

Genitalia and terminal abdominal segments of male basal Hymenoptera (Insecta): morphology and evolution**

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Abstract

The results of a morphological study of the terminal abdominal segments, particularly the reproductive organs, of male Hymenoptera are presented in the form of 87 morphological characters. The external male genitalia of at least one member of each of the 14 sawfly families are illustrated. The 87 characters comprise sclerites and muscles of the external genitalia, the abdominal sclerites, and the internal reproductive organs. The groundplan of all Hymenoptera and the evolution of the terminal segments of the male genitalia within Hymenoptera are deduced on the basis of a recent simultaneous analysis of basal Hymenoptera which includes the characters from the present work.

Key words: groundplan, male genitalia, sawflies, Symphyta

Introduction

Many parts of the hymenopteran body have already been examined in detail for their use in phylogenetic studies of the basal lineages of Hymenoptera (“Symphyta”). The phylogenetic analysis of Vilhelmsen (2001) included characters from the mouthparts and preoral cavity (Vilhelmsen 1996), other parts of the head including antennae (Vilhelmsen 1997a, 1999), cervix and prothorax (Vilhelmsen 2000a), mesothorax (Gibson 1985, Heraty et al. 1994), metathorax and anterior abdomen (Königsmann 1977, Vilhelmsen 2000b, Whitfield et al. 1989), legs (Basibuyuk & Quicke 1995), wings (Basibuyuk & Quicke 1997, Rasnitsyn 1988, Ronquist et al. 1999), pregenital abdomen (Vilhelmsen 2001), male genitalia (Königsmann 1976, 1977), and ovipositor (Quicke et al. 1994, Vilhelmsen 2000c), as well as larval morphology (Yuasa 1922).

These 236 characters included only 6 characters of the male genitalia, adopted from the literature study of

Königsmann (1976, 1977) and from Ronquist et al. (1999). Of these six characters, two were coded as invariant in the Hymenoptera, and therefore only four were potentially informative for the phylogenetic relationships within Hymenoptera. The terminal segments of the male abdomen (including genitalia and internal reproductive organs) are the part of the adult hymenopteran body that has been studied the least for the use in phylogenetic analysis. This is due to the fact that previous comparative studies of the male external genitalia (Crampton 1919, Boulangé 1924, Snodgrass 1941) and male internal reproductive organs (Togashi 1970) of a broad sample of sawfly taxa were not done in a cladistic context. The detailed investigation of the morphology of the terminal abdominal segments of male Hymenoptera presented here is aimed at filling this gap.

The terminal abdominal segments of the males of 59 hymenopteran species from 57 genera were examined in detail, and significant differences were coded in 87 characters covering the terminal sternites and ter-

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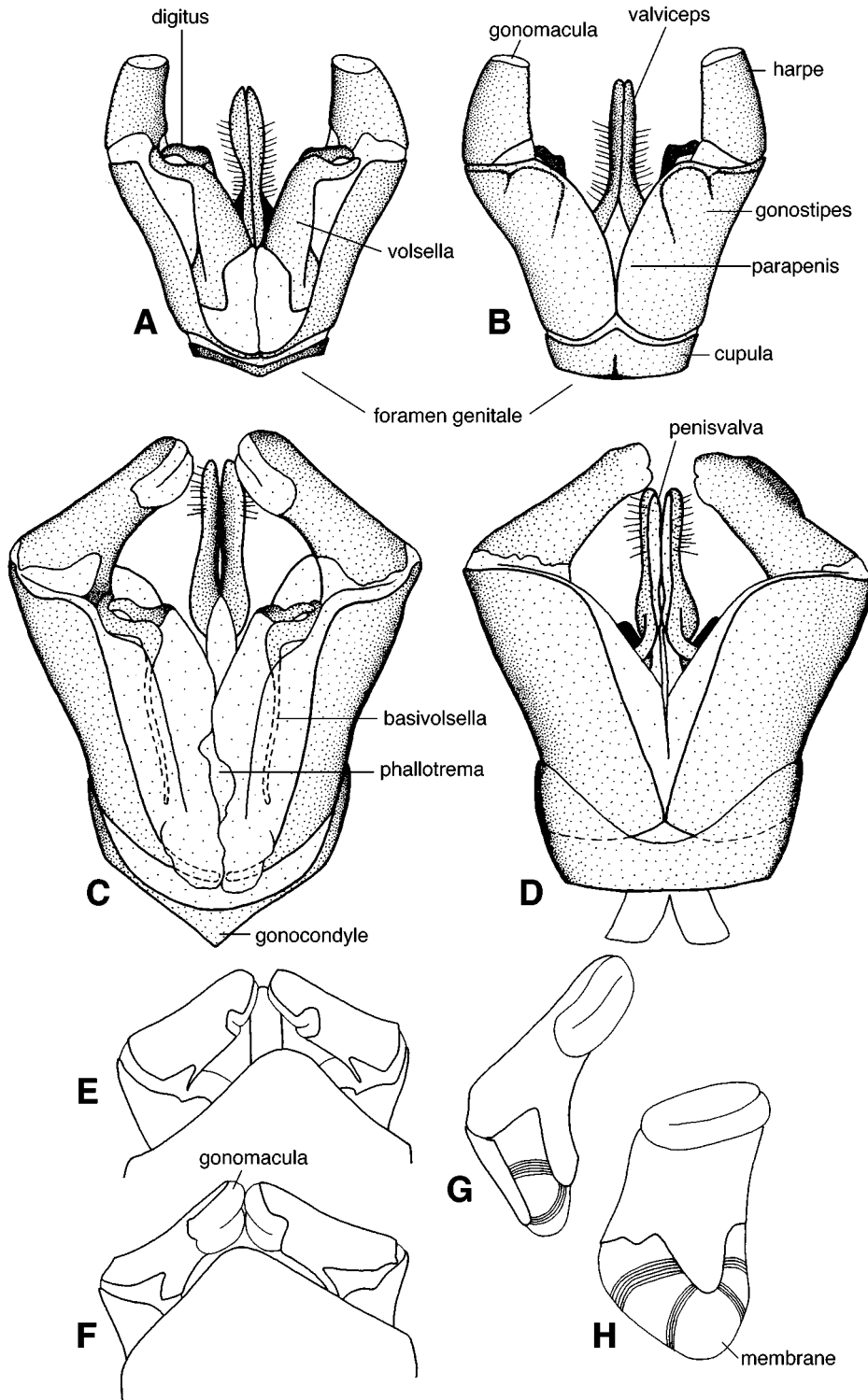


Fig. 1. Male external genitalia of Xyelidae. A. *Xyela* sp., ventral. B. *Xyela* sp., dorsal. C. *Macroxyela ferruginea*, ventral. D. *M. ferruginea*, dorsal. E. Terminal abdomen of male *M. ferruginea* with 'hidden' gonomaculae, ventral. F. Same, gonomaculae in relaxed position. G. Harpe and part of gonostipes of *M. ferruginea*, showing internal membrane, lateral view. H. Same, medial view.

gites, the internal reproductive organs and the sclerites and muscles of the copulatory apparatus.

