinal ridge; squamose setae are always present and more or less densely clustered near the anterior apex of this ridge; in *Haenydra* and most species of *Hydraena* s.str. (e.g. *H. riparia*, *H. grandis*) the squamose setae are usually very small and inconspicuous, whereas in *H. circulata* and *Phothydraena* they are more distinct; the apex of the ridge is surrounded by a group of scattered hairs. In *Hydraenopsis* the antennal cleaner is usually shorter than in the remaining subgenera, being characterized by a conspicuous apical or subapical process (directed posterolaterad) to which the squamose setae are confined. Finally, in *Adelphydraena* the antennal cleaner is probably secondarily lost due to the complete closure of the antennal pocket.

In *Parhydraena* and some related genera there is a short brush of densely set hairs placed at the anterior margin of the prosternum. This brush was regarded as an antennal cleaner by PERKINS (1997). However, this structure is obviously not homologous with the more complex antennal cleaner s.str. of *Davidraena*, *Laeliaena*, *Limnebius* and *Hydraena* s.l., which is probably a derivate of the notosternal suture. See Figs. 32, 52, 59, 66, 85, 98, 108, 119, 133, 143, 149, 163, 203, 229, 238, 239, 240, 254, 271, 295, 331, 343, 345, 346, 349.

### 13. Prosternum: median projection of anterior margin (0) absent or inconspicuous; (1) prominent.

In Hydraeninae, the anterior margin of the prosternum is usually evenly arched or inconspicuously toothed medially. In *Hydraena* s.l. such a small tooth is for instance present in *Haenydra* (e.g. *H. gracilis*, *H. scitula*), in few species of *H.* s.str. (e.g. *H. armipalpis*, *H. cordata*, *H. unca*, *H. servilia*), and in all species of *Hydraenopsis* examined (except *H. cordiformis*, *H. paucistriata* and *H. tubuliphallis*). In *H. circulata* this tooth was found to be present (although very small) in certain individuals but lacking in many others. See Figs. 31, 49, 50, 57, 64, 83, 96, 107, 117, 131, 142, 147, 161, 198, 222, 296, 329. In *Limnebius* the median projection of the anterior prosternal margin is conspicuously long and acute; this acute process brakes off easily when the specimens are handled (see Figs. 49, 50).

### 14. Hypomeron and prosternum: sutural gap at posterior end (0) distinctly divergent; (1) parallel or closed.

The posterior (coxal) apex of the prosterno-hypomeral suture is often distinctly gaping in Hydraeninae. In *Davidraena*, *Laeliaena*, *Limnebius*, *Hydraenopsis* (except *H. paucistriata*), and in a few species of *H.* s.str. (those related with *H. rugosa* and *H. circulata*) it is even distinctly divergent posteriorly; in several cases its edges are so widely separated that the trochantin is completely exposed (e.g. *Limnebius*, *Hydraena isolinae, H. leechi*). See Figs. 30, 49, 50, 57, 60, 64, 65, 83, 86, 87, 96, 106, 107, 117, 118, 131, 142, 147, 160, 198, 200, 222, 227, 228, 232, 252, 268, 269, 293, 328.

### 15. Hypomeron and prosternum: prosternal postcoxal process and hypomeral postcoxal process (0) not contiguous; (1) contiguous (or overlaping or acetabuliform).

In most hydraenine genera the procoxae are not closed posteriorly. However, in *Hydraena* s.l. and *Adelphydraena*, the postcoxal prosternal process meets the postcoxal hypomeral process. In *Adelphydraena* these two processes simply touch each other, whereas they clearly overlap each other dorsoventrally (prosternal process in ventral position) in *Haenydra* and most species of *Hydraena* s.str. (rarely the hypomeral process can be semi-acetabulate - not engulfing hypomeral process ventrally). In *Hydraena frondsicola*, in *Phothydraena* and in most species of *Hydraenopsis* the hypomeral postcoxal process usually forms a distinct pocket (acetabulum) for reception of the tip of the prosternal branch. For an accurate examination of this character specimens must be dissected.

## Mesothorax:

### 16. Elytron: number of striae (in anterior half): (0) eight to eleven; (1) twelve to fourteen; (2) fifteen or more; (3) without distinct rows of elytral punctures.

The number of longitudinal rows of elytral punctures (striae) is remarkably variable in Hydraeninae. Duplication and fusion of striae are very common, and may occur between closely related species or even within the same species (see JÄCH & DÍAZ 1998). *Limnebius* is the only genus among Hydraeninae without distinct striae. The assumption by BERTHÉLEMY (1986) and PERKINS (1997) that all species with 10 striae have retained the primitive condition is most questionable. See Figs. 35, 88, 111, 136, 168, 206, 299, 335.

### 17. Mesosternum (mesosternal angle): mesosternal intercoxal process projecting from mesosternal disc (0) in more or less the same plane; (1) at an obtuse angle of ca. 150° - 170°; (2) at an obtuse angle of ca. 100° - 130°.

In *Davidraena*, *Gondraena*, *Laeliaena*, *Parhydraena*, and *Hydraenida* the mesosternal process is lying more or less in one plane with the mesosternum. In most species of *Hydraenopsis*, and for instance in *Discozantaena*, the mesosternal process and the mesosternum form an obtuse angle of ca. 150° - 170° (Fig. 334). Finally, in *Limnebius*, *Coelometopon*, *Haenydra*, *Hydraena* s.str., *Phothydraena* and a few species of *Hydraenopsis* (e.g. *H. cordiformis*, *H. cristatigena*, *H. paeminosa*, *H. paucistriata*) the mesosternal process is even more steeply sloping toward the mesosternum (Fig. 60).

## Metathorax:

### 18. Paired metasternal glabrous plaques (0) absent; (1) present (one pair); (2) present (two pairs).

Paired metasternal glabrous plaques are lacking in most hydraenine genera (e.g. *Davidraena*, *Gondraena*, *Limnebius*, *Discozantaena*, *Laeliaena*, *Parhydraena*, *Hydraenida*). There is usually one pair in *Haenydra*, *Adelphydraena*, *Hydraena* s.str. and *Hydraenopsis*, but they are absent in a number of species of *Hydraena* s.str. and *Hydraenopsis*: *H. armipalpis*, *H. rugosa*, *H. leechi*, *H. cordiformis*, *H. paucistriata*, and *H. tubuliphallis*. In *Hydraena monikae* and a number of species of *Hydraenopsis* their margins are not very distinctly defined. In *Phothydraena* there are always two pairs, although the second (lateral) pair is very small in *H. serricollis* and *H. putearius*. In a number of species of *Hydraena* s.str., the presence or absence of metasternal glabrous plaques is sexually dimorphic (e.g. *H. melas*). See Figs. 33, 86, 87, 109, 110, 134, 164, 166, 167, 204, 205, 255, 297.

## Abdomen:

### 19. Abdominal sternite II (intercoxal sternite) (0) entirely glabrous; (1) at least partly pubescent.

The intercoxal sternite is glabrous in *Laeliaena*, *Limnebius*, *Haenydra*, *Phothydraena* and in several species of *Hydraena* s.str. and *Hydraenopsis*. See Figs. 42, 90, 91, 113, 137, 174, 210, 261, 262, 298, 304, 305, 337.

### 20. Abdominal sternite II (intercoxal sternite) and abdominal sternite III (ventrite I): intercoxal cavity (0) absent; (1) present.

In Hydraeninae the middle of the anterior margin of ventrite I is usually flat and firmly connected with the posterior margin of the intercoxal sternite. However, in *Davidraena*, *Hydraena* s.str. (*H. circulata*, *H. monikae*, *H. rugosa*), *Hydraenopsis* (*H. tubuliphallis*) and *Phothydraena* (*H. hernandoi*) there is a remarkable, deeply impressed cavity (here termed intercoxal cavity) in the middle of the anterior margin of ventrite I, immediately behind the intercoxal sternite. In most cases the intercoxal sternite is strongly concave (at least posteriorly) and thus forming part of this conspicuous cavity. See Figs. 42, 90, 91, 113, 137, 174, 175, 210, 261, 262, 298, 304, 305, 337.

### 21. Abdominal sternite III (ventrite I): non-pubescent areas behind coxal pits (0) absent; (1) present.

The abdominal sternite III (ventrite I) is usually unmodified behind the coxal pits in most genera of Hydraeninae. However, in all species of *Hydraena* s.str. and *Haenydra*, in most species of *Phothydraena* and in very few species of *Hydraenopsis* there is a conspicuous non-pubescent area which varies greatly in its extent. See Figs. 41, 90, 91, 112, 113, 137, 173, 209, 260 - 262, 300, 301, 336.

### 22. Abdominal sternite VII (ventrite V) (0) entirely glabrous or entirely pubescent; (1) or pubescent with (more or less) semicircular glabrous posterior portion.

A semicircular glabrous posterior portion of abdominal sternite VII is present in *Hydraena* s.l. and is also common in Orchymontinae. See Figs. 41, 89, 112, 137, 172, 207, 208, 213, 216, 260, 300, 301, 306, 307, 336.

**23. Gonocoxite: median longitudinal suture (0) absent; (1) present (complete or incomplete).**

The outer plate of the gonocoxite is usually not divided by a longitudinal suture in Hydraeninae. However, such a suture is present in *Orchymontia* BROUN, *Phothydraena*, in a few species of *Hydraena* s.str. (*H. circulata*, *H. monikae*, *H. rugosa*) and in one species of *Hydraenopsis* (*H. paeminosa*). See Fig. 41, 112, 139, 213 - 215, 306.

**24. Gonocoxite: pseudostyli (tufts) (0) absent; (1) present.**

In Hydraeninae, pseudostyli are developed in *Adelphydraena* and *Hydraena* s.l. only. They are very small in *Hydraena cristatigena*. Pseudostyli are probably not homologous with the styli (sensu LINDROTH & PALMÉN 1970) of other beetles. See Figs. 139, 214, 215.

**25. Male sternite X and spicula (= sternite IX) (0) not firmly connected with each other, at most loosely connected by a membrane; (1) firmly connected with each other.**

The male sternite X (Figs. 140, 307, 336) and the spicula (= sternite IX) are firmly connected with each other in *Davidraena boukali* and in several, presumably derived species of *Hydraenopsis* (*H. cyclops*, *H. isolinae*, *H. vulgaris*, *H. anisonycha*).

Legs:

**26. Protrochanter (0) (at least partly) pubescent; (1) not pubescent.**

The protrochanter is pubescent in *Davidraena*, *Laeliaena*, *Limnebius*, *Parhydraena*, *Hydraenida*, *Discozantaena*, *Hydraenopsis*, *Phothydraena* and a few species of *Hydraena* s.str. (*H. circulata*, *H. monikae*, *H. rugosa*, *H. frondsicola*, *H. cordata*). It is not pubescent in *Adelphydraena*, *Haenydra* and in the majority of *Hydraena* s.str.

Genitalia:

**27. Number of setae on aedeagal main piece: (0) none (at most with a group of spines); (1) four; (2) one to three; (3) more than four.**

The number of aedeagal setae is most variable within Hydraeninae and within certain genera. BERTHÉLEMY (1965: 14) suggested that the main piece of the aedeagus was originally provided with four setae (arranged in two pairs) in *Hydraena* s.l. In fact, the presence of four aedeagal setae is quite common in *Haenydra*, *Hydraena* s.str. and *Phothydraena*, but so far no species of *Hydraenopsis* is known to have four setae on the aedeagal main piece.

In *Limnebius atomus*, the setal groups may indicate parameral remnants (cf. *Laeliaena* !).

**28. Number of parameres: (0) two; (1) one; (2) none.**

Most species of Hydraenidae have two parameres. Both parameres are lost in certain species of *Limnebius* and they are generally absent in *Haenydra*. Loss of a single paramere can be observed in *Limnebius* and (very rarely) in *Hydraena* s.str. (e.g. *H. mylasae* JÄCH).

**29. Base of paramere(s): (0) free, articulated with main piece; (1) (at least one paramere) immovably fused to main piece.**

Parameres, if present, are usually movably articulated with the main piece. In *Laeliaena*, *Limnebius*, several species of *Hydraenopsis* (e.g. *H. isolinae*, *H. paeminosa*) and

*Hydraena* s.str. (e.g. *H. armipalpis*) the parameres (or at least one paramere) are (is) immovably fused to the main piece.

**30. Base of paramere(s): (0) proximal, close to base of aedeagus; (1) at least one paramere shifted distad.**

Parameres are usually inserted immediately behind the phallobase in Hydraeninae. In all species of *Laeliaena* and *Limnebius*, in the majority of *Hydraenopsis*, and in few species of *Phothydraena* (*H. hernandoi*) and *Hydraena* s.str. (e.g. *H. armipalpis*, *H.* cf. *cirrata*) the parameral base is positioned further distal (either due to fusion with main piece or due to transposition). In *Phothydraena* the transposition is generally very moderate.

**31. Pseudospermatheca (vaginal plate) (0) absent; (1) present.**

Accessory vaginal sclerites are present in all species of *Phothydraena*, in all species of *Laeliaena* so far examined, in at least one species of *Davidraena* (*D. antennalis* JÄCH), and in very few species of *Hydraena* s.l. (*H. monikae*, *H. paeminosa*, in *H. cordiformis* there is a very small sclerotized rod, which might represent a vaginal plate).

These vaginal sclerites can be very simple or very intricately shaped. In *Phothydraena*, they resemble a spermatheca.

## List of complementary characters (not entered in data matrix)

Apart from the selected 31 characters which were entered in the data matrix (table 1), we have detected 22 additional characters (or character groups), which seem to be of phylogenetic relevance (at least at species group level). However, we have not used them for the data matrix, partly because we have not yet worked them out thoroughly and partly because some of them turned out to be not applicable or ambiguous in certain species.

### Vestiture:

1. In Hydraeninae, there are considerable differences in the density and length of the hairs (pubescence, plastron) on the ventral side (see also BERTHÉLEMY 1986: 188). In *Hydraena* s.str. and *Haenydra*, the hairs are usually shorter and more densely arranged than in *Hydraenopsis* and *Phothydraena* (except *H. putearius*). See Figs. 41, 60, 87, 109, 166, 167, 171, 172, 205, 207, 336 - 339.

2. The shape of the hairs, especially on head and pronotum, seems to be quite diverse. In *H. circulata* (Figs. 180, 196) they appear to be rather thick, especially when compared with species related with *H. riparia* (Figs. 120, 129) or with *Haenydra* (Figs. 67, 69).

### Head:

3. Labrum: The anterior labral margin is usually moderately deeply emarginate/excised in Hydraeninae. Occasionally, this emargination/excision is very shallow (*Limnebius*, *Discozantaena*) or very deep (*Hydraena*, *Davidraena*). In *Hydraena* s.str. it is generally deeper than in *Hydraenopsis*. See Figs. 19, 69, 99, 121, 150, 178, 241, 278, 309.

4. Mandibles: The mandibles of *Hydraena* s.l. are characterized by a conspicuous, broad dorsolateral process which is part of the labral-mandibular interlocking device (sensu

PERKINS 1989). It is less clearly separated from the dorsomesal mandibular surface in *H. cyclops* than in *H. circulata*. The shape of the prostheca and of the semimembranous subapical lobe, and especially the shape of the strongly asymmetrical left and right mola will probably contribute to the understanding of the phylogeny of *Hydraena* s.l. (and Hydraenidae). However more study of these structural details is required. See Figs. 76, 77, 183, 184, 281 - 285, 318, 319.

5. Remaining mouthparts: So far we have not yet carried out comprehensive comparative analyses of the remaining mouthparts (maxillae, labium, epipharynx, hypopharynx). Shape and setation of these appear to be generally diverse. See Figs. 74, 75, 78 - 80, 122 - 126, 153, 179, 185 - 187, 243, 279, 280, 286, 287, 316, 317.

6. Antennae: The shape of the so-called cupule (= segment 6 of the 11-segmented antenna = segment 4 of 9-segmented antenna of *Hydraena* s.l.) is quite diverse within Hydraeninae, varying from almost symmetrical to strongly asymmetrically "cup-shaped". In *Haenydra* its apex is always rounded, whereas in the other lineages of *Hydraena* s.l. it is strongly pointed. See Figs. 25, 26, 70, 71, 100, 123, 152, 181, 182, 277, 313 - 315.

7. Vertex: The posterior, narrowed part of the head (vertex, neck region) reveals a couple of interesting characters dorsally. It is generally covered with a fine, posteriorly directed pubescence (however, in *Haenydra* it is glabrous anteriorly). A distinct median longitudinal concentration of trichia is well developed in *Hydraenopsis* and (less apparent) in *Phothydraena* but more or less absent in the remaining lineages. A few sublateral setae are present in many species. The shape of the distinct ridge separating the neck region from the frons is remarkably diverse: it can be evenly arcuate or sinuous, flattened or prominent, thin or wide. See Figs. 67, 68, 99, 120, 150, 177, 180, 241, 272, 274, 308, 312.

8. Postocular area: Various cuticular microstructures and rows or groups of long setae (postocular setae and genal antennal groove setae) are found anterior and posterior of the genal antennal groove. In *Haenydra* a conspicuous convex spiculate area is developed (posterior of the genal antennal groove), whereas the postocular genal setae are less distinctly developed than in other lineages. See Figs. 56, 63, 95, 103, 116, 128, 146, 189 - 191, 236, 245, 267, 290, 321, 324, 325.

## Thorax:

9. Pronotum: There are clusters of sensory setae on the anterior corners of the pronotum in *Hydraena* s.l. These clusters are quite diverse and worth being examined more thoroughly. See Figs. 82, 105, 129, 159, 196, 197, 250, 251, 292, 327.

10. Pronotum: Punctation and reticulation of the pronotum are usually rather evenly distributed. However, in *Hydraena* s.str. and *Haenydra* the lateral pronotal margin is usually more densely (rugosely) punctate and/or more distinctly reticulate than the disc. See Figs. 81, 104, 129, 158, 195, 196, 249, 250, 291, 292, 326.

11. Hypomera: In *Hydraena* s.l. the lateral hypomera are usually slightly arched and moderately wide. However, in *H. vulgaris*, *H. leechi*, and *H. tubuliphallis* they are conspicuously wide, whereas in *Haenydra* and *H. armipalpis* they are very narrow and strongly arched. Accordingly, the hypomeral carina can be more or less straight, or slightly or strongly arched. See Figs. 57, 64, 83, 96, 106, 117, 118, 131, 142, 147, 160, 198, 222, 227, 232, 237, 252, 268, 293, 328, 342, 348.

12. Hypomeral carina: The hypomeral carina is rather wide and flattened in most species of *Hydraena* s.str. and *Haenydra*. However, in *H. circulata*, *H. monikae*, and *H. rugosa* it is flattened but slightly narrower and in *Phothydraena* it is very narrow and convex. In *Hydraenopsis* it is rather variable: in *H. paucistriata*, *H. cordiformis* and *H. leechi* it is similar to *H. circulata*, *H. monikae*, and *H. rugosa*; in *H. tubuliphallis* and *H. cristatigena* it is narrow and convex, flattened only anteriorly; in *H. cyclops* it is distinctly widened anteriorly and posteriorly, but strongly narrowed in between. In *H. cristatigena* the hypomeral carina is furthermore devious in being microreticulate instead of glabrous anteriorly. See Figs. 57, 58, 64, 65, 83, 84, 96, 97, 106, 107, 117, 118, 131, 142, 147, 160, 162, 198, 201, 222, 223, 227, 228, 232, 233, 238, 238, 252, 268 - 270, 293, 294, 328, 330, 342, 343, 344, 348.

13. Prosternum: The anterior margin of the prosternum is usually provided with a fringe of longer setae. These setae are conspicuously long and densely arranged in *Hydraenopsis* (Figs. 237, 252, 268, 293, 329, 329, 342) and *Phothydraena* (Figs. 161, 162), whereas they are short in *Hydraena* s.str. (Figs. 96, 106, 107, 117, 118, 131, 147, 198, 201, 222, 227, 232) and more or less absent in *Haenydra* (Figs. 57, 64, 83).

14. Procoxal sockets and prosternal intercoxal process: The procoxal sockets are usually more or less distinctly transverse in *Limnebius*, *Laeliaena* and in most species of *Hydraenopsis* and in few species of *Hydraena* s.str. (*H. cordata* [*H. palustris* group], *H. circulata* group, *H. monikae*, and *H. rugosa*). In *Haenydra*, in most species of *Hydraena* s.str. and in *H. paucistriata* the outlines of the procoxal sockets are more or less round.

Analogously, the (minimum) width of the prosternal process between the procoxae is rather variable in *Hydraena* s.l. It is generally moderately or conspicuously wide, however, in a few species of *Hydraenopsis* (e.g. *H. vulgaris*, *H. leechi*) it is very narrow, reduced to a thin carina. In a few cases, the width of the prosternal process between the procoxae may be sexually dimorphic to some extent. See Figs. 31, 49, 50, 57, 64, 83, 96, 106, 117, 131, 142, 147, 160, 161, 198, 222, 227, 232, 237, 252, 268, 293, 328, 342.

15. Epipleura and pseudepipleura: The width of the epipleura and pseudepipleura as well as the angle between them varies considerably within *Hydraena* s.l. *Hydraena armipalpis* deviates greatly by its exceptionally wide epipleura, which lie in one plane with the pseudepipleura. See Figs. 60, 86, 87, 204.

16. Patches of spicules on ventral surface of elytra: The ventral side of the elytra bears cuticular micro-structures (spicules), which are arranged in conspicuous patches. According to HAMMOND (1979), these may function as binding patches (elytron-wing, elytron-abdomen, or elytron-pterothorax) and/or as stridulatory devices (plectra). These structures were found in all genera and species examined so far (see also JÄCH 1986, BERTHÉLEMY 1986, ORDISH 1984). They vary in extension, density, shape, and position on the elytra. See Figs. 36 - 38, 169, 170, 258, 259.

17. Scutellum: The scutellum is remarkably diverse in Hydraeninae, worth being examined more thoroughly in future! In *Hydraena* s.l. it is characterized by a remarkably long apical projection. In *Hydraenopsis* the scutellum is generally more transverse than in *Hydraena* s.str. and *Haenydra*. For an accurate examination the scutellum must be entirely dissected.

### Legs:

18. Setation of legs: Generally, the setation of the legs is enormously diverse in Hydraenidae, and deserves more detailed comparative analyses in future.

### Abdomen:

19. Trichia on dorsal surface: The dorsal surface of the abdomen (especially tergites VII - VIII, and pleurites) is covered with numerous trichia: e.g. tergal wing-folding spicules, palisade fringe (along posterior nargin of tergite VII), and stridulatory files (see also HAMMOND 1979). Preliminary investigations revealed interesting differences between hydraenine genera and within *Hydraena* s.l. See Figs. 39, 40, 43, 92, 217.

20. Male tergite X: The shape of the male tergite X is remarkably diverse and diagnostic (at least at species group level) in Hydraeninae. The apex is usually modified: truncate, notched, excavate or impressed subapically. It is very deeply and widely excavate in *Haenydra* (Fig. 89), but more or less truncate in *Phothydraena*. See also Figs. 140, 208, 216, 260, 300, 307, 340.

### Genitalia:

21. Phallobase: The basal orifice of the aedeagus can be either symmetrical or asymmetrical; it can be either ring-shaped or semicircular (dorsally or ventrally open).

22. Secondary sexual characters: Pronounced secondary sexual characters appear to be lacking or faintly developed in the presumably basal lineages of *Hydraena* s.str. and in *Phothydraena*. In *Hydraenopsis*, pronounced external sexual characters are often concerning male profemora and protibiae. In *Haenydra*, external sexual characters are often found on male meso- and metatibiae. In the presumably derived species of *Hydraena* s.str. external sexual characters are often concerning male meso- and metatibiae and male maxillary palpi (terminal segment strongly asymmetrical).

## List of characters of minor phylogenetic relevance

Maxillary palps: The length (proportional length of segments and total length) of the maxillary palpi is highly variable in Hydraeninae. Maxillary palps are for instance very short in *Hydraenida*, *Coelometopon* and *Davidraena*; they are moderately long in *Laeliaena*, *Limnebius*, considerably long in certain species of *Parhydraena* and very long in most species of *Hydraena* s.l. (with few exceptions). In *Hydraena* s.l. the length of the palps may vary greatly between closely related species (e.g. *H. palustris* and *H. curta* KIESENWETTER). This feature may be correlated with the habitat. See Figs. 18, 45, 48, 78, 124, 153, 185, 243, 286, 316.

Legs: The length of the legs is similarly variable in *Hydraena* s.l. and may be correlated with the habitat.

Intercoxal sternite: The shape and size of the intercoxal sternite varies greatly within Hydraeninae and within *Hydraena* s.l. See Figs. 42, 90, 91, 113, 137, 174, 210, 261, 262, 298, 304, 305, 337.

Parameres: The size, shape and symmetry of the parameres are enormously diverse in *Hydraena* s.l. Furthermore, the base of the parameres can be ventrolateral or exactly lateral (e.g. *Laeliaena*, most species of *Hydraena* s.str. (except *H. circulata*, *H. monikae*, *H. rugosa*, *H. cordata*), and in almost all species of *Hydraenopsis* (except *H. cordiformis*, *H. paucistriata*)).

## Hitherto unrecorded characters

Several characters, hitherto unrecorded in *Hydraena* s.l., were detected in the course of this study:

Presence of a pronotal membrane (*Phothydraena*, *Hydraena frondsicola* and *H. paeminosa*). See Figs. 158, 159.

Genae with paired, small, paramesal protuberances on smooth area between submentum and anterior transverse genal ridge, immediately posterior of faint transversely arranged lines denoting margin between submentum and genae. Detected in *H. isolinae* (see Figs. 320, 321, 323).

Ventrites 1 - 4 each with conspicuous glabrous (unpubescent) spot at middle of posterior margin. Observed in *Hydraena vedrasi* (see Figs. 89 - 91).

Anterior corners of ventrites modified in several species, e.g. lacking pubescence (*H. cyclops*, Figs. 302, 303) or with elongate, densely set, squamose sclerotized structures (*H. isolinae*, Fig. 339).

## Results of the cladistic analysis

A first analysis (heuristic search) with all characters equally weighted resulted in 287 minimal length trees with 99 steps length (CI: 0.465, HI: 0.535, RC: 0.350; Fig. 15: majority rule consensus tree, 50%). Only nine trees were obtained after successive reweighting. The sets of trees were identical after two consecutive searches. All unambiguous and some ambiguous apomorphies of clades in tree 3 are listed below (Figs. 16, 17). Characters that are unreversed and unique (Cl: 1.000) are indicated by an asterisk in the following.

***Hydraena* s.l.**: 1.1 (labrum abruptly constricted posteriorly, 2.2* (setae of penultimate segment of labial palp closely set), 3.1* (apex of mentum with acute median projection), 10.3* (antennal pocket seta on anterior apex of modified longitudinal hypomeral carina), 15.1* (prosternal postcoxal process and hypomeral postcoxal process contiguous, ovelapping or acetabuliform), 16.2 (elytra with 15 or more striae; reversal in several species), 17.2 (mesosternum and mesosternal process forming obtuse angle of ca. 100° - 130°; reversal in most species of *Hydraenopsis*), 21.1 (sternite III with non-pubescent areas behind coxal pits; reversal in several species), 22.1* (abdominal sternite VII pubescent with semicircular glabrous posterior region), 24.1* (gonocoxite with pseudostyli).

***Hydraenopsis***: 5.1 (longitudinal median genal suture incomplete or absent; parallelism in *Laeliaena*), 7.1 (pregula absent or very short, not triangular; parallelism in *Laeliaena*), 12.2* (hypomeral antennal cleaner with squamose setae distributed on process, which is always directed posterolaterad), 27.2 (number of setae on aedeagal main piece one to three; parallelism in *Hydraena gracilis* and *H. monikae*).

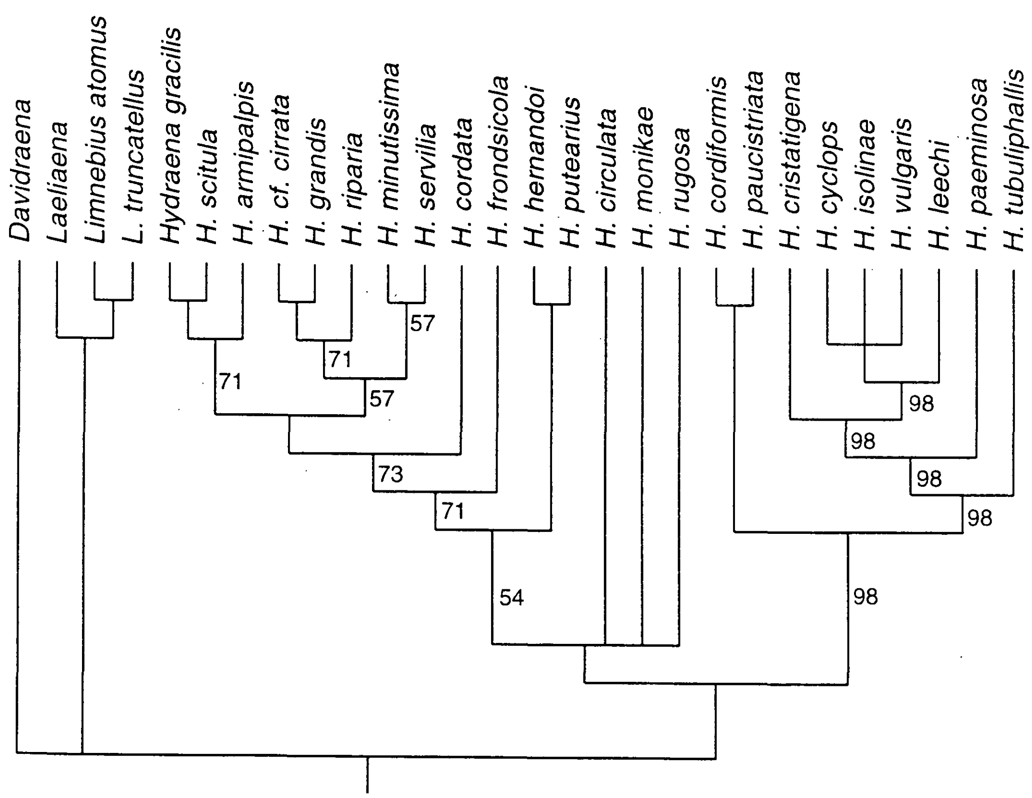


Fig. 15: Majority rule consensus tree (50%) of 287 minimal length trees.

