

Head anatomy of Xyelidae (Hexapoda: Hymenoptera) and phylogenetic implications

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Abstract

External and internal head structures of *Macroxyela ferruginea* (Say) and *Xyela julii* (Brébisson) were examined. A detailed description is provided for *Macroxyela*. The results are compared to the conditions found in other basal hymenopterans and representatives of other groups of endopterygote insects. Hitherto unnoticed autapomorphies of Hymenoptera are the concavity of the posterior head capsule, the very dense, regular vestiture of hairs, the collar-like, strongly developed posterior tentorium, and a large epipharyngopharyngeal lobe. Microphagous habits and associated features (asymmetric mandibular molae, epipharyngeal brush, infrabuccal pouch) are possibly groundplan features of Hymenoptera and Endopterygota. A switch to more or less liquefied food took place early in the evolution of Hymenoptera. The sitophore plate and a constricted, elongated prepharyngeal tube are likely synapomorphies of Hymenoptera and Mecoptera. Monophyly of Hymenoptera excluding Xyelidae is supported by the reduction of the mandibular molae and epipharyngeal brush. These changes are likely related to modified feeding habits. Widely separated mandibular bases, the loss of the median labral retractor (parallel loss in Xyelidae), and the presence of a hypostomal bridge are potential apomorphies of Hymenoptera excluding Xyelidae and Tenthredinoidea. Monophyly of Xyelinae and Macroxyelinae, respectively, is well supported by the results of our study. There is conflicting evidence as to whether Xyelidae is monophyletic. The presence of a subdivided galea is a putative autapomorphy of the family. The presence of unsclerotised paraglossae with dense fringes of thin hairs and the presence of a muscle connecting the anterior tentorial arm with the posterior edge of the sitophore plate are features shared by Xyelinae and members of non-xyelid families.

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Introduction

Xyelidae is a small family of herbivorous wasps comprising 82 extant species (Blank 2002). They have a

comparatively well-documented fossil record extending to the Triassic (Rasnitsyn 2002; Grimaldi and Engel 2005), farther back than in any other hymenopteran taxon. Moreover, Xyelidae has been retrieved repeatedly as the sister group of the remaining Hymenoptera in recent phylogenetic treatments of the order (Vilhelmsen 2001; Schulmeister et al. 2002; Schulmeister 2003). Monophyly of the family appears well corroborated by

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these studies. Blank (2002) lists a number of putative autapomorphies, though many of them are questionable (Vilhelmsen 2001). The difficulties in establishing convincing autapomorphies is caused in part by the highly derived state of many characters in Hymenoptera and by the basal position of Xyelidae within the order, resulting in doubtful polarisations of most informative characters at the base of the hymenopteran cladogram. In addition, inclusion of some of the fossil taxa in Xyelidae probably renders the family paraphyletic (Grimaldi and Engel 2005). Regardless of its cladistic status, the inclusion of representatives of the Xyelidae is a must for any study attempting to elucidate groundplan features of the Hymenoptera.

Adult Xyelidae have been observed to feed on pollen (e.g. *Xyela*) and other plant parts such as leaves and buds (*Macroxyela*) (see Jervis and Vilhelmsen 2000; Krenn et al. 2005). Feeding on pollen is at least 140 My old in the family, as documented by the gut contents of an early Cretaceous xyelid (Rasnitsyn 2002, fig. 332). Apparently, the entire mouthpart apparatus of Xyelidae is modified for ingesting pollen (Vilhelmsen 1996; Blank 2002). Many of the features observed in the mouthparts of Xyelidae bear a striking resemblance to those of Micropterigidae (Hannemann 1956). This moth family, members of which also feed on pollen, is the putative sister group of the remainder of Lepidoptera (Kristensen 1999a). Details of the mouthpart apparatus of Xyelidae are illustrated in Vilhelmsen (1996), Jervis and Vilhelmsen (2000), and Blank (2002).

Several studies (Taylor 1931; Matsuda 1957; Dhillon 1966) dealt with the head anatomy in some detail, including musculature, of representatives of the Tenthredinoidea, another basal hymenopteran taxon. Vilhelmsen (1996) treated the musculature associated with the labrum and labium in Xyelidae. However, a comprehensive study of the skeleto-musculature system of the head has been wanting. With the present study, we aim to remedy this to provide additional information about the groundplan of Hymenoptera, which hopefully will help to establish more firmly the phylogenetic position of this morphologically isolated order. Furthermore, we review the information pertaining to the basalmost splitting events within the order, including the cladistic status of Xyelidae.

Material and methods

List of taxa examined

Hymenoptera

Xyelidae: *Macroxyela ferruginea* (Say, 1824), *Xyela julii* (Brébisson, 1818)

Tenthredinidae: *Tenthredo vespa* Retzius, 1783

Diprionidae: *Gilpinia frutetorum* (Fabricius, 1793)

Argidae: *Arge* sp.

Pamphiliidae: *Onycholyda luteicornis* (Norton, 1869)

Siricidae: *Urocerus gigas* (Linnaeus, 1758)

Vespidae: *Vespula vulgaris* (Linnaeus, 1758)

Strepsiptera

Mengenillidae: *Mengenilla* sp., *Eoxenos laboulbenei* de Peyerimhoff, 1919

Mecoptera

Panorpidae: *Panorpa communis* (Linnaeus, 1758)

Boreidae: *Boreus hyemalis* (Linnaeus, 1758)

Diptera

Tipulidae: *Tipula* spp.

Culicidae: *Culex* sp.

Bibionidae: *Bibio* sp.

Megaloptera

Sialis spp.

Neuroptera

Chrysopidae: *Chrysopa* sp.

Myrmeleontidae: undetermined species from Argentina

Raphidioptera

Raphidiidae: *Xanthostigma xanthostigma* (Schummel, 1832)

Specimens of *Macroxyela ferruginea* and *Xyela julii* were fixed in Bouin's fluid and stored in 70% ethanol. Skeletal preparations of the head were made after maceration in KOH. For the reconstruction of musculature, digestive tract, endoskeleton and brain, serial cross sections and longitudinal sections were made. The specimens were embedded in Araldit[®], cut at 1 µm with a Microm microtome (HM 360), and the Azan-staining technique was applied.

Additional specimens were cleaned with ultrasound, and sputter-coated with gold for scanning electron microscopy. Pictures were taken with an FEI scanning electron microscope (XL 30 ESEM).

Drawings were made with a camera lucida or with an ocular grid, and processed and evaluated with Adobe Photoshop[®] and Macromedia Freehand[®] software. AnalySIS[®] software was used for the documentation of serial sections and slide preparations.

Muscle terminology follows von Kéler (1963).

Results

Head morphology of *Macroxyela ferruginea*

External head capsule (Fig. 1)

The head is orthognathous and not retracted into the prothorax. It articulates with a well-developed lateral cervical sclerite, which is partly fused with the

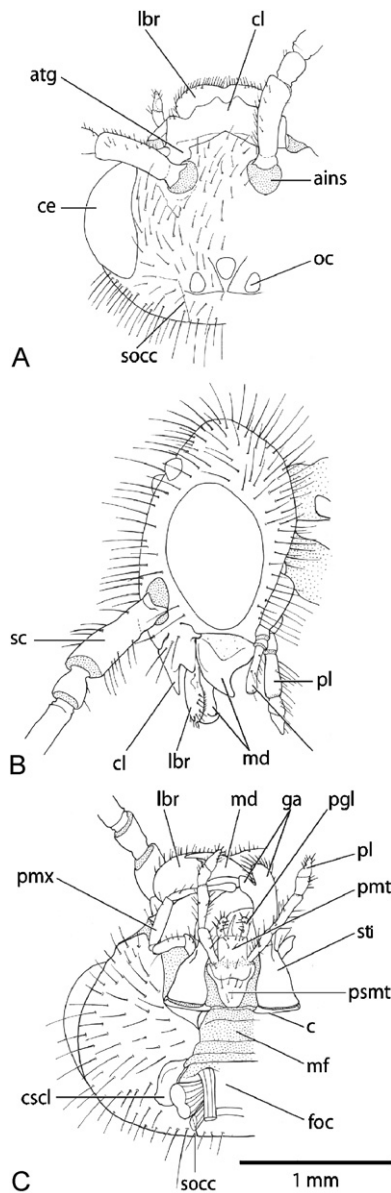


Fig. 1. *Macroxyela ferruginea*; head: (A) frontal view; (B) lateral view; (C) posterior view. Abbreviations: ains = antennal articulatory area, atg = anterior tentorial groove, c = cardo, ce = compound eye, cl = clypeus, cscl = cervical sclerite, foc = foramen occipitale, ga = galea, lbr = labrum, md = mandible, mf = membranous fold, oc = ocellus, pgl = paraglossa, pl = palpus labialis, pmt = prementum, pmx = palpus maxillaris, psmt = postmentum, sc = scapus, socc = occipital sulci, sti = stipes.

propleuron posteriorly. The foramen occipitale is narrow, but a postgenal bridge is absent (Fig. 1C). The head capsule is distinctly compressed antero-posteriorly, distinctly broader than long, and evenly rounded laterally and posterolaterally. The posterior surface is slightly concave. The thin cuticle is strongly sclerotised and densely covered with regularly distributed long, fine setae (Fig. 1), which are inserted in distinct pores. Most parts are shiny, of green-metallic colour, and slightly rugulose; dorsal areas between the compound eyes are brownish; the clypeus is yellow. The compound eyes are very large, with numerous ommatidia. Three well-developed ocelli are present; the median ocellus is slightly larger than the slightly elevated lateral ones, and enclosed by oblique ridges. The clypeus is separated from the frons by a very distinct frontoclypeal suture, which encloses a trapezoid area anterior of and between the antennal insertions (Fig. 1A). It is plate-like and of roughly trapezoidal shape, with parallel lateral margins, anterolateral convexities, and a distinct anteromedian incision; it is inflected anteriorly with a sharp secondary anterior edge. The coronal, frontal and genal sutures are absent. A posteriorly widening membranous area closes the space between the large articulation area of the retracted ventral mouthparts and the foramen occipitale (Fig. 1C). Occipital sulci are distinctly present; they converge above the foramen occipitale and diverge again on the frontal side of the head; anteriorly they reach the lateral ocelli.

Cephalic endoskeleton (Figs. 5B, C, 6)

Laterally, the foramen occipitale is enclosed by a low but distinct postoccipital ridge. The ridge is continuous dorsally with the occipital ridges corresponding to the occipital sulci, ventrally with the very broad and strongly sclerotised tentorial bridge and the broad posterior tentorial arms, and with a low ridge delimiting the maxillary groove posterolaterally. The posterior arms and the bridge together form a very extensive and strongly sclerotised collar-like structure, which stands approximately vertical relative to the posterior head surface. The dorsal tentorial arms are flattened and moderately broad; apically they are fused with the dorsal wall of the head capsule. The anterior arms are very strongly developed, broadened, with a medially directed rounded extension; they arise from very large anterior tentorial grooves between the lateral margin or the anteromedian part of the frons and the adjacent posterior part of the clypeus, anterior to the antennal insertion.

Labrum (Figs. 1A, 2B, C; Table 1)

The free labrum is connected with the clypeus by an internal membranous fold. It is broad, laterally rounded and slightly emarginated anteromedially. The anterior and lateral margins are set with moderately long hairs.

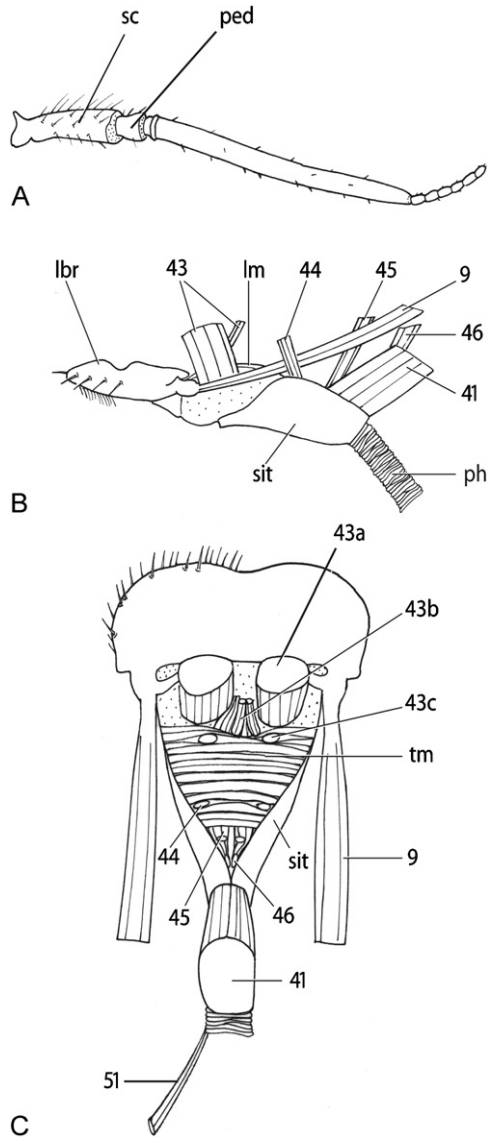


Fig. 2. *Macroxyela ferruginea*; antenna, labrum and foregut: (A) antenna; (B) labrum, prepharynx and pharynx; lateral view; (C) labrum, prepharynx and pharynx; anterior view. Abbreviations: lbr = labrum, lm = longitudinal muscle, ped = pedicellus, ph = pharynx, sc = scapus, sit = sitophore plate, tm = transverse muscle, 9 = *M. frontoepipharyngalis*, 41 = *M. frontohypopharyngalis*, 43a–c = subcomponents of *M. clypeopalatalis*, 44 = *M. clypeobuccalis*, 45 = *M. frontobuccalis anterior*, 46 = *M. frontobuccalis posterior*, 51 = *M. verticopharyngalis*.

Tormae are present at the dorsal margin, slightly mesad of the posterolateral edge; beyond a short basal part they are divided into a shorter, posteriorly directed process and a longer, anteromesally directed rod. A small brush of dense setae associated with the left torma is situated submedially.