The morphology of the terminal abdominal segments of male Hymenoptera is described in detail in Crampton (1919), Boulangé (1924), Peck (1937), Snodgrass

(1941), Togashi (1970), Smith (1969, 1970a, b, 1972), Birket-Smith (1981) and Schulmeister (2001). Below, only those findings will be discussed that have not previously been mentioned. Instead, the morphological differences found in the examined species will be presented

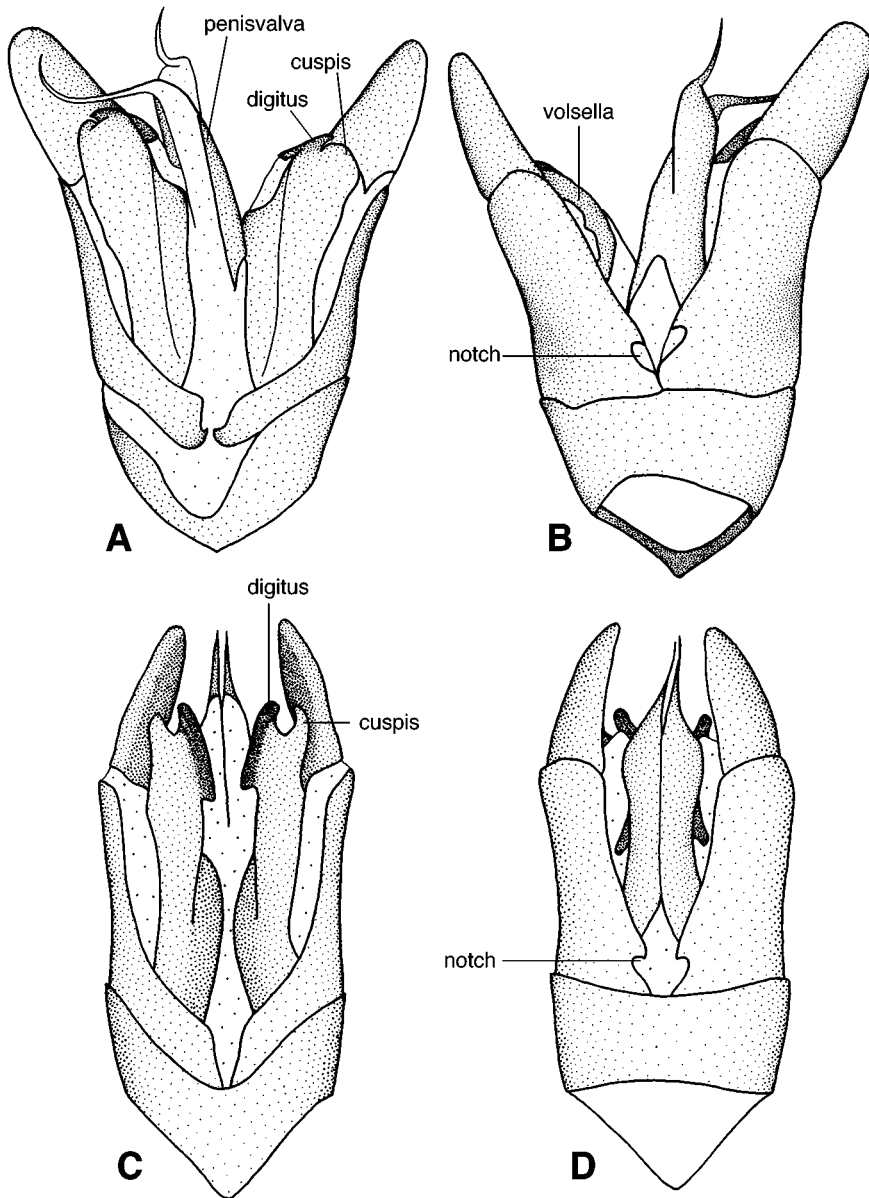


Fig. 2. Male external genitalia of Blasticotomidae. A. *Runaria reducta*, ventral. B. *R. reducta*, dorsal. C. *Paremphtytus flavipes*, ventral. D. *P. flavipes*, dorsal.

in the form of character lists and matrices. In addition, the external genitalia of at least one member of each sawfly family are depicted.

The following sections on morphology and functional morphology attempt to provide purely descriptive findings, without reference to phylogeny. In the discussion, the groundplan and evolution of the terminal abdominal regions of male Hymenoptera is described, based on a phylogeny determined by a recent simultaneous analysis of morphological and molecular characters (Schulmeister 2003b), which included the characters presented here.

The terminology employed here for the parts of the male genitalia is that of Schulmeister (2001). For a de-

tailed description of the morphology, and for definitions and discussion of the terms, please refer to that paper.

Material and methods

The species examined for morphology of the male genitalia are listed in Appendix 1. Most specimens were fixed in Bouin's fluid and kept in ethanol (70%) until preparation. Others were pinned museum specimens, which were softened prior to dissection by keeping them in a box the bottom of which was covered with 30% ethanol. The preservation method for each species is listed in Appendix 1. If possible, two or more exemplars from each species were examined. Dissections were done under a Zeiss stereomicroscope Stemi SV