***Hydraena cordiformis* + *H. paucistriata***: 4.0 (posterior transverse genal ridge more or less flat; parallelism in *Hydraena cyclops*, *H. isolinae*, *H. leechi*, and *H. vulgaris*).

***Hydraenopsis* excl. (*Hydraena cordiformis* + *H. paucistriata*)**: 8.1 (transverse anterior inner gular carina absent; parallelism in outgroup taxa), 17.1 (mesosternal intercoxal process projecting from mesosternal disc at an obtuse angle of 150° - 180°), 30.1 (at least one paramere shifted distad; parallelism in several species).

***Hydraena cyclops* + *H. isolinae* + *H. vulgaris***: 25.1 (male sternite X and spicula firmly connected with each other; parallelism in *Davidraena*).

**(*Hydraena cyclops* + *H. isolinae* + *H. vulgaris*) + *H. leechi***: 4.0 (posterior transverse genal ridge more or less flat; parallelism in *Hydraena cordiformis* and *H. paucistriata*).

((*Hydraena cyclops* + *H. isolinae* + *H. vulgaris*) + *H. leechi*) + *H. cristatigena*: 6.2 (longitudinal inner genal carina absent; parallelism in outgroup taxa).

**(((*Hydraena cyclops* + *H. isolinae* + *H. vulgaris*) + *H. leechi*) + *H. cristatigena*) + *H. paeminosa***: 18.1 (one pair of metasternal glabrous plaques present; reversal in *H. leechi*; parallelism in several species), 19.1 (abdominal sternite II at least partly pubescent), 21.0 (abdominal sternite III without non-pubescent areas behind coxal pits; reversal in several species).

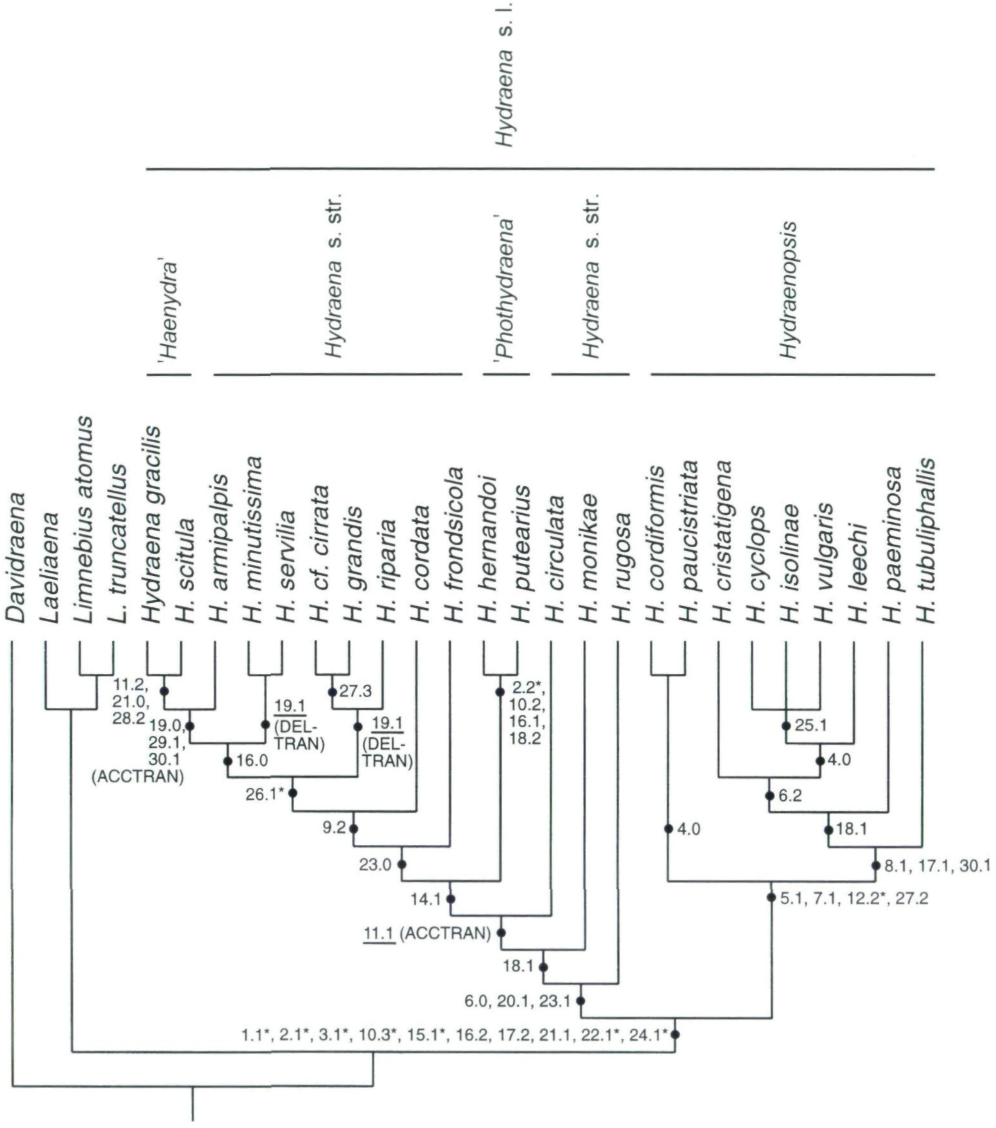


Fig. 16: Tree 3 of 9 minimal length trees obtained after successive reweighting. All unambiguous and some ambiguous apomorphies mapped on cladogram (ACCTRAN: accelerated transformation; DELTRAN: delayed transformation). Non-homoplasious apomorphies marked by an asterisk.

***Hydraena* s.l. excl. *Hydraenopsis***: 6.0 (longitudinal inner genal carina complete), 20.1 (intercoxal cavity of abdominal sternites II and III present; reversal in many species), 23.1 (median longitudinal suture of gonocoxite present; reversal in many species; parallelism in *H. paeminosa*).

***Hydraena* s.l. excl. *Hydraenopsis* and *Hydraena rugosa***: 18.1 (one pair of metasteral glabrous plaques; parallelism in several species; reversal in *H. armipalpis*).

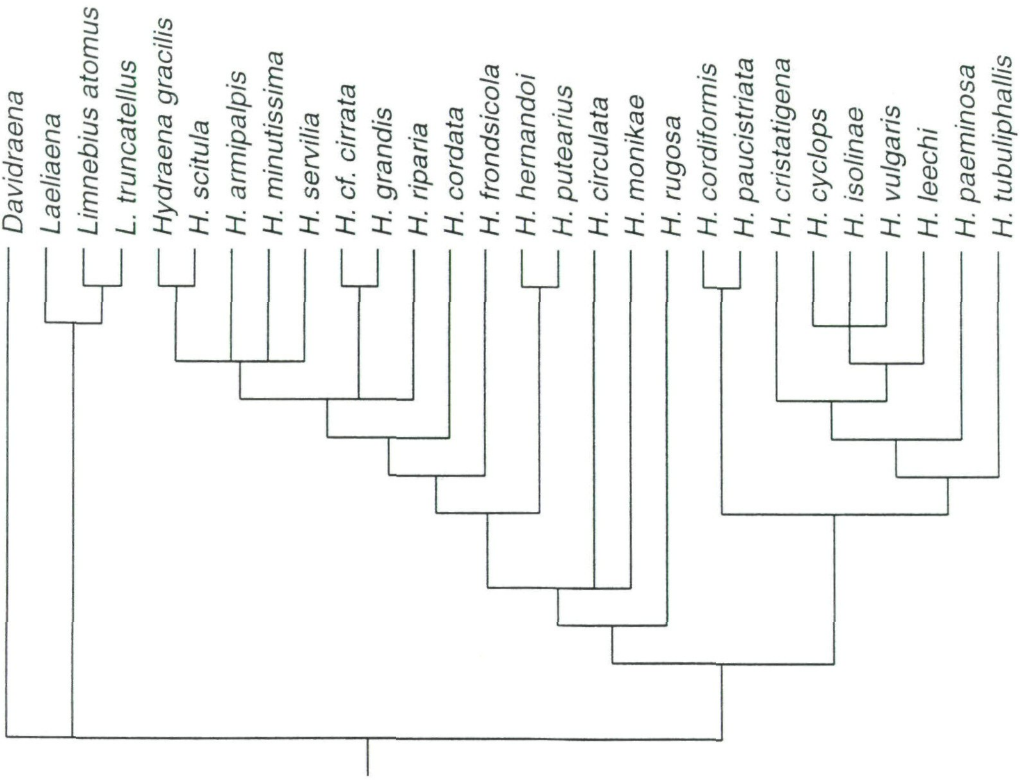


Fig. 17: Strict consensus tree of 9 minimal length trees obtained after successive reweighting.

***Hydraena* s.l. excl. *Hydraenopsis, Hydraena rugosa* and *H. monikae***: not supported by unambiguous apomorphy (11.1 - only in accelerated transformation).

***Hydraena* s.l. excl. *Hydraenopsis, Hydraena rugosa, H. monikae* and *H. circulata***: 14.1 (sutural gap at posterior end of hypomeron and prosternum parallel or closed; parallelism in *H. paucistriata*).

***Phothydraena* (*Hydraena hernandoi* + *H. putearius*)**: 2.1* (subapical setae of penultimate segment of labial palp widely separated from each other, located on outer and inner edge respectively), 10.2 (antennal pocket setae immediately behind anterior margin of ventrolateral wall of antennal pocket), 16.1 (elytra with 12 – 14 striae), 18.2 (two pairs of metasternal glabrous plaques).

((((*Haenydra* + *H. armipalpis*) + (*H. minutissima* + *H. servilia*)) + ((*H.* cf. *cirrata* + *H. grandis*) + *H. riparia*)) + *H. cordata*) + *H. fronsicola*: 23.0 (median longitudinal suture of gonocoxite absent; parallelism in most species of *Hydraenopsis*).

(((*Haenydra* + *H. armipalpis*) + (*H. minutissima* + *H. servilia*)) + ((*H.* cf. *cirrata* + *H. grandis*) + *H. riparia*)) + *H. cordata*: 9.2 (antennal pocket of hypomeron closed laterally; parallelism in *H. putearius*).

Table 1: Character state matrix used for cladistic analysis.

| CHARACTERS<br>SPECIES | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *Davidraena boukali* | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2. *Laeliaena sichuanensis* | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| 3. *Limnebius atomus* | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 2 | - | - | 0 |
| 4. *Limnebius truncatellus* | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 1 | 1 | 0 |
| 5. *Hydraena gracilis* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 3 | 2 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 2 | - | - | 0 |
| 6. *Hydraena scitula* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 4 | 2 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 2 | - | - | 0 |
| 7. *Hydraena armipalpis* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 3 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| 8. *Hydraena circulata* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 0 | 0 | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9. *Hydraena* cf. *cirrata* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 3 | 0 | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 3 | 0 | 0 | 1 | 0 |
| 10. *Hydraena cordata* | 1 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 3 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| 11. *Hydraena frondsicola* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 1 | ? | 0 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12. *Hydraena grandis* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 3 | 1 | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 3 | 0 | 0 | 0 | 0 |
| 13. *Hydraena minutissima* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 3 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 14. *Hydraena monikae* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 1 | 0 | 0 | 1 | 2 | 2 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 |
| 15. *Hydraena riparia* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 3 | 0(1) | 1 | 0 | 1 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 16. *Hydraena rugosa* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | 2 | 1 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 17. *Hydraena servilia* | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 3 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| 18. *Hydraena cordiformis* | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 3 | 0 | 2 | 0 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| 19. *Hydraena cristatigena* | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 3 | 1 | 2 | 0 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 0 |
| 20. *Hydraena cyclops* | 1 | 2 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 3 | 0 | 2 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 1 | 0 |
| 21. *Hydraena isolinae* | 1 | 2 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 3 | 0 | 2 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 | 1 | 0 |
| 22. *Hydraena leechi* | 1 | 2 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 3 | 0 | 2 | 0 | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| 23. *Hydraena paeminosa* | 1 | 2 | 1 | 1 | ?0 | 1 | 1 | 1 | 1 | 3 | 0 | ? | 0 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| 24. *Hydraena paucistriata* | 1 | 2 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 3 | 0 | 2 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| 25. *Hydraena tubuliphallis* | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 0 | 2 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 0 |
| 26. *Hydraena vulgaris* | 1 | 2 | 1 | 0 | 1 | 2 | 1 | 1 | 1 | 3 | 0 | 2 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 1 | 0 |
| 27. *Hydraena hernandoi* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 2 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| 28. *Hydraena putearius* | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |

((*Haenydra* + *H. armipalpis*) + (*H. minutissima* + *H. servilia*)) + ((*H.* cf. *cirrata* + *H. grandis*) + *H. riparia*): 26.1* (protrochanter not pubescent).

***Hydraena* cf. *cirrata* + *H. grandis***: 27.3 (more than four setae on aedeagal main piece; parallelism in *Limnebius*).

**(*Hydraena* cf. *cirrata* + *H. grandis*) + *H. riparia***: not supported by unambiguous apomorphy (19.1, abdominal sternite II at least partly pubescent - only in delayed transformation).

**(*Haenydra* + *H. armipalpis*) + (*H. minutissima* + *H. servilia*)**: 16.0 (elytra with 8 - 11 striae; parallelism in *Hydraena paucistriata* and outgroup taxa).

***Hydraena minutissima* + *H. servilia***: not supported by unambiguous apomorphy (19.1, abdominal sternite II at least partly pubescent - only in delayed transformation).

***Haenydra* + *Hydraena armipalpis***: not supported by unambiguous apomorphy (19.0, abdominal sternite II not pubescent; 29.1, base of parameres immovably fused to main piece; 30.1, at least one paramere shifted distad – all characters only in accelerated transformation).

***Haenydra***: 11.2 (none or two antennal pocket setae; parallelism in *H. rugosa*), 21.0 (non-pubescent areas behind coxal pits absent; parallelism in several *Hydraena* species and in outgroup taxa), 28.2 (parameres absent; parallelism in *Limnebius atomus*).

## Discussion

### 1. Mandibles and internal structures of head:

The complex and distinctly asymmetric mandibles (with an apical part inserting proximal to the cranial margin, a prostheca, and a semimembranous mesal lobe covered with microtrichia) are quite similar to the mandibles of myxophagan larvae, which are strictly algophagous as far as known at present (BEUTEL et al. 1999). The characteristic, broad dorsolateral process is probably not an exclusive feature of *Hydraena* s.l. (see *Adelphydraena*; PERKINS 1989: Fig. 6). However, in *Hydraena* s.l. it is apparently more prominent and interlocks with a lateral notch of the labrum. Another unusual feature of *Hydraena* s.l. is the markedly asymmetric proximal area, with a blunt left mola and a strongly broadened right mola with a pointed apex, which reaches deeply into the prepharynx. This structural peculiarity is less strongly expressed in the genus *Ochthebius*; and it has not been described for adults of other beetle families.

Muscular features of the head of adults of *Hydraena* s.str. and *Hydraenopsis* seem to be rather uniform, whereas internal skeletal structures differ considerably. The posterior transverse genal ridge and the longitudinal genal carina are either absent or obliterated in members of the latter subgenus (characters 4 and 6). Antennal muscles seem to be specialized in *Hydraena* s.l. and clearly different from those of ochthebiine hydraenids (*Meropathus*, *Ochthebius*) or representatives of other families examined (e.g. Leiodidae: *Neopelatops*, Helophoridae: *Helophorus*). The origin from the upper tentorial body and the separation of the unusually strong extrinsic muscles into a lower and an upper group may be correlated with the special shape and function of the antennae. This may turn out as an additional autapomorphy of *Hydraena* s.l. or as a synapomorphy of this genus and other hydraenine representatives. Another characteristic feature of adults of *Hydraena* s.l. is the origin of a very strong M. frontohypopharyngalis from the posterior vertex in

*Hydraena* s.l. A similar condition is found in some representatives of other groups of Coleoptera (e.g. *Helophorus*), but not in *Ochthebius* and *Meropathus*. An unusual, presumably apomorphic feature shared by adults of the latter genera is the very strong sclerotization of the dorsal tentorial arms and the origin of lateral pharyngeal dilators from these structures. A similar condition is not found in members of *Hydraena* s.l. or other groups of Coleoptera.

Other internal features of the head of adult Hydraenidae such as the unusual condition of the hypopharynx or tentorium may turn out as helpful for future phylogenetic investigations in a broader taxonomic context.

## 2. Cladistic analysis:

Within *Hydraena* s.l. the branching pattern implies a considerable degree of homoplasy, i.e. reversals and parallelisms, which is reflected by the comparatively low consistency index (which is not surprising for a cladogram at the species level). The proposed phylogeny seems to be well founded at different branching points.

One of the major results of this analysis is the well supported monophyly of *Hydraenopsis*, which was described as a new genus by JANSSENS (1972). PERKINS (1980) synonymized *Hydraenopsis* with *Hydraena* s.str., whereas JÄCH (1986) treated it as a subgenus of *Hydraena*. Eventually, PERKINS (1997: 163) corroborated his earlier opinion by reducing *Hydraenopsis* once more to synonymy (with *Hydraena* s.str.); however, the arguments, which he provided in support of his synonymic theory are not convincing: "the subgenus *Hydraena* (sensu stricto) is based on the derived elytral strial configuration, which is both practical and accurate". However, the number of elytral striae is extremely variable in *Hydraena* s.l. (even within species) and subject to numerous reversals and parallelisms (see character 16), and therefore neither accurate nor practical.

*Hydraenopsis* is characterized by 3 unambiguous autapomorphies (see above). Other diagnostic characters are: labrum usually less abruptly constricted posteriorly; posterior transverse genal ridge very rarely crested; longitudinal inner genal carina absent or incomplete; transverse anterior inner gular carina absent in most species (except: *H. cordiformis*, *H. paucistriata*); pronotum on average almost parallel-sided (or slightly convergent anteriad) in anterior half; anteroexternal and posteroexternal pronotal foveae usually shallowly impressed; punctation and reticulation of lateral pronotal margin as on disc; hypomeral antennal pocket open ventrally; anterior and mesial margin of hypomeral antennal pocket usually forming a gently arched, continuous line, only rarely forming a distinct angle (e.g.: *H. cristatigena*, *H. vulgaris*); hypomeral antennal pocket usually with five or more longer setae; anterior margin of prosternum with median projection (except: *H. cordiformis*, *H. paucistriata*, *H. tubuliphallis*) and with fringe of long setae; prosterno-hypomeral suture distinctly gaping at posterior (coxal) apex (except: *H. paucistriata*); connection between prosternal postcoxal process and hypomeral postcoxal process acetabuliform; prosternal postcoxal process short and transverse, parallel-sided (never triangular); procoxal sockets transverse (except: *H. paucistriata*); elytra in most cases with fifteen striae (except: *H. paucistriata*); mesosternal process and mesosternum usually form an obtuse angle of ca. 150° - 170° (rarely, e.g. *H. cordiformis*, *H. cristatigena*, *H. paeminosa* and *H. paucistriata*, the mesosternal process is more steeply declivitous toward the mesosternum); margins of metasternal plaques usually not very distinctly defined; sclerotization of first abdominal tergite usually interrupted medially;

abdominal sternite II (intercoxal sternite) usually pubescent (except: *H. paucistriata*, *H. tubuliphallis*); intercoxal cavity very rarely present (*H. tubuliphallis*); ventrite I with or without non-pubescent area behind coxal pits; gonocoxite very rarely with median longitudinal suture (e.g. *H. paeminosa*); male abdominal sternite X often with a pair of short lateral projections near base, firmly connected with spicula in at least several species; protrochanter always pubescent; aedeagal main piece with one, three or without (e.g. *H. quadricollis*) setae; aedeagus usually with two parameres, their bases usually shifted distad, rarely inserted near phallobase (*H. cordiformis*, *H. paucistriata*); a distinct accessory vaginal sclerite is usually absent (except: *H. paeminosa*); distal tip of spermathecal duct swollen and slightly sclerotized (except: *H. tubuliphallis*); secondary sexual characters of males never include strongly asymmetrical labial palps.

*Hydraena cordiformis* and *H. paucistriata* share numerous plesiomorphic characters, which are also found in *Hydraena* s.l. (excl. *Hydraenopsis*). Their aedeagi are remarkably similar (see JÄCH & DÍAZ 2000: Figs. 11, 13), which corroborates the assumption of their close relationship.

*Hydraena tubuliphallis* is a remarkable species with numerous deviating characters: lateral hypomera very wide; legs very short; tarsal claws toothed; female tergite X with very wide glabrous area anteriorly; apical third of female tergite X clearly demarcated from basal two thirds by a distinct edge; aedeagal distal lobe inside sheath-like apical part of main piece; spermathecal duct not enlarged apically.

*Hydraena paeminosa* shares irregular elytral punctation with at least one undescribed species of *Hydraenopsis* from South Africa. A very narrow membrane is present on the anterior pronotal margin and (at least partly) on the anterior margin of the hypomeral antennal pocket (parallelism in *Phothydraena* and *Hydraena frondsicola*). This character was previously not recorded for *Hydraena* s.l. (in Hydraeninae it was so far recorded only from *Protozantaena* PERKINS).

The second great lineage and sistergroup of *Hydraenopsis* (= *Hydraena* s.l. (excl. *Hydraenopsis*)) includes all other subgenera described so far: each of the first three lineages, i.e. *H. rugosa* [= *Holcohydraena*], *H. monikae*, and *H. circulata* [= *H. circulata* species group], are not supported by unambiguous apomorphies in the analysis. However, these lineages share a few conspicuous symplesiomorphies: e.g. 14.0 (sutural gap at posterior end of hypomeron and prosternum); 26.0 (protrochanter pubescent). The first of these characters is shared with the outgroup and *Hydraenopsis*, whereas the second character is shared with the outgroup, *H. frondsicola*, *H. cordata*, *Hydraenopsis* and *Phothydraena*. A possible synapomorphy for these three lineages (*H. rugosa*, *H. monikae*, *H. circulata*) + *H. cordata* + *Phothydraena* could be character 20.1 (intercoxal cavity of abdominal sternites II and III present). Character 23.1 (median longitudinal suture of gonocoxite present) might be a possible synapomorphy of these first three lineages + *Phothydraena*. *Hydraena circulata* and its allies (*H. circulata* species group) are well characterized by the peculiar aedeagal morphology (main piece flattened dorsoventrally, with dorsal scales or bristles; distal lobe simple, membraneous).

A sistergroup relationship between *H. monikae* und *H. rugosa* is suggested by the overall external similarity (e.g. pronotal longitudinal keel) and is confirmed in 49 of 287 minimal length trees based on unweighted characters, but not in nine trees obtained after successive reweighting.

The monophyly of *Phothydraena* (*Hydraena hernandoi* + *H. putearius*) is well supported by autapomorphic characters (see above). Another apomorphic character (not included in the data matrix) is the presence of a very narrow membrane on anterior pronotal margin and on anterior margin of hypomeral antennal pocket (parallelism in *H. paeminosa*; parallelism or synapomorphy in *Hydraena frondsicola*). In addition, the hypomeral postcoxal process forms a distinct pocket (acetabulum) for reception of tip of prosternal branch (shared with *H. frondsicola*; parallelism in *Hydraenopsis*). Prosternal postcoxal process short and transverse, parallel-sided. A faint longitudinal pronotal keel can be developed in at least one (? basal) species of *Phothydraena* (*H. serricollis*). Furthermore, the morphology of the aedeagus and the pseudospermatheca clearly corroborate the monophyly of this lineage. On the other hand, the presence of a second pair of metasternal plaques (character 18.2), which is the most frequently used distinguishing character is not the most significant feature, because in at least one species (*H. serricollis*) it is more or less obsolete.

The following branch in the *Hydraena* s.l. (excl. *Hydraenopsis*) lineage is *H. frondsicola* [= *Spanglerina*], which, although being not supported by apomorphic characters in the cladogram (Fig. 15) presents several deviating characters: fronto-clypeal suture strongly arched; postcoxal mesosternal ridges complete; pseudepipleura very wide; pronotum strongly attenuated anteriorly and posteriorly. Hypomeral postcoxal process forms a distinct pocket (acetabulum) for reception of tip of prosternal branch (shared with *Phothydraena*; parallelism in *Hydraenopsis*); hyaline membrane on anterior margin of pronotum, on anterior margin of hypomeral antennal pocket, and on middle of posterior margin (? synapomorphy with *Phothydraena*); a very wide intercoxal sternite is shared with some species (e.g. *H. armipalpis*), obviously due to parallelism. A prominent longitudinal pronotal keel is also developed (shared with *H. rugosa*, *H. monikae* and one species of *Phothydraena*). Male tergite X only slightly notched apically.

The following branch (*H. cordata* [= *H. palustris* species group]) in the *Hydraena* s.l. (excl. *Hydraenopsis*) lineage is the last one before the large lineage that includes all derived species groups (incl. *Haenydra* and the *Hydraena riparia* group). In the computer analysis this lineage is not supported by an unambiguous apomorphy. The intercoxal cavity is shared with *H. rugosa*, *H. circulata*, *H. monikae*, and *Phothydraena*. Furthermore, the aedeagus is obviously of a very primitive type, not unsimilar to that of *H. rugosa*.

The following lineage [here termed: (*H. riparia* group + allied groups) + *Haenydra* lineage] includes all species of *Haenydra* and the majority of the species which were hitherto assigned to *Hydraena* s.str. (autapomorphy: protrochanter not pubescent). Several clades within this lineage are not supported by unambiguous apomorphies in the analysis (see above). The apomorphy supporting the (*Haenydra* + *H. armipalpis*) + (*H. minutissima* + *H. servilia*) lineage (16.0, elytra with 8 - 11 striae) is misleading because there are numerous species (not included in the analysis), which are closely related with *H. armipalpis* and the *H. minutissima* + *H. servilia* lineage and clearly have more than 11 elytral striae (e.g. *H. audisioi*, and numerous undescribed species from East Asia). *Hydraena* cf. *cirrata* + *H. grandis* are united by the presence of clusters of aedeagal setae. However, duplication of setae may have occurred more than once and therefore provides weak evidence for a monophyly.

Only one lineage within the (*H. riparia* group + allied groups) + *Haenydra* lineage is very well supported by unambiguous apomorphies: *Haenydra*. In this monophylum, the hypomeral setae are largely reduced (in size and number), often completely lacking. The parameres are totally absent. Although HANSEN (1991: 34) stressed that the shape of the antennal cupule (segment 4 in *Haenydra*) is generally variable in *Hydraena* s.l. we found this character to be indeed diagnostic for *Haenydra* because its apex is never rounded in any other lineage of *Hydraena* s.l. (see also JÄCH 1988: 241). Furthermore, the closure of the hypomeral antennal pocket of *Haenydra* is almost exclusively formed by the mesial (instead of the lateral) hypomeron; and the elytral striae are remarkably straight and their number is comparatively constant (10 - 11). The tip of the median subapical projection of the gonocoxite is distinctly raised (autapomorphy). The secondary sexual characters are not comprising strongly asymmetrical labial palps.

## Conclusions

*Hydraena* s.l. splits into two large monophyletic lineages: 1) *Hydraenopsis* and 2) *Hydraena* s.l. excl. *Hydraenopsis*.

Within the *Hydraenopsis* lineage there are again two rather distinct lineages: (*Hydraena cordiformis* + *H. paucistriata*) and *Hydraenopsis* excl. (*Hydraena cordiformis* + *H. paucistriata*). There is no subgeneric name available for the *Hydraena cordiformis* + *H. paucistriata* lineage (if it were credited subgeneric rank).

At the base of the *Hydraena* s.l. excl. *Hydraenopsis* lineage there are six lineages (*H. rugosa*, *H. monikae*, *H. circulata*, (*H. hernandoi* + *H. putearius*), *H. frondsicola*, and *H. cordata*), that are (with the exception of *H. hernandoi* + *H. putearius*) mostly characterized by plesiomorphic features (see strict consensus tree, Fig. 17). Should they all turn out to represent well supported monoplyletic groups, they all could stand as distinct subgenera: *Holcohydraena* (for *H. rugosa*), subg.n. (for. *H. monikae*), subg.n. (for *H. circulata*), *Phothydraena* (for *H. hernandoi* + *H. putearius*), *Spanglerina* (for *H. frondsicola*), and subg.n. (for *H. cordata*). Should they all be found to represent one monophyletic lineage, this subgenus would have to be named *Holcohydraena*, *Phothydraena*, or *Taenhydraena*, because all these names were introduced in 1888! Sexual characters are not well pronounced in these six lineages and apparently do not include modified maxillary palps.

As we mentioned above, the (*H. hernandoi* + *H. putearius*) lineage (= *Phothydraena*) is the only lineage near the base of the *Hydraena* s.l. excl. *Hydraenopsis* lineage, that is well supported by unambiguous apomorphies. Regarding this lineage as a distinct subgenus of *Hydraena* would make the remaining part of the *Hydraena* s.l. excl. *Hydraenopsis* lineage paraphyletic (unless we regard *H. rugosa*, *H. monikae* and *H. circulata* as subgenera).