Musculature (Figs. 6, 7C, D). Musculus (M.) labroepipharyngalis (M. 7) strongly developed, composed of numerous bundles; origin (O) in central region of

external wall of labrum, insertion (I) medial on ventral wall of labrum, posterior part between anteromesal rods of tormae. *M. frontolabralis* (M. 8) absent. *M. frontoepipharyngalis* (M. 9): O in frontal region, anterior to *M. frontohypopharyngalis* (M. 41) and *M. frontopharyngalis anterior* (M. 45); I on posterolateral edge of labrum, on basal part of tormae. *M. epistomolabralis* (M. 10) absent.

Antenna (Figs. 1A, 2A)

The antenna is inserted in a moderately sized membranous articulatory area on the anterior side of the head capsule, close to the posterior clypeal margin. The distance between the articulatory areas is about 1.5 times their diameter. The large scapus is about 3.5 times as long as wide; the radicle is separated from the elongated distal part by a distinct incision; a distinct anterior notch articulates with a narrow and pointed articulatory process of the head capsule. The pedicellus is short and slightly widened distally. The extremely elongated third antennomere is almost 3 times as long as the scapus and more than 8 times as long as the pedicellus; a short basal part is separated from the rest by a distinct circular ridge. The following six antennomeres are very small and together about as long as the scapus. Longer hairs are present on the scapus, very short hairs on the long third segment and the small distal antennomeres. Multiporous plate sensilla are absent.

Musculature (Figs. 5C, 6, 7D, 8A; Table 1) strongly developed. *M. tentorioscapalis anterior* (M. 1) large; origin (O) on upper surface of anterior part of anterior tentorial arm, insertion (I) anterolateral on scapal base. *M. tentorioscapalis posterior* (M. 2) large; O mesal from proximal part of dorsal tentorial arm and mesal from posterior part of anterior arm; I posterior on scapal base. *M. tentorioscapalis lateralis* (M. 3) moderately sized; O lateral from proximal part of dorsal tentorial arm and lateral from posterior part of anterior tentorial arm; I posterolateral on scapal base, distinctly separated from M. 1. *M. tentorioscapalis medialis* (M. 4) large; O on anterior tentorial arm, anteromesad to M. 1; I mesal at articulatory scapal base. *M. scapopedicellaris lateralis* (M. 5) well developed; O posteromesal on proximal part of scapus; I lateral on base of pedicellus. *M. scapopedicellaris medialis* (M. 6) smaller than M. 5; O on anterolateral wall of scapus; I mesal on base of pedicellus.

Mandibles (Figs. 1B, 3, 7A, B)

The mandibles have two articulations with the head capsule (Fig. 7A). They are conspicuously asymmetrical, with the right mandible distinctly broader at its base. The proximolateral parts of the mandibles are not strongly sclerotised and largely unpigmented (Fig. 1B). The distal part is fairly slender and acuminate at its

Table 1. Head muscles of Xyelidae and representatives of other insect groups, part 1: Appendages

Muscle	Taxon (reference)	<i>Macroxylela</i>	<i>Xyela</i>	<i>Macrophya</i> (Matsuda 1957)	<i>Pteronidea</i> (Taylor 1931)	<i>Tentredo</i>	<i>Zorotypus</i> (Beutel and Weide 2005)	<i>Rhyacophila</i> (Klemm 1966)	<i>Micropteryx</i> (Hannemann 1956)	<i>Panorpa</i> (Heddergott 1938)	<i>Mengenilla</i> (Beutel and Pohl 2005)	<i>Priacma</i> (Hörnshemeyer et al. 2002)	<i>Sialis</i> (Röber 1942)	<i>Chaetiodex</i> (Maki 1936)	<i>Agulla</i> (Matsuda 1956)
1. M. tent.-scap. ant.	++	++	19?	+	+	+	+	1	+	+	+	+	+	6	6
2. M. tent.-scap. post.	++	+	20?	+	+	+	+	2	+	+	+	+	+	4	7
3. M. tent.-scap. lat.	+	+	–?	–?	+	–	+	3?	–	–	–	–	–	–	–
4. M. tent.-scap. med.	++	+	21?	+	+	+	+	4	+	+	+	+	+	5	8
5. M. scapoped. lat.	+	+	22	+	+	+	+	5, 6	+	+	+	+	+	7	9
6. M. scapoped. med.	+	+	23	+	+	+	+	7, 8	+	+	+	+	+	8	10
7. M. labroepipharyngalis	++	+	3, 4	–?	+	+	–?	21	+	–	+	+	+	1	1, 2
8. M. frontolabralis	–	–	1	–?	+	+	–	–	–	–	–	+	+	2	3
9. M. frontoepipharyngalis	+	+	2	+	+	+	+	19 ^a	–	–	–	–	Mt	3	4
10. M. epistomolabralis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
11. M. craniomand. int.	+	+	22	+	+	+	+	22	+/4	+	+	+	+/2	9	12
12. M. craniomand. ext.	+	+	23	+	+	+	+	23	+	+	+	+	+	10	11
13. M. hypopharyngo-mand.	+	–?	–	–?	?	+	–	–	–?	–	–	–	?	11	–?
14. M. zygomat. mand.	–	–	–	–	?	–	–	–	–	–	–	–	–	–	–
15. M. craniocard. ext.	+	+	?	?	?	+	+	24	–	–	+	+	+	12	15, 16
16. M. craniocard. int.	–	–	–	–	?	–	–	–	–	–	–	–	–	–	–
17. M. tent.-card.	+	+	25	+	+	+	+	26	+	–	+	+	+	13	13
18. M. tent.-stip.	++	+	26?	?	+	+/2	+	27, 29?	+	–	+	+	+	14	14
19. M. craniolacinalis	+	+	?	+	?	+	+	25, 29?	+/2?	–	+	+	+	15	–?
20. M. stipitolacinalis	+	–	27	+	?	+	+	28	–	–	–	–	+	16	19
21. M. stipitogalealis	+/2	+	30	+	+	+	–	30	–	–	–	–	+	17	21
22. M. stipitopalpalis ext.	+	+	29	+	+	+	+	32	+	–	22/ 23	+	+	19	20
23. M. stipitopalpalis int.	+	+	28	+	+	+	+	31	–	–	–	–	+	18	–
24. M. palpopalp. max. prim.	+	+	31	+	+	+	+	33	+	–	–	–	–	20–21	22–23
25. M. palpopalp. max. sec.	+	+	32	+	?	+	+	34	+	–	–	–	–	22–23	24
26. M. palpopalp. max. tert.	+	+	33	+	?	+	+	35	+	–	–	–	–	24–25	25
27. M. palpopalp. max. quart.	+	–?	34	–?	?	+	+	36	–	–	+	?	–	26–27	26, 27?
28. M. submentopraem.	+	+	38	+	?	+/2	+	41	+	–	+	+	+	29	29
29. M. tent.-praem. inf.	+	+	36	+	+	+	+	40	–	–	+	+	+	30	28
30. M. tent.-praem. sup.	+	+	37	+	+	+	+	39	–	–	+	+	+	31	35
31. M. praementoparaglossalis	++	+	39	?	++	+	+	37	–	–	31/32	–	–	–	–
32. M. praementoglossalis	+	+	41	?	++	+	–	38	–	–	–	–	–	–	–
33. M. praementopalpalis int.	+	+	40	+	+	+	+	42	–	–	–	–	–	–	–
34. M. praementopalpalis ext.	+	+	42	+	+	+/2	+	43	+	–	+	32	32	32	30
35. M. palpopalp. lab. prim.	+	+	44, 45	+	+	+	–?	44	–	–	+	33	33	33	31
36. M. palpopalp. lab. sec.	+	+	46, 47	+	?	+	–?	–	–	–	+	34	34	34	32–34?

Muscle numbers in far left column (also used in the descriptive texts) adopted from v. Kéler (1963), numbers or letters in other columns were introduced by other authors; – = absent, + = present, ++ = unusually large.

^aWith lateral origin (2 separate bundles).

^bDegenerated or reduced in most specimens.

apex. On the right mandible, a mesal groove is enclosed by a blade-like cutting edge on the posterior side and four subapical teeth on the anterior side. The molar part is strongly protruding, with a fairly deep concavity enclosed by a curved edge on the posterior side and a serrate ridge on the anterior side; the serrate edge ends with a posteriorly directed pointed tooth. The basal part of the mola is covered with very small pointed tubercles

on the anterior side. The subapical teeth on the left mandible differ strongly from those of the right mandible. The tooth following the mandibular apex is fairly large and the mesal edge is serrate. The following four teeth are small and arranged on one prominence. The large tooth distal to the mola bears a small subapical projection. The mola is much less prominent. An edge is present posteriorly, a large serrate projection

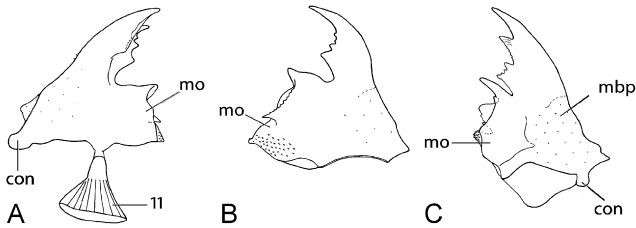


Fig. 3. *Macroxyela ferruginea*; mandibles: (A) right mandible, posterior view; (B) right mandible, anterior view, part of base removed; (C) left mandible, posterior view. Abbreviations: con = condyle (primary joint), mbp = membranous basal part, mo = mola, 11 = *M. craniomandibularis internus*.

anterodistally, and a smaller projection, which is covered with spine-like tubercles, proximally.

Musculature (Figs. 5B, 6–8; Table 1). *M. craniomandibularis internus* (*M. 11*), the largest muscle of the head capsule, composed of numerous fibres; origin (*O*) in large areas of dorsal and posterodorsal wall of head capsule, insertion (*I*) at strongly developed adductor tendon. *M. craniomandibularis externus* (*M. 12*): *O* posterolateral of head capsule; *I* at abductor tendon. *M. hypopharyngo-mandibularis* (*M. 13*) extremely thin, composed of 3 fibrillae; *O* ventrolateral from anterior part of anterior tentorial arm; *I* dorsomesal on inner surface of mandible. *M. zygomaticus mandibulae* (*M. 14*) absent.

Maxillae (Figs. 1C, 4A, 5C, 7)

The maxillae and the labium form a functional unit. Both parts are closely connected by a narrow membranous area. A mesal articulatory membrane is not developed. The labio-maxillary complex is strongly retracted; it is separated from the foramen occipitale by a broad membranous area. The cardo is short and triangular and almost vertically oriented. It is broadly connected with the stipes by a narrow articulatory membrane. The stipes is the largest part of the maxilla. It is not divided into basistipes and mediostipes, and slightly narrowing towards the maxillary appendages. The 5-segmented palp is inserted laterally; palpomere 1 is short and curved; palpomere 2 is c. 2.5 times as long as 1; it is followed by a very small, wedge-shaped palpomere 3 resembling a trochanter; palpomere 3 is about 1.5 times as long as 2; palpomere 4 is slightly longer than 2 and 3 together; palpomere 5 is strongly elongated, and slightly narrowed in the middle section. The galea is fused with the stipes, strongly elongated and apically divided into two lobes by a deep narrow cleft; the lateral lobe carries mesally directed long spines. The lacinia is about half as long as the galea and arises from the stipes anteromesally; it is flat, distally widening and apically truncate: the apical margin is densely set with spines.

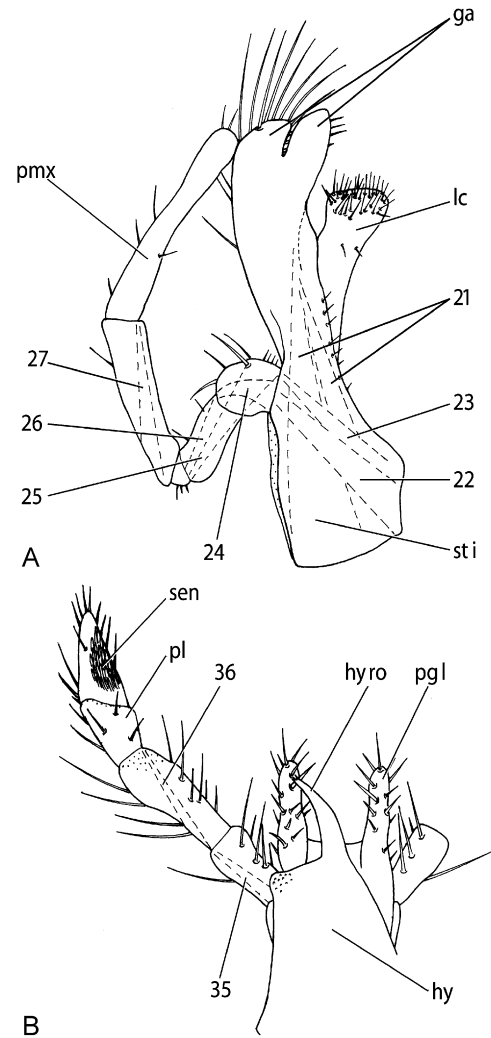


Fig. 4. *Macroxyela ferruginea*; maxilla, labium and hypopharynx: (A) maxilla; posterior view, cardo removed; (B) labium and hypopharynx; anterior view. Abbreviations: ga = galea, hy = hypopharynx, hyro = hypopharyngeal rod, lc = lacinia, pgl = paraglossa, pl = palpus labialis, pmx = palpus maxillaris, sen = field of sensilla, sti = stipes, 21 = *M. stipitogalealis*, 22/23 = *M. stipitopalpalis ext./int.*, 24 = *M. palpopalpalis max. prim.*, 25 = *M. palpopalpalis max. sec.*, 26 = *M. palpopalpalis max. tert.*, 27 = *M. palpopalpalis max. quart.*, 35 = *M. palpopalpalis lab. prim.*, 36 = *M. palpopalpalis lab. sec.*

Musculature (Figs. 4A, 5C, 6, 7; Table 1). *M. craniocardinalis externus* (*M. 15*) flat, triangular; origin (*O*) posteromesal from head capsule, posteromesad to attachment area of *M. 19* and above foramen occipitale (see above), insertion (*I*) lateral on base of cardo by means of a thin tendon. *M. craniocardinalis internus* (*M. 16*) absent. *M. tentoriocardinalis* (*M. 17*) moderately sized; *O* mesal from ventral surface of posterior part of anterior tentorial arm, close to origin of posterior subcomponent of *M. tentoriostipitalis*; *I* lateral on inner surface of cardo and at a ridge along