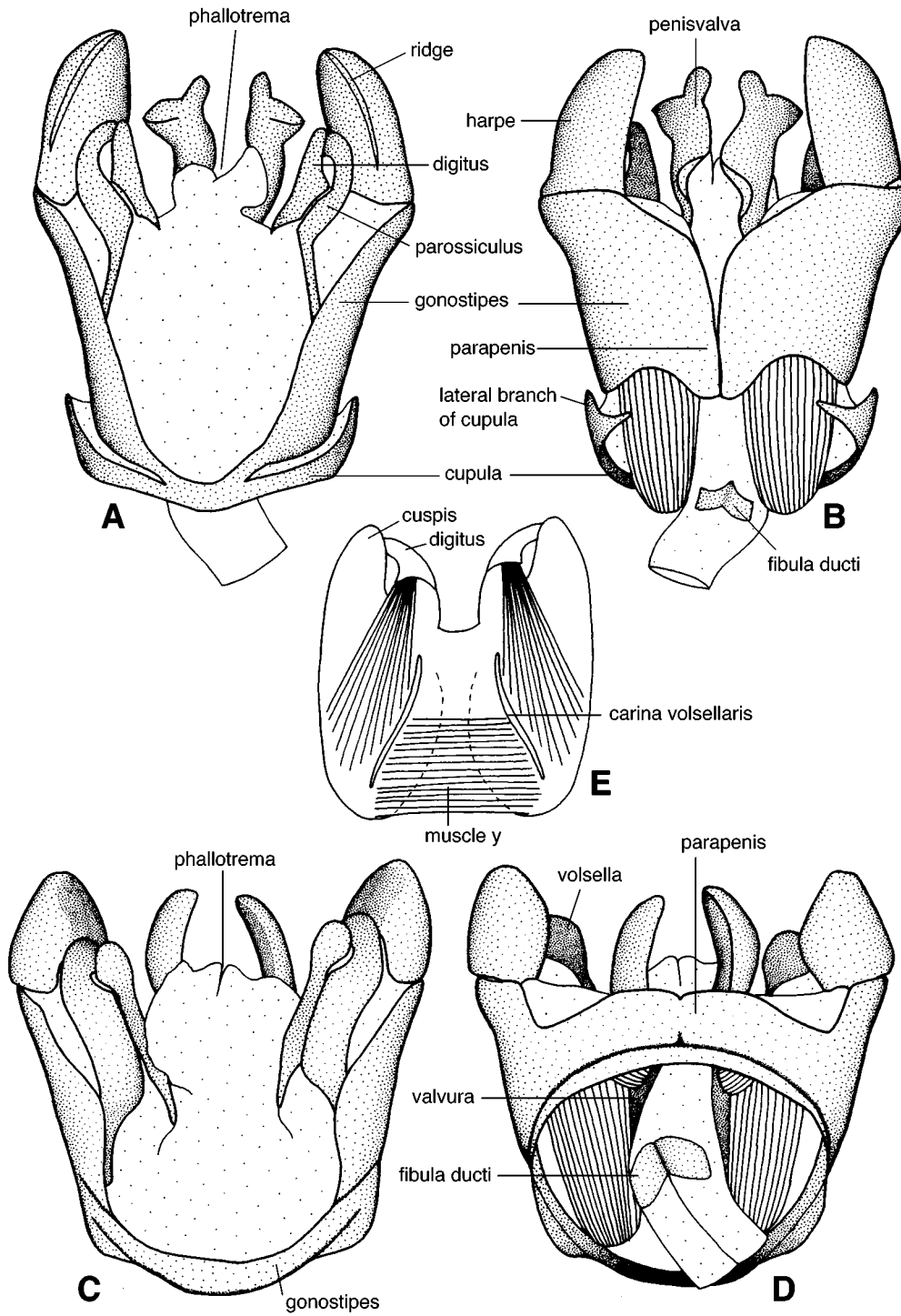


Fig. 3. Male external genitalia of Argidae (A–B) and Pergidae (C–E). A. *Arge cyanocrocea*, ventral. B. *A. cyanocrocea*, dorsal. C. *Decameria* sp., ventral. D. *Decameria* sp., dorsal. E. Volsellae of *Lophyrotoma analis*, internal.

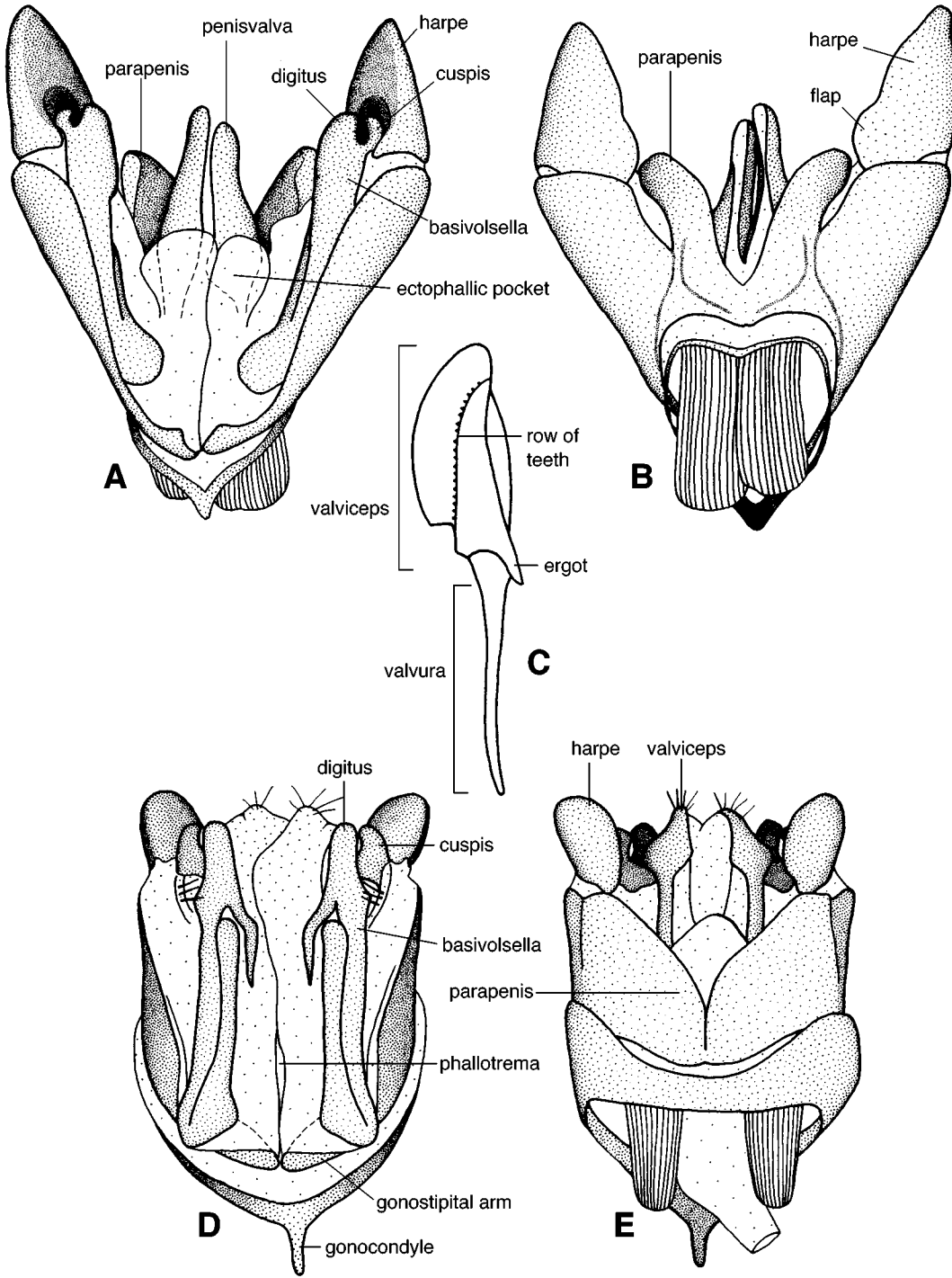


Fig. 4. Male external genitalia of Diprionidae (A–C) and Cimbicidae (D–E). A. *Diprion pini*, ventral. B. *D. pini*, dorsal. C. Penisvalva of *Monoctenus juniperi*, lateral. D. *Corynis crassicornis*, ventral. E. *C. crassicornis*, dorsal.