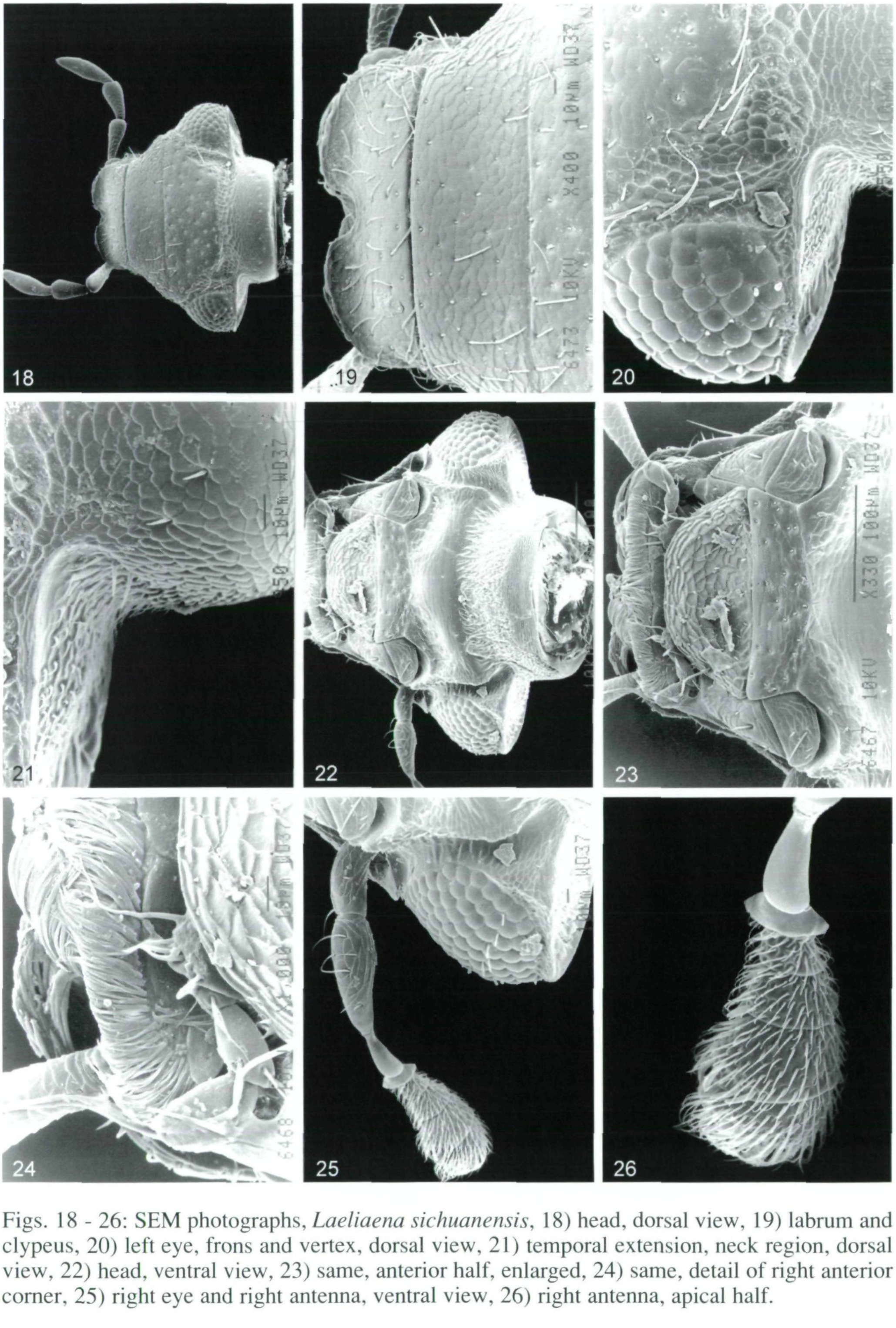
At the top end of the *Hydraena* s.l. excl. *Hydraenopsis* lineage there are a few well supported monophyla, e.g. *Haenydra* (respectively (*H. riparia* group + allied groups) + *Haenydra*). However, these lineages are apparently quite young (and very successful) evolutionary offshoots within the genus and therefore not eligible for being recognized as subgenera unless the phylogenetic relationships of all earlier lineages are fully understood. The rather restricted and compact geographical distribution of the *Haenydra* lineage (respectively (*H. riparia* group + allied groups) + *Haenydra* lineage) also corroborates the assumption that it represents a young offshoot.

The (*H. riparia* group + allied groups) + *Haenydra* lineage includes the type species of *Hadrenya* and *Hydraena* s.str. Therefore, the synonymy between *Hadrenya* and *Hydraena* s.str. is clearly confirmed by this analysis.

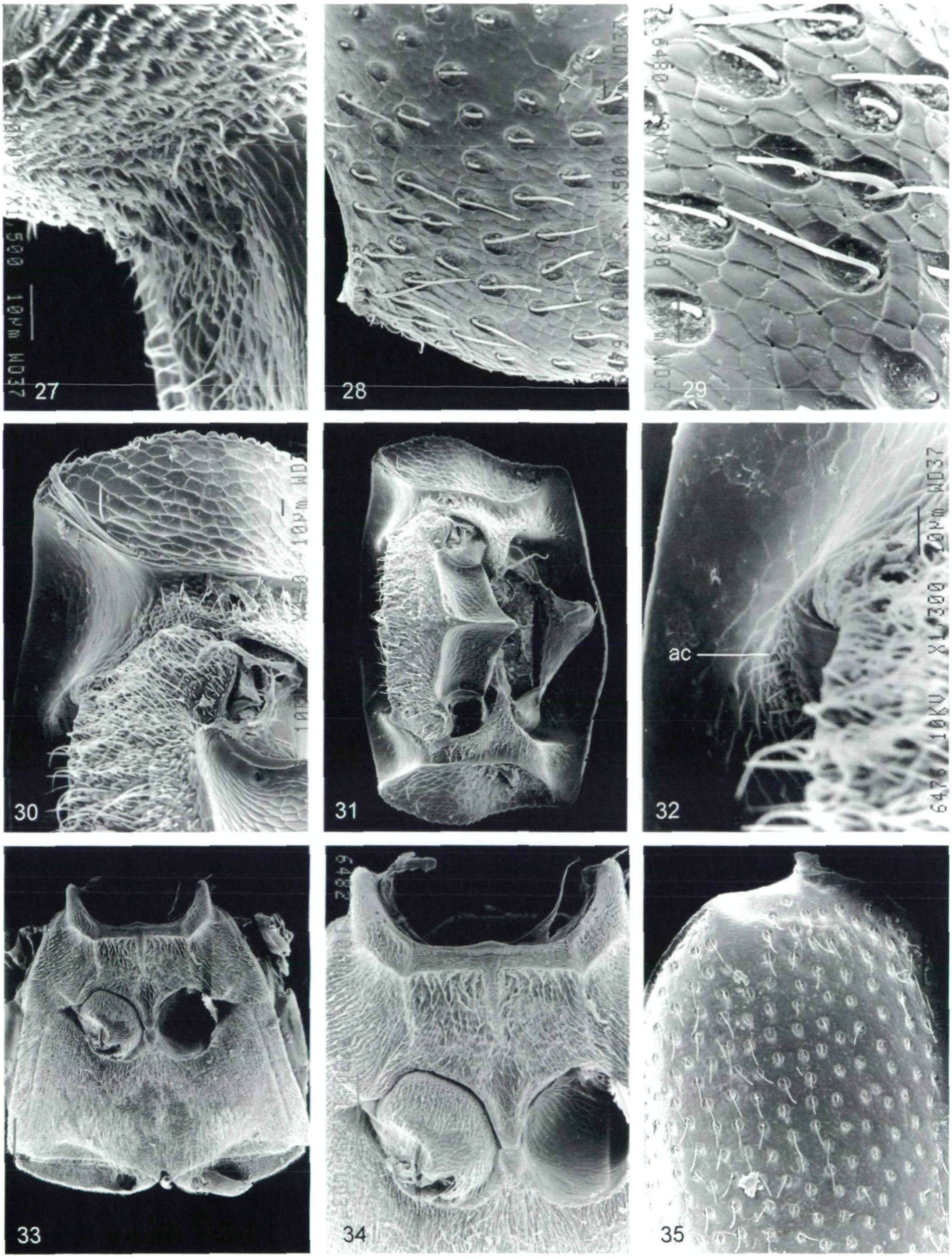
Following the results of the present phylogenetic computer analysis we suggest to maintain only two subgenera within *Hydraena* s.l. at present. These subgenera are identical with the two major phylogenetic lineages: *Hydraena* s.str. (= *Hydraena* s.l. excl. *Hydraenopsis*) and *Hydraenopsis*. These two subgenera are well distinguished by several significant characters (see above). Indeed, some of these characters are very well concealed (e.g. character 12) and it will often be found necessary to dissect or scan certain species for correct subgeneric assignation (unfortunately, development of clear-cut distinguishing characters is not a principal goal in evolution!). Apart from the morphological characters, these two lineages are also well distinguished by the geographical distributions, which clearly indicate a Gondwana origin for *Hydraenopsis* and a Laurasia origin for *Hydraena* s.str.

We know from experience that modern cladistic analyses often evoke drastic rearrangements of traditionally accepted classifications. The present analysis is not an exception in this respect: *Haenydra* and *Phothydraena*, which have hitherto been treated as good subgenera should – at present – be regarded as synonyms of *Hydraena* s.str., although both are represented by well supported monophyla! Those who do not want to renounce these well established names (*Haenydra*, *Phothydraena*) and, at the same time, do not wish to accept a paraphyletic *Hydraena* s.str. should – for practical reasons – refer to *Haenydra* and *Phothydraena* as the '*Haenydra*' lineage and the '*Phothydraena*' lineage of *Hydraena* s.str.

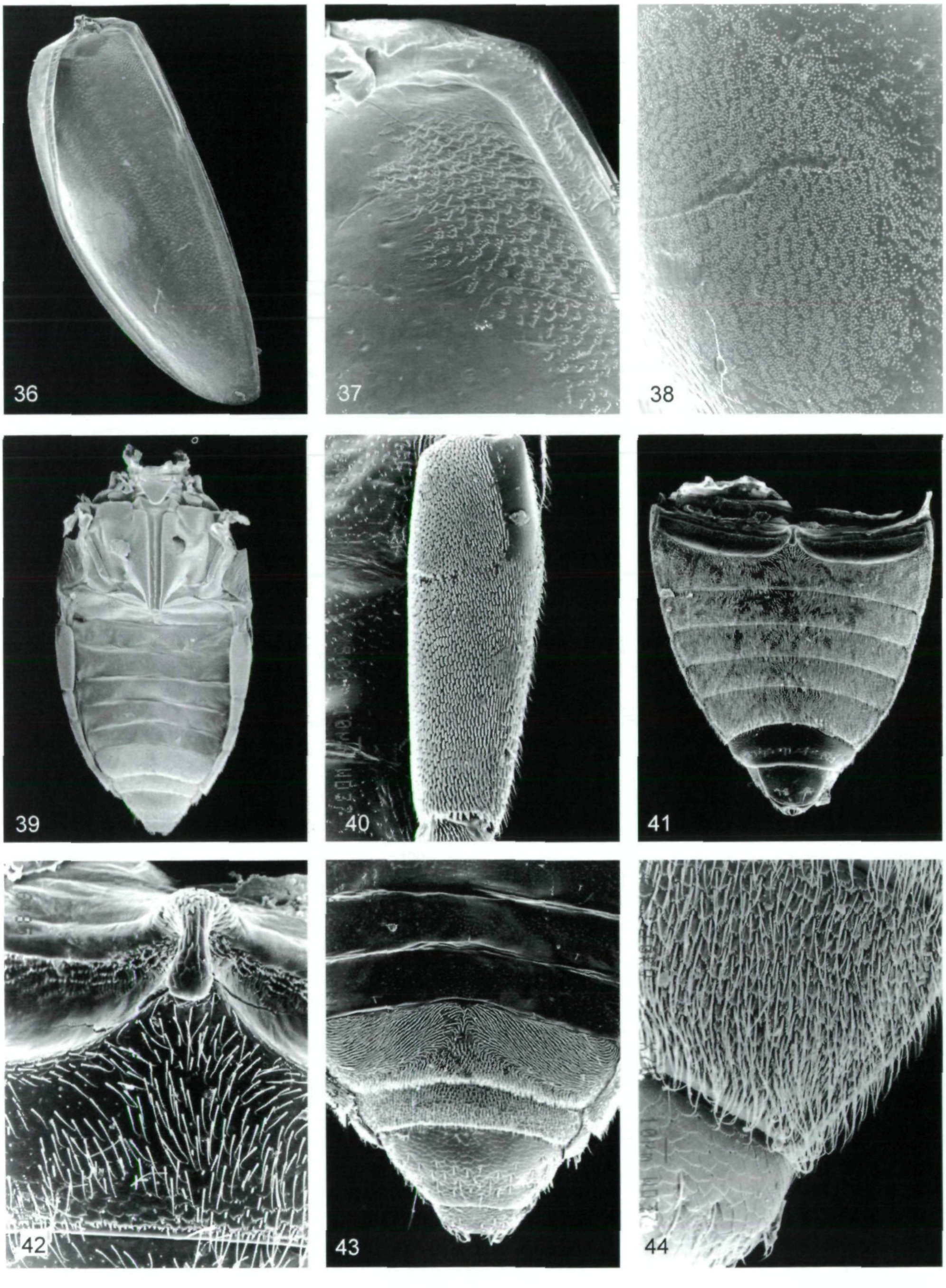
Although the phylogenetic relationships and evolutionary trends outlined by our computer analysis appear to be well confirmed by complementary data not included in the matrix, the model presented here must be regarded as preliminary. Further studies should focus on a more precise resolution of the basal branches within the *Hydraena* s.l. excl. *Hydraenopsis* lineage. We hope that our contribution will ignite further research which should also comprise larval morphology, isozyme analyses, karyological characters, and DNA-sequence data (e.g. 12S rDNA, ITS2, ND1). A stable and phylogenetically sound subgeneric concept should be based on a broad spectrum of characters. A better knowledge of the phylogeny will not only improve the classification but will be the basis for a more profound understanding of the evolution of the world's "most successful" water beetle genus.



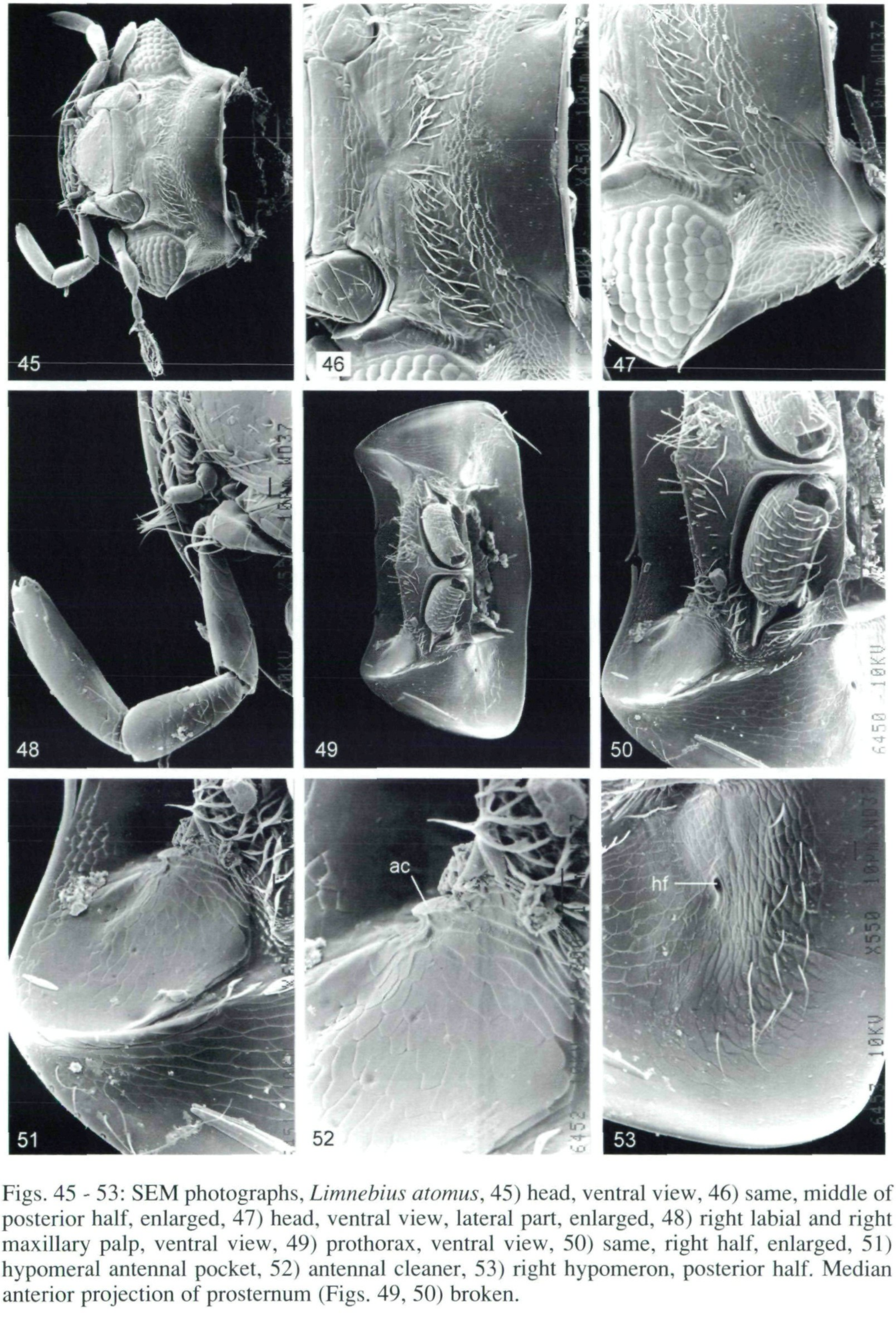
Figs. 18 - 26: SEM photographs, *Laeliaena sichuanensis*, 18) head, dorsal view, 19) labrum and clypeus, 20) left eye, frons and vertex, dorsal view, 21) temporal extension, neck region, dorsal view, 22) head, ventral view, 23) same, anterior half, enlarged, 24) same, detail of right anterior corner, 25) right eye and right antenna, ventral view, 26) right antenna, apical half.



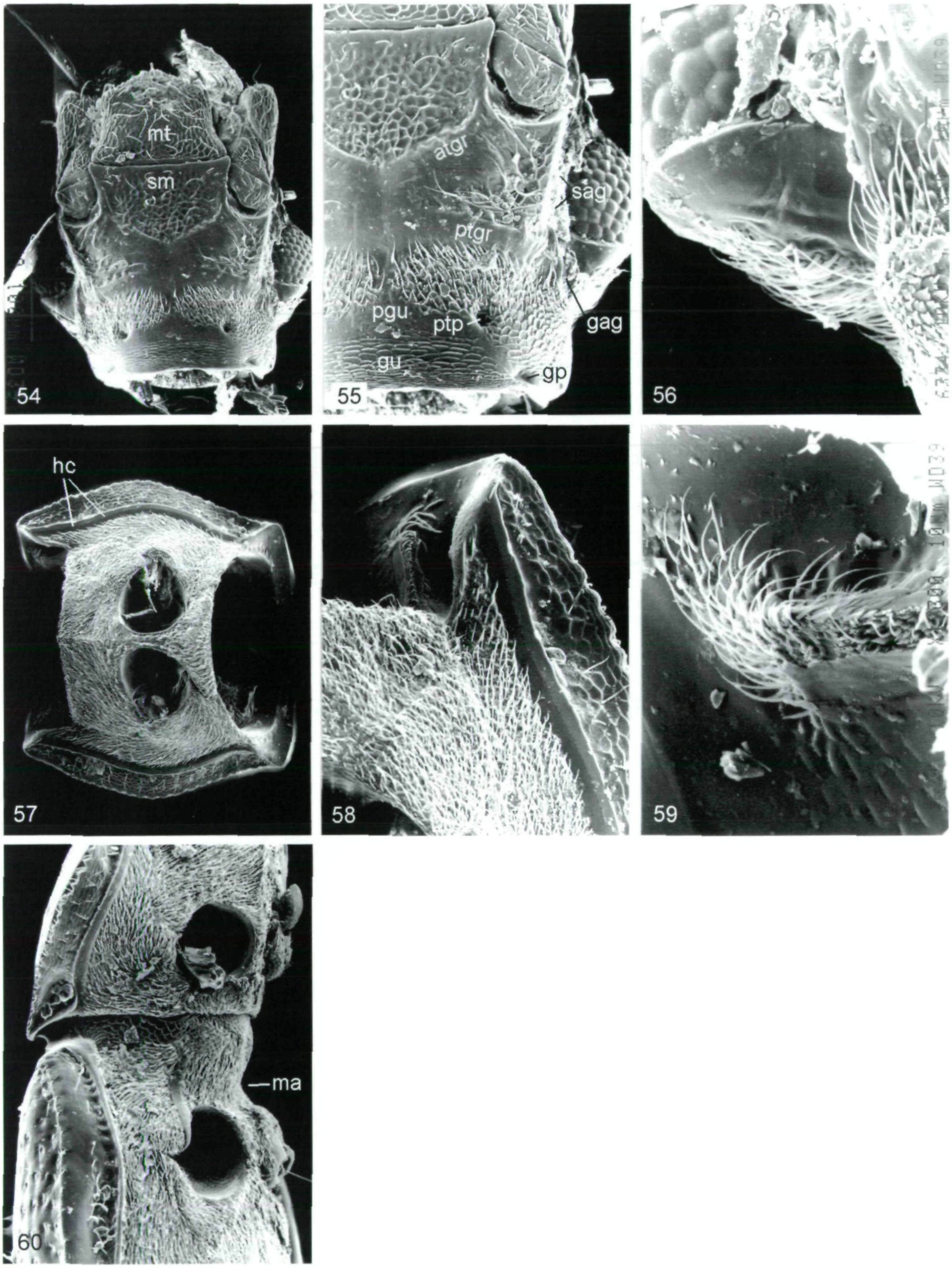
Figs. 27 - 35: SEM photographs, *Laeliaena sichuanensis*, 27) neck region and temporal extension, enlarged, 28) pronotum, left anterior corner, 29) same, detail, 30) hypomeral antennal pocket, 31) prothorax, ventral view, 32) antennal cleaner, 33) meso- and metasternum, 34) mesosternum, 35) left elytron, anterior half, dorsal view.



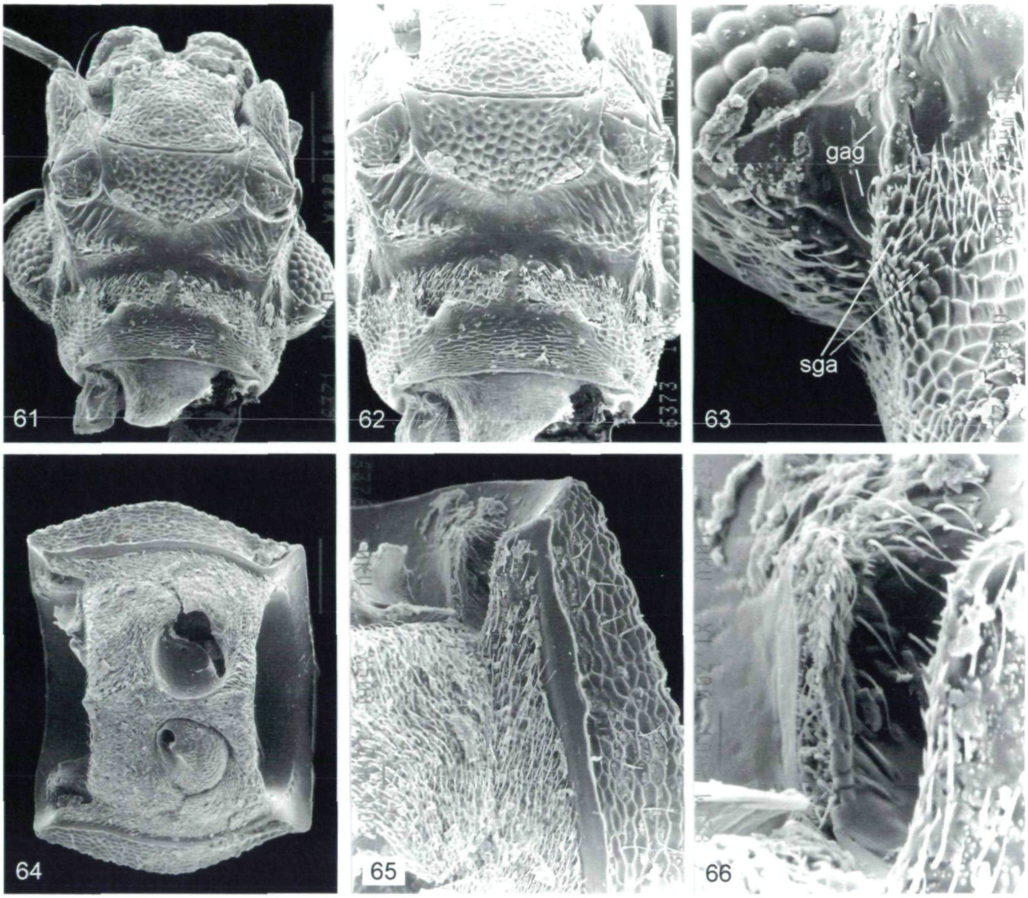
Figs. 36 - 44: SEM photographs, *Laeliaena sichuanensis*, 36) right elytron, ventral view, 37) same, anterior mesal corner, enlarged, 38) right elytron, detail near middle of lateral margin, 39) meso-, metathorax and abdomen, dorsal view, 40) abdomen, anterior right corner, dorsal view, 41) abdomen, ventral view, 42) intercoxal sternite, metacoxal sockets and middle of ventrite I, 43) abdominal apex, dorsal view, 44) ventrites V and VI, lateral margin.



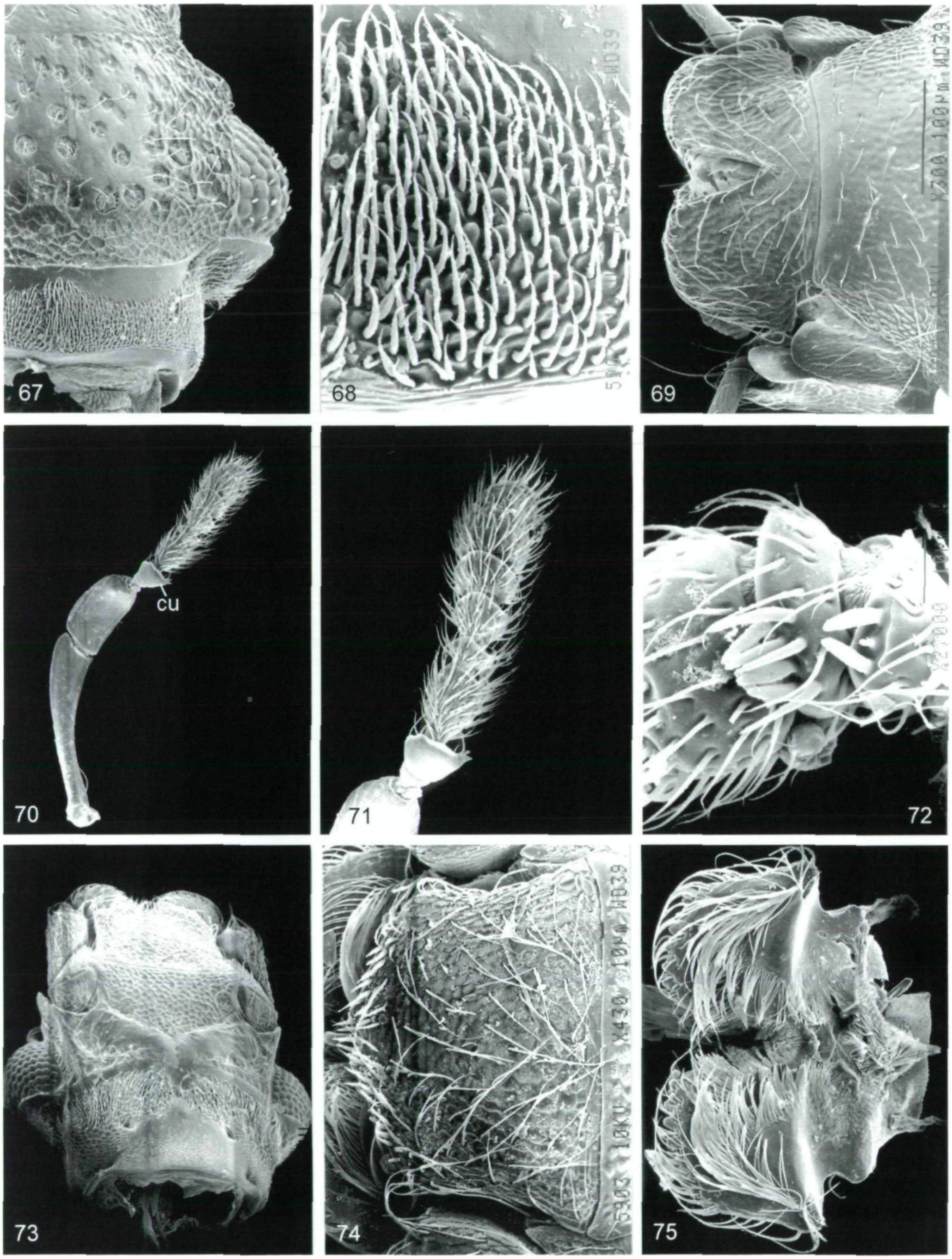
Figs. 45 - 53: SEM photographs, *Limnebius atomus*, 45) head, ventral view, 46) same, middle of posterior half, enlarged, 47) head, ventral view, lateral part, enlarged, 48) right labial and right maxillary palp, ventral view, 49) prothorax, ventral view, 50) same, right half, enlarged, 51) hypomeral antennal pocket, 52) antennal cleaner, 53) right hypomeron, posterior half. Median anterior projection of prosternum (Figs. 49, 50) broken.