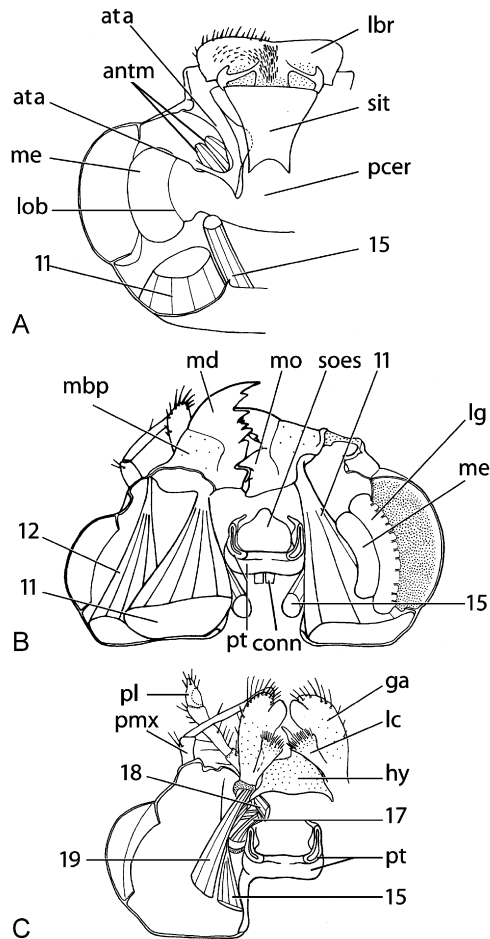


Fig. 5. *Macroxyela ferruginea*; head: (A) horizontal section, anterior part, mandibles removed; (B) horizontal section, posterior part, maxillary muscles partly omitted; (C) horizontal section, posterior part, mandibles removed. Abbreviations: antm = antennal muscles, ata = anterior tentorial arm, conn = connective, ga = galea, hy = hypopharynx, lbr = labrum, lc = lacinia, lg = lamina ganglionaris, lob = lobula, mbp = membranous basal part, md = mandible, me = medulla, mo = mola, pcer = protocerebrum, pl = palpus labialis, pmx = palpus maxillaris, pt = posterior tentorium, sit = sitophore plate, soes = suboesophageal ganglion, 11 = M. craniomandibularis internus, 12 = M. craniomandibularis externus, 15 = M. craniocardinalis, 17 = M. tentoriocardinalis, 18 = M. tentoriostipitalis, 19 = M. craniolacinialis.

its anterior margin. M. tentoriostipitalis (M. 18) composed of four strong subcomponents; O on ventral side of posterior part of anterior tentorial arm, anterad to M. 17; I on inner surface of posterior stipes (M. 18a), inner surface of the anterior stipes (M. 18b), lateral on membrane connecting stipes with head capsule (M. 18c), and on a low ridge at anteromesal margin of stipes (M. 18d). M. craniolacinialis (M. 19) flat; O on posterior wall of head capsule, anteromesad of attachment area of M. craniomandibularis externus (M. 12); I on basal edge of lacinia, without tendon. M. stipitolacinialis (M. 20)

well developed; O lateral on inner surface of stipes, laterad to attachment of M. 18b; I on base of lacinia, close to insertion of M. 19. M. stipitogalealis (M. 21) composed of two bundles: M. 21a well developed; O on ventromesal surface of stipes, anterior to M. 22 and very close to M. 23, I on base of inner lobe of galea; M. 21b with O mesal on stipes, very close to M. 22, I on a thin tendon; attachment of tendon not clearly identified, probably together with M. 21a. M. stipitopalpalis externus (M. 22): O on inner surface of anteromesal stipes; I posterior on base of palpomere 1. M. stipitopalpalis internus (M. 23): O anterior to M. stipitopalpalis externus; I anterior on base of palpomere 1. M. palpopalpalis maxillae primus (M. 24): O on base of palpomere 1; I mesal on base of palpomere 2. M. palpopalpalis secundus (M. 25): O on anterior margin of palpomere 1; I lateral on vestigial palpomere 3. M. palpopalpalis tertius (M. 26): O on base of palpomere 2; I on base of palpomere 3. M. palpopalpalis quartus (M. 27): O lateral on basal part of palpomere 4; I mesal on base of palpomere 5.

Labium (Figs. 1C, 4B, 6, 7)

Inserted between stipes and connected with them by a membrane. Composed of a small, posteriorly rounded postmentum and a slightly broader, well-developed prementum. The 3-segmented palp is inserted laterally on the prementum, distinctly posterior to its anterior margin; the palpomeres are elongate and about equally long; palpomere 3 is spindle-shaped; the setation is shown in Figs. 1C, 4B, and 6; palpomere 3 is subdivided by a transverse, weakly sclerotised zone (see Vilhelmsen 1996, fig. 8A) into roughly equal parts, but they are not connected by muscles; a concavity accommodating numerous short sensillae is situated subapically on the distal part of palpomere 3. Curved, palp-like paraglossae insert at the anterolateral edge of the prementum; they are equipped with strong spines. A glossa is not developed; the anterior premental margin between the paraglossae is straight.

Musculature (Figs. 6, 7; Table 1). M. submentopraementalis (M. 28): origin (O) posteromedial on posterior margin of postmentum; insertion (I) medial on posterior margin of prementum. M. tentoriopraementalis inferior (M. 29): O lateral from posterior part of anterior tentorial arm, below attachment of posterior antennal muscles and posterior to origin of M. 17; I ventrolateral on posterior margin of prementum, laterad of M. 28. M. tentoriopraementalis superior (M. 30): O mesal at base of tentorial bridge; I dorsolateral on anterior part of prementum. M. praementoparaglossalis (M. 31), M. praementoglossalis (M. 32) well developed; O medial from posterior premental margin; I on mesal margin of paraglossa and anterior wall of prementum. M. praementopalpalis internus (M. 33) absent. M. praementopalpalis externus (M. 34): O lateral from ventral wall of

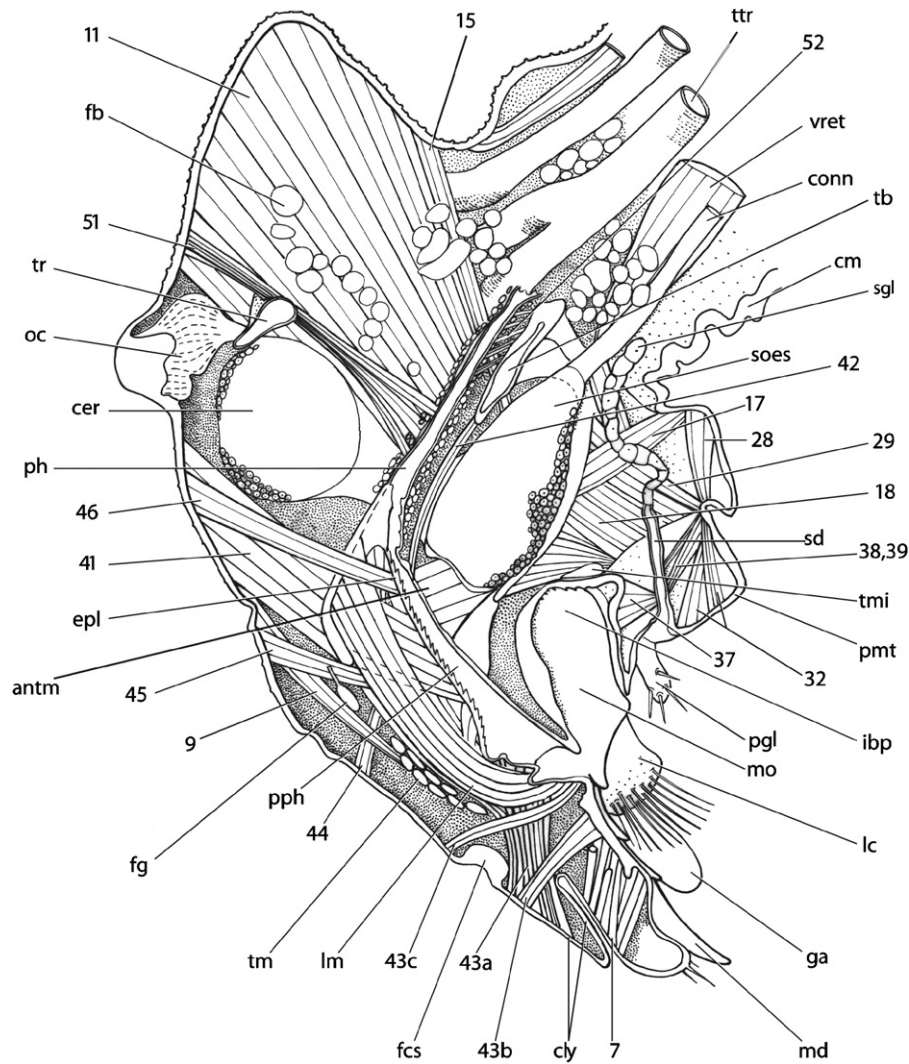


Fig. 6. *Macroxyela ferruginea*; head, sagittal section. Abbreviations: antm = antennal muscles, cly = clypeus, cer = cerebrum, cm = cervical membrane, conn = connectives, epl = epipharyngopharyngeal lobe, fb = fat body, fcs = frontoclypeal suture, fg = frontal ganglion, ga = galea, ibp = infrabuccal pouch, lc = lacinia, lm = longitudinal muscle, md = mandible, mo = mola, oc = ocellus, pgl = paraglossa, ph = pharynx, pmt = prementum, pph = prepharynx, sd = salivary duct, sgl = salivary gland, soes = suboesophageal complex, tb = tentorial bridge, tm = transverse muscle, tmi = transverse muscle of infrabuccal pouch, tr = trachea, ttr = tracheal trunk, vret = ventral retractor of head, 7 = *M. labroepipharyngalis*, 9 = *M. frontoepipharyngalis*, 11 = *M. craniomandibularis int.*, 15 = *M. craniocardinalis*, 17/18 = *Mm. tentorio-cardinalis/-stipitalis*, 28 = *M. submentopraementalis*, 29 = *M. tentoriopraementalis inf.*, 32 = *M. praementoglossalis*, 37 = *M. hypopharyngosalivaris*, 38/39 = *Mm. praementosalivaris ant./post.*, 41 = *M. frontohypopharyngalis*, 42 = *M. tentoriohypopharyngalis*, 43a–c = components of *M. clypeopalatalis*, 44 = *M. clypeobuccalis*, 45/46 = *Mm. frontobuccalis ant./post.*, 51 = *M. verticopharyngalis*, 52 = *M. tentoriharyngalis*.

prementum; I lateral on base of palpomere 1. *M. palpopalpalis labii primus* (*M.* 35): O on base of palpomere 1; I lateral on base of palpomere 2. *M. palpopalpalis labii secundus* (*M.* 36): O on lateral wall of palpomere 2; I mesal on base of palpomere 3.

Epipharynx (Figs. 5A, 6, 7)

The ventral semimembranous epipharynx (posterior wall of labrum) bears a very dense, slightly asymmetrical median field of dorsally directed macrotrichiae (epihar-

yngeal brush), and areas with shorter hairs arranged in a semicircle lateral to it (Fig. 5A). The dorsal (postlabral) epipharynx forms a very large, prominent buccal lobe which is fused with the dorsolateral edge of the sclerotised hypopharynx (= sitophore plate), thus forming a closed, elongated tube (= prepharynx), which is approximately U-shaped in cross section. The posterolateral edges of the sitophore plate are strongly bent upwards and adjacent in the midline. The surface of the buccal lobe is densely covered with dorsally directed,