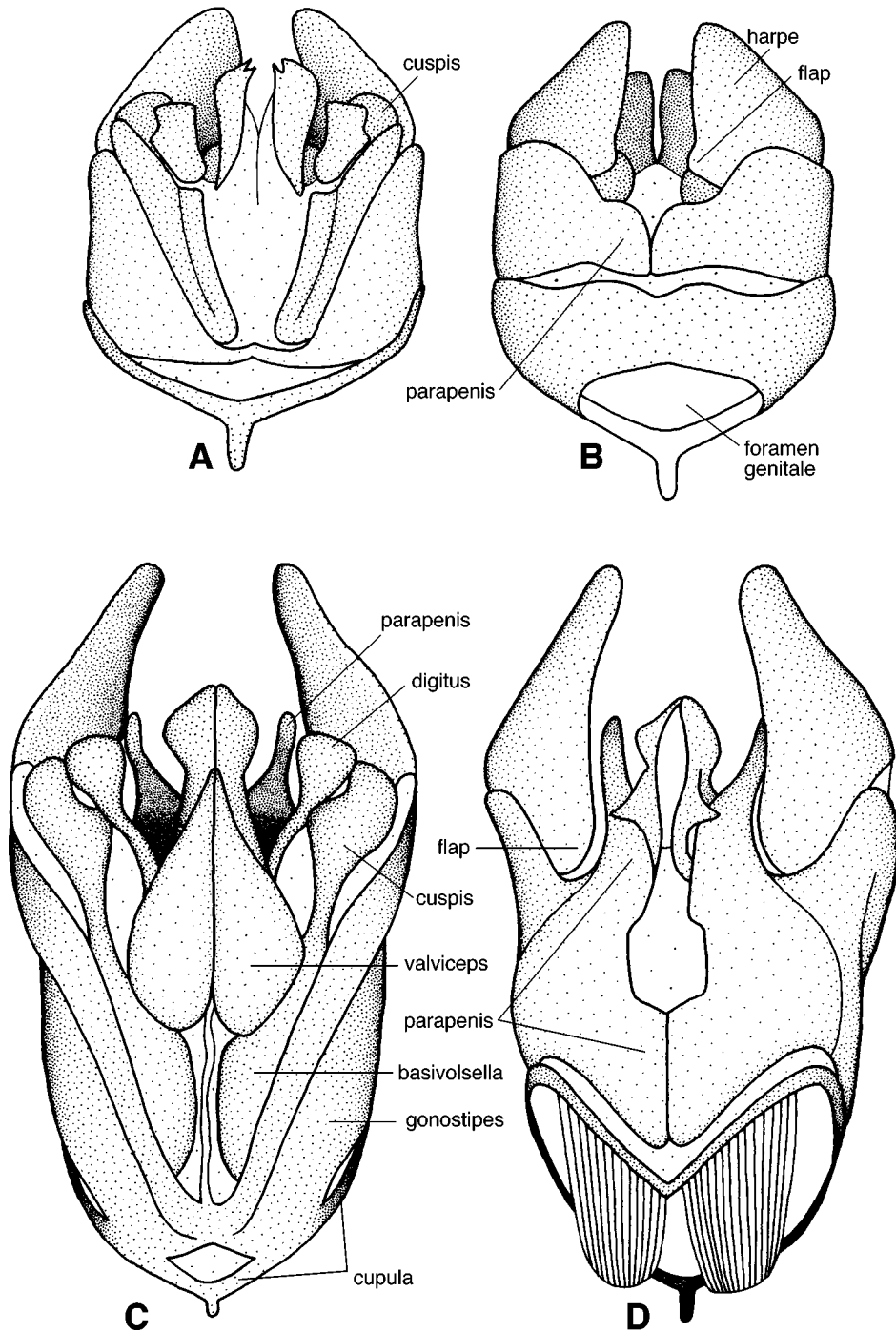


Fig. 5. Male external genitalia of Tenthredinidae. A. *Athalia rosae*, ventral. B. *A. rosae*, dorsal. C. *Dolerus gonager*, ventral. D. *D. gonager*, dorsal.

11 (maximum magnification 66x). Viewing the objects under light coming from the side proved sufficient for discrimination of the parts, so that staining was not necessary. Drawings were made with the aid of a camera lucida. In the figures of external male genitalia below, the distal end of the latter is always oriented towards the top of the page; setae are usually not shown.

Morphology

Male external genitalia

The male external genitalia of many hymenopteran species, including exemplars from all sawfly families,

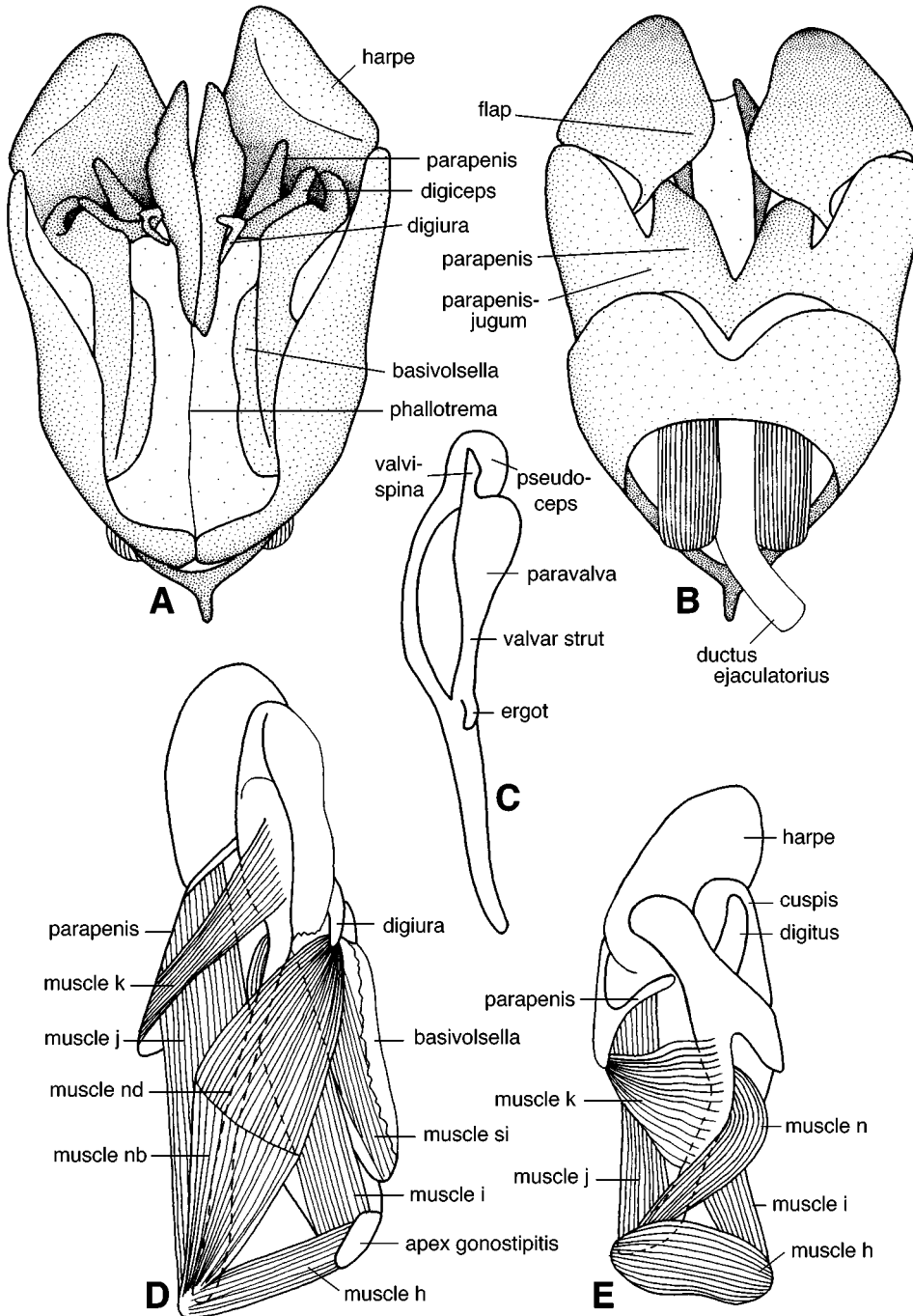


Fig. 6. Male external genitalia of Tenthredinidae. A. *Nematus* sp., ventral. B. *Nematus* sp., dorsal. C. Penisvalva of *Nematus* sp., lateral. D. Medio-sagittal section of external male genitalia of *Tenthredo campestris*. E. Medio-sagittal section of external male genitalia of *Aglaostigma lichtwardti*.