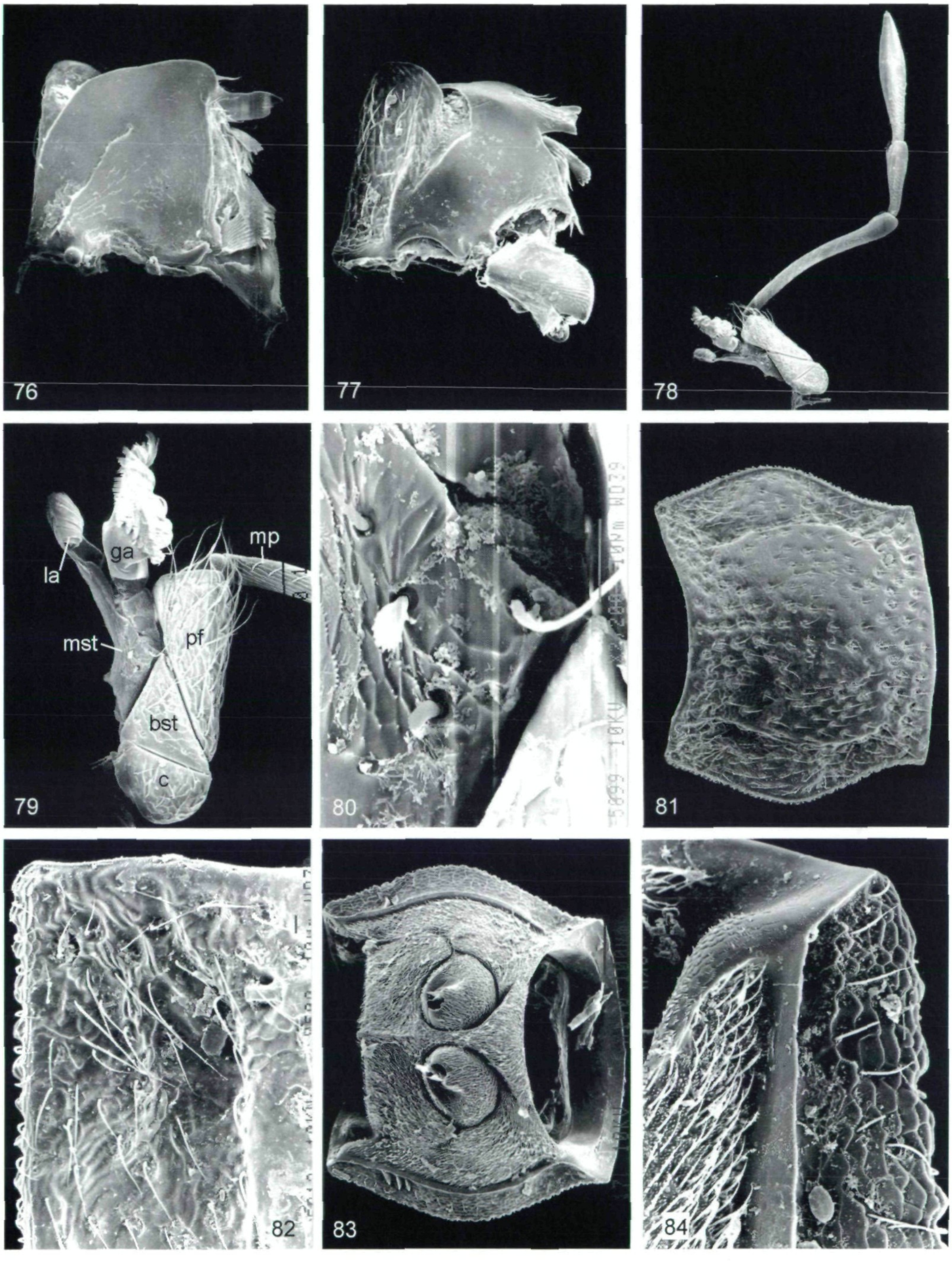
Figs. 54 - 60: SEM photographs, *Hydraena gracilis*, 54) head, ventral view, 55) same, posterior half, enlarged, 56) posterior part of eye, temporal extension, ventral view, 57) prothorax, ventral view, 58) hypomeral antennal pocket, 59) antennal cleaner, 60) pro-, meso- and metasternum, lateral view.



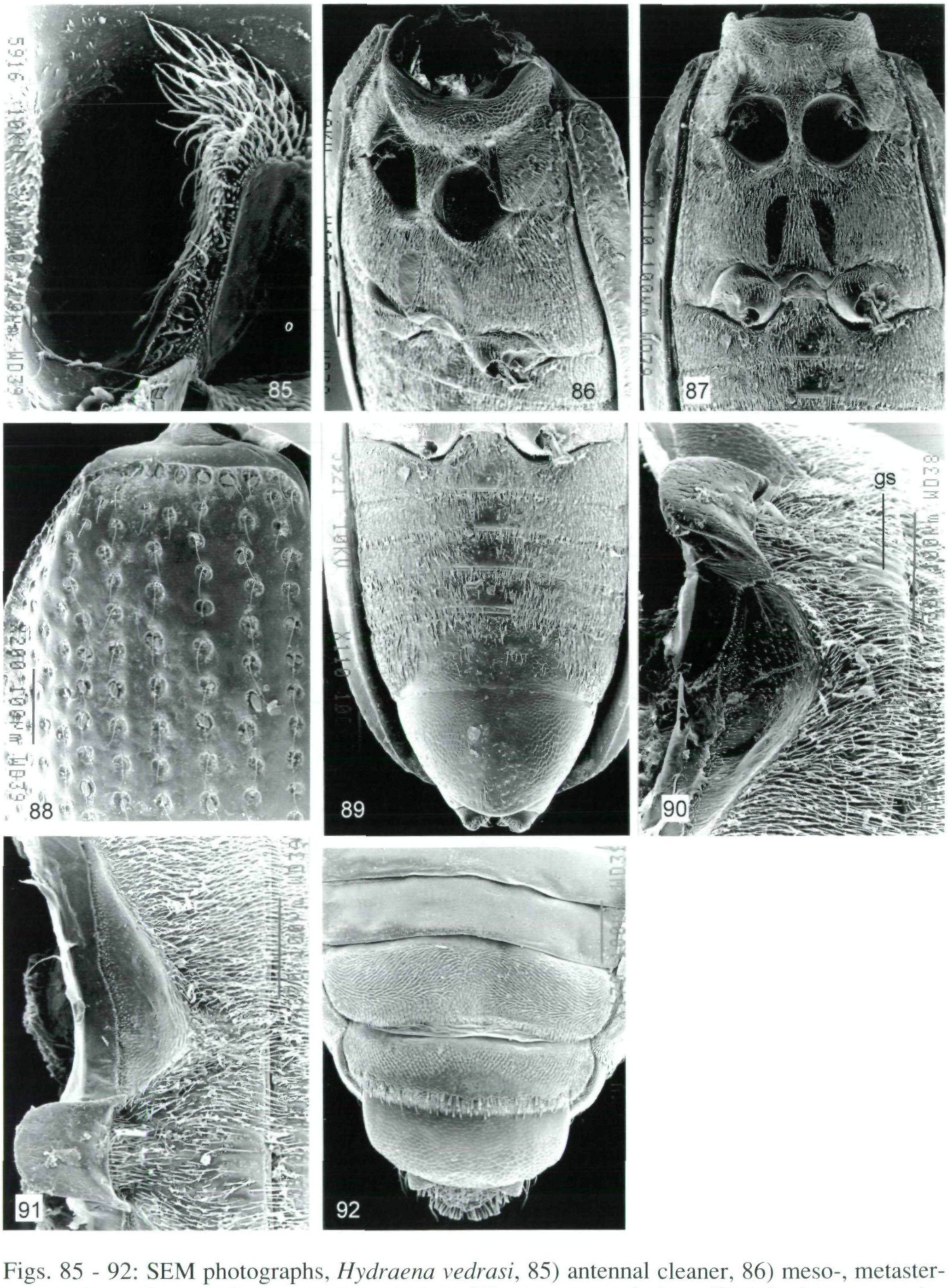
Figs. 61 - 66: SEM photographs, *Hydraena scitula*, 61) head, ventral view, 62) same, posterior part, enlarged, 63) posterior part of eye, temporal extension, lateral genal area, ventral view, 64) prothorax, ventral view, 65) hypomeral antennal pocket, 66) antennal cleaner.



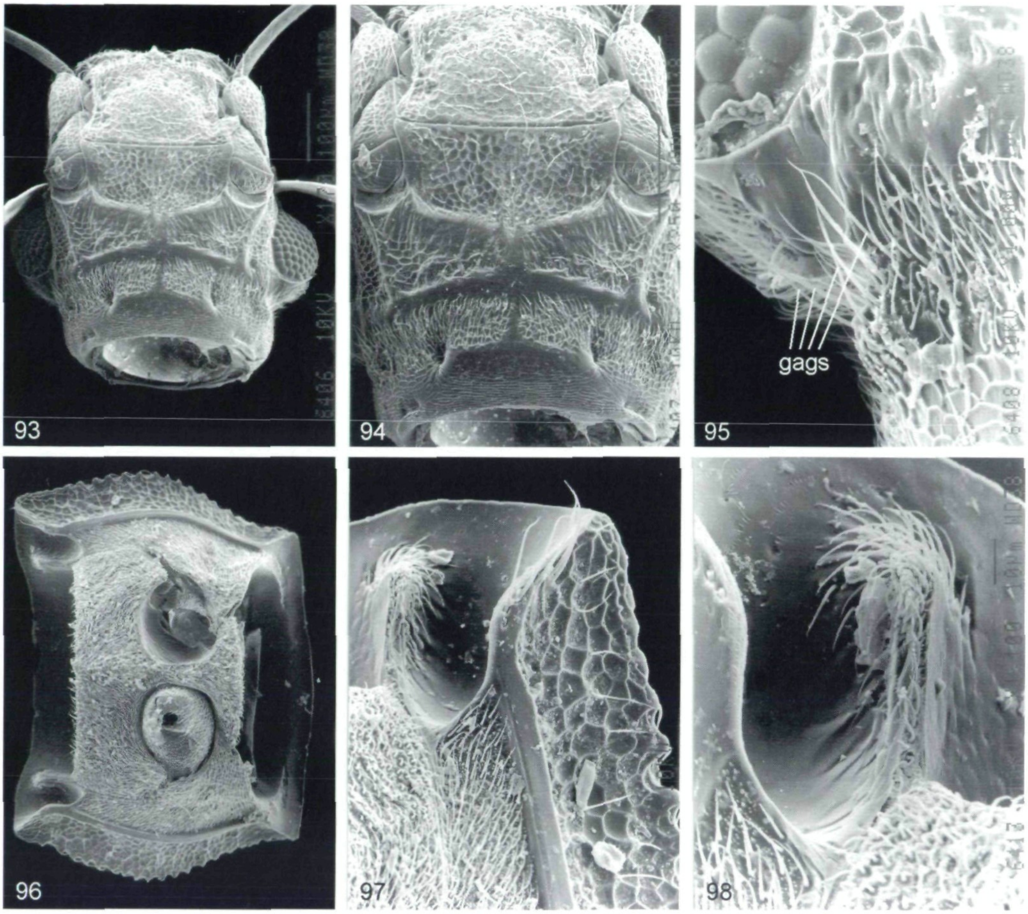
Figs. 67 - 75: SEM photographs, *Hydraena vedrasi*, 67) head, right side of posterior half, 68) pubescence near middle of neck region, 69) labrum and clypeus, 70) antenna, 71) same, apical half, 72) same, detail of basal club segments, 73) head, ventral view, 74) mentum, 75) epipharynx.



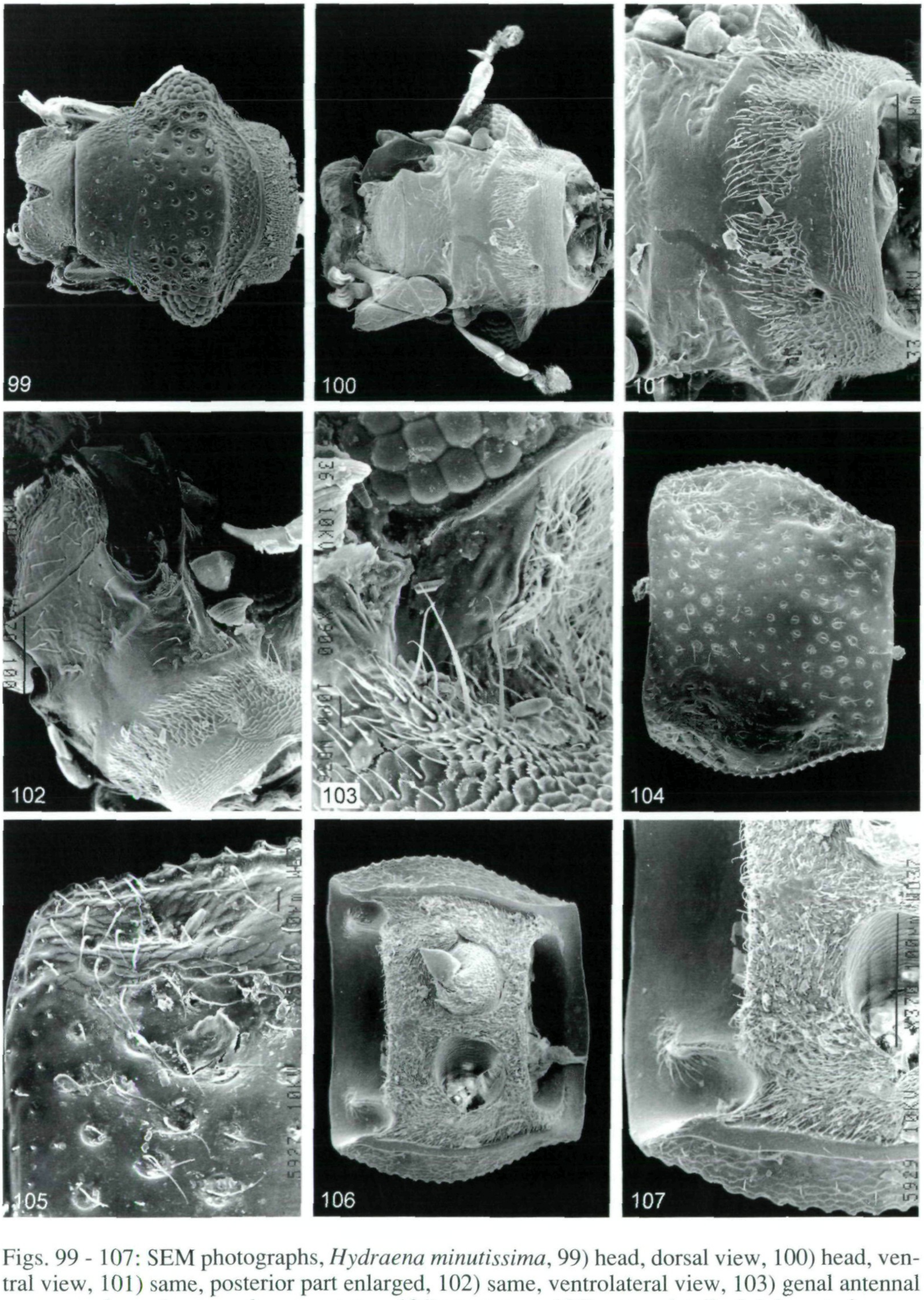
Figs. 76 - 84: SEM photographs, *Hydraena vedrasi*, 76) right mandible, ventral view, 77) left mandible, dorsal view, 78) left maxilla, ventral view, 79) same, detail, 80) mediostipes, detail, 81) pronotum, 82) same, left anterior corner, sensory setae, 83) prothorax, ventral view, 84) left hypomeron, anterior apex.



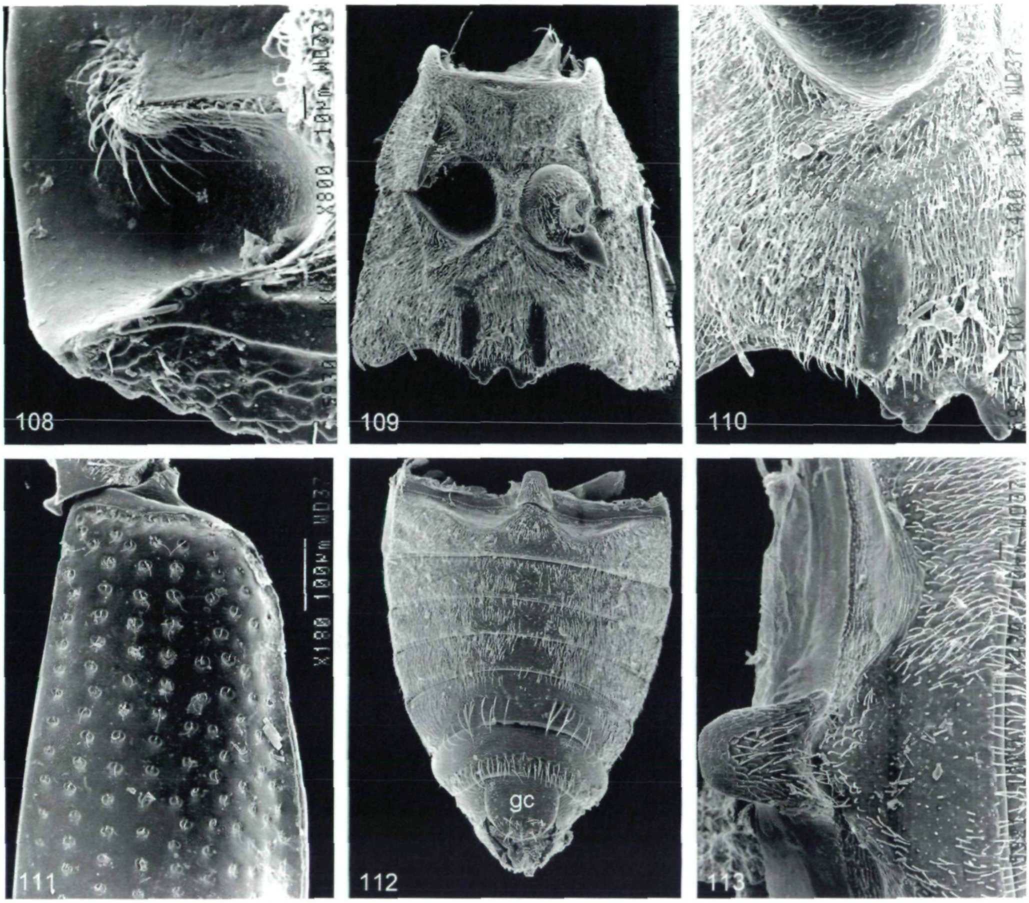
Figs. 85 - 92: SEM photographs, *Hydraena vedrasi*, 85) antennal cleaner, 86) meso-, metasternum and anterior ventrites, ventrolateral view, 87) same, ventral view, 88) left elytron, anterior half, dorsal view, 89) male abdomen, ventral view, 90) intercoxal sternite, metacoxal socket and middle of ventrite I, ventrolateral view, 91) same, ventral view, 92) female abdomen, dorsal view.



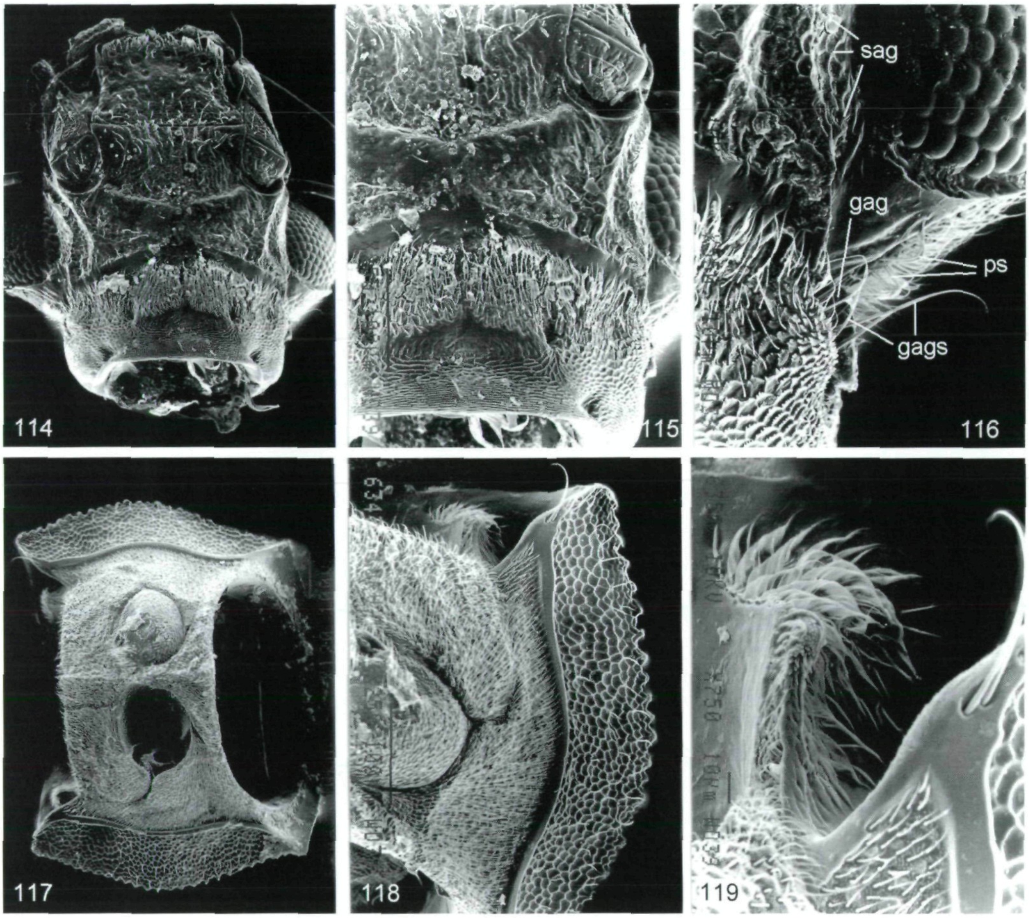
Figs. 93 - 98: SEM photographs, *Hydraena* cf. *armipalpis*, 93) head, ventral view, 94) same, posterior part enlarged, 95) eye, temporal extension, lateral genal area, ventral view, 96) prothorax, ventral view, 97) hypomeral antennal pocket, 98) antennal cleaner.



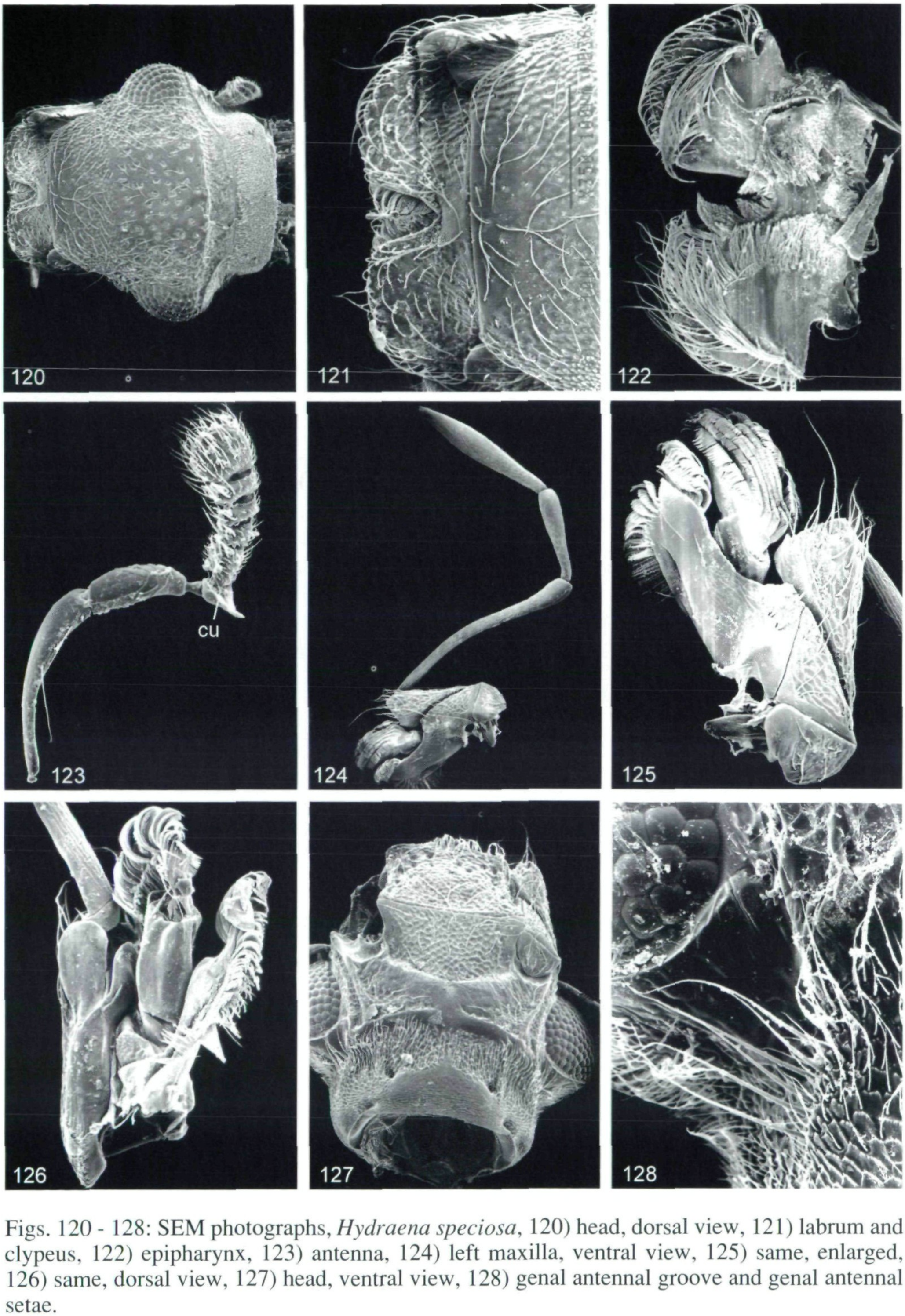
Figs. 99 - 107: SEM photographs, *Hydraena minutissima*, 99) head, dorsal view, 100) head, ventral view, 101) same, posterior part enlarged, 102) same, ventrolateral view, 103) genal antennal groove and genal antennal groove setae, 104) pronotum, 105) same, detail of right anterior corner, 106) prothorax, ventral view, 107) hypomeral antennal pocket.



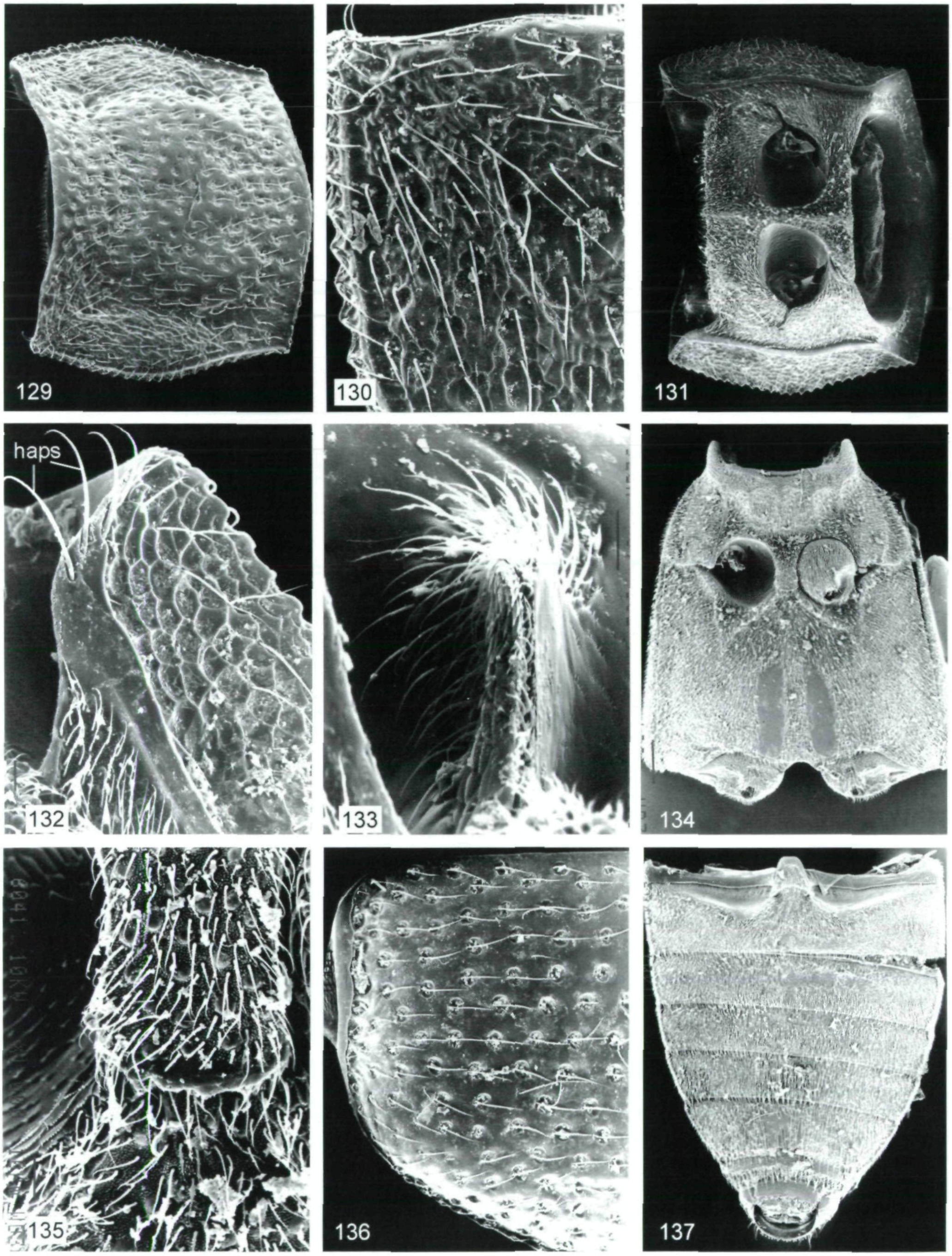
Figs. 108 - 113: SEM photographs, *Hydraena minutissima*, 108) antennal cleaner, 109) meso- and metasternum, 110) detail of metasternum, 111) anterior half of right elytron, dorsal view, 112) abdomen, ventral view, 113) intercoxal sternite and median parts of ventrite I.



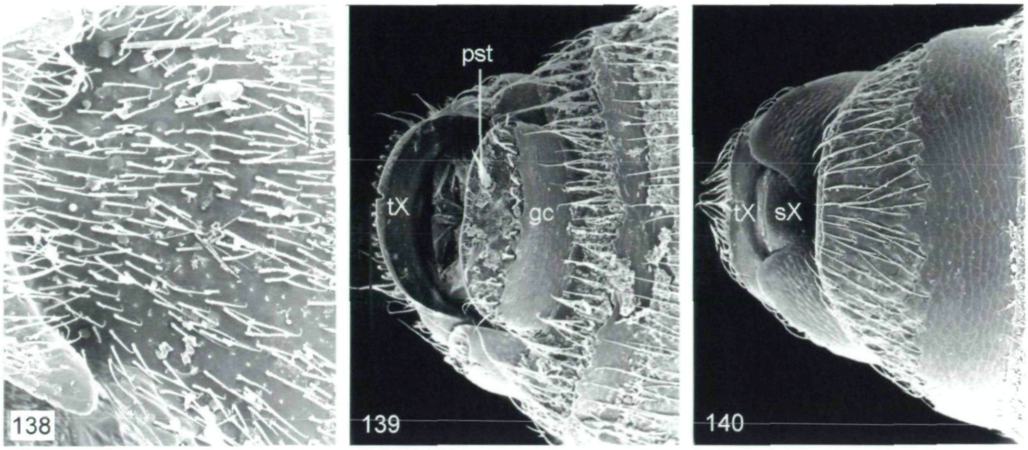
Figs. 114 - 119: SEM photographs, *Hydraena grandis*, 114) head, ventral view, 115) same, posterior part enlarged, 116) eye, temporal extension, lateral genal area, ventral view, 117) prothorax, ventral view, 118) same, left side, enlarged, 119) hypomeral antennal pocket.