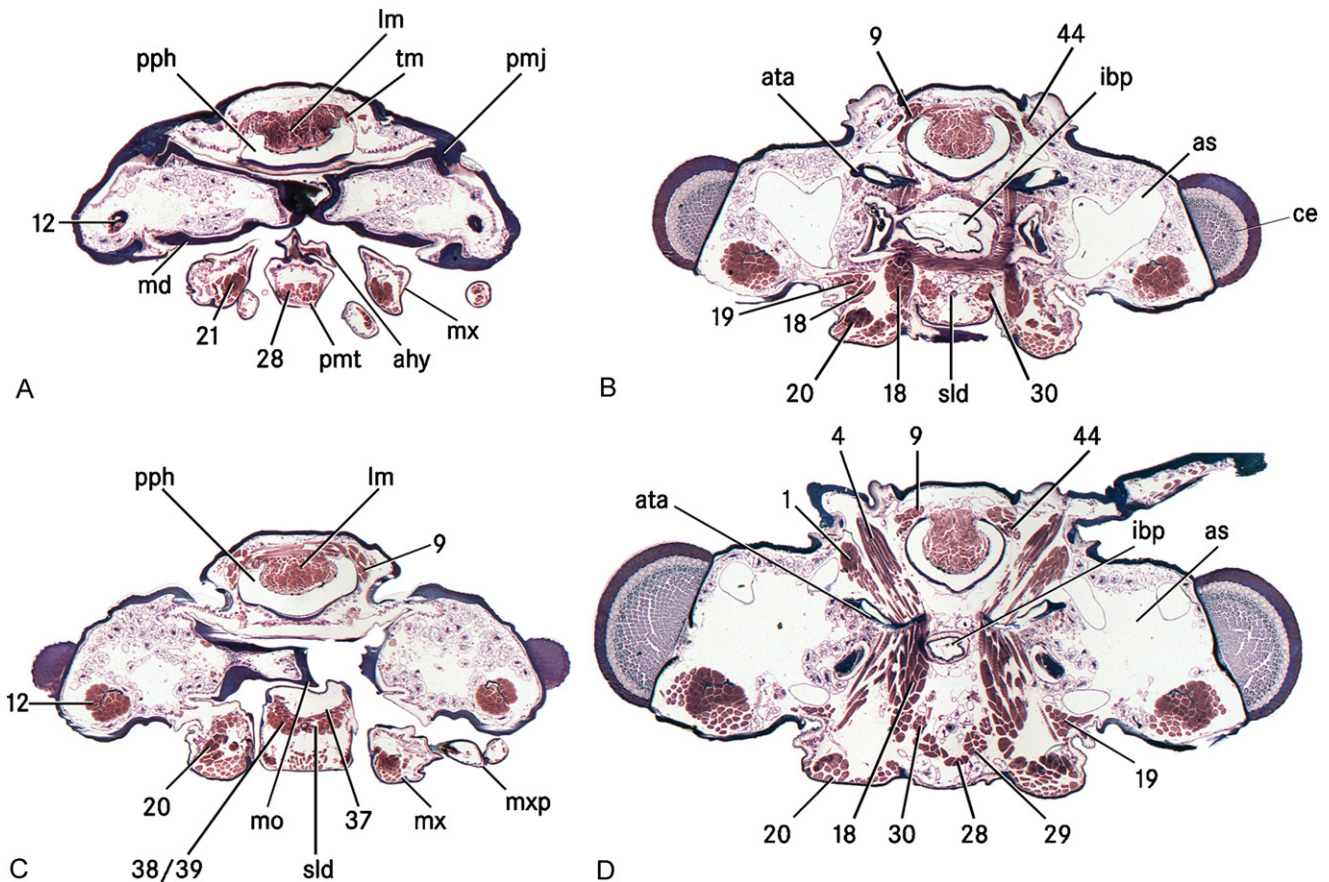


Fig. 7. *Macroxyela ferruginea*; head, cross sections: (A) clypeal region; (B) anterior frontal region; (C) anterior prepharyngeal region; (D) posterior prepharyngeal region. Abbreviations: ahy = anterior hypopharynx, as = airsac, ata = anterior tentorial arms, ce = compound eye, ibp = infrabuccal pouch, lm = longitudinal muscle, md = mandible, mo = mola, mx = maxilla, mxp = maxillary palp, pmj = primary mandibular joint, pmt = prementum, pph = prepharynx, sld = salivary duct, tm = transverse muscle, 1/4 = Mm. tentorioscapalis ant./med., 9 = M. frontoepipharyngalis, 12 = M. craniomandibularis ext., 18 = M. tentoriostipitalis, 19 = M. craniolacinalis, 20 = M. stipitolacinalis, 21 = M. stipitogalealis, 28 = M. submentopraementalis, 29/30 = Mm. tentoriopraementalis inf./sup., 37 = M. hypopharyngosalivaris, 38/39 = Mm. praementosalivaris ant./post., 44 = M. clypeobuccalis.

non-articulated spine-like structures ventrally, laterally and dorsolaterally. Fairly long, sclerotised, paired processes reach into the pharyngeal tube dorsally. Considering the attachment of the anterior and posterior frontobuccal muscles (Mm. 45, 46; see below), we assume that the anterior pharynx also forms part of this conspicuous structure.

Musculature (Figs. 2B, 6; Table 2). *M. clypeopalatalis* (M. 43) strongly developed, composed of many fibres and two subcomponents: M. 43a with origin (O) in central region of clypeus and insertion (I) on ventral epipharynx; M. 43b thin, composed of few fibres running parallel to longitudinal muscle of cibariopharyngeal lobe, with O on dorsal margin of clypeus, dorsal to main component of *M. clypeopalatalis*, and I posterolateral on sitophore plate.

A thin muscle which arises from the ventral frons and is attached to the ventral epipharynx (Fig. 6) probably is a part of *M. clypeopalatalis*, which has shifted its origin (M. 43c). An extremely strong longitudinal muscle

(Fig. 6: lm) connects the ventral epipharynx with the sclerotised dorsal edge of the sitophore plate (below the attachment of *M. frontopharyngalis* = M. 41), the dorsal parts of the lobe, and with the dorsal side of the anterior pharynx. A very large transverse muscle connects the upper edges of the anterior part of the sitophore plate (Fig. 6: tm), which encloses the lobe.

Salivarium and salivary glands (Figs. 6, 7B)

The small, tube-like salivary glands enter the narrow salivary duct at the level of the postmento-mental suture. The posterior part of the duct is fully sclerotised, whereas the upper side is membranous at the attachment area of *M. praementosalivaris* anterior. It opens between the upper premental surface and the ventral part of the hypopharynx.

Musculature (Figs. 6, 7B; Table 2). *M. hypopharyngosalivaris* (M. 37): origin (O) dorsolateral from anterior part of hypopharynx; insertion (I) dorsolateral on salivary duct. *M. praementosalivaris* anterior and

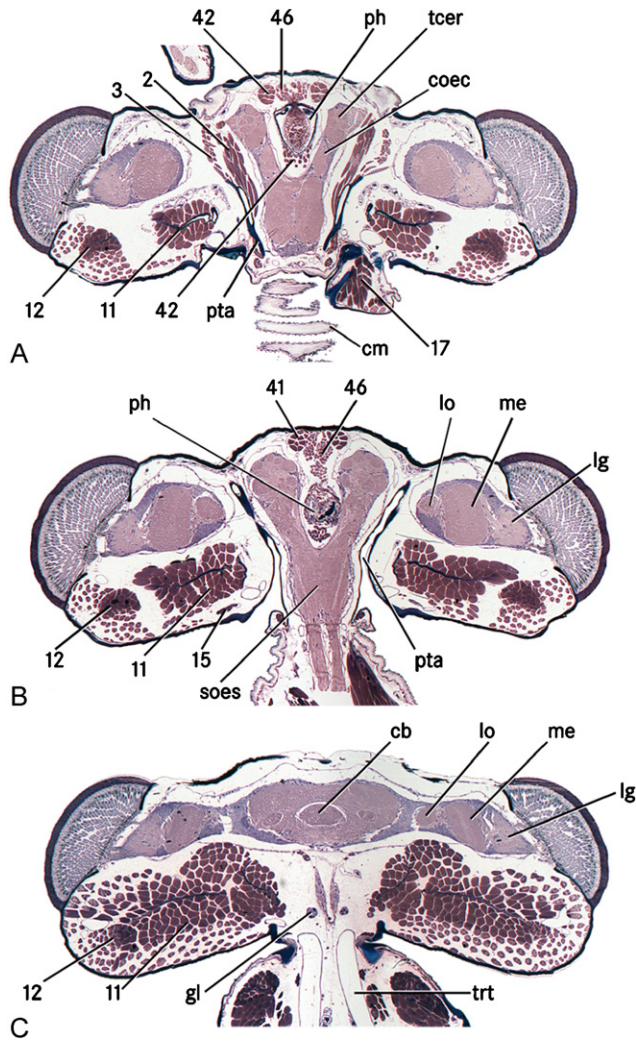


Fig. 8. *Macroxyela ferruginea*; head, cross sections: (A) anterior neck region; (B) middle neck region; (C) posterior neck region. Abbreviations: cb = central body, cm = cervical membrane, coec = circumoesophageal connective, gl = gland, lg = lamina ganglionaris, lo = lobula, me = medulla, pta = posterior tentorial arm, ph = pharynx, soes = suboesophageal complex, tcer = tritocerebrum, trt = tracheal trunk, 2/3 = Mm. tentorioscapalis post./lat., 11/12 = Mm. craniomandibularis int./ext., 15 = M. craniocardinalis, 17 = Mm. tentorio-cardinalis, 41 = M. frontohypopharyngalis, 42 = M. tentoriohypopharyngalis, 46 = M. frontobuccalis post.

posterior (M. 38, 39) of two bundles with a common origin but slightly separated points of insertion: O ventrolateral on posterior prementum; I ventrolateral on sclerotised part of salivary duct. M. annularis salivarii (M. 40) reduced; it cannot be ruled out that a thin layer of tissue around the anteriormost part of the salivary duct represents a vestigial M. annularis salivarii.

Hypopharynx (Figs. 4B, 6, 7A, B)

The anteroventral part of the hypopharynx is represented by a small, asymmetrical, semimembranous

structure with a curved blade-like rod above the opening of the salivary duct. The large anterodorsal part forms the wall of a deep infrabuccal pouch (Figs. 6, 7C, D), which functions as working space for the molar parts of the mandibles (Fig. 6). Cuticular teeth are arranged in transverse rows on its surface. The ventral margin of the anterior wall of the infrabuccal pouch forms a sharp edge (Fig. 6). The proximal part of the hypopharynx is laterally fused with the epipharynx and forms a large, trough-like, sclerotised structure (= sitophore plate; see above), which encloses the large buccal lobe (Figs. 2B, C, 5A, 6). Paired dorsolateral sclerotised processes of the sitophore plate reach deeply into the pharynx (Figs. 6, 8B).

Musculature (Figs. 2B, 6, 8A, B; Table 2). M. frontohypopharyngalis (M. 41) strong; origin (O) on frons, anterior to median ocellus; insertion (I) on sclerotised posterolateral edge of sitophore plate. M. tentoriohypopharyngalis (M. 42): O on tentorial bridge; I ventromedial on posterior part of sitophore plate.

The ventrolateral edges of the infrabuccal pouch are connected by numerous thin transverse fibrillae without the typical structure of cross-striated muscle fibres. The homology is unclear.

Pharynx and oesophagus (Figs. 2B, 6, 8A, B)

The pharynx is very strongly folded in longitudinal direction; the lumen is very narrow (Figs. 6, 8A, B). The anterior part probably forms a structural complex with the dorsal epipharynx (see above: epipharyngopharyngeal lobe).

Musculature (Figs. 2B, 6, 8A, B; Table 2). M. clypeobuccalis (M. 44) moderately sized; origin (O) dorsal on clypeus, ventral to antennal insertion. M. frontobuccalis anterior (M. 45) well developed; O on frons, anteromesad of M. 41; insertion (I) dorsolateral on dorsal part of cibariopharyngeal lobe. M. frontobuccalis posterior (M. 46) well developed; O on frons, anterior to cerebrum and mesad of M. 41; I on dorsal part of cibarial lobe. M. frontobuccalis lateralis (M. 47) absent. M. tentoriobuccalis anterior (M. 48) absent. M. tentoriobuccalis lateralis (M. 49) absent. M. tentoriobuccalis posterior (M. 50) absent. M. verticopharyngalis (M. 51): O dorsal on frons, posterior to ocelli; I dorsal on postcerebral pharynx. M. tentoriopharyngalis (M. 52) composed of numerous thin fibrillae; O on basal part of posterior tentorial arm and posterior part of tentorial bridge; I ventral on posterior pharynx, posterior to attachment of M. 51. M. transversalis buccae (M. 67) absent. M. annularis stomodaei (M. 68) present as strongly developed ring muscle layer over whole length of pharynx. M. longitudinalis stomodaei (M. 69) present as moderately developed, longitudinal muscles on dorsal and ventral sides of pharynx, covered by the ring musculature (Fig. 6).

Table 2. Head muscles of Xyelidae and representatives of other insect groups, part 2: Digestive tract and salivarium

Muscle	Taxon reference	<i>Macroxyela</i>	<i>Xyela</i>	<i>Macrophya</i> (Matsuda 1957)	<i>Pteronidea</i> (Taylor 1931)	<i>Tenthredo</i>	<i>Zoroxyptus</i> (Beutel and Weide 2005)	<i>Rhyacophila</i> (Klemm 1966)	<i>Micropterix</i> (Hannemann 1956)	<i>Panorpa</i> (Heddergott 1938)	<i>Mengenilla</i> (Beutel and Pohl 2005)	<i>Priacma</i> (Hörschemeyer et al. 2002)	<i>Stalis</i> (Röber 1942)	<i>Chauliodes</i> (Maki 1936)	<i>Agnilla</i> (Matsuda 1956)
37. M. hypophar.-saliv.		+	+	48, 49	+	+	+	–	56, 57	+ M. dil.spp.	–	–	+	35	–?
38. M. praementosaliv. ant.		+	+		+	+	+		–		–	–	+	37	–?
39. M. praementosaliv. post.							+		58 ^a		–	–	–	36	–?
40. M. annularis salivarii		–	–	?	?	–	+?	+?	+	+	–	–	?	–	–?
41. M. frontohypophar.		11	+	9,10, 12?	+	+	+/?	3dlphy?	?	–	+	+	+	44	
42. M. tent.-hypophar.		15	+	13	+	+	+	+	46	–	–	–	+	28?, 48?	35?, 41?
M. tent.-hypophar. ant.			+	–?	–?	+	–	–	–	?	–	–	?	?	?
43. M. clypeopalatalis		++	+	5–8	+	+	++	++	45	++/?	+	+	+	38–39	36, 37
M. longitudinalis epiphar.		++	++	?	++	+	+	+	?	?	+	–	–?	–?	?
44. M. clypeobuccalis		+	–	–	?	–?	–	1dlphy	48, 49?	–	–	–	+	40?	?
45. M. frontobuccalis ant.		+	+	11	+	+	+	+	50	+	+	+	+	41?	38?
46. M. frontobuccalis post.		+	+	–?	–?	+	++	+	–?	+	+	+	+	–?	39?
47. M. frontobuccalis lat.		–	–	–	–	–	+?	3dlphy?	–	–	–	–	–	45	–
48. M. tent.-buccalis ant.		–	–	–	–	–	–	–	–	–	–	–	+	–?	42?
49. M. tent.-buccalis lat.		–	–	–	–	–	–	–	–	–	–	–	–	46	–
50. M. tent.-buccalis post.		–	–	–	–	–	+	+	54	–	–	–	+	49	43, 44
51. M. verticopharyngalis		+	+	15	+	+	+	+	51, 52, 53?	+	+	–	+/?	42–43, 47?	40
52. M. tentoriophar.		+	+	14	?	+	+	+	55	+	+	+	+ ^b	50, 51?	–
67a. M. transv. epiphar.		++	++	++	+	++	++	+	+	+	++	–	–?	?	?
67b. M. transvers. buccae		–	–	?	?	+	+	+	47	+	+	–	–?	?	?
68. M. annularis stomodaei		++	+	+	+	+	+	+	+	+	++	+	+	+	+
69. M. longitud. stomodaei		+	r	?	?	+	++	+	+	+	++	+	+	?	?