are depicted in Figs. 1–12. They consist of four main sclerotized parts (depicted in Schulmeister 2001: Fig. 2), which are present in all Hymenoptera, except that the cupula is missing in Pergidae.

1. The cupula (= basal ring), which is a ring surrounding the base of the genitalia.
2. The two latimeres, which constitute the main frame of the copulatory apparatus. Each consists of a basal

gonostipes and a distal harpe. If the harpe is absent or fused to the gonostipes, the resulting structure is called gonoforceps.

3. The two volsellae, which are a pair of pincers on the ventral surface of the genitalia. Each consists of a digitus (= gonossiculus) and parossiculus. In some hymenopterans, the bases of the volsellae are linked by a sclerotized bridge (Fig. 11C), the basivolsellar bridge.

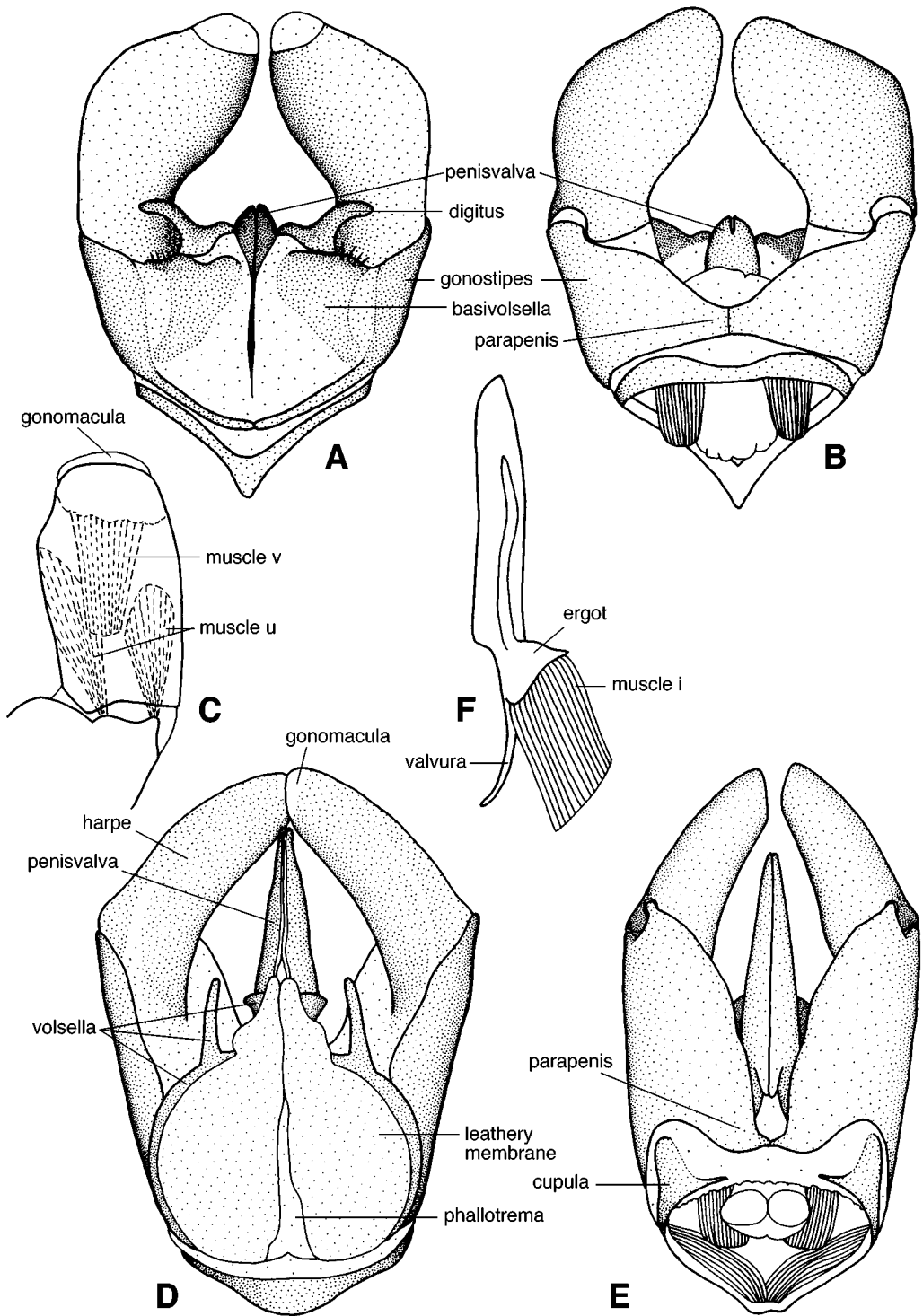


Fig. 7. Male external genitalia of Pamphiliidae (A–C) and Megalodontesidae (D–F). A. *Onycholyda amplexa*, ventral. B. *O. amplexa*, dorsal. C. External dorso-lateral view of harpe of *Cephalcia* sp. D. *Megalodontes cephalotes*, ventral. E. *M. cephalotes*, dorsal. F. Penisvalva of *M. cephalotes*.