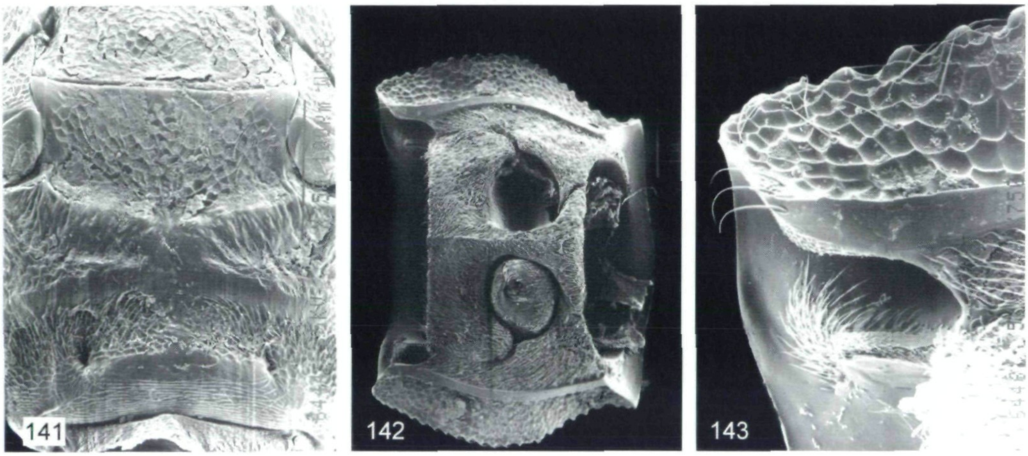


Figs. 120 - 128: SEM photographs, *Hydraena speciosa*, 120) head, dorsal view, 121) labrum and clypeus, 122) epipharynx, 123) antenna, 124) left maxilla, ventral view, 125) same, enlarged, 126) same, dorsal view, 127) head, ventral view, 128) genal antennal groove and genal antennal setae.



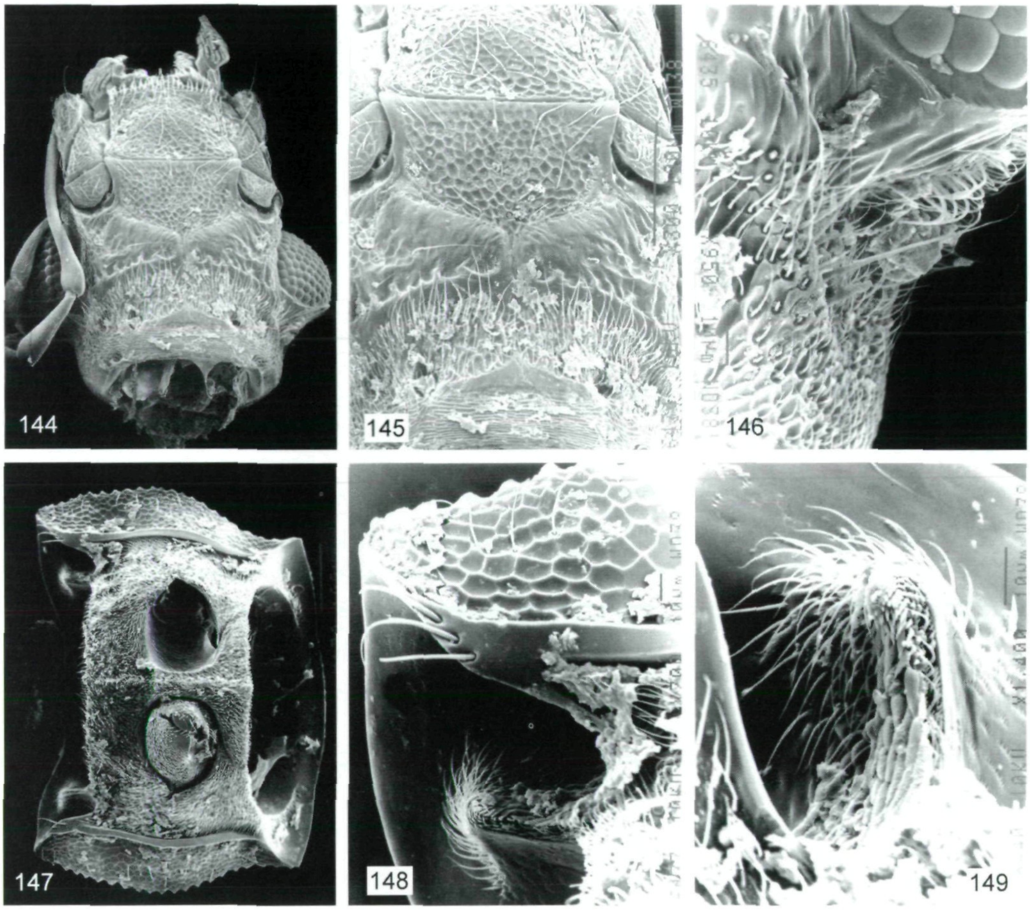
Figs. 129 - 137: SEM photographs, *Hydraena speciosa*, 129) pronotum, 130) same, left anterior corner, 131) prothorax, ventral view, 132) left hypomeron, anterior apex, 133) antennal cleaner, 134) meso- and metasternum, 135) mesosternal process, 136) left elytron, anterior half, dorsal view, 137) female abdomen, ventral view.



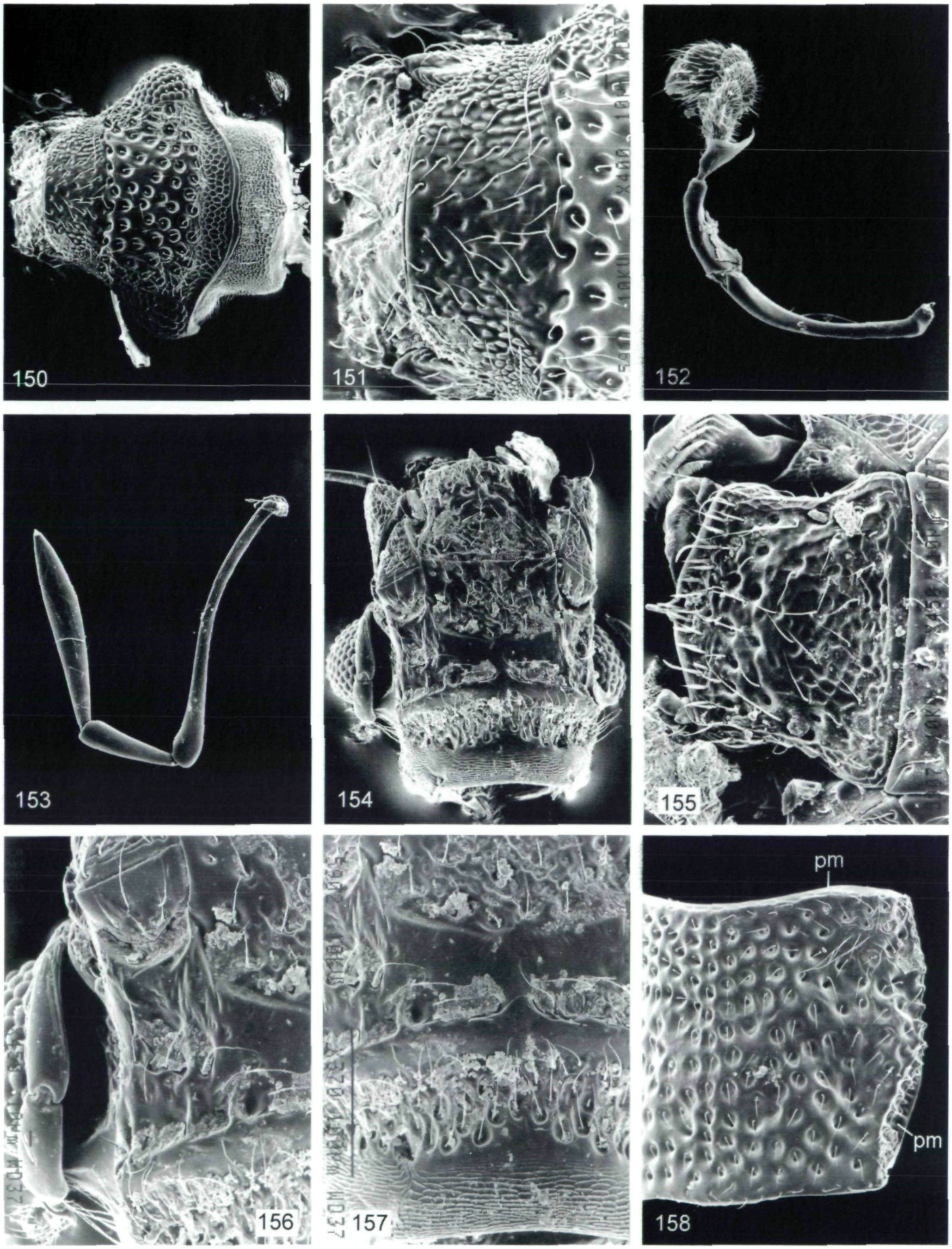


Figs. 138 - 140: SEM photographs, *Hydraena speciosa*, 138) posterior margin of intercoxal sternite and middle of ventrite I, 139) apex of female abdomen, ventral view, 140) apex of male abdomen, ventral view.

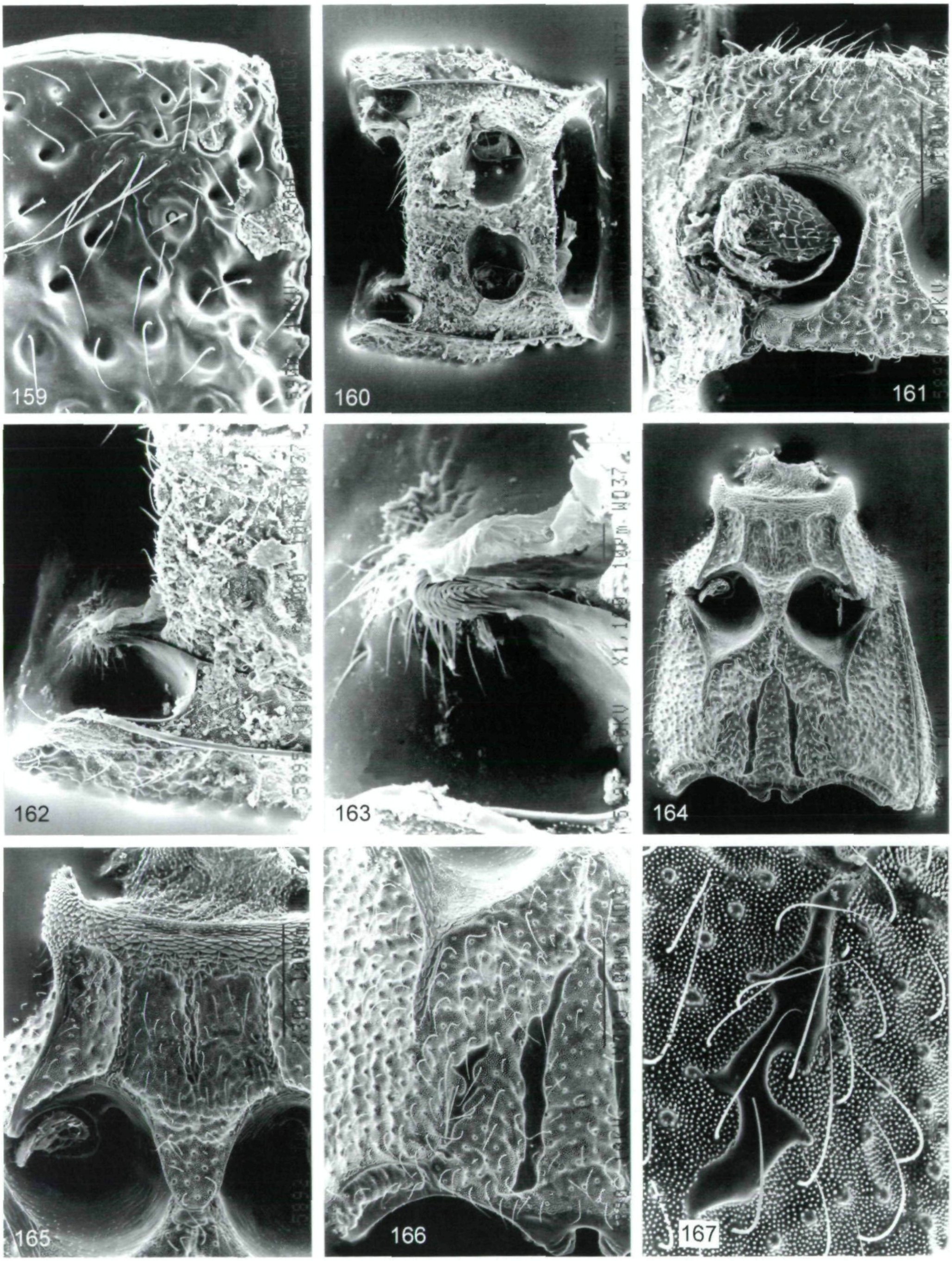
Figs. 141 - 143: SEM photographs, *Hydraena yoshitomii*, 141) head, ventral view, 142) prothorax, ventral view, 143) hypomeral antennal pocket.



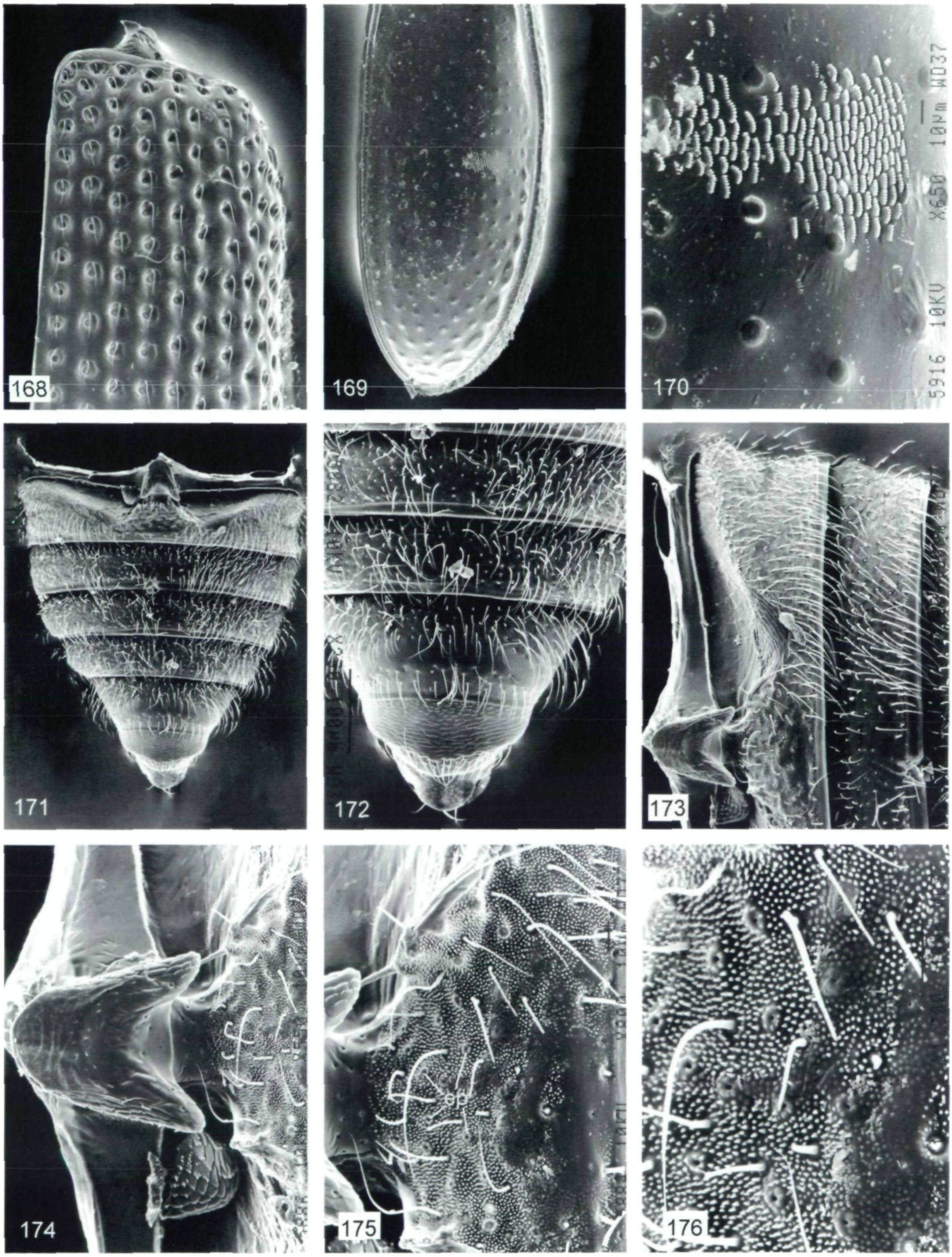
Figs. 144 - 149: SEM photographs, *Hydraena cordata*, 144) head, ventral view, 145) same, posterior part enlarged, 146) eye, temporal extension, lateral genal area, ventral view, 147) prothorax, ventral view, 148) hypomeral antennal pocket, 149) antennal cleaner.



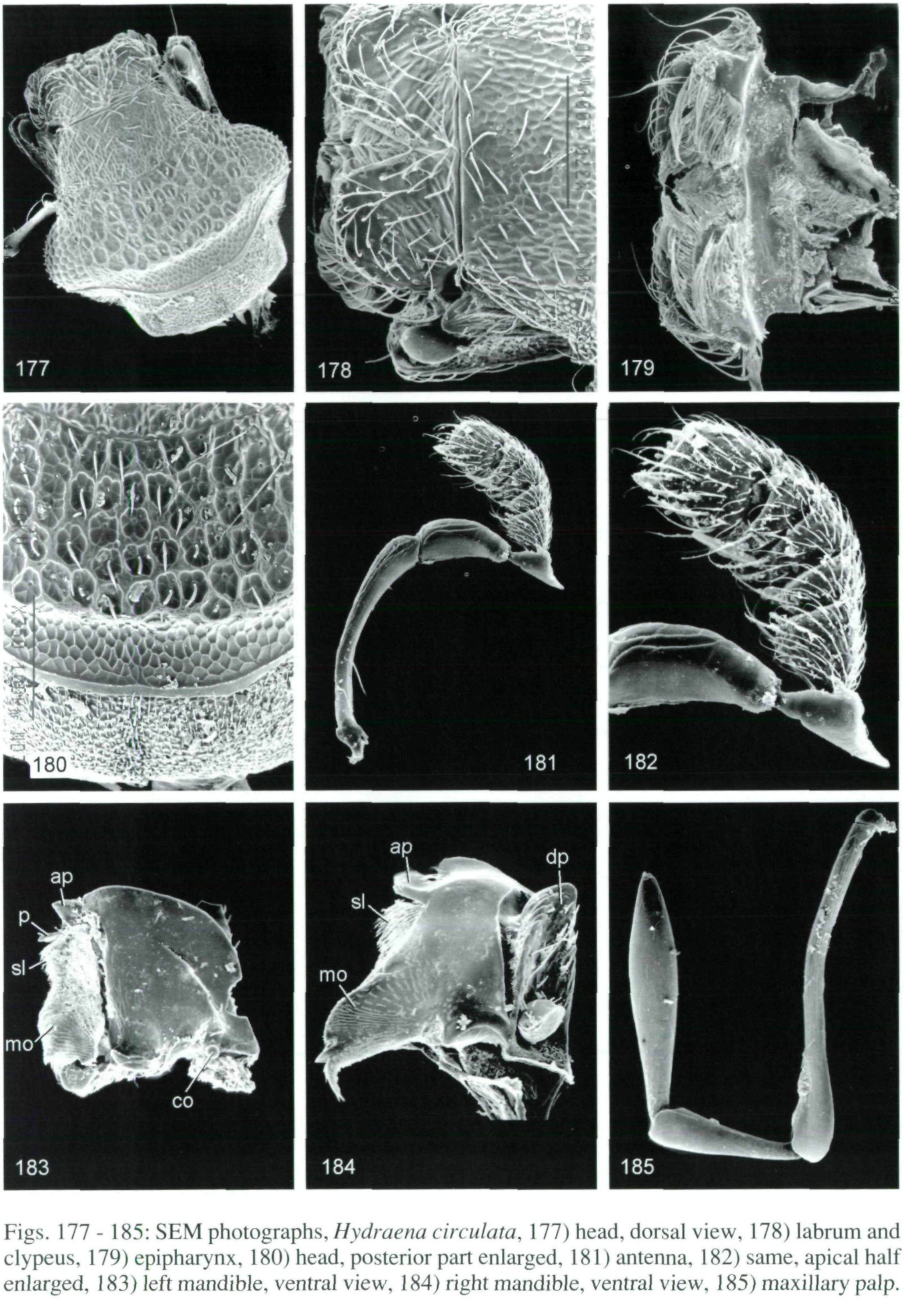
Figs. 150 - 158: SEM photographs, *Hydraena hernandoi*, 150) head, dorsal view, 151) labrum and clypeus, 152) antenna, 153) maxillary palp, 154) head, ventral view, 155) mentum, 156) head, right side enlarged, ventral view, 157) genal ridges and gula, 158) pronotum, right side.



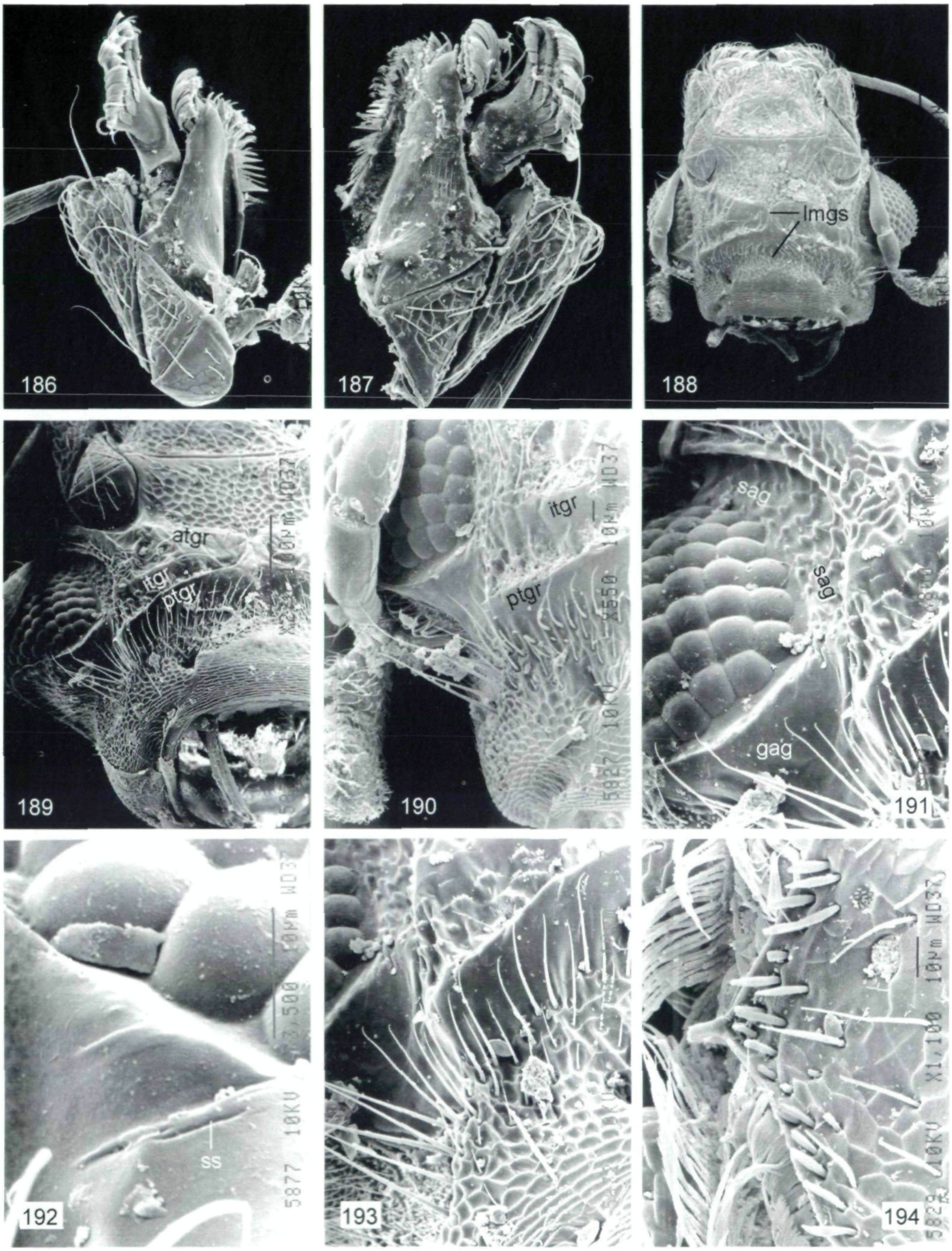
Figs. 159 - 167: SEM photographs, *Hydraena hernandoi*, 159) pronotum, right anterior corner, 160) prothorax, ventral view, 161) same, right side enlarged, 162) hypomeral antennal pocket, 163) antennal cleaner, 164) meso- and metasternum, 165) mesosternum, 166) metasternal plaques, 167) same, enlarged.



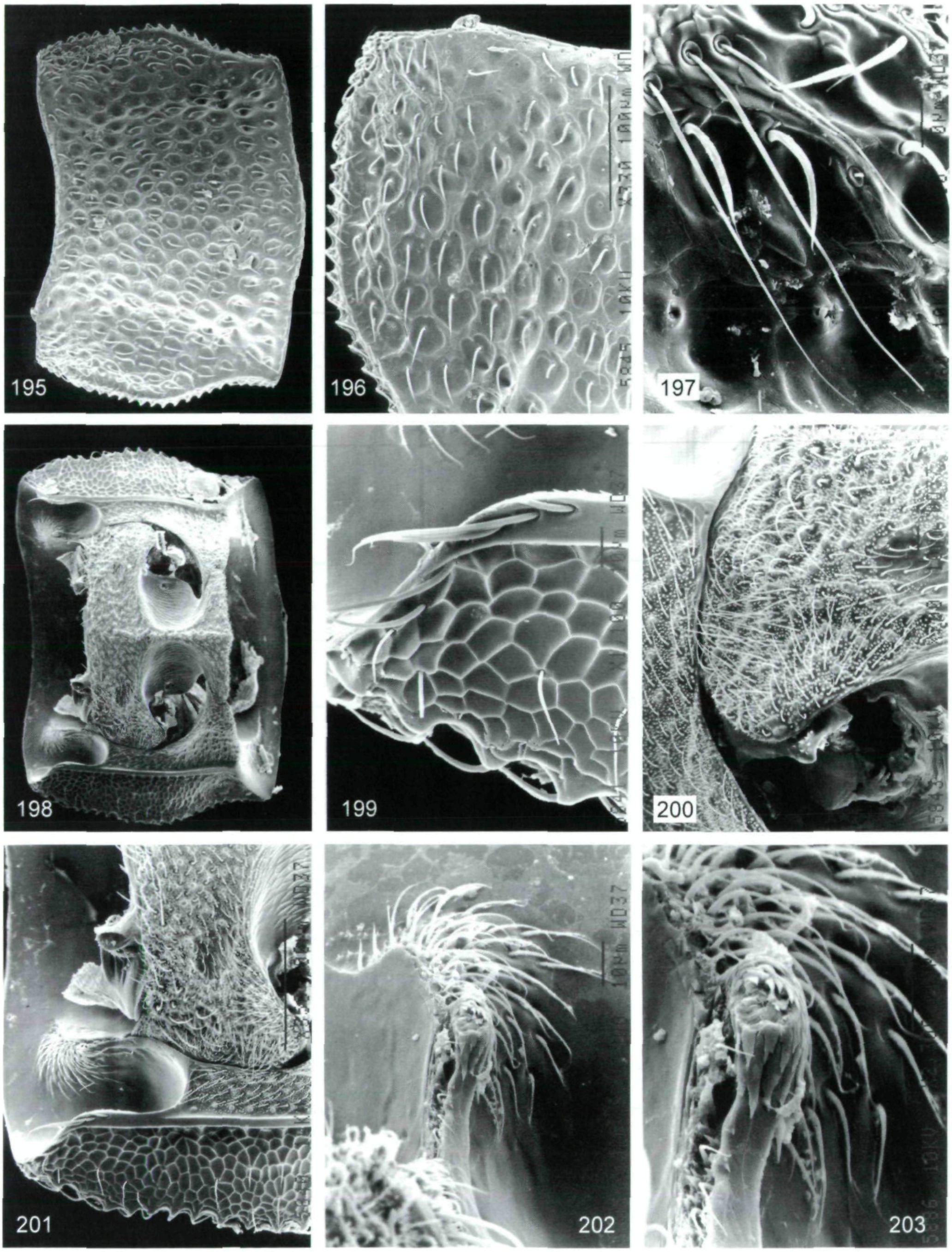
Figs. 168 - 176: SEM photographs, *Hydraena hernandoi*, 168) right elytron, dorsal view, 169) left elytron, ventral view, 170) same, detail, 171) abdomen, ventral view, 172) same, posterior part enlarged, 173) intercoxal sternite and anterior ventrites, 174) intercoxal sternite, intercoxal cavity and middle of ventrite I, 175) same, exocrine pores, enlarged, 176) middle of ventrite I, detail.