Muscle numbers in far left column (also used in the descriptive texts) adopted from v. Kéler (1963), numbers or letters in other columns were introduced by other authors; – = absent, + = present, ++ = unusually large.

^aOriginates from mentum.

^bOriginates from posterior head capsule.

Brain and suboesophageal complex (Figs. 5A, 6, 8A–C)

The brain and the suboesophageal complex are moderately sized in relation to the head size (Figs. 6, 8C). The brain is dumb-bell-shaped and transverse (Fig. 8C), and inserted between the compound eyes. The central body, the first commissure, the optical commissure, and the corpora pedunculata are distinct. The optic neuropils are strongly developed.

Fat body (Fig. 6)

A voluminous but loosely aggregated fat body is distributed in most parts of the head capsule, in the labrum and the basal parts of the mandible.

Tracheae and airsacs (Figs. 6, 7D)

Two pairs of large tracheal trunks enter the head. The lower divides into two branches immediately anterior to the foramen occipitale. Within the head capsule the large tracheae form a strongly branched system of air-filled cavities, especially between subcomponents of M. craniomandibularis internus (M. 11).

Head morphology of *Xyela julii*

External head capsule (Figs. 9, 10)

The general shape is similar to *Macroxyela*, but the head is slightly less compressed. The vestiture of hairs is less dense and the setae are much shorter. The cuticle is without metallic sheen. Most parts are brownish, but fairly extensive testaceous areas are present around the large compound eyes and the occipital sulci. The anterior tentorial grooves are more rounded. The clypeus in lateral view joins the medioventral part of the frons at an angle of almost 90° (Fig. 9A). The occipital sulci are more conspicuous than in *Macroxyela*, and anteriorly converging.

Cephalic endoskeleton

Similar to *Macroxyela*, but the dorsal arms are very slender and approximately round in cross section.

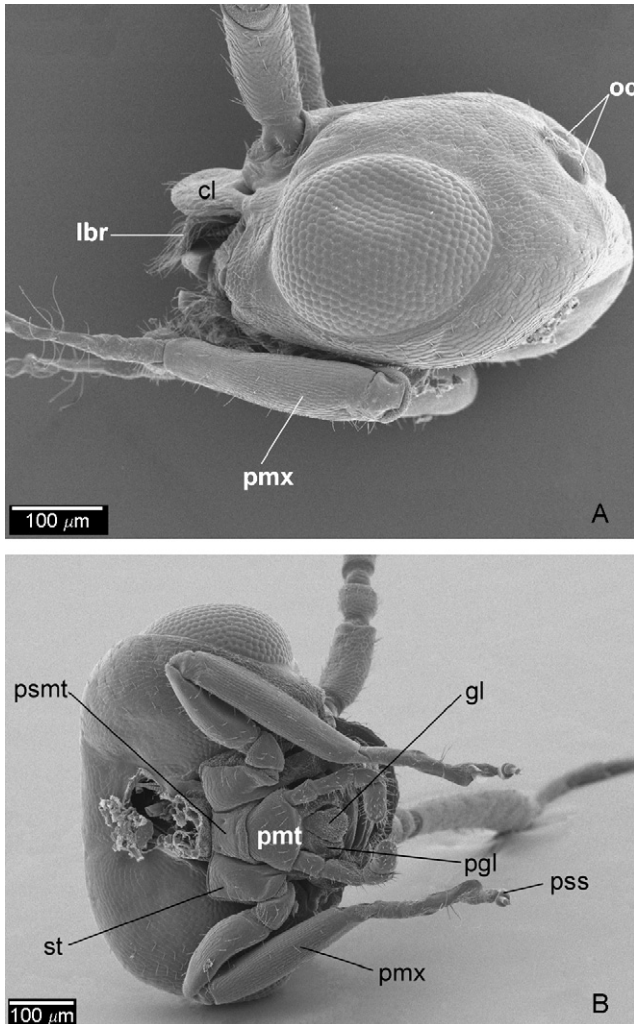


Fig. 9. *Xyela julii*; SEM micrographs: (A) head, lateral view; (B) head, ventral view. Abbreviations: cl = clypeus, gl = glossa, lbr = labrum, oc = ocelli, pgl = paraglossa, pmt = prementum, pmx = maxillary palp, psmt = postmentum, pss = pseudosegments of maxillary palp, st = stipes.

Labrum (Fig. 10A)

The labrum is slightly narrower than in *Macroxyela*, asymmetric, more rounded in outline and almost as high as wide (Vilhelmsen 1996, fig. 2B). A group of strong, conspicuous setae are present submedially on the left part of the posterodorsal labral wall. They interact with a dense fringe of hairs along the posterior margin of the mola of the right mandible.

Musculature (Table 1) similar to *Macroxyela* (Vilhelmsen 1996, fig. 9B).

Antenna (Figs. 9A, 11)

The distance between the antennal insertions is very short. The basal part of the antenna is similar to *Macroxyela*, but the long distal part of the scapus is separated from a subproximal portion by a ring-like, low

ridge. The strongly elongated antennomere 3 has numerous multiporous plate sensilla (Fig. 11; see Basibuyuk and Quicke 1999). Antennomere 3 is followed by 9 additional ones, which form a larger part of the total length of the antenna than the distal antennomeres in *Macroxyela*.

Musculature (Table 1) strongly developed, similar to *Macroxyela*.

Mandibles (Fig. 10B)

The general shape and the asymmetry are similar to the condition in *Macroxyela*. The proximolateral area is also less strongly sclerotised than the other parts. The apical area is less complex. There are only two fairly large subapical teeth; a blade-like cutting edge is not developed. A long, moveable, apically rounded appendage is inserted on the anterior base of the strongly prominent right mola; the hind margin of the right mola is set with a dense fringe of short hairs. The mesal surface of the distinctly smaller left mola is strongly concave.

Musculature (Table 1) similar to *Macroxyela*.

Maxillae (Figs. 9B, 12A)

The basal parts of the maxilla are similar to the condition in *Macroxyela*. The two parts of the galea are very deeply separated. The lacinia is more distinctly separated from the dorsal stipital surface; its fairly long mesal edge is set with a row of spines dorsally. A group of unusual small molars with a smooth and rounded surface is present below this row. The apical palpomeres are strongly modified. Palpomere 4, which follows the very small, wedge-shaped palpomere 3, is distinctly longer than in *Macroxyela*. Palpomere 5 is also elongated and strongly twisted in its apical part. It is followed by a small, triangular segment 6. The apical segment 7 is also small, with a narrowed distal part, a subapical and an apical sensory field, and two short apical setae.

Musculature (Table 1) similar to condition in *Macroxyela*. M. palpopalpalis tertius probably absent.

Labium (Figs. 9B, 12A, B)

The posterior part of the labium and the palp are similar to the condition found in *Macroxyela*. The paraglossae are not sclerotised as in *Macroxyela*, and not set with strong spines; an extremely dense fringe of long hairs is present along the margin. A large, predominantly membranous glossa is present; small pegs are present dorsally, and the ventral surface is covered with very fine hairs which are inserted on small tubercles; an extremely long fringe of hairs, which likely creates capillary forces, is present along the lateral and anterior margins.

Musculature (Table 1) similar to *Macroxyela*. M. praementoglossalis (M. 32) very strongly developed.

Epipharynx

The distribution of macrotrichia on the ventral epipharyngeal wall is highly asymmetric: most are

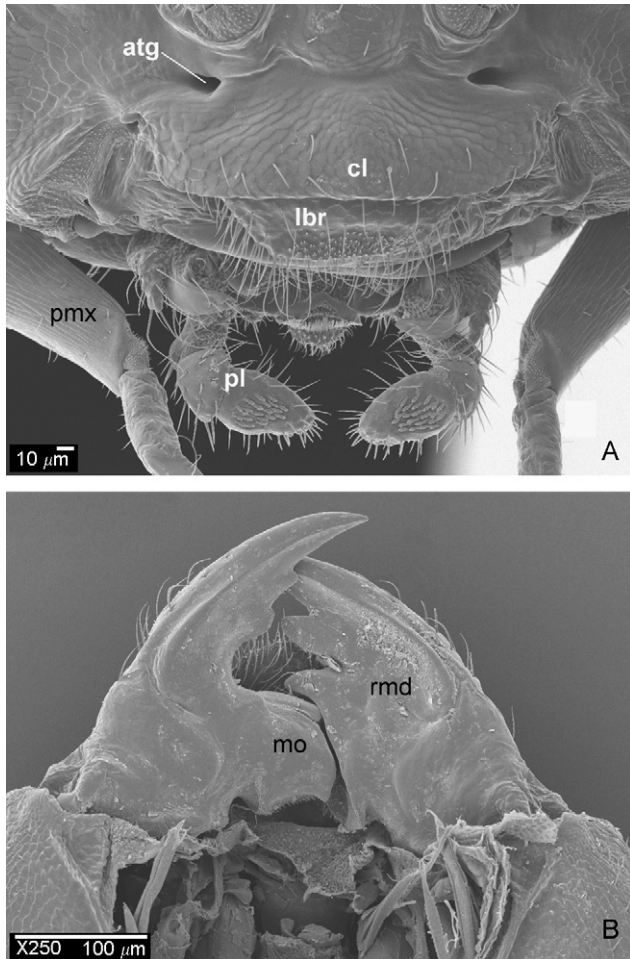


Fig. 10. *Xyela julii*; SEM micrographs: (A) clypeolabral region, frontal view; (B) mandibles, anterior view. Abbreviations: atg = anterior tentorial groove, cl = clypeus, lbr = labrum, mo = mola, pl = labial palp, pmx = maxillary palp, rmd = right mandible.

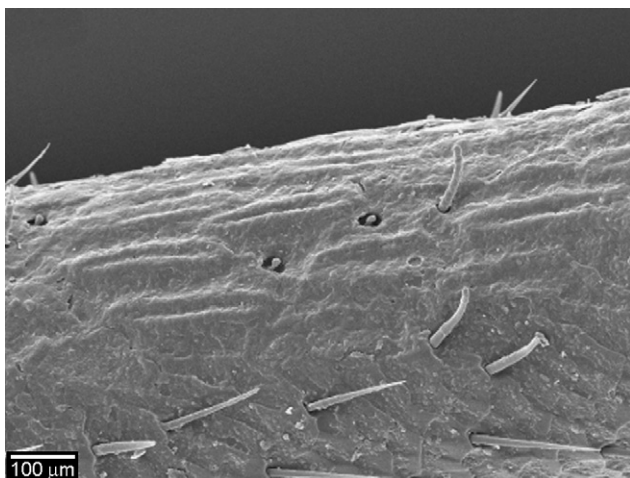


Fig. 11. *Xyela julii*; antennomere 3, sensilla.

situated on the right side (Vilhelmsen 1996, fig. 2B). The buccal lobe is also strongly developed. It is set with strong, dorsally directed spines, and short but strongly sclerotised paired processes are developed at its posterior end.

Musculature (Table 2) similar to the condition in *Macroxyela*.

Salivarium and salivary glands

The salivary duct is distinctly flattened posteriorly and distinctly wider relative to the head size.

Musculature (Table 2) similar to the condition in *Macroxyela*.

Hypopharynx (Fig. 12A)

The anteroventral part of the hypopharynx is more or less incorporated into the wall of the infrabuccal pouch. The asymmetric rod is absent. Small, overlapping microtrichia with minute spines at their proximal margins are situated in a narrow zone on the anterior surface of the hypopharynx (Vilhelmsen 1996, fig. 6B). A transverse sclerotised bar interacts with the mesal edge of the lacinia, and an area with non-articulated spines with the small molars below it. The surface of the infrabuccal pouch is strongly folded. The sitophore plate formed by the proximal part of the hypopharynx is rectangular; the posterolateral edges are not strongly bent upwards as in *Macroxyela*.

Musculature (Table 2). An unusual muscle, *M. tentoriohypopharygalis* anterior, originates from the anterior base of the anterior tentorial arm. Otherwise similar to the condition in *Macroxyela*.

Pharynx and oesophagus

The pharynx is very narrow.

Musculature (Table 2). *M. clypeobuccalis* (*M.* 44) absent. Otherwise similar to the condition in *Macroxyela*.

Brain and suboesophageal complex

The brain is distinctly larger in relation to the head size, and more compact. The circumoesophageal connectives are shorter.

Fat body

The fat body is more strongly developed than in the head of *Macroxyela*.

Tracheae and airsacs

The air sacs are much less developed than in *Macroxyela*.

Phylogenetically relevant characters

(see Table 3)

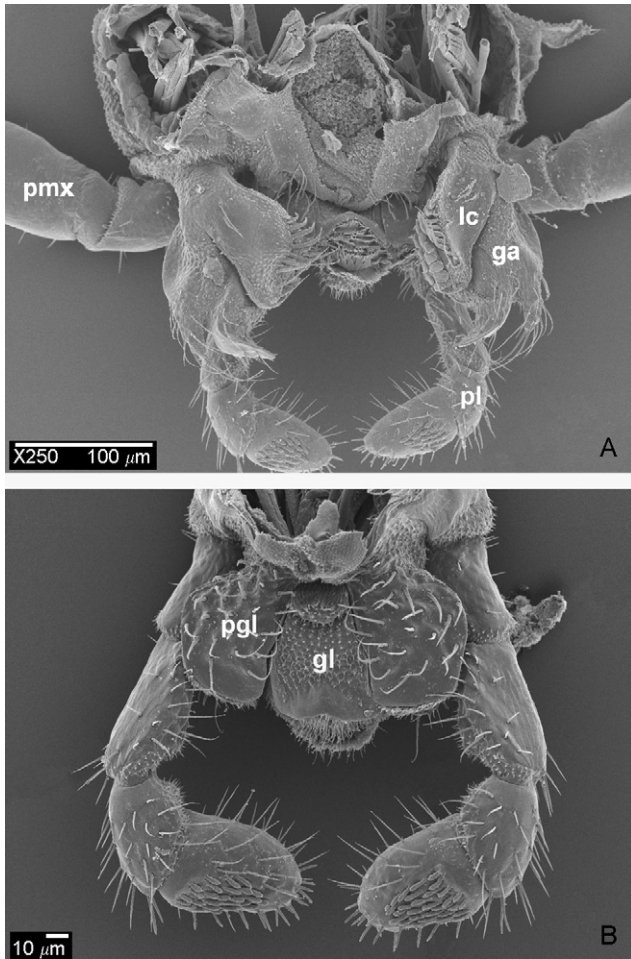


Fig. 12. *Xyela julii*; SEM micrographs: (A) maxillolabial complex, dorsal view; (B) labium with glossa and paraglossae, dorsal view. Abbreviations: ga = galea, gl = glossa, lc = lacinia, pgl = paraglossa, pl = labial palp, pmx = maxillary palp.