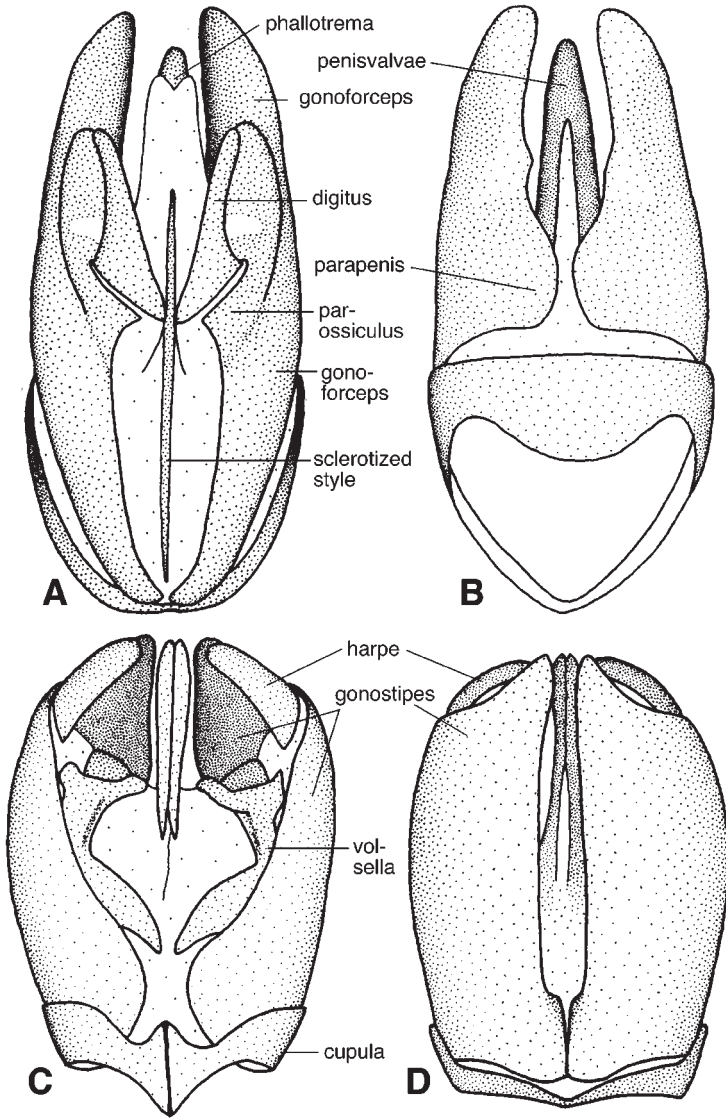


Fig. 8. Male external genitalia of Cephidae and Anaxyelidae. A. *Calameuta filliformis*, ventral. B. *C. filliformis*, dorsal. C. *Syntexis libocedrii*, ventral. D. *S. libocedrii*, dorsal.

4. The two penisvalvae. The distal, disc-shaped part of each penisvalva is called valviceps; the basal, elongated part is the valvura.

Some hymenopterans have additional sclerites associated with the male genitalia. The following were found in the sample examined in the present study.

A. The median sclerotized style is found in Cephidae and Siricidae (Figs. 8A; 9A, C). It closes the phallotrema basally, so that the phallotrema opens only distally, between the valviceps.

B. The fibula ducti (Schulmeister 2001), if present, usually is a tiny sclerite inside of the ductus ejaculatorius. In Pergidae and Argidae it is large and has two plates dorsally and ventrally on the ductus (Fig. 3B, D).

C. The dorsal rod (Snodgrass 1941) is a sclerite on the dorsal surface of the external genitalia, between the

penisvalvae (Fig. 11D). Snodgrass (1941) also assigned this term to a basal extension of dorsally fused penisvalvae in other taxa, but the homology is not clear.

The muscles of the male genitalia and their insertion sites are listed in Table 1. They are illustrated in Schulmeister (2001).

Muscle n was described by Schulmeister (2001) as having a basal and a distal part, here called nb and nd. In the present study, some taxa were found to have a lateral muscle, called nl, which runs from the basivolsella to the distal end of nb and/or the basal end of nd. In *Arge*, a muscle connects the left and right digiurae and could be homologous to the muscles nd. In *Perga*, *Lophyrotoma*, *Decameria* and *Acordulecera*, a muscle connects the left and right basivolsellae (Fig. 3E). This muscle was not assumed to be homologous to any other described muscle

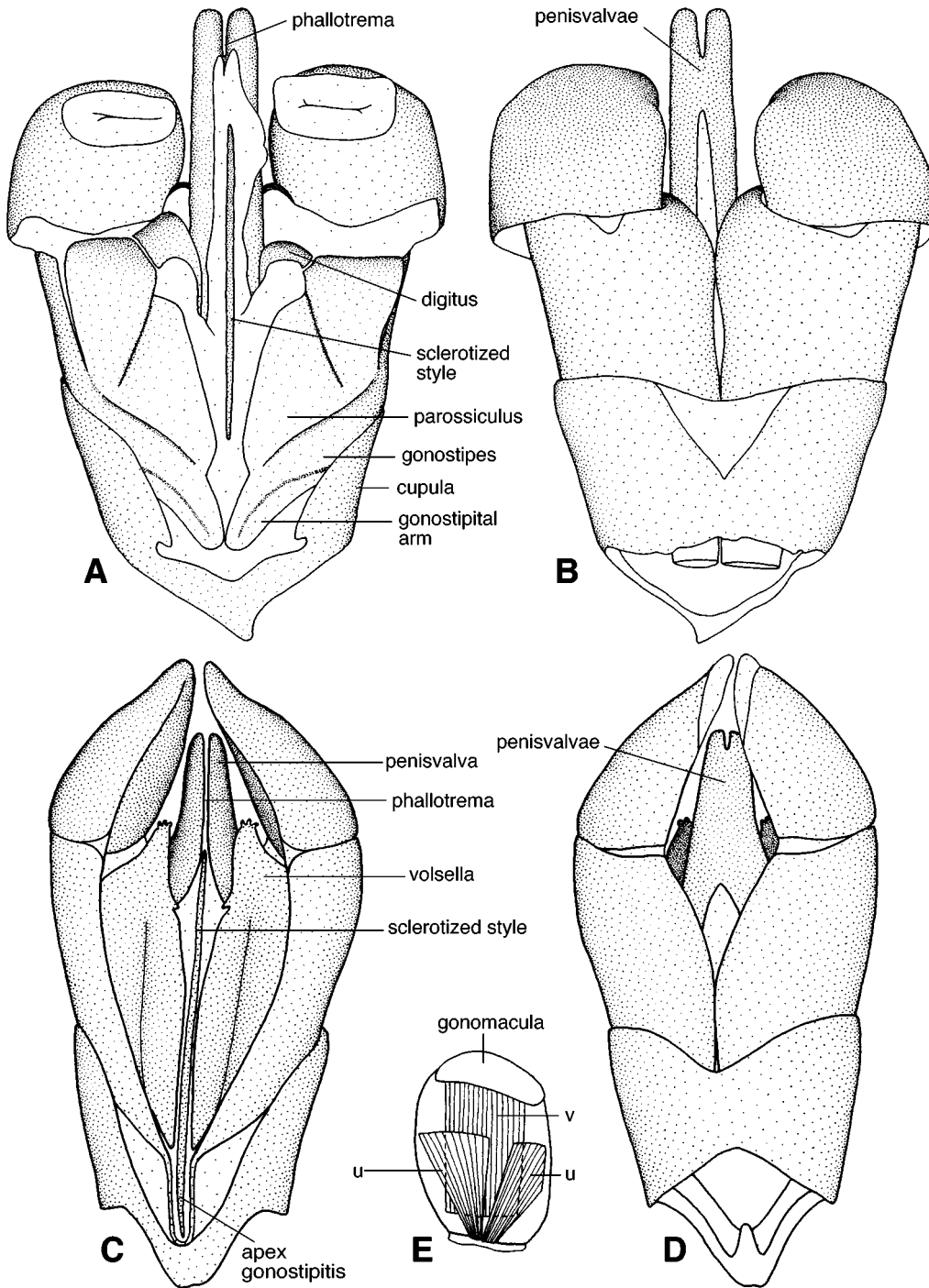


Fig. 9. Male external genitalia of Siricidae. A. *Xeris spectrum*, ventral. B. *X. spectrum*, dorsal. C. *Tremex columba*, ventral. D. *T. columba*, dorsal. E. Internal view of lateral part of harpe of *Urocerus gigas*.

and was termed y. In *Dolichovespula*, a muscle (named w) was found to run from the dorsal to the ventral part of the wall of the gonostipes. Its function is unclear.