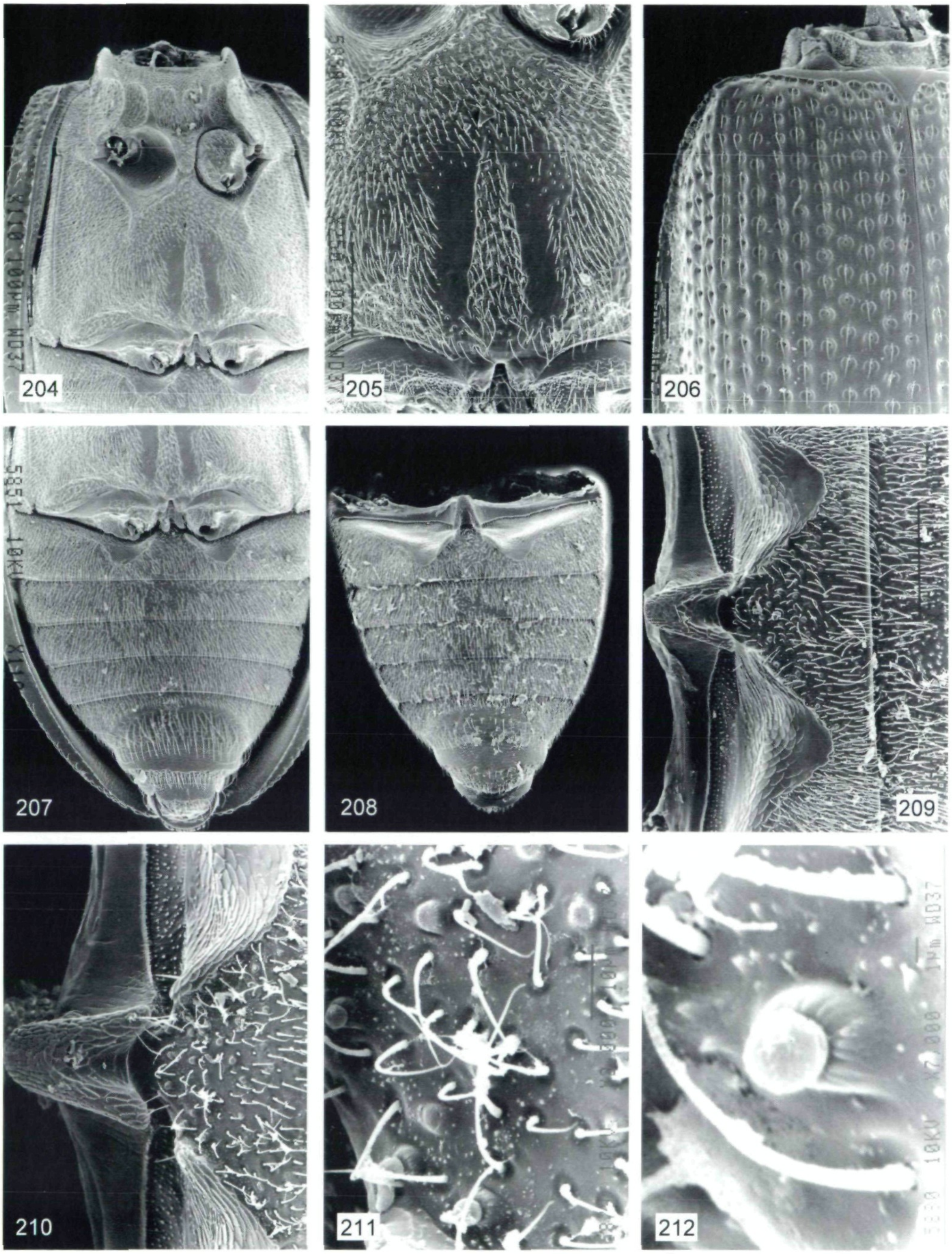
Figs. 177 - 185: SEM photographs, *Hydraena circulata*, 177) head, dorsal view, 178) labrum and clypeus, 179) epipharynx, 180) head, posterior part enlarged, 181) antenna, 182) same, apical half enlarged, 183) left mandible, ventral view, 184) right mandible, ventral view, 185) maxillary palp.



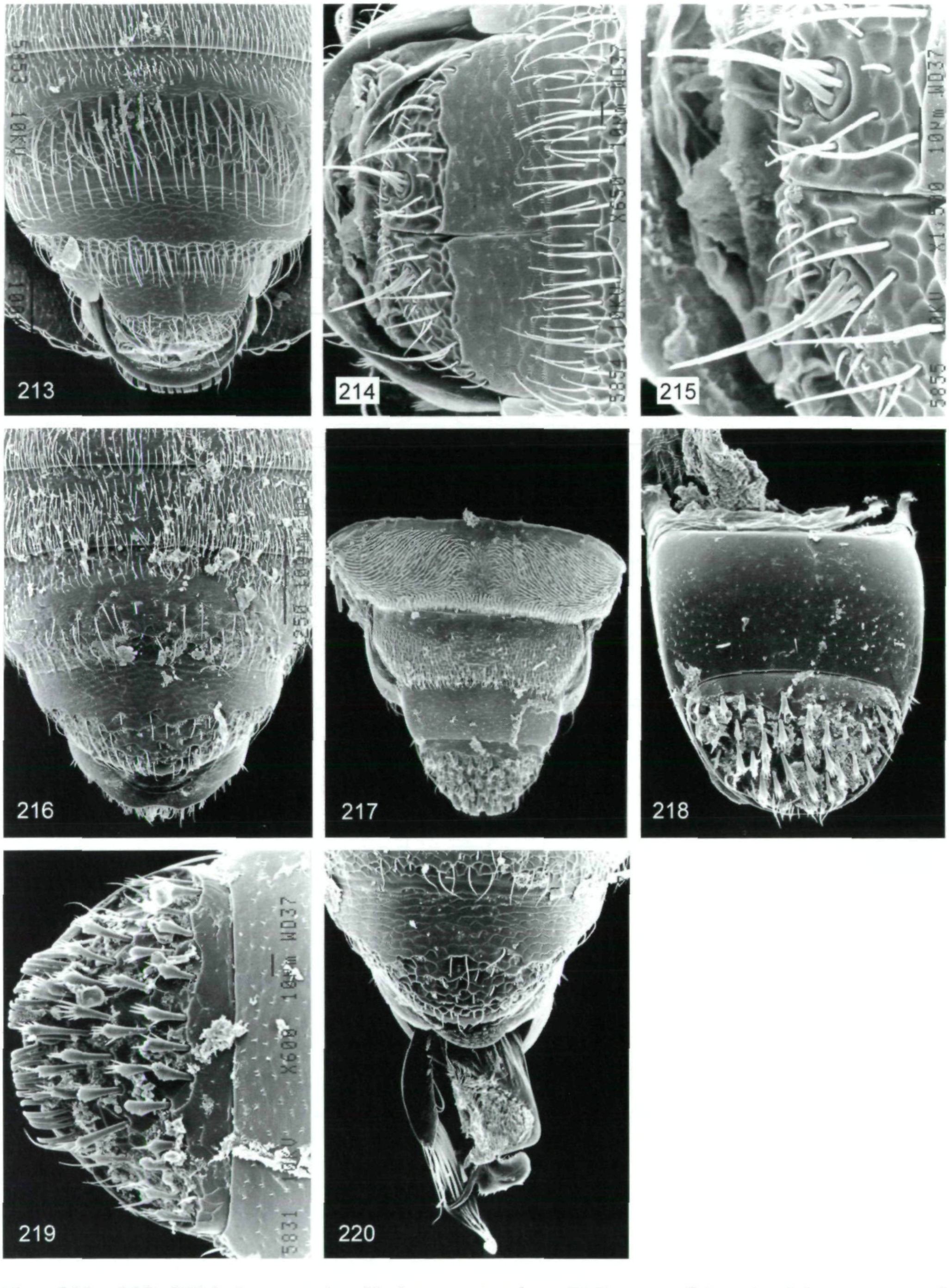
Figs. 186 - 194: SEM photographs, *Hydraena circulata*, 186) right maxilla, ventral view, 187) left maxilla, ventral view, 188) head, ventral view, 189) same, right side enlarged, 190) antenna, eye, temporal extension and lateral genal area, ventral view, 191) eye, subocular antennal groove, genal antennal groove and genal antennal groove setae, 192) facets and temporal extension, secretion sulci, enlarged, 193) genal antennal groove and genal antennal groove setae, 194) apex of mentum.



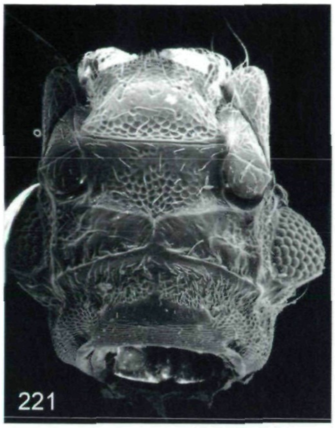
Figs. 195 - 203: SEM photographs, *Hydraena circulata*, 195) pronotum, 196) same, left anterior corner, 197) same, sensory setae, enlarged, 198) prothorax, ventral view, 199) right hypomeron, anterior apex, 200) prosterno-hypomeral suture, 201) hypomeral antennal pocket, 202) antennal cleaner, 203) same, enlarged.

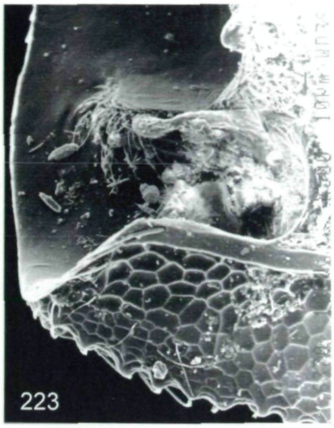


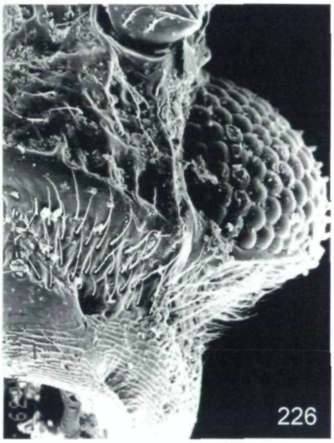
Figs. 204 - 212: SEM photographs, *Hydraena circulata*, 204) meso-, metasternum and ventrite I, 205) metasternum, 206) left elytron, anterior half, dorsal view, 207) female abdomen, ventral view, 208) male abdomen, ventral view, 209) intercoxal sternite, intercoxal cavity and middle of ventrite I, 210) same, enlarged, 211) middle of ventrite I, detail, 212) same, exocrine pore and secretion cap, enlarged.

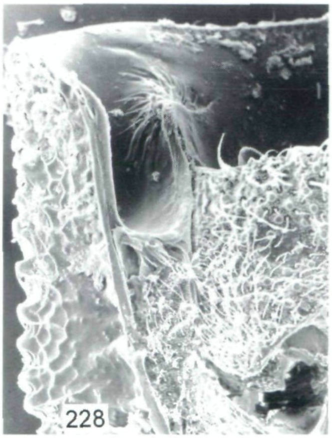


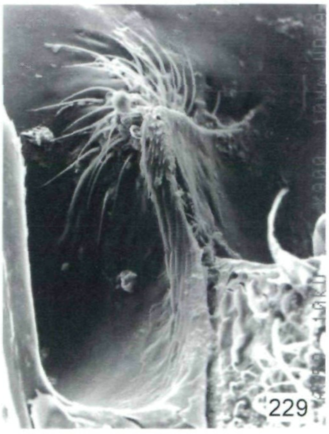
Figs. 213 - 220: SEM photographs, *Hydraena circulata*, 213) apex of female abdomen, ventral view, 214) gonocoxite, 215) same, apical part enlarged, 216) apex of male abdomen, ventral view, 217) apex of female abdomen, dorsal view, 218) apex of male abdomen, dorsal view, 219) female tergite X, 220) male abdominal apex and apical half of aedeagus, ventral view.





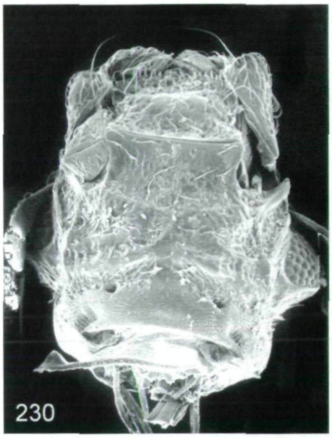






Figs. 221 - 224: SEM photographs, *Hydraena monikae*, 221) head, ventral view, 222) prothorax, ventral view, 223) hypomeral antennal pocket, 224) left hypomeron, anterior part.

Figs. 225 - 229: SEM photographs, *Hydraena cornelli*, 225) head, ventral view, 226) same, posterior part of left side, enlarged, 227) prothorax, ventral view, 228) hypomeral antennal pocket, 229) antennal cleaner.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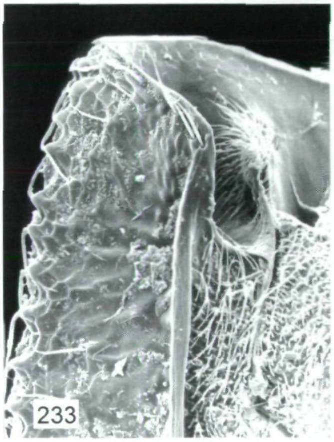
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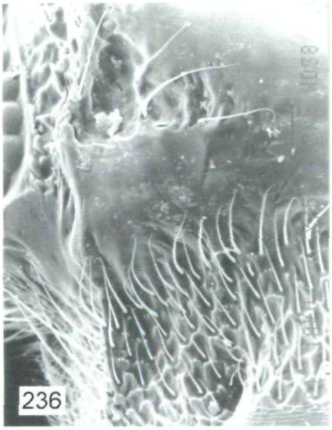
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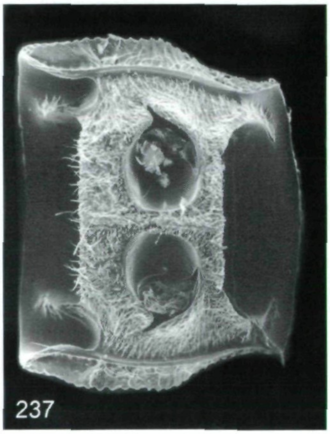
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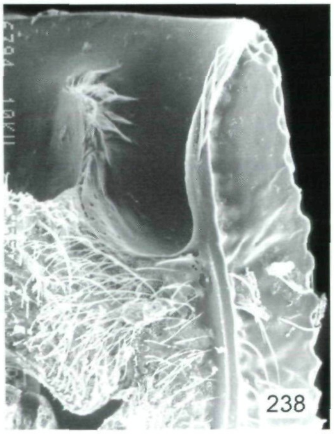
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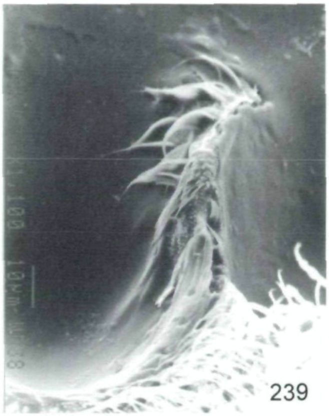
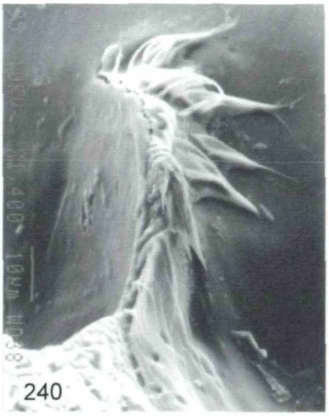
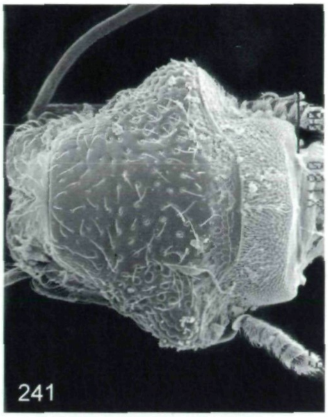
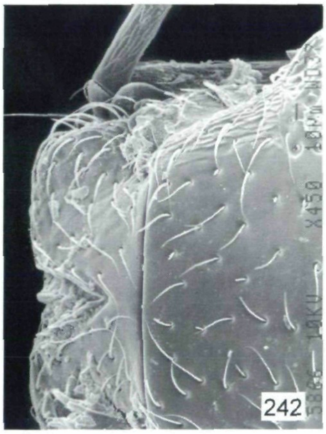
Figs. 230 - 233: SEM photographs, *Hydraena rugosa*, 230) head, ventral view, 231) same, posterior part, enlarged, 232) prothorax, ventral view, 233) hypomeral antennal pocket.

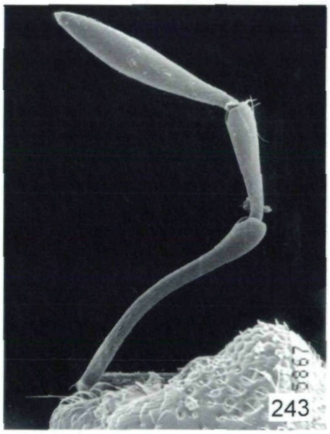
Figs. 234 - 238: SEM photographs, *Hydraena cordiformis*, 234) head, ventral view, 235) same, posterior part, enlarged, 236) right lateral genal area, enlarged, 237) prothorax, ventral view, 238) hypomeral antennal pocket.

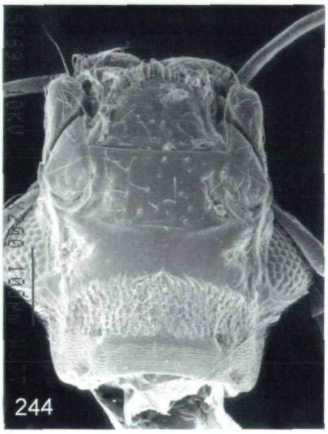


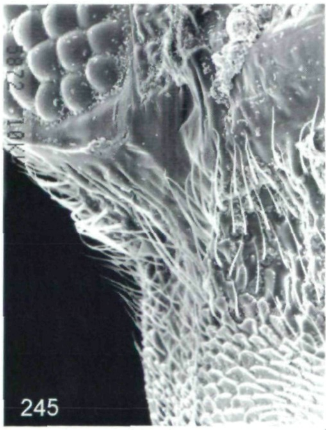


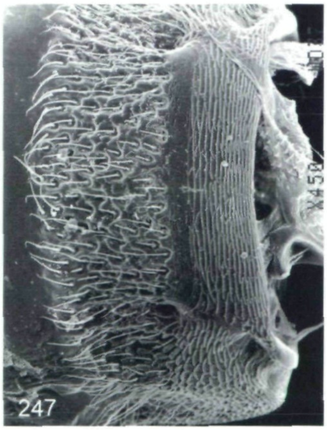






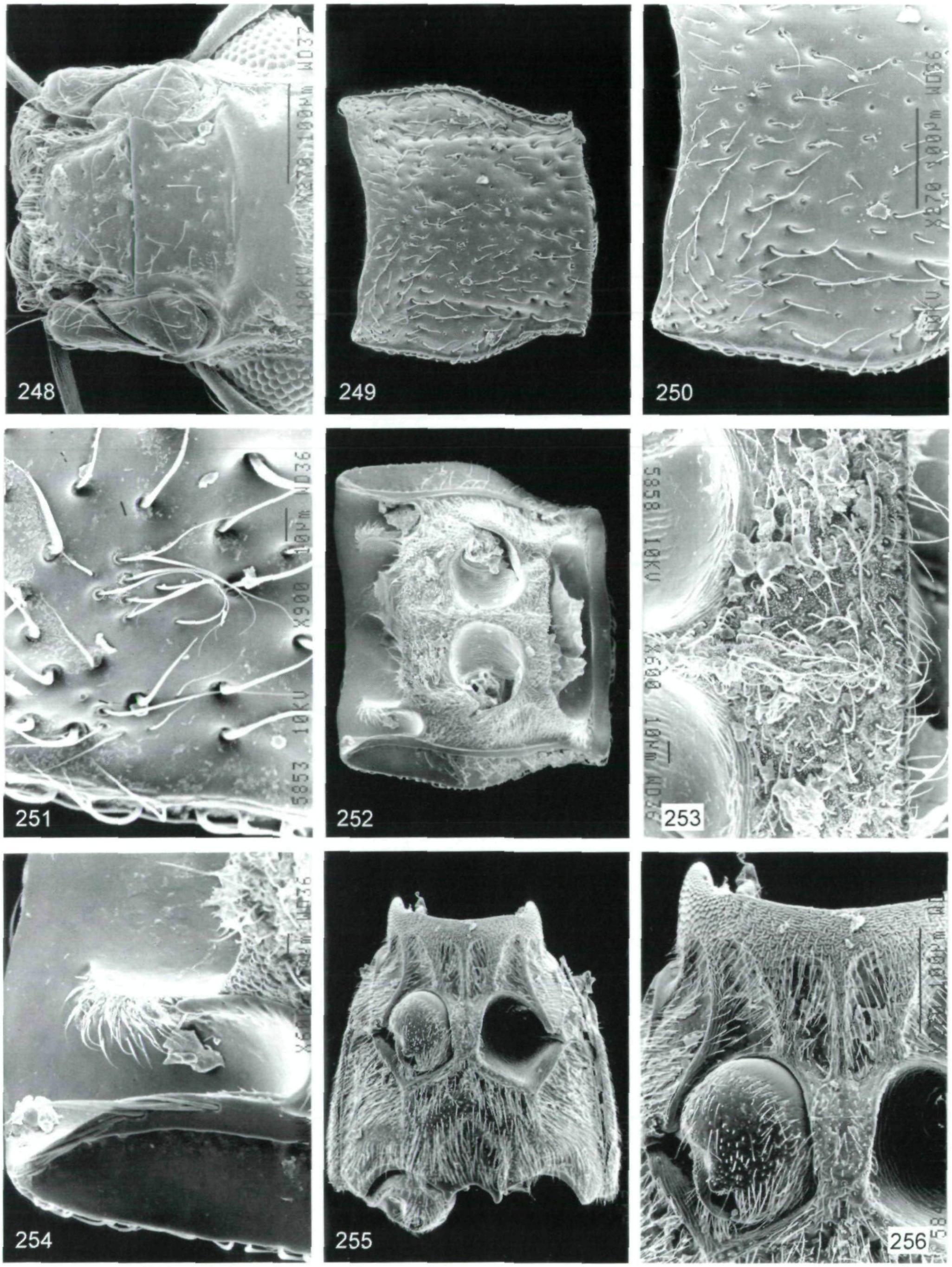




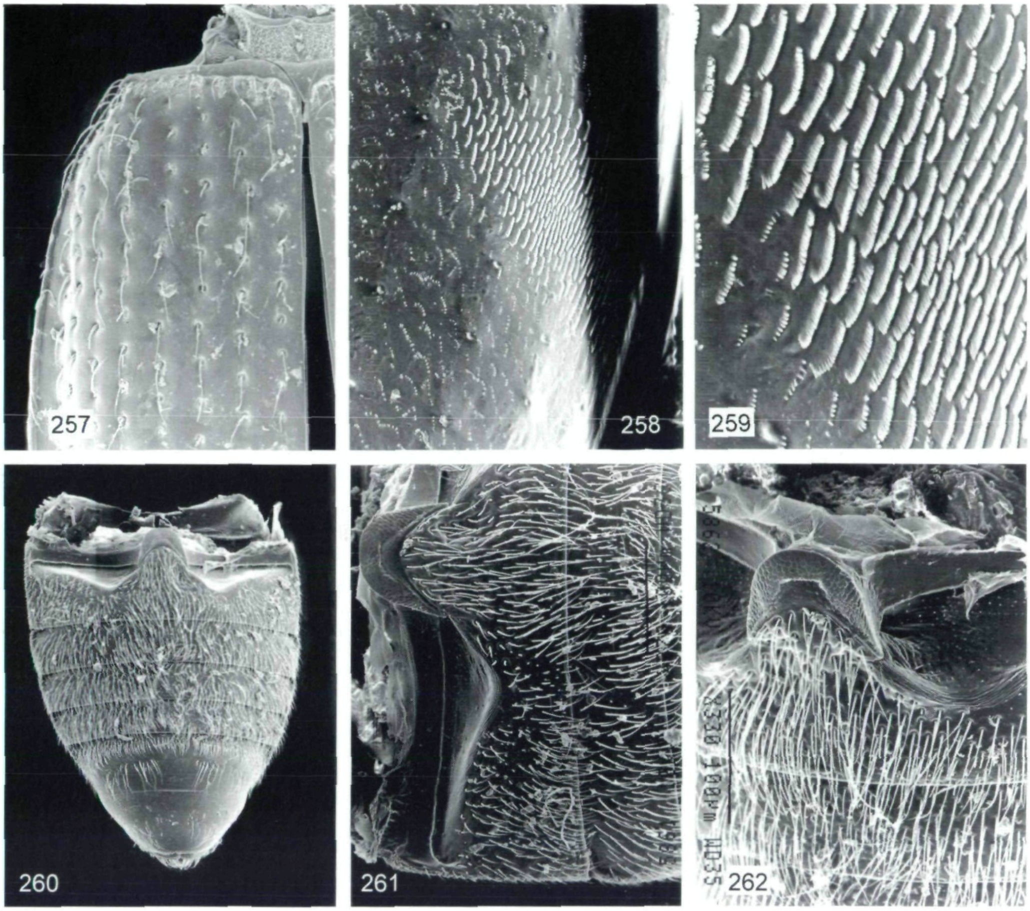


Figs. 239 - 247: SEM photographs, *Hydraena cordiformis*, 239) right antennal cleaner, 240) left antennal cleaner.

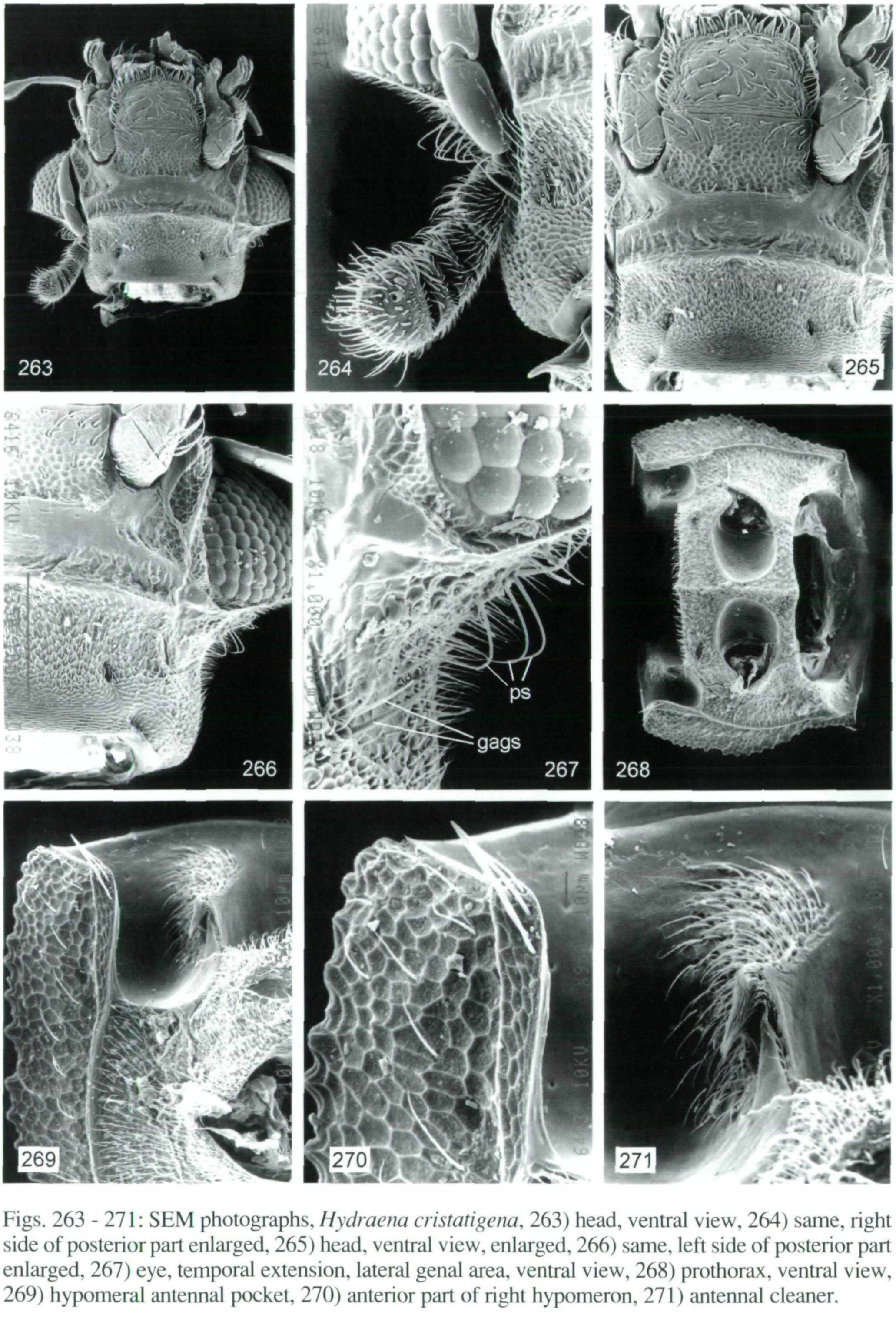
Figs. 241 - 247: SEM photographs, *Hydraena paucistriata*, 241) head, dorsal view, 242) labrum and clypeus, 243) right side of head and maxillary palp, dorsal view, 244) head, ventral view, 245) eye, temporal extension and lateral genal area, ventral view, 246) eye, subocular ridge, subocular antennal groove and lateral parts of transverse genal ridges, 247) gula and posterior parts of genae.