1. Exposure of posterior head region: (0) fully exposed; (1) at least partly retracted.

The head is not retracted into the prothorax in any species examined among basal Hymenoptera (Fig. 1B). Only the Siricidae have the head capsule closely associated with the pronotum (Vilhelmsen unpubl.), and evidently this is not a groundplan feature of the order. An exposed head is found in Zoraptera, Strepsiptera, most subgroups of Mecoptera (incl. Nannochoristidae; Kaltenbach 1978) and in Diptera (e.g. Colless and McAlpine 1991). The posterior head region is covered by an anterior collar of the prothorax in Coleoptera, Megaloptera and Neuroptera (Maki 1936; Röber 1942; Hörnschemeyer et al. 2002). This could be considered as a potential synapomorphy of Coleoptera and the neuropterid orders, with partial reversal in Raphidioptera which displays an intermediate stage (Aspöck and Aspöck 1971). An intermediate condition is also found in *Boreus*, where the anterior

margin of the pronotum slightly overlaps with the posterodorsal head region. The dorsal part of the head capsule of *Ctenocephalus* forms a fold which overlaps the pronotum, and the occipital region is retracted into the prothorax.

2. Orientation of head: (0) orthognathous; (1) prognathous or slightly inclined.

The head is orthognathous in Xyelidae (Fig. 1B) and all other hymenopteran representatives examined. The prognathous condition is very uncommon within the order and only encountered within the higher, apocritan wasps (e.g. Bethyloidea). Obviously, orthognathous is a groundplan feature of Hymenoptera, and a similar condition is found in most Strepsiptera (Beutel and Pohl 2005), Trichoptera (Klemm 1966; Malicky 1973), Lepidoptera (groundplan; Kristensen 2003), Mecoptera (Kaltenbach 1978), Siphonaptera, Diptera, and also in most hemimetabolous groups such as, e.g., Zoraptera, Blattodea and Plecoptera. The prognathous or slightly inclined head in Coleoptera and Neuroptera (e.g. Röber 1942; Aspöck and Aspöck 1971; Hörnschemeyer et al. 2002) is a potential synapomorphy of these taxa.

3. Foramen occipitale: (0) not distinctly narrowed or wide; (1) narrow, without tube-like neck region; (2) narrow, with tube-like neck region.

The foramen occipitale is narrow in all hymenopteran species examined (Figs. 1C, 9B), even though a hypostomal or postgenal bridge is clearly absent in the groundplan (Vilhelmsen 1999). A similar condition is found in Diptera (e.g. Rees and Ferris 1939; Hennig 1973, fig. 75), Siphonaptera (Wenk 1953, fig. 3), and some mecopterans (e.g. *Nannochorista*; Hepburn 1969, fig. 31). The foramen is moderately narrow in most mecopterans (e.g. Heddergott 1938, fig. 3; Hepburn 1969, e.g. fig. 30 [*Boreus*]), Trichoptera (Klemm 1966, fig. 4), basal Lepidoptera (Hannemann 1956, figs. 3, 4), and Strepsiptera (Beutel and Pohl 2005), whereas it is wide in most representatives of Coleoptera (narrow in *Lytta*; Schneider 1981, fig. 2), Neuroptera, and Megaloptera (Röber 1942; Hörnschemeyer et al. 2002). The foramen occipitale is also narrow in Raphidioptera (Aspöck and Aspöck 1971), but in a manner different from that in Hymenoptera and Diptera. In contrast to these groups, the posterior part of the strictly prognathous head of Raphidioptera forms a narrow, almost tube-like neck region. The narrow foramen results in high moveability of the head in Hymenoptera and Diptera, which is not the case in snake flies.

It is difficult to outline well-defined character states, as intermediate stages occur and different structures are involved in the formation of the foramen. Therefore, the character is of minor phylogenetic value, even though the condition in Hymenoptera and Diptera appears distinct.

4. Shape of posterior side of head: (0) not concave; (1) concave.

The head is compressed between its frontal and posterior surface in Xyelidae (Fig. 1B) and other hymenopteran representatives examined, and the posterior side is distinctly concave (e.g. Tait 1962). Apparently this is a groundplan feature of Hymenoptera and a potential autapomorphy. A similar condition has evolved within Diptera (especially Brachycera; Hennig 1973), but this is certainly the result of parallel evolution, as the posterior part of the head is clearly convex in members of basal lineages such as Tipulidae and Culicidae. The posterior surface of the head is primarily flattened in Lepidoptera (Kristensen 2003), but more or less strongly convex in other groups of endopterygote insects (e.g. Neuropterida, Coleoptera, Strepsiptera, Mecoptera; Röber 1942; Hepburn 1969; Hörnschemeyer et al. 2002; Beutel and Pohl 2005).

5. Vestiture of hairs: (0) sparse, few setae; (1) dense, regular vestiture of longer setae; (2) dense, regular vestiture of short setae; (3) dense, irregular distribution of long setae; (4) dense vestiture of hair scales; (5) fewer very strong setae; (6) dense vestiture of microtrichia.

The head capsule is densely covered with long hairs in *Macroxyela* (Fig. 1) and members of other hymenopteran groups examined (see also Tait 1962). This is probably a groundplan feature of Hymenoptera and a potential autapomorphy, even though the vestiture is rather sparse and the hairs are distinctly shorter in *Xyela* (Fig. 9). A similar condition is found in adults of Trichoptera (Malicky 1973), but the distribution of hairs is less regular. Long hair scales are present in Lepidoptera (Kristensen 2003). Some members of Diptera (e.g. Bibionidae) show a similar pattern to that found in Hymenoptera. However, fewer very strong setae are typical for the order. A dense vestiture of shorter hairs is present in *Sialis*, and most parts of the surface of the head are covered with very short microtrichia in Strepsiptera (Beutel and Pohl 2005). Sparse setation is present in most adult beetles and in the representatives of Neuroptera, Raphidioptera and Mecoptera examined.

6. Hypostomal bridge: (0) absent; (1) present.

The hypostomal bridge is absent in Xyelidae (Figs. 1C, 9B) and Tenthredinoidea (Rasnitsyn 1988; Vilhelmsen 1999). It is present in Cephidae, Anaxyelidae, Xiphidriidae (partim; Vilhelmsen 1999, fig. 3C), and possibly in Pamphilioidea (Vilhelmsen 1999, fig. 2A). According to Rasnitsyn (1988) this structure belongs to the groundplan of Hymenoptera excl. Xyelidae and Tenthredinoidea, and was replaced twice independently by a postgenal bridge (see following character).

7. Postgenal bridge: (0) absent; (1) present.

A postgenal bridge is absent in Xyelidae (Figs. 1C, 9B) and most other basal Hymenoptera (Vilhelmsen

1999). It has probably evolved independently in Siricidae and the common ancestor of Orussidae and Apocrita. The configuration of the region between the foramen occipitale and the mouthpart cavity is highly variable in Hymenoptera where those areas are separated by a sclerotisation (all taxa except Xyelidae and Tenthredinoidea). Separation of the different types of sclerotisation (hypostomal bridge, postgenal bridge, gula, etc.) is defined by its relation to other anatomical features, primarily the posterior tentorial grooves (Vilhelmsen 1999). However, the configuration of these features is variable, too, compromising their reliability as anatomical ‘landmarks’. Thus the differences between the types of ventral sclerotisation might be more a question of definition rather than reflecting profound ontogenetic divides, i.e. the ventral head sclerotisation might be homologous for all Hymenoptera possessing it, and the different types might have evolved later as the ontogeny of the region diversified. In any case, it is reasonable to assume that ventral head sclerotisation is not part of the hymenopteran groundplan. The postgenal bridge, which occurs in Siphonaptera (Wenk 1953, fig. 3), certainly has evolved independently.

8. Occipital sulci: (0) absent; (1) present.

The presence of anteriorly diverging occipital sulci (Fig. 1A) on the posterodorsal head capsule of most ‘symphytan’ taxa (e.g. Dhillon 1966, fig. 2; absent in *Zaraea*, *Xiphidria*, *Orussus*; Vilhelmsen 1999) likely is a groundplan feature of Hymenoptera. The sulci are probably not homologous with intersegmental fusion lines (‘occipital sutures’), as pointed out in Vilhelmsen (1999). Similar structures are also present in other groups of Endopterygota (e.g. *Chrysopa* [Neuroptera], *Micropterix* [Lepidoptera], *Rhyacophila* [Trichoptera], *Panorpa* [Mecoptera], *Bibio* [Diptera]; see Vilhelmsen 1999), which indicates that this is a plesiomorphy for Hymenoptera. The sulci are absent in Coleoptera, Megaloptera (e.g. Maki 1936, fig. 3; Röber 1942), Raphidioptera (Aspöck and Aspöck 1971), *Boreus* (Mecoptera), *Ctenocephalus* (Siphonaptera; Wenk 1953), *Tipula* (Diptera), and Strepsiptera (Beutel and Pohl 2005). Whether the very widely separated lines in Neuroptera (Ferris 1940; furrow-like depression) are homologous with the occipital sulcus of Hymenoptera and members of other groups is an open question.

9. Epicranial suture (coronal and frontal sutures): (0) present; (1) partly reduced; (2) absent.

The Y-shaped epicranial suture is completely reduced in all hymenopteran representatives examined (Fig. 1A). It is also absent in adults of Diptera (Hennig 1973), Strepsiptera (e.g. Beutel and Pohl 2005), Coleoptera (e.g. Hörnschemeyer et al. 2002), Raphidioptera (partim; Aspöck and Aspöck 1971), and *Chrysopa* (Beutel pers. obs.), but distinctly present in *Sialis* (Röber 1942, fig. 16) and *Mantispa* (Ferris 1940, fig. 6). A mid-cranial

sulcus, which is likely homologous with the coronal suture, occurs in some representatives of *Raphidia* (Crampton 1921, fig. 33), Neuroptera (e.g. *Myrmeleon*; Crampton 1921, figs. 58, 59; Beutel pers. obs.), Trichoptera (posterodorsally; Klemm 1966, fig. 4; Malicky 1973), and Lepidoptera (anterodorsally; Kristensen 2003); vestiges of a Y-shaped suture are present in some Mecoptera (e.g. *Panorpa*, *Brachypanorpa*, *Chorista*; Heddergott 1938, fig. 1; Hepburn 1969). It appears likely that different degrees of reduction of head sutures have evolved several times independently within Endopterygota.

10. Clypeus: (0) not inflected; (1) inflected.

An inflected clypeus (Figs. 1B, 10A) with a more or less sharp anterior edge is an autapomorphy of Hymenoptera (Vilhelmsen 1996). The inflected clypeus of fleas (*Ctenocephalus*; Wenk 1953, “Clypealwulst”, fig. 38) has certainly evolved independently.

11. Shape of posterior tentorium: (0) not collar-like; (1) strongly developed, collar-like; (2) absent.

The very extensive and strongly sclerotised vertical collar-like structure formed by the posterior tentorial arms and the tentorial bridge (Fig. 5B, C; Taylor 1931, figs. 2, 3; Tait 1962, “central body”) is likely an autapomorphy of Hymenoptera. The tentorium is less strongly developed in other endopterygote groups such as Coleoptera (e.g. Beutel 1986; Hörnschemeyer et al. 2002; Anton and Beutel 2004), Mecoptera (Hepburn 1969, figs. 30–34) and Lepidoptera (Hannemann 1956, fig. 4), and is absent in Strepsiptera (Beutel and Pohl 2005) and Diptera (Tipulidae; Rees and Ferris 1939). The posterior parts of the tentorium are also strongly developed in *Sialis* (Röber 1942). However, they do not form a collar-like structure as in Hymenoptera.

12. Labrum: (0) anterior to mandibular apices; (1) posterior to mandibular apices.

The presence of a free and exposed labrum is a plesiomorphic groundplan feature of Hymenoptera, which is found in Xyelidae (Figs. 1A, 10A) and Tenthredinoidea, and in most other groups of endopterygote insects (e.g. Megaloptera; Röber 1942; Coleoptera; Hörnschemeyer et al. 2002; strongly reduced in Siphonaptera; Wenk 1953, fig. 38). In other Hymenoptera, the labrum is inflected, displaced posteriorly to the tips of the mandibles, and often reduced in size (Vilhelmsen 1996). Thus the mandibles are separated from the other mouthparts and have the potential of working independently of those (e.g. as tools in nest-building [bees, digger wasps] or food-collecting [harvester ants]; Jervis and Vilhelmsen 2000). This condition is a potential autapomorphy of Hymenoptera excl. Xyelidae and Tenthredinoidea.

13. M. frontolabralis (M. 8) (Table 1): (0) present; (1) absent.

The muscle is absent in *Macroxyela* (Figs. 6, 7), *Xyela* and all other Hymenoptera examined, except in some Tenthredinoidea (Matsuda 1957; Vilhelmsen 1996, character 13; Beutel pers. obs.). The loss is a potential autapomorphy of Xyelidae, unless presence in Tenthredinoidea is a reversal from absence in the hymenopteran groundplan. The latter is the most parsimonious explanation. The muscle is usually present in endopterygote insects, but absent in Mecoptera (Heddergott 1938), Coleoptera (e.g. Beutel 1986; Hörnschemeyer et al. 2002; Anton and Beutel 2006).

14. Insertion of antennae: (0) anteriorly between compound eyes, adjacent; (1) anteriorly between compound eyes, not adjacent; (2) laterally.