Boulangé (1924) reported muscle x to be present in *Abia*. I dissected a well-preserved male of *Abia* sp. but

could not find the muscle x. The few muscle fibers running medially from the valvurae probably belonged to muscle nb.

Not included in Table 1 is a large muscle which was found in *Orussus abietinus* and *O. minutus*, running dor-

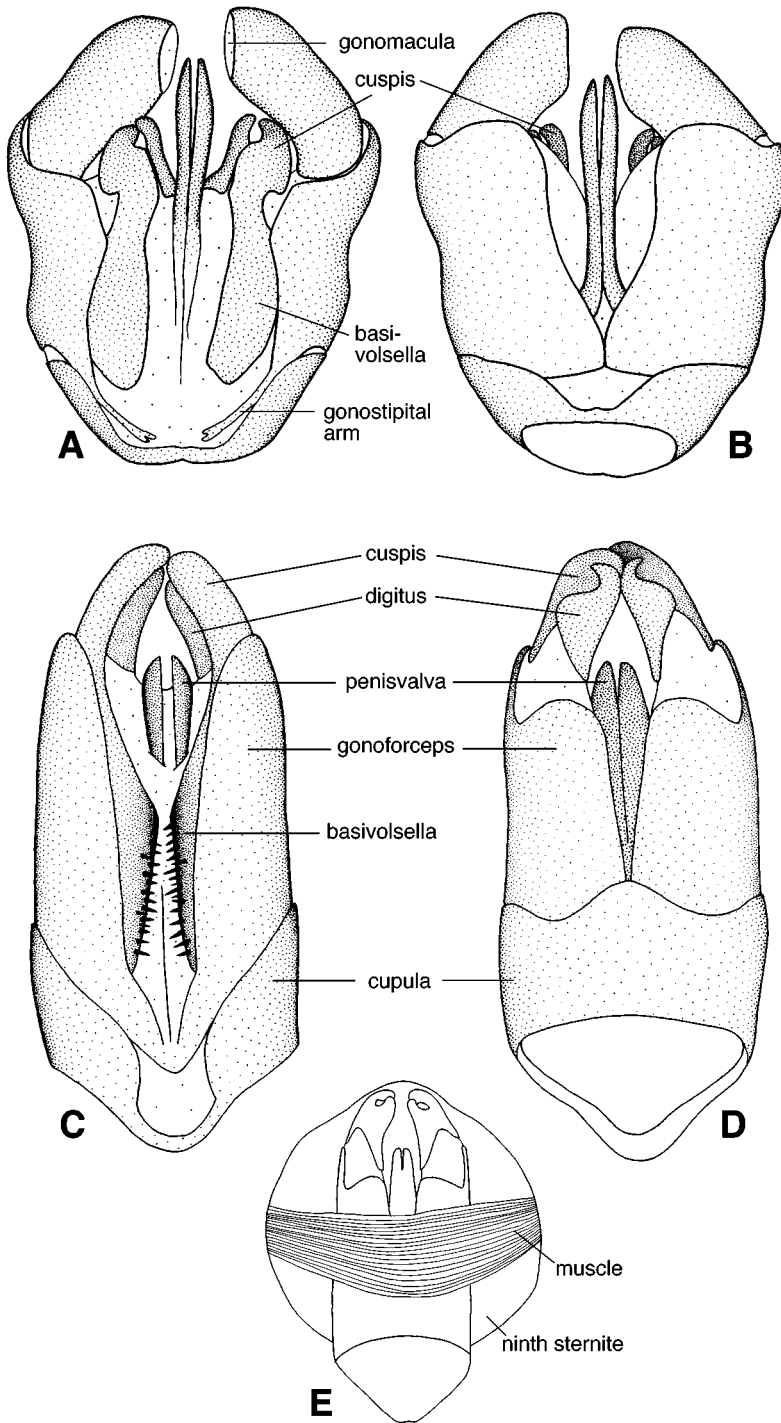


Fig. 10. Male external genitalia of Xiphydriidae (A–B) and Orussidae (C–E). A. *Xiphydria camelus*, ventral. B. *X. camelus*, dorsal. C. *Orussus abietinus*, ventral. D. *O. abietinus*, dorsal. E. External genitalia, ninth sternite, and undescribed muscle of *O. abietinus*.

sally across the copulatory apparatus and pressing it against the ninth sternite (Fig. 10E). This muscle inserts on the left and right margins of the ninth sternite and not on the external genitalia. It has not been found in any other hymenopteran.

Male internal reproductive organs

The internal reproductive organs of many sawfly species are depicted in Togashi (1970). The vasa deferentia lead from the testes to the glandulae mucosae (Fig. 13B, C).