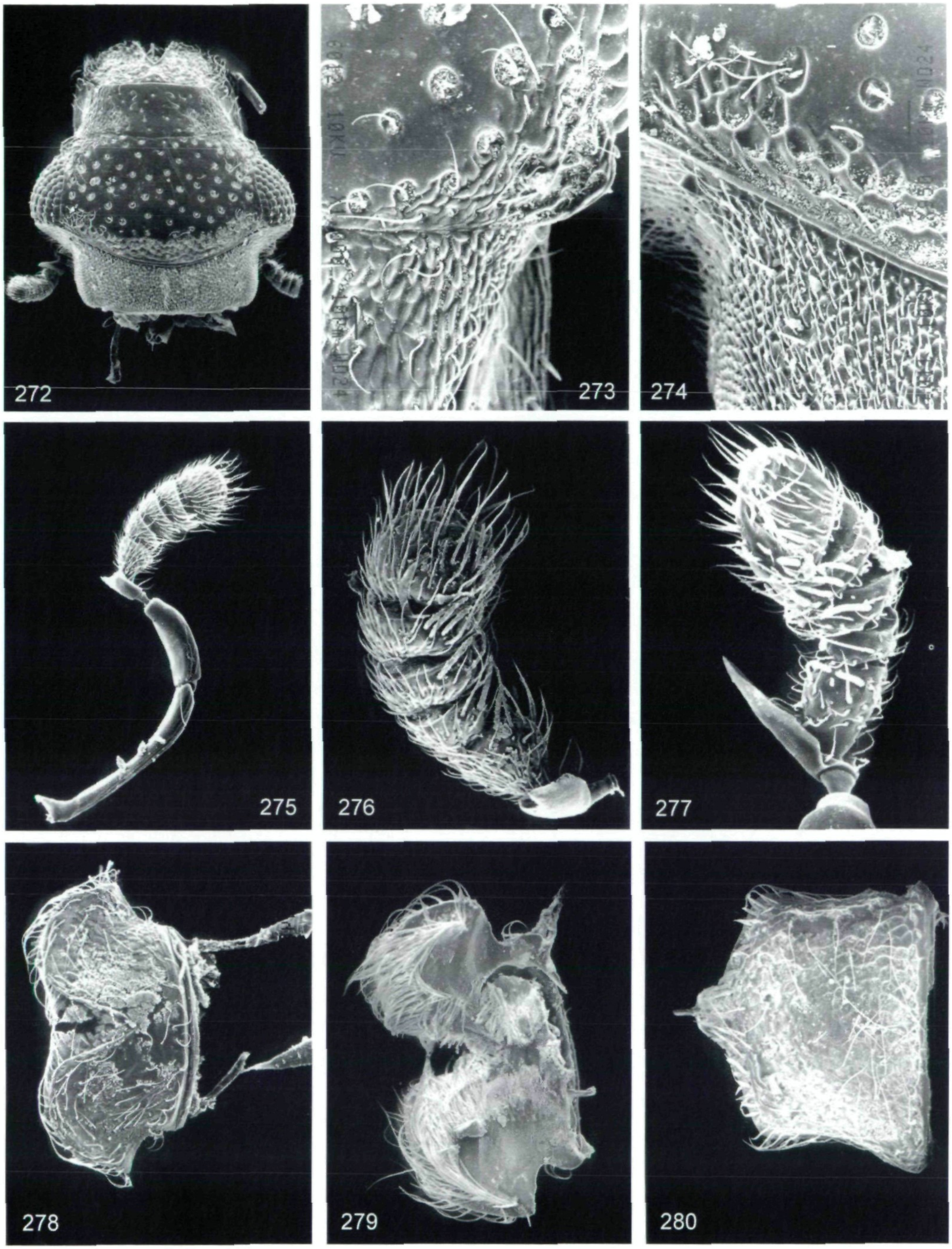
Figs. 248 - 256: SEM photographs, *Hydraena paucistriata*, 248) anterior part of head, ventral view, 249) pronotum, 250) same, left anterior corner, enlarged, 251) same, sensory setae, 252) prothorax, ventral view, 253) middle of prosternum, 254) hypomeral antennal pocket, 255) meso- and metasternum, 256) mesosternum.



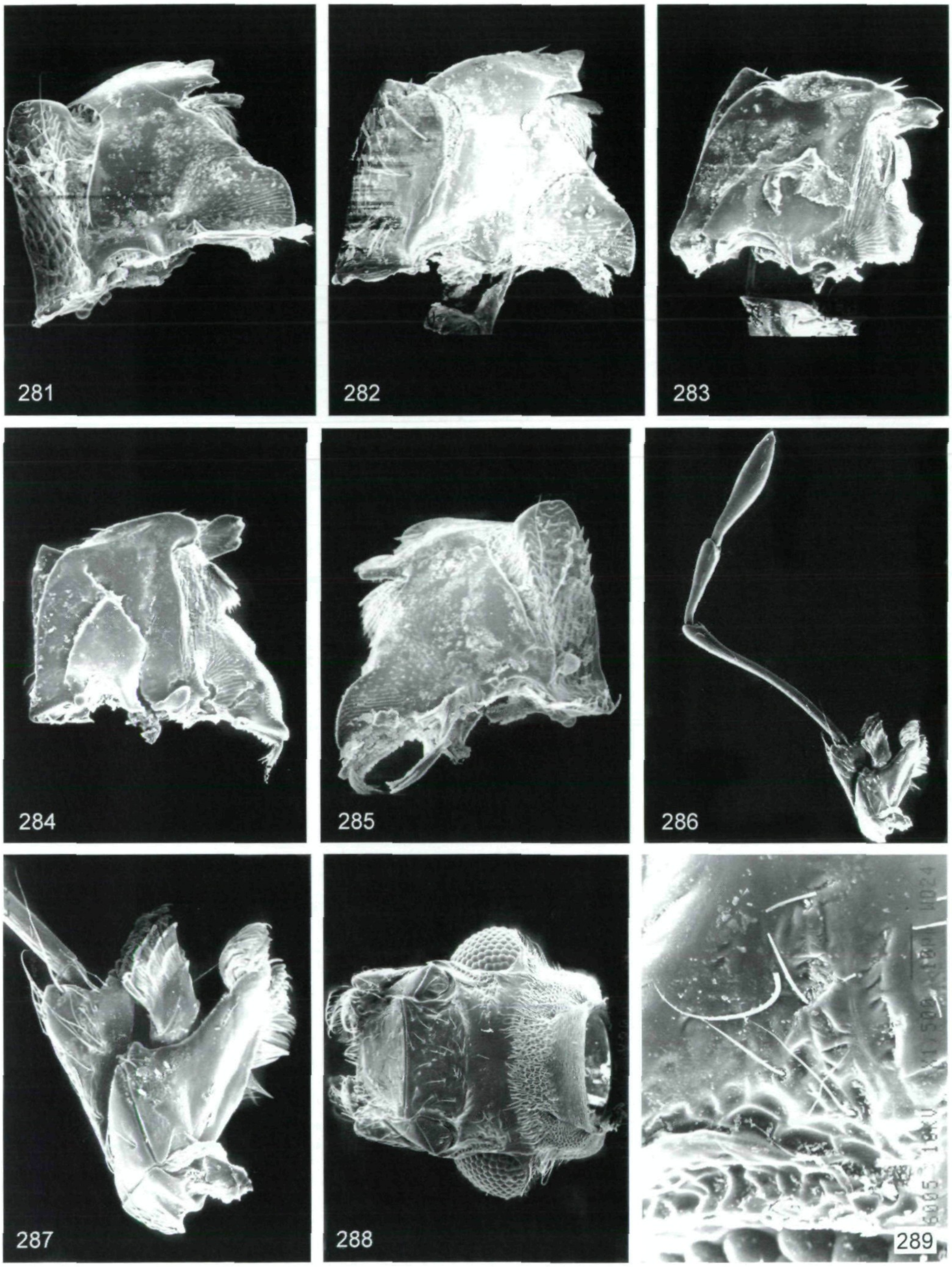
Figs. 257 - 262: SEM photographs, *Hydraena paucistriata*, 257) anterior half of left elytron, dorsal view, 258) elytron, ventral view, detail, 259) same, enlarged, 260) male abdomen, ventral view, 261) intercoxal sternite, metacoxal socket and ventrites I and II, 262) same, ventrolateral view.



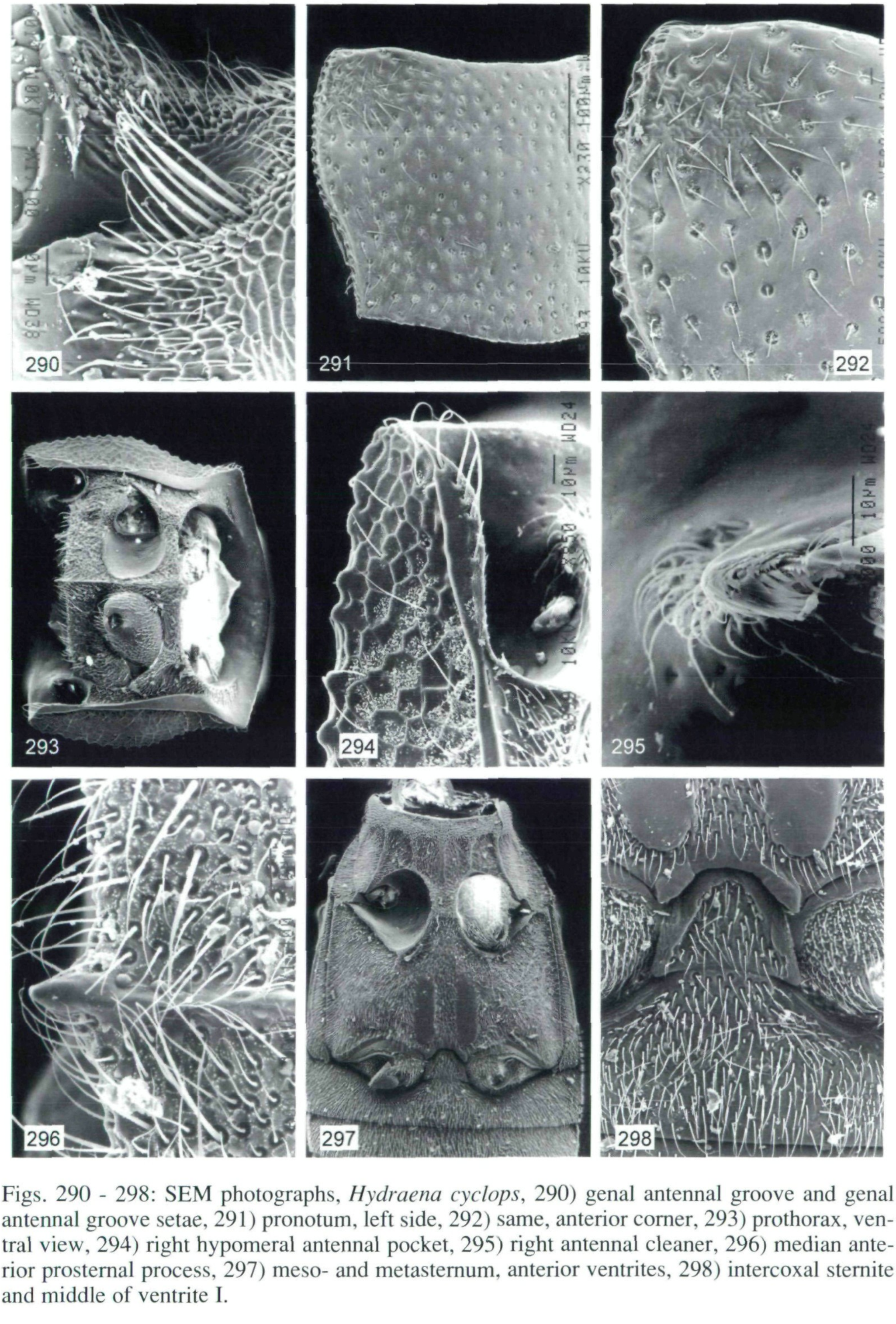
Figs. 263 - 271: SEM photographs, *Hydraena cristatigena*, 263) head, ventral view, 264) same, right side of posterior part enlarged, 265) head, ventral view, enlarged, 266) same, left side of posterior part enlarged, 267) eye, temporal extension, lateral genal area, ventral view, 268) prothorax, ventral view, 269) hypomeral antennal pocket, 270) anterior part of right hypomeron, 271) antennal cleaner.



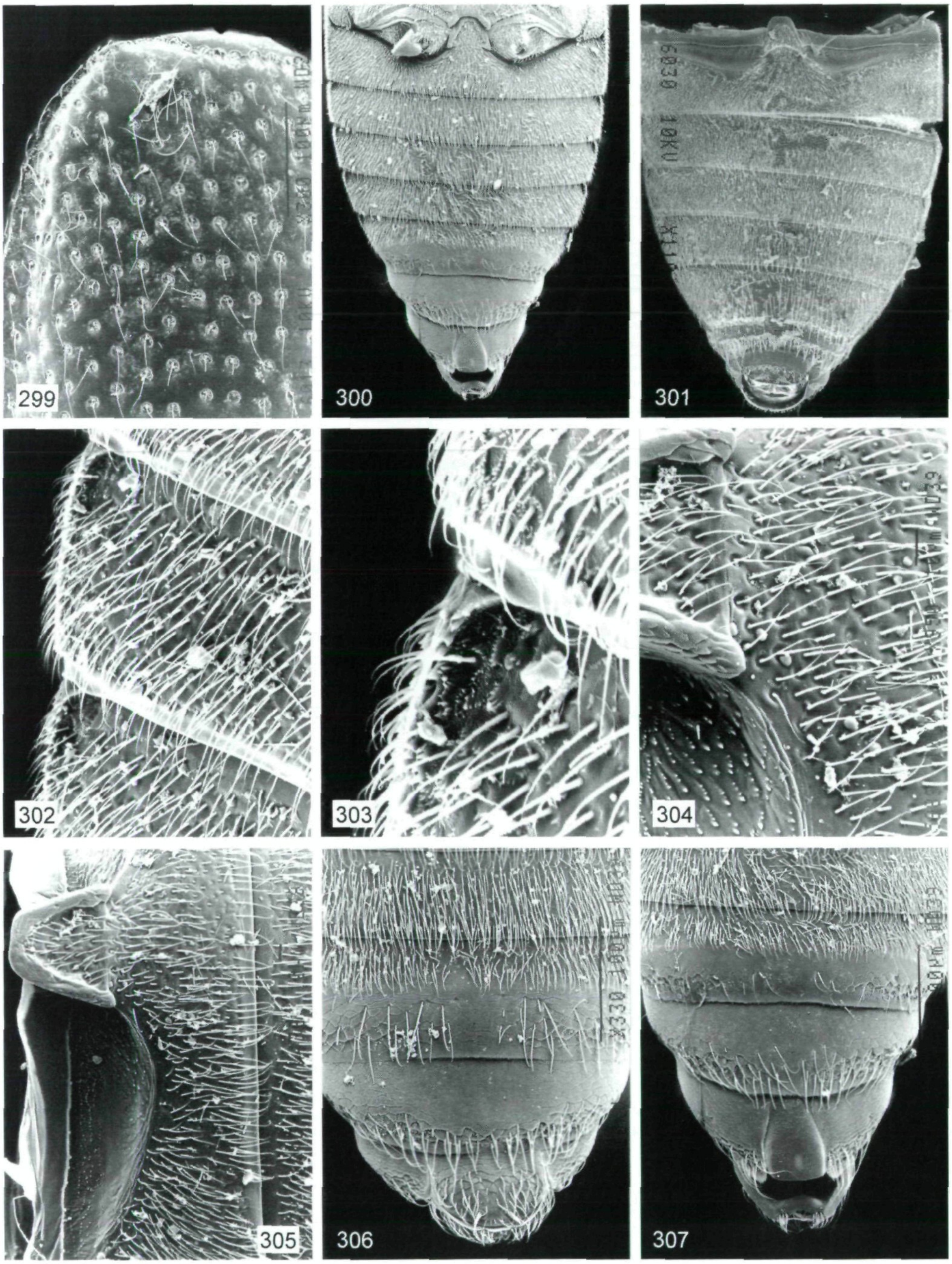
Figs. 272 - 280: SEM photographs, *Hydraena cyclops*, 272) head, dorsal view, 273) left margin of clypeus and frons, 274) ridge separating frons and neck region, 275) antenna, 276) antennal club, 277) same, different view, 278) labrum, 279) epipharynx, 280) mentum.



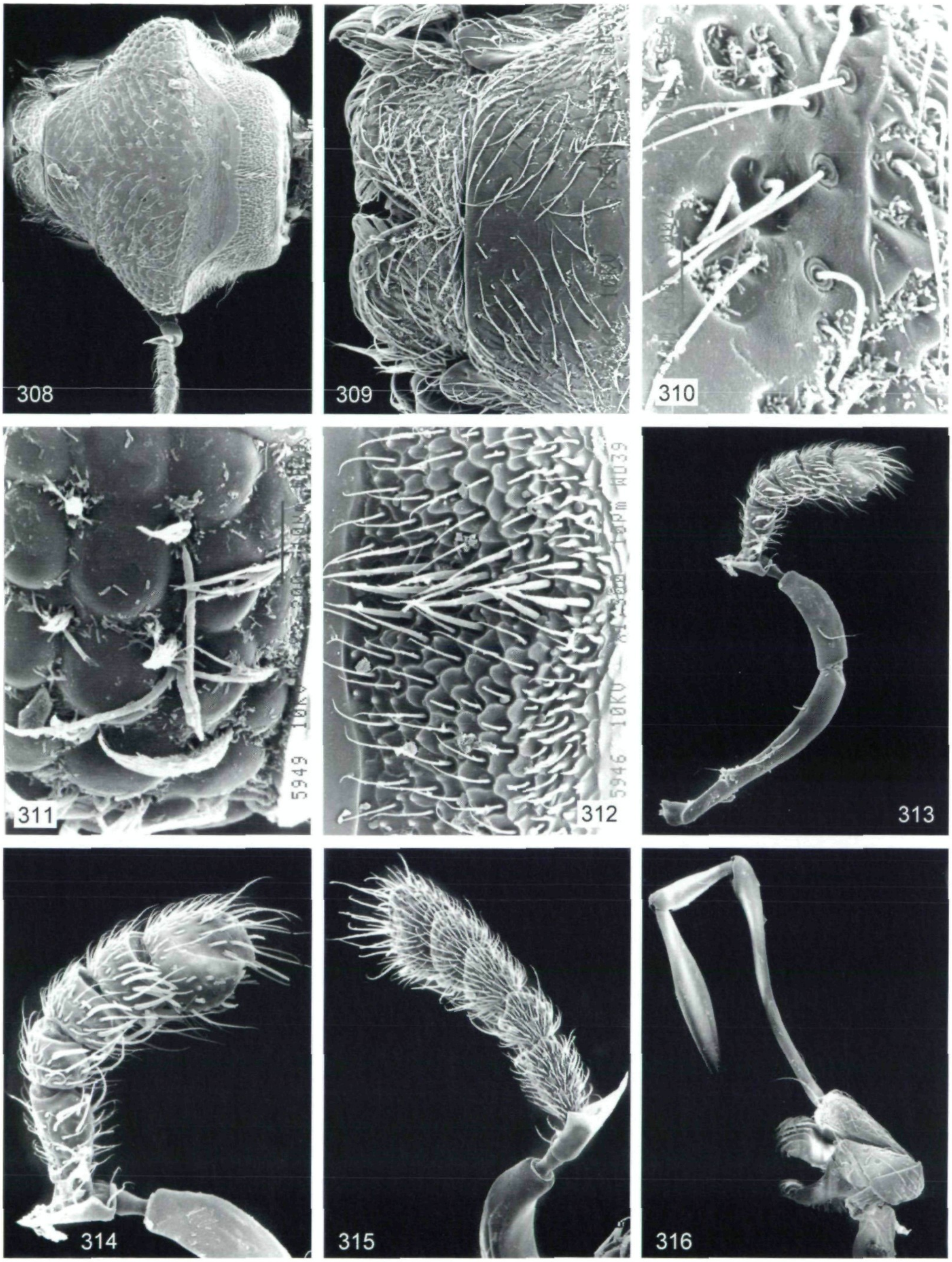
Figs. 281 - 289: SEM photographs, *Hydraena cyclops*, 281) left mandible, dorsal view, 282) same, slightly deviating orientation, 283) right mandible, ventral view, pointed apex of mola broken, 284) same, pointed apex of mola intact, 285) right mandible, dorsal view, 286) right maxilla, ventral view, 287) same, detail, 288) head, ventral view, 289) subocular antennal groove and subocular antennal ridge.



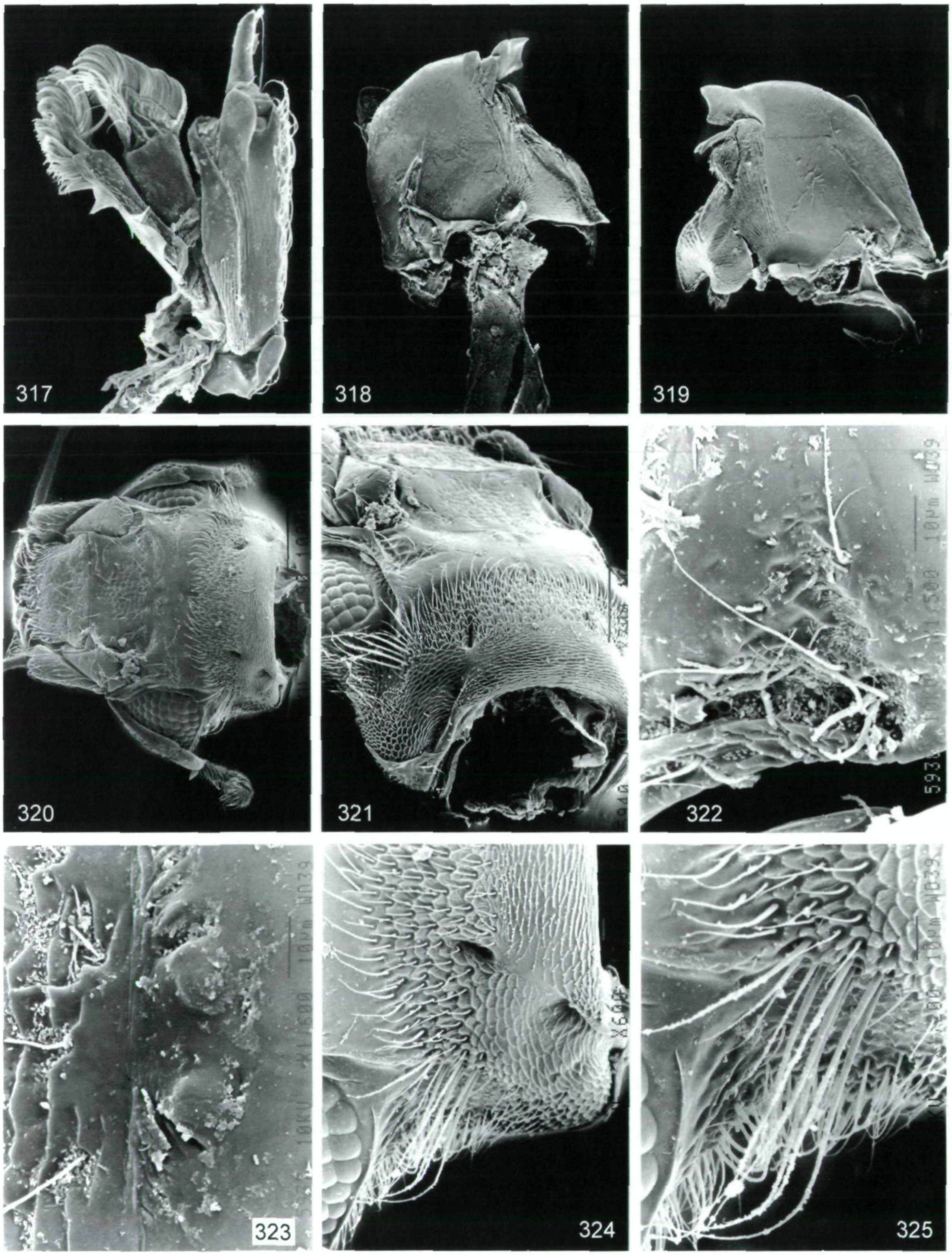
Figs. 290 - 298: SEM photographs, *Hydraena cyclops*, 290) genal antennal groove and genal antennal groove setae, 291) pronotum, left side, 292) same, anterior corner, 293) prothorax, ventral view, 294) right hypomeral antennal pocket, 295) right antennal cleaner, 296) median anterior prosternal process, 297) meso- and metasternum, anterior ventrites, 298) intercoxal sternite and middle of ventrite I.



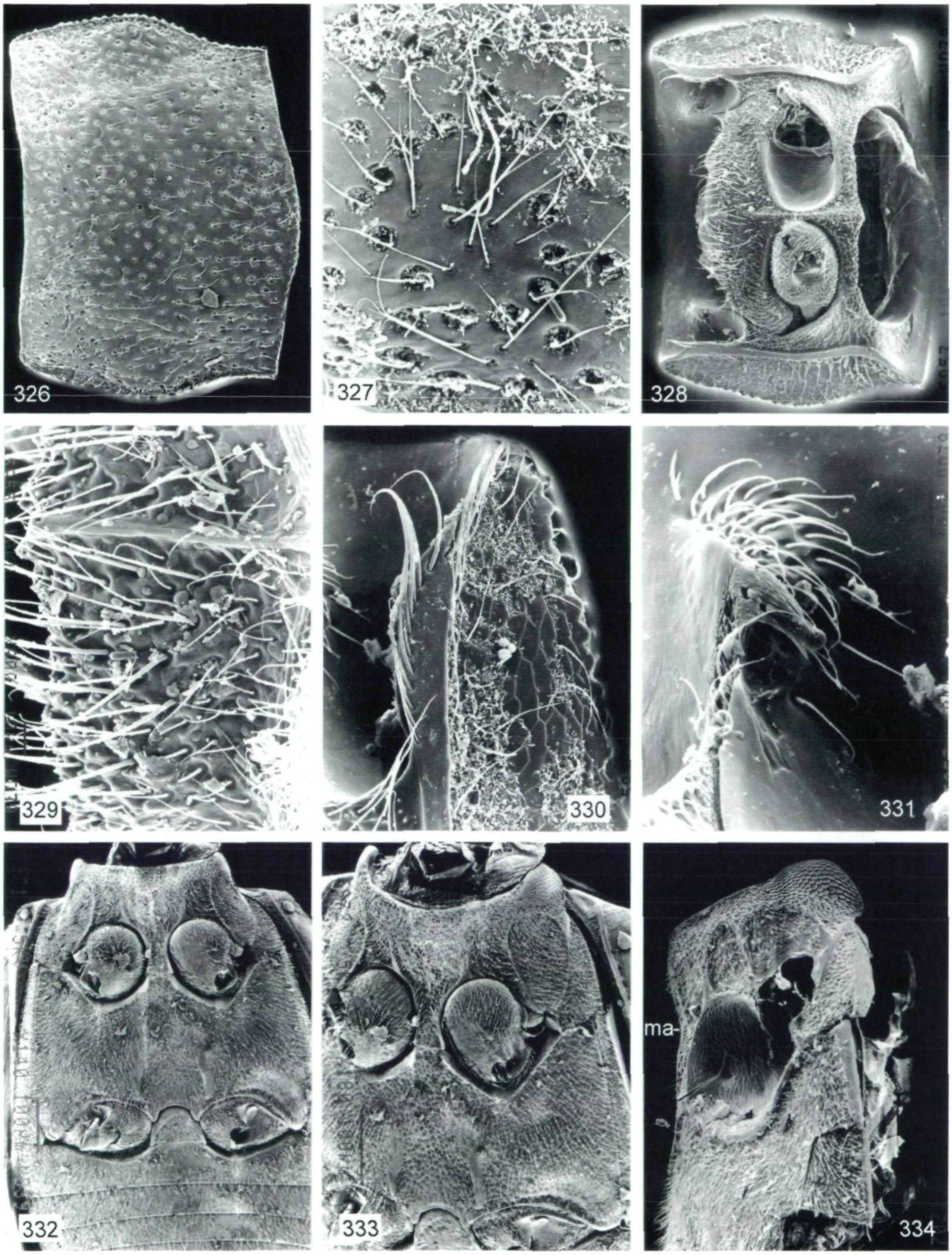
Figs. 299 - 307: SEM photographs, *Hydraena cyclops*, 299) left elytron, anterior half, dorsal view, 300) male abdomen, ventral view, 301) female abdomen, ventral view, 302) ventrites II and III, lateral margin, 303) posterior corner of ventrite I and anterior corner of ventrite II, enlarged, 304) posterior half of intercoxal sternite and middle of ventrite I, 305) intercoxal sternite and ventrite I, 306) apex of female abdomen, ventral view, 307) apex of male abdomen, ventral view.



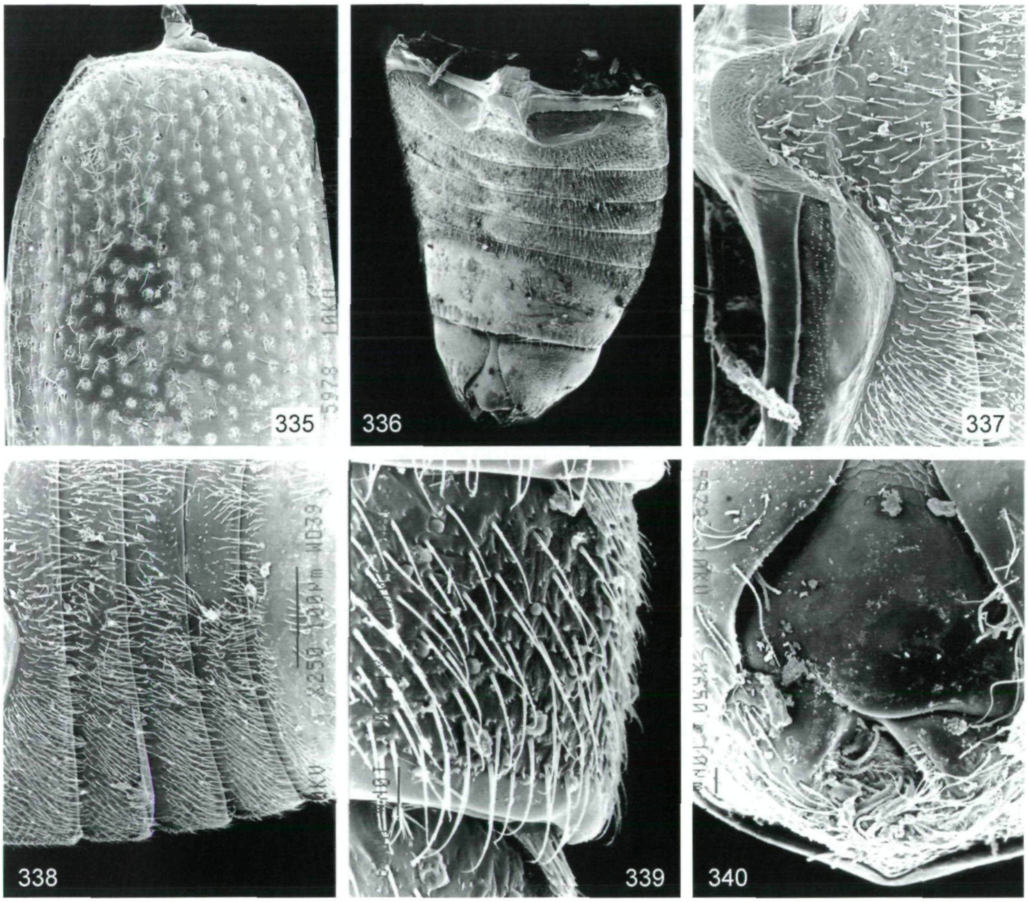
Figs. 308 - 316: SEM photographs, *Hydraena isolinae*, 308) head, dorsal view, 309) labrum and clypeus, 310) clypeus, lateral margin, sensory setae, enlarged, 311) left eye, posterior corner, dorsal view, fascicular sensilla, 312) middle of neck region (vertex), 313) antenna, 314) antennal club, 315) same, different view, 316) left maxilla, ventral view.