The antennal insertions lie closely together on the anterior side of the head capsule between the compound eyes in Xyelidae (Figs. 1A, 10A) and other representatives of Hymenoptera examined (e.g. *Arge*, *Gilpinia*, *Tenthredo*). This is also the case in *Perga* (Tait 1962) and *Urocerus*, but the articulatory areas are more widely separated. A similar condition is found in *Chauliodes* (Megaloptera) (Maki 1936) and Raphidioptera (partim; Aspöck and Aspöck 1971). The antennal insertions are also inserted anteriorly and adjacent in *Inocella* (Aspöck and Aspöck 1971, fig. 6), Trichoptera (Klemm 1966), Lepidoptera (Kristensen 2003), Mecoptera (Hepburn 1969), and Diptera (e.g. Rees and Ferris 1939; Hennig 1973). The antennae insert anterolaterally in front of the compound eyes in most Coleoptera and in *Sialis* (e.g. Röber 1942; Hörnschemeyer et al. 2002), a feature possibly correlated with the prognathous condition.

15. Shape of antennomere 3: (0) not distinctly elongated; (1) distinctly elongated.

A markedly elongated antennomere 3 is present in Xyelidae (Fig. 2A), Tenthredinidae (e.g. *Tenthredo*; Taylor 1931, fig. 1), Blasticotomidae, Cimbicidae, Argidae, and in some representatives of Pamphiliidae and Xiphydriidae (Rasnitsyn 1988; Ronquist et al. 1999; Blank 2002). As a similar condition is found in a number of fossil hymenopteran lineages (Rasnitsyn 1988), this is probably a groundplan feature and autapomorphy of Hymenoptera (Blank 2002).

16. Basal circular ridge of antennomere 3: (0) absent; (1) present.

A circular ridge separates a short basal part of antennomere 3 from a very long distal portion in *Macroxyela* (Fig. 3A) and *Xyela*. A similar condition is present in *Tenthredo*. It is possible that this is an autapomorphy of Hymenoptera, with secondary loss in most groups.

17. Asymmetry of mandible: (0) present; (1) absent or indistinct.

The mandibles are strongly asymmetric in Xyelidae, especially with regard to the development of the right

and left mola (Figs. 3, 10B). This is possibly a groundplan feature of Hymenoptera. A similar condition is present in basal Lepidoptera (Hannemann 1956), Zoraptera (Beutel and Weide 2005), and in at least some Psocodea (Jervis and Vilhelmsen 2000). The asymmetry is indistinct in other groups of Hymenoptera (e.g. Argidae) or the mandibles are symmetrical. This is correlated with reduction of the molae (see character 19). Distinctly asymmetric mandibles apparently occur in groups with a strong interaction between the basal parts of the mandibles, and are typical for insects with microphagous habits.

18. Membranisation of mandible: (0) absent; (1) laterobasal parts; (2) entire mandibles.

A large basolateral part of the mandible in *Macroxyela* (Figs. 3, 5A–C), *Xyela*, and *Arge* is not fully sclerotised and unpigmented. A less strongly pigmented, fairly small area is also present at the mandibular base in *Tenthredo*, *Onycholyda* and *Gilpinia* (Diprionidae). It is possible that this is an autapomorphy of Hymenoptera. The entire mandibles are weakly sclerotised in adults of Trichoptera (e.g. Klemm 1966).

19. Mandibular mola: (0) distinctly developed; (1) strongly reduced or absent.

The mandibular mola is strongly developed in Xyelidae (Figs. 3, 10B). It is still recognisable in *Arge*, but distinctly reduced. Only a small grinding area at about midlength of the mesal mandibular margin is present in *Tenthredo*. In most groups of Hymenoptera the mola is absent and the mesal edges of the mandibular bases are widely separated (e.g. Pamphiloidea). The presence of a strongly developed mola is possibly a plesiomorphic groundplan feature, and the partial reduction a synapomorphy of Hymenoptera excl. Xyelidae. A well developed mola is also present in subgroups of Coleoptera (Myxophaga, Polyphaga partim; e.g. Anton and Beutel 2004), in basal groups of Lepidoptera (Kristensen 2003), and in most hemimetabolous insects (e.g. Psocoptera; Badonnel 1934; Zoraptera; Beutel and Weide 2005). It is absent in Strepsiptera, Archostemata, Adephaga (Coleoptera), Neuropterida, Trichoptera (pupae and adults; Malicky 1973), Mecoptera (Hepburn 1969; Kaltenbach 1978), and in the groups with strongly modified (or reduced) mandibles.

20. Labio-maxillary complex: (0) absent; (1) present.

The presence of a labio-maxillary complex, i.e. the close connection between labium and maxillae that are moved in almost exclusively vertical direction, likely is an autapomorphy of Hymenoptera (Figs. 1C, 9B). Many Hymenoptera (e.g. bees, pollen wasps; Krenn et al. 2005) have evolved a proboscis for imbibing liquid food while retaining functional mandibles (see above). This always involves at least parts of the labio-maxillary

complex and has happened numerous times independently within the order (Jervis 1998; Jervis and Vilhelmsen 2000), as reflected by the variety of proboscis configurations.

21. Subdivision of galea: (0) absent; (1) present.

Subdivision of the galea into an outer lobe with long hairs along its lateral, anterior and mesal edges and an inner lobe with a largely or completely (*Macroxyela*) smooth margin is a potential autapomorphy of Xyelidae (Figs. 4A, 12A; Blank 2002, his character 18).

22. Lacinia: (0) not apically rounded and with apical tuft of hairs, with mesally directed spines; (1) apically rounded and with apical tuft of hairs, without mesally directed spines.

The specific condition of the lacinia of *Macroxyela*, i.e. the complete absence of mesally directed spines and the presence of a dense field of hairs on the rounded apical area (Figs. 4A, 5C), is a potential autapomorphy of Macroxyelinae.

23. Field of small molars on lacinia: (0) absent; (1) present.

A field of small, sclerotised molars is present on the mesal side of the lacinia in *Xyela* (Fig. 12A). This unusual condition is a potential autapomorphy of Xyelinae. It interacts with a sclerotisation of the infrabuccal pouch (Fig. 12A) and is probably used for grinding pollen.

24. Length of maxillary palpomere 5: (0) not elongated; (1) moderately elongated; (2) strongly elongated.

The subapical maxillary palpomere is moderately elongated in *Macroxyela* (Fig. 4A), and strongly elongated in most species of *Xyela* (Fig. 9B), in *Xyelecia*, and in *Pleroneura* (Blank 2002). The latter condition is probably an autapomorphy of Xyelinae.

25. Torsion of apical maxillary palpomere: (0) absent; (1) present.

The terminal palpomere is twisted in *Pleroneura* (Blank 2002) and *Xyela* (Fig. 9B). This unusual condition is considered as a synapomorphy of both genera.

26. Subdivision of apical maxillary palpomere: (0) absent; (1) present.

The apical palpomere is subdivided and strongly modified in *Pleroneura* (Blank 2002) and *Xyela* (Fig. 9B). This highly unusual condition is another synapomorphy of both genera. Subdivision of the palp, however differently shaped, does also occur in other groups of Hymenoptera (e.g. Tenthredinidae; Dhillon 1966).

The configuration of the distal part of the palp is apparently correlated with the collection of pollen prior to mastication (Blank 2002). The maxillary palps of *Micropterix* have a similar function (Hannemann 1956),

but it is not parsimonious to assume that these similar structural peculiarities are homologous.

27. Subdivision of labium: (0) submentum, mentum and prementum; (1) postmentum and undivided prementum; (2) postmentum and subdivided prementum.

The postmentum is always undivided in Hymenoptera (Figs. 1C, 9B), and this is also the case in Mecoptera (Hepburn 1969), Diptera (Rees and Ferris 1939), and Siphonaptera (Wenk 1953, fig. 20). A distinct separation into a posterior submentum, often fused with a gula, and an anterior mentum is found in Coleoptera, Megaloptera (Röber 1942), Neuroptera (Crampton 1921), and Raphidioptera (Aspöck and Aspöck 1971, fig. 9c). The labium is also divided into three subunits in basal Lepidoptera (Kristensen 2003). However, the arrangement of the muscles suggests that this condition is different from what is found in the other groups with a subdivided postmentum (Kristensen 2003). The postmentum is reduced in adults of Trichoptera (Klemm 1966; Malicky 1973, “erloschen”) and the prementum forms the haustellum together with the hypopharynx. It is apparently also absent in Siphonaptera (Michelsen 1997), and not recognisable as a separate structure in Strepsiptera (Beutel and Pohl 2005).

28. Subdivision of apical labial palpomere: (0) absent; (1) indistinct, (2) distinct, appearing as two separate palpomeres.

The apical palpomere is subdivided into a proximal and a distal portion in *Macroxyela* (Fig. 1C) and *Xyela* (Fig. 12B). This is probably a groundplan feature and autapomorphy of Hymenoptera (Blank 2002). The additional distal element is very clearly separated from the proximal part of segment 3 in other groups of Hymenoptera (e.g. Dhillon 1966; see also Blank 2002), thus appearing as a separate palpomere. It is not connected to the penultimate segment by a muscle. The undivided apical palpomere in *Perga* (Tait 1962, fig. 1C) is probably due to reversal.

29. Sensorial field on apical labial palpomere: (0) absent; (1) present.

A round field of peg-like sensilla is present on the dorsal side of the ultimate labial palpomere in Xyelidae (figs. 4B, 12B) and some other basal Hymenoptera (e.g. Blasticotomidae, Siricidae; Vilhelmsen 1996). This is a potential autapomorphy of the order, with secondary losses in several groups.

30. Glossa: (0) present; (1) absent or vestigial.

The absence of the glossa in Macroxyelinae (Figs. 1C, 4B; Vilhelmsen 1996; Blank 2002) is likely an autapomorphy of this subfamily. A well-developed glossa with a very dense fringe of hairs is present in *Xyela* (Figs. 9B, 12B) and other basal hymenopterans (Vilhelmsen 1996). The glossa is absent or vestigial in Coleoptera (fused with paraglossae in *Priacma*; Hörnschemeyer et al.

2002), Megaloptera (Röber 1942, fig. 15), Raphidioptera (recognisable as small membranous lobes; Aspöck and Aspöck 1971), Trichoptera (Malicky 1973), Mecoptera (Hepburn 1969), Diptera (Hennig 1973), and Siphonaptera (Wenk 1953). Whether the ligula of Neuroptera (Miller 1933; Ferris 1940, fig. 7D) is homologous with a glossa is uncertain. It appears rather unlikely, as no muscles associated with this structure are present (Miller 1933). A small glossa is present in *Micropterix* and the groundplan of Lepidoptera (Hannemann 1956, fig. 16), but it is not nearly as developed as in *Xyela*.

31. Paraglossa: (0) without very dense fringes of fine hairs; (1) unsclerotised, with dense fringes of fine hairs; (2) absent or strongly reduced.

It is unclear whether the groundplan of Hymenoptera includes sclerotised paraglossae with strong setae as are present in *Macroxyela* (Figs. 1C, 4B) or unsclerotised, larger paraglossae with a very dense fringe of hairs. The latter condition is found in *Xyela* and other basal hymenopterans (e.g. *Arge*, *Tenthredo*). In these taxa, the labial endites form a functional unit probably serving as a sponge to absorb water or liquid food and/or to dispense saliva during mastication. In *Macroxyela*, the latter function is perhaps taken over by the blade-like rod above the salivarial orifice, as the reduced endites in this taxon seem unsuitable for that purpose. The paraglossa of *Micropterix* (Hannemann 1956, fig. 16), apparently resembles the condition found in *Macroxyela* more than *Xyela*. Comparatively few long hairs are present along the mesal and lateral margins. Paraglossae are absent or largely reduced in Siricidae (Vilhelmsen 1996), Coleoptera, Neuropterida (Miller 1933; Ferris 1940, fig. 7D; Röber 1942, fig. 15; Aspöck and Aspöck 1971), Trichoptera (Malicky 1973), and Antliophora (Wenk 1953; Hepburn 1969; Hennig 1973).

32. Sclerotised sitophore plate: (0) absent; (1) present.

This structure is present in Hymenoptera (Figs. 2C, 5A, 6) and most representatives of Amphiesmenoptera and Antliophora (excl. Strepsiptera) (Heddergott 1938; Hannemann 1956; Klemm 1966; Vilhelmsen 1996). It is a putative synapomorphy of these lineages of Endopterygota (Kristensen 1999b); However, it is also present in Hemiptera. The presence of a strongly sclerotised cibarial floor is probably correlated with the presence of sucking mouthparts, the sitophore being a prerequisite for the development of a proboscis (Vilhelmsen 1996; Jervis and Vilhelmsen 2000).

33. Prepharyngeal tube: (0) short or absent; (1) present, elongated.

The presence of a constricted and more or less elongated prepharyngeal tube anterior to the anatomical mouth is probably a groundplan feature of Hymenoptera. This condition is possibly correlated with the presence of the sitophore plate and a sucking pump

anterior to the anatomical mouth. A closed prepharynx is also present in *Rhyacophila* (Trichoptera; Klemm 1966, figs. 15, 16), Lepidoptera (Hannemann 1956, fig. 9; Kristensen 2003, “cibario-pharyngeal sucking pump”), *Panorpa* (Heddergott 1938, fig. 12), Diptera (Hennig 1973, “Cibarialpumpe”), Strepsiptera (Beutel and Pohl 2005), and also in Raphidioptera (Matsuda 1956, fig. 1A). It is absent in *Priacma* (Hörnschemeyer et al. 2002) and very short in other beetles (e.g. *Helophorus*; Anton and Beutel 2004), *Chrysopa* (Beutel pers. obs.), and probably also in Sialidae (Röber 1942, fig. 23). A short prepharynx is also present in *Zorotypus* (Beutel and Weide 2005).

34. Epipharyngeal brush: (0) absent; (1) present.

A brush of microtrichia on the ventral epipharynx, which interacts with the mandibles, is present in Xyelidae (Fig. 5A). This feature was suggested as an autapomorphy of Xyelidae by Vilhelmsen (1996). However, considering the correlation with the mesal mandibular parts, the presence of the epipharyngeal brush could alternatively be a groundplan feature of Hymenoptera secondarily lost in the non-xyelid groups. An epipharyngeal brush is also present in other groups of insects with microphagous feeding habits and well-developed mandibles with molae, such as in basal Lepidoptera (Hannemann 1956), Polyphaga (partim), Myxophaga (Anton and Beutel 2006), Zoraptera (Beutel and Weide 2005), and Psocoptera (v. Kéler 1966, figs. 1, 2; Jervis and Vilhelmsen 2000). It is absent in *Sialis* (Röber 1942, fig. 23), *Priacma* (Hörnschemeyer et al. 2002), Strepsiptera (Beutel and Pohl 2005), *Rhyacophila* (Klemm 1966), *Panorpa* (Heddergott 1938, figs. 7, 11–13), Diptera (Hennig 1973), and Siphonaptera.

35. Epipharyngopharyngeal lobe: (0) absent; (1) present.

The presence of a large epipharyngopharyngeal lobe with spines on its surface, and with sclerotised posterolateral processes that reach fairly deeply into the pharynx, is possibly an autapomorphy of Hymenoptera (Figs. 6, 7). The lobe is absent in other groups of endopterygote insects such as Coleoptera (e.g. Hörnschemeyer et al. 2002; Anton and Beutel 2006), Strepsiptera (Beutel and Pohl 2005), Megaloptera (Röber 1942), Lepidoptera (Hannemann 1956; Kristensen 2003), Mecoptera (Heddergott 1938), and Diptera (Schiemenz 1957; Hörnschemeyer et al. 2002). In basal Hymenoptera, the spines on the lobe are developed to varying degrees and may vary in orientation. In Siricidae, the dorsal epipharynx is smooth and partly sclerotised (Vilhelmsen 1996, fig. 12) and the longitudinal epipharyngeal muscle (see below) is reduced. This is probably correlated with the absence of adult feeding in this family.

36. Longitudinal muscle of epipharynx (Table 2): (0) normally developed; (1) strongly developed.

The very large size of the longitudinal muscle of the epipharynx (Figs. 6, 7A–D) is very likely correlated with the presence of the epipharyngopharyngeal lobe. This muscle is enlarged in Xyelidae, Argidae, Pamphiliidae and members of other ‘symphytan’ families (Vilhelmsen 1996). It is secondarily small in Siricidae and Orussidae (Vilhelmsen 1996, figs. 12, 13), as well as in apocritans (e.g. *Vespula*). We assume that the large size is another derived groundplan feature of Hymenoptera.

In Xyelidae, the strongly developed epipharyngopharyngeal lobe and longitudinal muscle may function in pollen feeding, helping to convey the masticated pollen grains further into the digestive tract for the consumption of their contents (i.e. like a tongue). The dorsally directed spines may serve as a ratchet, preventing backflow of the food particles.

The longitudinal muscle is moderately developed or absent in other groups of Endopterygota (e.g. Heddergott 1938; Röber 1942; Wenk 1953).

37. Infrabuccal pouch: (0) absent; (1) present.

A deep infrabuccal pouch, which is completely separated from the prepharyngeal tube, is present in Xyelidae (Figs. 6, 7C, D) and most other groups of Hymenoptera (Vilhelmsen 1996). The gradual size reduction (small in, e.g., Tenthredinoidea excl. Cimbicidae; Vilhelmsen 1996) is probably correlated with the reduction of the mola (see above), as the pouch is primarily a working space for these basal grinding parts of the mandible (in Xyelidae). The presence is very likely a groundplan feature of Hymenoptera, but it is unclear whether it is an apomorphic condition. A similar infrabuccal pouch is present in basal lineages of Lepidoptera (Hannemann 1956; Kristensen 2003) and in Psocoptera (v. Kéler 1966; Jervis and Vilhelmsen 2000). The infrabuccal pouch is absent in other groups of endopterygote insects such as Coleoptera (e.g. Hörnschemeyer et al. 2002), Strepsiptera (Beutel and Pohl 2005), Megaloptera (*Sialis*; Röber 1942), Mecoptera (*Panorpa*; Heddergott 1938, fig. 7), and Diptera (Schiemenz 1957; Hennig 1973).

38. Transverse muscle connecting posterolateral edges of infrabuccal pouch: (0) absent; (1) present.

This unusual muscle without the typical cross-striated structure is known from *Macroxyela* only (Figs. 6, 7C).

39. Hypopharyngolabial complex: (0) absent; (1) present

The hypopharynx forms a structural unit together with the anterior labium in Hymenoptera (Figs. 6, 7, 12A) and other groups of holometabolous insects (e.g. Coleoptera; Hörnschemeyer et al. 2002). The lateral walls of both structures are fused and the salivarium is only represented by a more or less narrow duct. A similar condition is found in Zoraptera (Beutel and Weide 2005, fig. 7A, B). The hypopharynx forms a distally free, tongue-like lobe in representatives of the

'lower neopteran orders' (e.g. Blattodea; Snodgrass 1935; Matsuda 1965; Grylloblattodea; Walker 1931; Embioptera; Rähle 1970) and the salivarium is not reduced to a tube- or syringe-like structure.

40. Asymmetric, blade-like hypopharyngeal rod: (0) absent; (1) present.

An asymmetric, blade-like hypopharyngeal rod is present in *Macroxyela* (Figs. 1C, 4B), but absent in other representatives of Hymenoptera or Endopterygota examined. It is not known whether it is present in *Megaxyela*.

41. M. tentoriohypopharyngalis anterior: (0) absent; (1) present.

A highly unusual muscle arising from the anterior tentorial arm and inserted on the posterolateral edge of the sitophore plate is present in *Xyela* and *Tenthredo*, but absent in *Macroxyela* and *Onycholyda* as well as in representatives on non-hymenopteran groups examined. The interpretation of this unusual feature is problematic. It cannot be excluded that the muscle is secondarily absent in *Macroxyela*, or it may have evolved several times independently. Otherwise it would indicate a closer relationship between Xyelinae and the non-xyelid hymenopteran families. The function of the muscle is probably to hold the sitophore plate in its position, together with M. frontohypopharyngalis, when the epipharyngopharyngeal lobe is pulled back.

Discussion

Monophyly of Hymenoptera has never been seriously challenged, and the present study reveals further autapomorphies of the order. It is very likely that a large epipharyngopharyngeal lobe and the associated conspicuously developed longitudinal muscle of the epipharynx are derived groundplan features of the order. Together they form a specific preoral pumping apparatus not described from any other insect group. Further potential autapomorphies are the concavity of the posterior head capsule, the very dense, regular vestiture of hairs, the collar-like posterior tentorium, and the sensorial field on the apical labial palpomere. It is also possible that the strongly elongated antennomere 3 with a circular ridge, and an unsclerotised zone of the external mandibular base are apomorphic groundplan features of Hymenoptera. However, this would imply secondary modification in many groups. The almost complete loss of the head sutures likely is a derived condition as well. However, reduction of sutures has almost certainly taken place many times in endopterygote insects.

Some other features of the hymenopteran head are probably plesiomorphic. The exposed posterior head region and the orthognathous orientation of the head

are considered groundplan conditions of Endopterygota, with the corresponding apomorphic states, i.e. retracted posterior head region and prognathism, in Coleoptera and Neuropterida. Contiguous antennal insertions between the compound eyes and a narrow foramen occipitale are also likely plesiomorphic features. The wide foramen occipitale in most groups of Coleoptera and Neuropterida is probably correlated with prognathism. Phylogenetic interpretation of the presence of occipital sulci is difficult. In any case the presence is a groundplan feature of Hymenoptera and a potential autapomorphy of Endopterygota with secondary loss in several lineages.

A feature which doubtlessly belongs to the groundplan of Hymenoptera is the presence of a more or less deep infrabuccal pouch (Vilhelmsen 1996). This is probably primarily correlated with microphagous habits (feeding on, e.g., fungal spores or pollen), as a very similar condition is also present in basal Lepidoptera and in Psocoptera (v. Kéler 1966). It appears plausible to assume that feeding on small particles is a groundplan feature of Hymenoptera, and that a switch to feeding on more or less liquefied food took place once or twice (Xyelinae) very early in the evolution of Hymenoptera. Alternatively, interpretation of liquid-feeding and the acquisition of a liquid-uptake apparatus (anterior part of the labiohypopharyngeal complex, primarily the labial endites) as groundplan features of Hymenoptera (e.g. Vilhelmsen 1996; Krenn et al. 2005) would imply reversal in Macroxyelinae. However, microphagy and liquid-feeding are not necessarily mutually exclusive.

It is conceivable that the microphagous habit associated with the presence of asymmetric mandibles with molae, an epipharyngeal brush, and possibly an infrabuccal pouch, is plesiomorphic for the entire Endopterygota, even though this condition is currently observed only in basal groups of Lepidoptera and Hymenoptera and in myxophagan and polyphagan beetles. Outside of Endopterygota, these features are observed in varying combinations in taxa with microphagous adults, such as Zoraptera and Psocoptera. However, even if the latter were chosen as outgroups, the microphagous condition would probably not be optimised to be the groundplan state of holometabolous insects in a numerical cladistic character evaluation. Almost all endopterygote groups have evolved very different types of feeding apparatuses either in correlation with predacious habits (e.g. Raphidioptera; Coleoptera partim, e.g. Beutel 1986), carrion-feeding (Mecoptera), suctorial feeding (most Lepidoptera), blood-feeding (Siphonaptera, Diptera partim), or non-feeding (Strepsiptera, Beutel and Pohl 2005; Trichoptera, Klemm 1966; Sialidae, Röber 1942).

An apomorphic feature, which clearly links Hymenoptera with the Mecopterida is the presence of a fully sclerotised hypopharyngeal floor, the sitophore plate

(Vilhelmsen 1996). The presence of a constricted and elongated prepharyngeal tube is a derived feature probably correlated with that condition. An undivided postmentum is a trait shared by Hymenoptera and some groups of Mecoptera. However the polarity interpretation remains ambiguous, and the postmentum is strongly reduced or modified in several groups.

Monophyly of Hymenoptera excluding Xyelidae is well supported by the results of our study. The distinct or complete reduction of the mola and the epipharyngeal brush are likely synapomorphic features that are correlated with a shift in feeding behaviour. Hymenoptera excluding Xyelidae have apparently abandoned microphagous feeding habits (see above) and lost the associated structures.

A large lineage comprising Hymenoptera exclusive of Xyelidae and Tenthredinoidea is corroborated by the widely separated mandibular bases with completely reduced molae that do not interact during the feeding process, and by the presence of a retracted labrum that is often reduced in size (Vilhelmsen 1996). The loss of the median labral retractor is also a possible apomorphy of this clade. However, this implies parallel reduction in Xyelidae (Vilhelmsen 1996). Another potential synapomorphy of this lineage is the presence of ventral head sclerotisation between the occipital foramen and the mouthpart cavity, initially in the form of a hypostomal bridge (Rasnitsyn 1988). The presence of a postgenal bridge probably is a later development in Siricidae and Orussidae + Apocrita, respectively (Vilhelmsen 1999).

Monophyly of Xyelidae is not unambiguously supported by the results of our study. The family was retrieved in all recent cladistic treatments of basal Hymenoptera (e.g. Vilhelmsen 2001; Schulmeister et al. 2002; Schulmeister 2003), as well as in Blank (2002), but most of the features considered as autapomorphies for the family are correlated with microphagous feeding and frequently occur outside Hymenoptera (see above). The best putative autapomorphy for Xyelidae appears to be the subdivision of the galea (character 21). However, Xyelinae and other basal hymenopterans apparently share some features in the labial endites associated with liquid-feeding (glossa and paraglossae densely set with long and flexible hairs) that are absent in *Macroxyela*. Elongation and modifications of the distal maxillary palp are also conditions found in Xyelinae and other groups of Hymenoptera (part of the CNEA = concealed nectar extraction apparatus; Jervis and Vilhelmsen 2000), but not in *Macroxyela* and *Megaxyela*; however, these modifications are not that similar and probably independently derived. It is also remarkable that *Xyela* shares an unusual apomorphic condition with *Tenthredo* (Beutel pers. obs.): The presence of a muscle arising from the anterior tentorial arm and inserted on the posterolateral edge of the sitophore plate.

It is conceivable that a distinct change in feeding habits took place twice independently: once in Xyelinae, and a second time in the stem lineage of the non-xyelid Hymenoptera. Alternatively, if Xyelinae are more closely related to other Hymenoptera than Macroxyelinae, they might have adapted to liquid-feeding while retaining the microphagous habit lost in non-xyelid Hymenoptera.

The monophyly of Macroxyelinae appears well founded. The strongly modified lacinia in *Macroxyela* and *Megaxyela* (Blank 2002), without a regular row of mesally directed setae, likely is an autapomorphy of the subfamily. Another autapomorphy is the absence of the glossa (Blank 2002). Whether the curved and strongly sclerotised paraglossae are derived or plesiomorphic is unclear. The asymmetric, blade-like hypopharyngeal rod found in *Macroxyela* is almost certainly derived, but the condition in *Megaxyela* is unknown. The observed feeding habit of *Macroxyela ferruginea* (feeding on buds; Garlick 1923) might also be apomorphic; apparently, feeding on pollen is not an option due to the absence of modifications for pollen-collecting at the tips of the maxillary palps.

An apomorphic feature found in *Xyela* is the presence of small, sclerotised molars on the mesal edge of the lacinia. However, it is unknown whether this condition is also present in other genera of Xyelinae. Xyelini (*Xyela* and *Pleroneura*) are strongly supported by the very unusually shaped apical part of the maxillary palp, probably correlated with collecting pollen. However, the maxillary palp of *Micropterix* is also modified for this purpose, indicating that at least the function of the palps may be a retained plesiomorphy.

It is noteworthy that the head structures in *Perga* (Pergidae; Tait 1962) differ strongly from those of other 'symphytan' representatives examined during this study. The antennal insertions are widely separated, the maxillary palps are short and 4-segmented, and the apical labial palpomere is apparently undivided and devoid of a field of sensilla (Tait 1962, fig. 1). As Pergidae are deeply nested within Tenthredinoidea (Vilhelmsen 2001; Schulmeister 2003), it appears plausible to consider these features as the result of reversals.

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