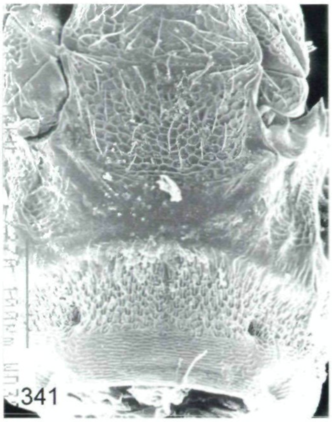
Figs. 317 - 325: SEM photographs, *Hydraena isolinae*, 317) right maxilla, 318) right mandible, ventral view, 319) left mandible, ventral view, 320) head, ventral view, 321) head, ventrolateral view, 322) lateral genal area, enlarged, 323) genal paramesal protuberances, 324) temporal extension, lateral posterior genal area and lateral half of gula, 325) genal antennal groove and genal antennal groove setae.



Figs. 326 - 334: SEM photographs, *Hydraena isolinae*, 326) pronotum, 327) same, left anterior corner, sensory setae, 328) prothorax, ventral view, 329) middle of prosternum, 330) left hypomeral antennal pocket, 331) left antennal cleaner, 332) meso-, metasternum and anterior ventrites, 333) same, ventrolateral view, 334) meso- and metasternum, lateral view.



Figs. 335 - 340: SEM photographs, *Hydraena isolinae*, 335) left elytron, anterior half, dorsal view, 336) male abdomen, ventrolateral view, 337) intercoxal sternite and ventrite I, 338) ventrites I – V, 339) lateral margin of ventrite II, 340) male abdominal apex.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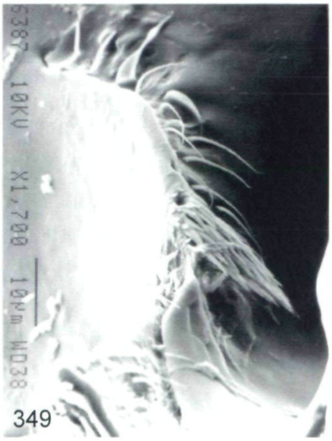
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Figs. 341 - 346: SEM photographs, *Hydraena leechi*, 341) head, ventral view, 342) prothorax (slightly damaged), ventral view, 343) hypomeral antennal pocket, 344) same, 345) left antennal cleaner, 346) right antennal cleaner.

Figs. 347 - 349: SEM photographs, *Hydraena tubuliphallis*, 347) head (slightly damaged), ventral view, 348) right half of prothorax (slightly damaged), ventral view, 349) left antennal cleaner.

## World Check List of the Species of *Hydraena* KUGELANN

In the following check list, all species of *Hydraena* described until 2000 are included. Subspecies and synonyms are excluded.

* = '*Haenydra*' lineage ** = '*Phothydraena*' lineage

### Subgenus *Hydraena* s.str. KUGELANN

1. *abbasigili* JÄCH, 1988
2. *achaica* JÄCH, 1995
3. *aethaliensis* BREIT, 1917
4. *affusa* d'ORCHYMONT, 1936
5. *africana* KUWERT, 1888
6. *akbesiana* (AUDISIO, DE BIASE & JÄCH, 1993)*
7. *albai* SAINZ-CANTERO, 1993
8. *alcantarana* IENIŞTEA, 1985
9. *algerina* KADDOURI, 1992
10. *alia* d'ORCHYMONT, 1934
11. *allomorpha* LAGAR & FRESNEDA, 1990
12. *alpicola* PRETNER, 1931*
13. *altamirensis* DÍAZ & GARRIDO, 1993*
14. *ambigua* GANGLBAUER, 1901
15. *americana* JÄCH, 1993
16. *amidensis* JÄCH, 1988
17. *anatolica* JANSSENS, 1963*
18. *ancylis* PERKINS, 1980
19. *ancyrae* JÄCH, 1992
20. *andalusa* LAGAR & FRESNEDA, 1990
21. *andreinii* d'ORCHYMONT, 1934
22. *angulicollis* NOTMAN, 1921
23. *angulosa* MULSANT, 1844
24. *angustata* STURM, 1836
25. *antiatlantica* JÄCH, AGUILERA & HERNANDO, 1998
26. *antiochena* JÄCH, 1988
27. *appalachicola* PERKINS, 1980
28. *arachthi* FERRO & JÄCH, 2000
29. *arenicola* PERKINS, 1980
30. *ariana* JANSSENS, 1962
31. *armata* REITTER, 1880
32. *armeniaca* JANSSENS, 1968
33. *armipalpis* JÄCH & DÍAZ, 2000
34. *armipes* REY, 1886
35. *assimilis* REY, 1885
36. *atrata* DESBROCHERS DES LOGES, 1891**
37. *attaleiae* FERRO, 1984
38. *audisioi* JÄCH, 1992
39. *aurita* JÄCH, 1988
40. *avuncula* JÄCH, 1988
41. *bactriana* JANSSENS, 1962
42. *balearica* d'ORCHYMONT, 1930
43. *balli* d'ORCHYMONT, 1940
44. *barrosi* d'ORCHYMONT, 1934
45. *bedeli* BERTHÉLEMY, 1992
46. *belgica* d'ORCHYMONT, 1930*
47. *bensae* GANGLBAUER, 1901*
48. *berytus* JÄCH, 1986
49. *beyarslani* JÄCH, 1988
50. *bicolorata* JÄCH, 1997
51. *bicuspidata* GANGLBAUER, 1901*
52. *bihamata* CHAMPION, 1920
53. *bimagua* JÄCH, 1986
54. *bisulcata* REY, 1884
55. *bitruncata* d'ORCHYMONT, 1934*
56. *bolivari* d'ORCHYMONT, 1936
57. *bononiensis* CHIESA, 1959*
58. *bosnica* APFELBECK, 1909*
59. *brachymera* d'ORCHYMONT, 1936
60. *brevis* SHARP, 1882
61. *britteni* JOY, 1907
62. *bromleyae* JÄCH, 1986
63. *bulgarica* BREIT, 1916
64. *calcarifera* JANSSENS, 1959
65. *californica* PERKINS, 1980
66. *canakcioglui* JANSSENS, 1965
67. *cappadocica* JÄCH, 1988
68. *capta* d'ORCHYMONT, 1936
69. *carbonaria* KIESENWETTER, 1849
70. *carica* JÄCH, 1988
71. *carniolica* PRETNER, 1970*
72. *cata* d'ORCHYMONT, 1943*
73. *catalonica* FRESNEDA, AGUILERA & HERNANDO, 1994*
74. *caucasica* KUWERT, 1888*
75. *cephalleniaca* JÄCH, 1985
76. *cervisophila* JÄCH, 1992
77. *chiesai* JANSSENS, 1965
78. *chifengi* JÄCH & DÍAZ, 1999
79. *chobauti* GUILLEBEAU, 1896
80. *christinae* AUDISIO, DE BIASE & JÄCH, 1996*
81. *ciliciensis* JÄCH, 1988
82. *circulata* PERKINS, 1980
83. *cirrata* CHAMPION, 1920

84. *cirratoides* JANSSENS, 1980
85. *colchica* JANSSENS, 1963
86. *cordata* SCHAUFUSS, 1883
87. *corinna* d'ORCHYMONT, 1936
88. *cornelli* JÄCH & DÍAZ, 1998
89. *corrugis* d'ORCHYMONT, 1934
90. *coryleti* JÄCH, 1992
91. *crepidoptera* JÄCH, 1992*
92. *croatica* KUWERT, 1888
93. *cryptostoma* JÄCH, 1992
94. *curta* KIESENWETTER, 1849
95. *czernohorskyi* MÜLLER, 1911*
96. *dalmatina* GANGLBAUER, 1901*
97. *damascaena* PIC, 1910
98. *decolor* SAINTE-CLAIRE DEVILLE, 1903*
99. *delia* BALFOUR-BROWNE, 1978
100. *dentipalpis* REITTER, 1888
101. *dentipes* GERMAR, 1842*
102. *devillei* GANGLBAUER, 1901*
103. *devincta* d'ORCHYMONT, 1940*
104. *discreta* GANGLBAUER, 1904*
105. *dolichogaster* JANSSENS, 1965
106. *ebriimadli* JÄCH, 1988
107. *egoni* JÄCH, 1986
108. *eichleri* d'ORCHYMONT, 1937
109. *elisabethae* JÄCH, 1992*
110. *emarginata* REY, 1885*
111. *epeirosi* FERRO, 1985*
112. *eucnemis* JANSSENS, 1970
113. *evanescens* REY, 1884*
114. *exarata* KIESENWETTER, 1866
115. *exasperata* d'ORCHYMONT, 1935*
116. *excisa* KIESENWETTER, 1849*
117. *explanata* PIC, 1905
118. *falcata* JÄCH, 1992
119. *filum* SAHLBERG, 1908
120. *finita* d'ORCHYMONT, 1943
121. *fiorii* PORTA, 1899
122. *fluvicola* (PERKINS, 1980)
123. *fontiscarsavii* (JÄCH, 1988)*
124. *fritzi* JÄCH, 1992
125. *frondsicola* (PERKINS, 1980)
126. *furthi* JÄCH, 1982
127. *gaditana* LAGAR & FRESNEDA, 1990*
128. *galatica* JANSSENS, 1970
129. *georgiadesi* d'ORCHYMONT, 1931
130. *glassmani* JÄCH, 1986
131. *gnatella* d'ORCHYMONT, 1945
132. *gnatelloides* d'ORCHYMONT, 1945
133. *gracilis* GERMAR, 1824*
134. *graciloides* (JÄCH, 1988)*
135. *grandis* REITTER, 1885
136. *graphica* d'ORCHYMONT, 1931
137. *grata* d'ORCHYMONT, 1944
138. *gregalis* d'ORCHYMONT, 1944
139. *gressa* d'ORCHYMONT, 1944
140. *griphus* d'ORCHYMONT, 1944
141. *guentheri* JÄCH, 1992
142. *hainzi* JÄCH, 1988
143. *helena* d'ORCHYMONT, 1929
144. *hernandoi* FRESNEDA & LAGAR, 1990**
145. *heterogyna* BEDEL, 1898*
146. *hiekei* JÄCH, 1992
147. *hispanica* GANGLBAUER, 1901*
148. *holdhausi* PRETNER, 1929
149. *hortensis* JÄCH & DÍAZ, 2000
150. *hosseinieorum* BILTON & JÄCH, 1998*
151. *hungarica* REY, 1884*
152. *iberica* d'ORCHYMONT, 1936*
153. *ilica* JÄCH, 1994
154. *imperatrix* KNISCH, 1919
155. *inapicipalpis* PIC, 1918
156. *ingens* (PERKINS, 1980)
157. *integra* PRETNER, 1931*
158. *intermedia* ROSENHAUER, 1847
159. *jaechiana* (AUDISIO & DE BIASE, 1990)*
160. *jailensis* BREIT, 1917
161. *janczyki* JÄCH, 1992
162. *janeceki* JÄCH, 1987
163. *karinkukolae* JÄCH, 1989
164. *kasyi* JÄCH, 1992
165. *kaufmanni* GANGLBAUER, 1901
166. *khnzoriani* JANSSENS, 1968*
167. *kocheri* BERTHÉLEMY, 1992
168. *kroumiriana* KADDOURI, 1992
169. *kuehnelti* JÄCH, 1989
170. *kurdistanica* JÄCH, 1988
171. *lapidicola* KIESENWETTER, 1849*
172. *lapissectilis* JÄCH, 1992
173. *larissae* JÄCH & DÍAZ, 2000*
174. *latebricola* JÄCH, 1986
175. *lazica* JANSSENS, 1963*
176. *leonhardi* BREIT, 1916*
177. *leprieuri* SAINTE-CLAIRE DEVILLE, 1905
178. *levantina* SAHLBERG, 1908
179. *ligulipes* JÄCH, 1988
180. *liriope* d'ORCHYMONT, 1943
181. *lucasi* LAGAR, 1984
182. *ludovicae* d'ORCHYMONT, 1931
183. *lusitana* (BERTHÉLEMY, 1977)*
184. *lycia* JÄCH, 1988
185. *macedonica* d'ORCHYMONT, 1931

186. *madronensis* CASTRO, GARCÍA & FERRERAS, 2000*
187. *magnessa* JÄCH, 1997*
188. *malickyi* JÄCH, 1989
189. *manfredjaechi* DELGADO & SOLER, 1991*
190. *marcosae* AGUILERA, HERNANDO & RIBERA, 1997
191. *mariannae* JÄCH, 1992
192. *mecai* MILLÁN & AGUILERA, 2000
193. *melas* DALLA TORRE, 1877
194. *meschniggi* PRETNER, 1929
195. *mignymixys* PERKINS, 1980
196. *minutissima* STEPHENS, 1829
197. *modili* JÄCH, 1988
198. *monikae* JÄCH & DÍAZ, 2000
199. *monscassius* JÄCH, 1988
200. *monstruosipes* FERRO, 1986*
201. *morio* KIESENWETTER, 1849
202. *mouzaiensis* SAINTE-CLAIRE DEVILLE, 1909
203. *muelleri* PRETNER, 1931*
204. *muezziginea* JÄCH, 1988
205. *mylasae* JÄCH, 1992
206. *nigra* HATCH, 1965
207. *nigrita* GERMAR, 1824
208. *nike* JÄCH, 1995*
209. *nilguenae* (JÄCH, 1988)*
210. *nivalis* JÄCH, 1992
211. *notsui* SATÔ, 1978
212. *numidica* SAINTE-CLAIRE DEVILLE, 1905
213. *nuratauensis* JÄCH, 1994
214. *occidentalis* PERKINS, 1980
215. *occitana* (AUDISIO & DE BIASE, 1995)*
216. *olidipastoris* JÄCH, 1988
217. *orientalis* BREIT, 1916
218. *ortali* JÄCH, 1986
219. *ovata* JANSSENS, 1961
220. *oxiana* JANSSENS, 1974
221. *pachyptera* APFELBECK, 1909
222. *pacifica* PERKINS, 1980
223. *paganettii* GANGLBAUER, 1901**
224. *pakistanica* JÄCH, 1992
225. *pallidula* SAINTE-CLAIRE DEVILLE, 1909**
226. *palustris* ERICHSON, 1837
227. *pamirica* JÄCH, 1992
228. *pangaei* JÄCH, 1992*
229. *parysatis* JANSSENS, 1981
230. *pelops* JÄCH, 1995*
231. *pensylvanica* KIESENWETTER, 1849
232. *persica* JANSSENS, 1981
233. *petila* PERKINS, 1980
234. *phallerata* d'ORCHYMONT, 1944
235. *phallica* d'ORCHYMONT, 1930*
236. *phassilyi* d'ORCHYMONT, 1931
237. *philyra* d'ORCHYMONT, 1944
238. *pici* SAINTE-CLAIRE DEVILLE, 1905
239. *pindica* JANSSENS, 1965
240. *planata* KIESENWETTER, 1849*
241. *plastica* d'ORCHYMONT, 1943*
242. *platycnemis* JÄCH, 1988
243. *platynaspis* JÄCH, 1988
244. *platysoma* JANSSENS, 1968
245. *plumipes* REY, 1886*
246. *polita* KIESENWETTER, 1849*
247. *pontica* JANSSENS, 1963
248. *praetermissa* JÄCH, 1987
249. *pretneri* CHIESA, 1927
250. *producta* MULSANT & REY, 1852*
251. *prusensis* JÄCH, 1992
252. *pseudoriparia* d'ORCHYMONT, 1945
253. *puetzi* JÄCH, 1994
254. *pulchella* GERMAR, 1824
255. *putearius* JÄCH & DÍAZ, 2000**
256. *pygmaea* WATERHOUSE, 1833
257. *quadricurvipes* PERKINS, 1980
258. *quetiae* CASTRO, 2000
259. *quilisi* LAGAR, FRESNEDA & HERNANDO, 1987
260. *reyi* KUWERT, 1888
261. *rhodia* JÄCH, 1985
262. *riberai* JÄCH, AGUILERA & HERNANDO, 1998
263. *richardimbi* JÄCH, 1985
264. *rigua* d'ORCHYMONT, 1931
265. *riparia* KUGELANN, 1794
266. *rivularis* GUILLEBEAU, 1896
267. *rufipennis* BOSCÁ BERGA, 1932
268. *rufipes* CURTIS, 1830
269. *rugosa* MULSANT, 1844
270. *saga* d'ORCHYMONT, 1930*
271. *samnitica* FIORI, 1904*
272. *sanfilippoi* (AUDISIO & DE BIASE, 1995)*
273. *sappho* JANSSENS, 1965*
274. *sardoa* BINAGHI, 1961
275. *scabrosa* d'ORCHYMONT, 1931
276. *schilfii* JÄCH, 1988
277. *schillhammeri* JÄCH, 1988
278. *schoedli* JÄCH, 1992
279. *schoenmanni* JÄCH, 1988
280. *schuelkei* JÄCH, 1992
281. *schuleri* GANGLBAUER, 1901*
282. *scitula* d'ORCHYMONT, 1943*
283. *scythica* JANSSENS, 1974

284. *septemlacuum* JÄCH, 1992*
285. *serpentina* JÄCH, 1988
286. *serricollis* WOLLASTON, 1864**
287. *servilia* d'ORCHYMONT, 1936
288. *sharpi* REY, 1886
289. *sicula* KIESENWETTER, 1849
290. *sierra* PERKINS, 1980
291. *similis* d'ORCHYMONT, 1930
292. *simonidea* d'ORCHYMONT, 1931
293. *smyrnensis* SAHLBERG, 1908
294. *solarii* PRETNER, 1930*
295. *speciosa* d'ORCHYMONT, 1944
296. *spinipes* BAUDI, 1882
297. *stussineri* KUWERT, 1888
298. *subacuminata* REY, 1884
299. *subgrandis* JÄCH, 1988
300. *subimpressa* REY, 1885
301. *subina* d'ORCHYMONT, 1944
302. *subinflata* d'ORCHYMONT, 1944
303. *subinoides* d'ORCHYMONT, 1944
304. *subintegra* GANGLBAUER, 1901*
305. *subinura* d'ORCHYMONT, 1944
306. *subirregularis* PIC, 1918
307. *subjuncta* d'ORCHYMONT, 1930
308. *sublamina* d'ORCHYMONT, 1945
309. *sublapsa* d'ORCHYMONT, 1945
310. *subsequens* REY, 1886
311. *tarvisina* (FERRO, 1992)*
312. *tatii* SAINZ-CANTERO & ALBA-TERCEDOR, 1989*
313. *tauricola* JÄCH, 1988
314. *taxila* JANSSENS, 1962
315. *terebrans* JÄCH, 1992
316. *testacea* CURTIS, 1830**
317. *truncata* REY, 1885*
318. *tuolumne* PERKINS, 1980
319. *turcica* JANSSENS, 1965
320. *tyrrhena* BINAGHI, 1961*
321. *unca* VALLADARES, 1989
322. *uzbekistanica* JÄCH, 1994
323. *vandykei* d'ORCHYMONT, 1923
324. *vedrasi* d'ORCHYMONT, 1931*
325. *verstraeteni* FERRO, 1984
326. *virginalis* JANSSENS, 1963
327. *vodozi* SAINTE-CLAIRE DEVILLE, 1908
328. *waldheimi* JÄCH, 1987
329. *watanabei* JÄCH & SATÔ, 1988
330. *wewalkai* JÄCH, 1988
331. *wrasei* JÄCH, 1992
332. *yosemitensis* PERKINS, 1980
333. *yoshitomii* JÄCH & DÍAZ, 1999
334. *zezerensis* DÍAZ & BILTON, 1995*

## Subgenus *Hydraenopsis* JANSSENS

1. *abdita* d'ORCHYMONT, 1948
2. *abyssinica* RÉGIMBART, 1905
3. *accurata* d'ORCHYMONT, 1948
4. *adrastea* d'ORCHYMONT, 1948
5. *alberti* BALFOUR-BROWNE, 1950
6. *alluaudi* RÉGIMBART, 1906
7. *alternata* PERKINS, 1980
8. *alterra* PERKINS, 1980
9. *ambiflagellata* ZWICK, 1977
10. *anaphora* PERKINS, 1980
11. *anisonycha* PERKINS, 1980
12. *arabica* BALFOUR-BROWNE, 1951
13. *argutipes* PERKINS, 1980
14. *arizonica* PERKINS, 1980
15. *australica* ZWICK, 1977
16. *balfourbrownei* BAMEUL, 1986
17. *barbipes* ZWICK, 1977
18. *barricula* PERKINS, 1980
19. *bergeri* (JANSSENS, 1972)
20. *billi* ZWICK, 1977
21. *bilobata* JÄCH & DÍAZ, 1998
22. *bispinosa* PU, 1951
23. *bituberculata* PERKINS, 1980
24. *blackburni* ZAITZEV, 1908
25. *boetcheri* d'ORCHYMONT, 1932
26. *borbonica* FAIRMAIRE, 1898
27. *bractea* PERKINS, 1980
28. *bractoides* PERKINS, 1980
29. *breedlovei* PERKINS, 1980
30. *brittoni* ZWICK, 1977
31. *browni* PERKINS, 1980
32. *campbelli* PERKINS, 1980
33. *canticacollis* PERKINS, 1980
34. *castanea* DEANE, 1937
35. *chenae* PU, 1951
36. *chiapa* PERKINS, 1980
37. *clavigera* ZWICK, 1977
38. *colombiana* PERKINS, 1980
39. *colymba* PERKINS, 1980
40. *compressipilis* JÄCH & DÍAZ, 1998
41. *concinna* d'ORCHYMONT, 1932
42. *confusa* PU, 1951
43. *connexa* d'ORCHYMONT, 1932
44. *coomani* d'ORCHYMONT, 1932
45. *cooperi* BALFOUR-BROWNE, 1954
46. *cordiformis* JÄCH & DÍAZ, 2000
47. *costiniceps* PERKINS, 1980
48. *cristatigena* JÄCH & DÍAZ, 2000
49. *crystallina* PERKINS, 1980
50. *curtipalpis* JÄCH & DÍAZ, 1998

51. *cuspidicollis* PERKINS, 1980
52. *cyclops* JÄCH & DÍAZ, 2000
53. *cygnus* ZWICK, 1977
54. *d-destina* PERKINS, 1980
55. *debeckeri* (JANSSENS, 1972)
56. *decipiens* ZWICK, 1977
57. *decui* SPANGLER, 1980
58. *delvasi* DELGADO & COLLANTES, 1996
59. *densa* FAUVEL, 1883
60. *dilutipes* FAIRMAIRE, 1898
61. *dimorpha* d'ORCHYMONT, 1922
62. *dinosaurophila* JÄCH, 1994
63. *discicollis* FAIRMAIRE, 1898
64. *eliya* JÄCH, 1982
65. *errina* d'ORCHYMONT, 1948
66. *erythraea* RÉGIMBART, 1905
67. *eryx* d'ORCHYMONT, 1948
68. *evansi* BALFOUR-BROWNE, 1945
69. *exilipes* PERKINS, 1980
70. *extorris* ZWICK, 1977
71. *feuerborni* d'ORCHYMONT, 1932
72. *fijiensis* BALFOUR-BROWNE, 1945
73. *fischeri* SCHÖNMANN, 1991
74. *fontana* d'ORCHYMONT, 1932
75. *formula* d'ORCHYMONT, 1932
76. *geminya* PERKINS, 1980
77. *germaini* d'ORCHYMONT, 1923
78. *grouvellei* d'ORCHYMONT, 1923
79. *guadelupensis* d'ORCHYMONT, 1923
80. *guatemala* PERKINS, 1980
81. *haitiensis* PERKINS, 1980
82. *hamifera* ZWICK, 1977
83. *hunanensis* PU, 1951
84. *hyalina* PERKINS, 1980
85. *hynesi* ZWICK, 1977
86. *iheya* JÄCH & DÍAZ, 1999
87. *impercepta* ZWICK, 1977
88. *impressicollis* FAIRMAIRE, 1898
89. *incurva* d'ORCHYMONT, 1932
90. *indiana* JÄCH, 1994
91. *indica* d'ORCHYMONT, 1920
92. *inopinata* JÄCH & DÍAZ, 1998
93. *insita* d'ORCHYMONT, 1932
94. *insolita* d'ORCHYMONT, 1932
95. *insularis* d'ORCHYMONT, 1945
96. *inusta* d'ORCHYMONT, 1932
97. *iriomotensis* JÄCH & DÍAZ, 1999
98. *isolinae* JÄCH & DÍAZ, 1998
99. *iterata* d'ORCHYMONT, 1948
100. *jacobsoni* d'ORCHYMONT, 1932
101. *janssensi* HANSEN, 1998
102. *jengi* JÄCH & DÍAZ, 1998
103. *jivaro* PERKINS, 1980
104. *kilimandjarensis* RÉGIMBART, 1906
105. *knischi* d'ORCHYMONT, 1928
106. *kwangsiensis* PU, 1951
107. *leechi* PERKINS, 1980
108. *leei* JÄCH & DÍAZ, 1998
109. *limpidicollis* PERKINS, 1980
110. *longicollis* SHARP, 1882
111. *lucernae* ZWICK, 1977
112. *luridipennis* MACLEAY, 1871
113. *maculicollis* CHAMPION, 1920
114. *magna* PU, 1951
115. *magnetica* ZWICK, 1977
116. *mahensis* SCOTT, 1913
117. *malkini* PERKINS, 1980
118. *marginicollis* KIESENWETTER, 1849
119. *maureenae* PERKINS, 1980
120. *mazamitla* PERKINS, 1980
121. *mexicana* PERKINS, 1980
122. *miyatakei* SATÔ, 1959
123. *nevermanni* PERKINS, 1980
124. *newtoni* PERKINS, 1980
125. *oaxaca* PERKINS, 1980
126. *oblio* PERKINS, 1980
127. *okinawensis* JÄCH & DÍAZ, 1999
128. *orchis* JÄCH & DÍAZ, 1998
129. *orcula* PERKINS, 1980
130. *ordishi* DELGADO & PALMA, 1997
131. *ozarkensis* PERKINS, 1980
132. *paeminosa* PERKINS, 1980
133. *paraguayensis* JANSSENS, 1972
134. *particeps* PERKINS, 1980
135. *parva* ZWICK, 1977
136. *paucistriata* JÄCH & DÍAZ, 2000
137. *pavicula* PERKINS, 1980
138. *perkinsi* SPANGLER, 1980
139. *perlonga* BALFOUR-BROWNE, 1950
140. *peru* PERKINS, 1980
141. *pilipes* ZWICK, 1977
142. *plaumanni* d'ORCHYMONT, 1937
143. *plurifurcata* JÄCH & DÍAZ, 1998
144. *pontequula* PERKINS, 1980
145. *porcula* JÄCH & DÍAZ, 1998
146. *premordica* PERKINS, 1980
147. *prieto* PERKINS, 1980
148. *princeps* FAUVEL, 1903
149. *pulsatrix* PERKINS, 1980
150. *punctata* LECONTE, 1855
151. *puncticollis* SHARP, 1882
152. *quadrata* (JANSSENS, 1980)
153. *quadricollis* WOLLASTON, 1864
154. *quechua* PERKINS, 1980

155. *regimbarti* ZAITZEV, 1908
156. *reticulata* ZWICK, 1977
157. *rhinoceros* (JANSSENS, 1972)
158. *ripaeaureae* (JANSSENS, 1972)
159. *robusta* ZWICK, 1977
160. *rudallensis* BLACKBURN, 1896
161. *ruinosa* ZWICK, 1977
162. *sabella* PERKINS, 1980
163. *sahlbergi* d'ORCHYMONT, 1923
164. *satoi* JÄCH & DÍAZ, 1999
165. *sautakei* JÄCH & DÍAZ, 1999
166. *sauteri* d'ORCHYMONT, 1913
167. *scabra* d'ORCHYMONT, 1925
168. *scintilla* PERKINS, 1980
169. *scintillabella* PERKINS, 1980
170. *scintillutea* PERKINS, 1980
171. *scolops* PERKINS, 1980
172. *scopula* PERKINS, 1980
173. *simplicicollis* BLACKBURN, 1896
174. *simplipes* ZWICK, 1977
175. *socius* JÄCH & DÍAZ, 1999
176. *sordida* SHARP, 1882
177. *spangleri* PERKINS, 1980
178. *splecoma* PERKINS, 1980
179. *squalida* d'ORCHYMONT, 1932
180. *szechuanensis* PU, 1951
181. *tenjikuana* SATÔ, 1979
182. *tenuis* (JANSSENS, 1980)
183. *terralta* PERKINS, 1980
184. *thienemanni* d'ORCHYMONT, 1932
185. *thyene* BALFOUR-BROWNE, 1958
186. *trapezoidalis* ZWICK, 1977
187. *tricantha* ZWICK, 1977
188. *trinidensis* PERKINS, 1980
189. *triparamera* JÄCH, 1982
190. *tubuliphallis* JÄCH, 1982
191. *tucumanica* PERKINS, 1980
192. *turrialba* PERKINS, 1980
193. *undulata* JÄCH & DÍAZ, 1998
194. *vela* PERKINS, 1980
195. *victoriae* JÄCH & DÍAZ, 1999
196. *vietnamensis* (JANSSENS, 1972)
197. *vulgaris* JÄCH & DÍAZ, 2000
198. *wangi* JÄCH & DÍAZ, 1998
199. *williamsensis* DEANE, 1931
200. *wittmeri* SATÔ, 1979
201. *youngi* PERKINS, 1980
202. *ypsilon* ZWICK, 1977
203. *yunnanensis* PU, 1942
204. *zapatina* PERKINS, 1980
205. *zelandica* ORDISH, 1984

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