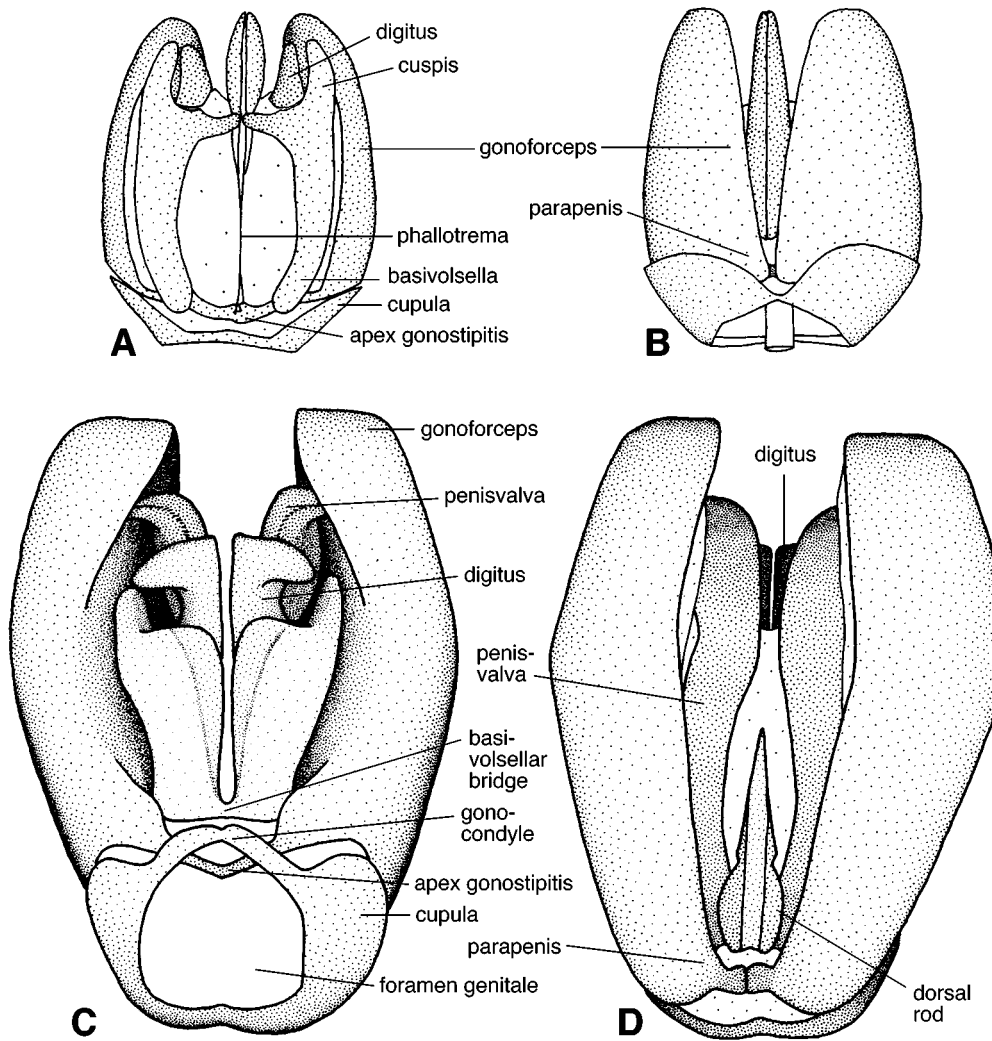


Fig. 11. Male external genitalia of Apocrita. A. *Stephanus serrator*, ventral. B. *S. serrator*, dorsal. C. *Sceliphron caementarium*, ventral. D. *S. caementarium*, dorsal.

In most groups, the vasa deferentia are coiled near the glandulae to form the vesiculae seminales. The glandulae mucosae are more or less round or oval in most groups, but can take a variety of shapes (Fig. 13). The ducti ejaculatorii lead from the glandulae mucosae to the external genitalia. They unite before becoming enlarged to the endophallus.

Sclerites of the terminal segments of the male abdomen

The male hymenopteran abdomen ends on the ventral side with the ninth sternite, and on the dorsal side with the tenth tergite including the cerci. The eighth sternite is

more or less rectangular in most sawfly groups, but medially constricted in some groups (Fig. 14). In Siricidae, the eighth sternite has a distinct triangular notch in its distal margin (Fig. 14P, Q). In Vespidae (in the present study observed in *Polistes* and *Dolichovespula*), the eighth sternite is closely attached to the ninth sternite (Fig. 14W). The ninth sternite forms a subgenital plate, which is more or less round in most Hymenoptera, particularly the basal groups. However, in some groups the form of the ninth sternite departs from this ‘standard’ (Fig. 14). The spiculum, an apodeme on the basal margin of the ninth sternite, varies greatly in size, from being completely absent to extending caudally beyond the eighth sternite (Fig. 14W).

The eighth tergite is the last prominent tergite of the male abdomen. The ninth and tenth tergites are more or

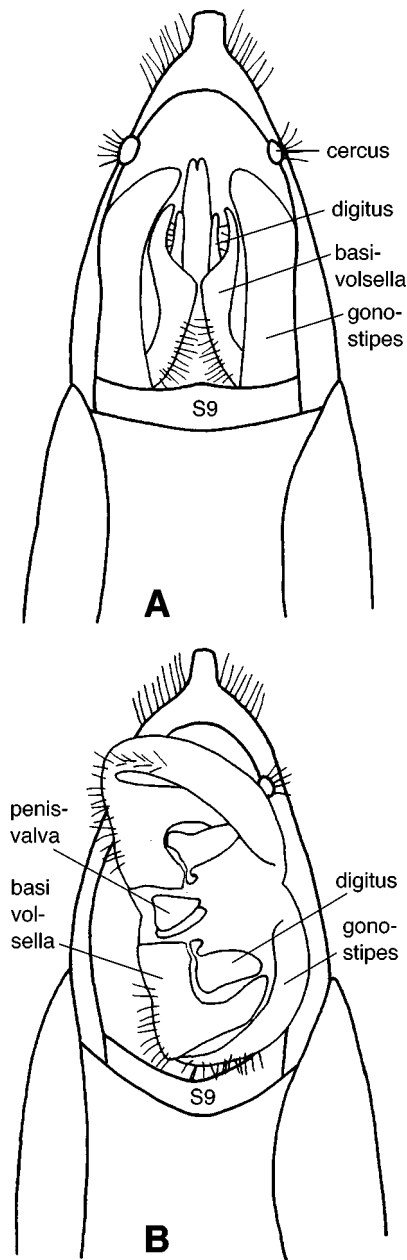


Fig. 12. Terminal segments of the abdomens of two specimens of *Schlettererius cinctipes*, ventral view. A. External genitalia 'closed'. B. External genitalia opened up.

Table 1. Muscles and their insertion sites in external genitalia of male Hymenoptera.

Muscles connecting the cupula to the ninth sternite		
a	gonocondyle	spiculum
b	laterally of gonocondyle	spiculum
c	gonocondyle	laterally on ninth sternite
Muscles connecting cupula and gonostipes		
d	ventro-medially next to gonocondyle	ventro-laterally on gonostipital arm
e	ventro-laterally on cupula	ventro-medially on gonostipital arm
f	dorso-medially on cupula	dorso-laterally on gonostipes
g	dorso-laterally on cupula	dorso-medially on gonostipes
Muscles connecting penisvalva and gonostipes		
h	apex of valvura	apex gonostipitis
i	ergot or equivalent	apex gonostipitis
j	apex of valvura	parapenis
k	median side of penisvalva	median edge of parapenis
l	ergot or equivalent	(dorso-)laterally on gonostipes
Muscles of the volsella		
m	apex of valvura	digiceps
n	nb apex of valvura	primary gonopore
	nd primary gonopore	digiura
	nl nb and nd or primary gonopore ?	basisvolsella
o	basisvolsella	distally on the gonostipes
p	distivolsellar apodeme	basally on the gonostipes
qr	distivolsellar apodeme	basal part of basisvolsella
s	digiura	medial basal part of basisvolsella
si	ergot or equivalent	medial part of basisvolsella
Muscles of the harpe		
t	gonostipes	medial face of harpe
u	distal edge of gonostipes	harpe (lateral or medial face)
v	harpe	gonomacula
Extraordinary muscles		
w	dorsal gonostipes	ventral gonostipes
x	left valvura	right valvura
y	left basisvolsella	right basisvolsella
z	valvura	median sclerotized style

less retracted below the eighth tergite (Fig. 15). They are not clearly separated in most taxa, and the tenth tergite is often membranous or completely absent (Fig. 15F). The ninth tergite can be separated into two disconnected lateral sclerites (Fig. 15F). The cerci are absent in some taxa, e.g. *Tremex* (Siricidae).

Functional morphology

Gonomaculae

In Xyelidae, Pamphiliidae, Megalodontesidae, Siricidae, and Xiphydriidae, there is a membranous area at the distal

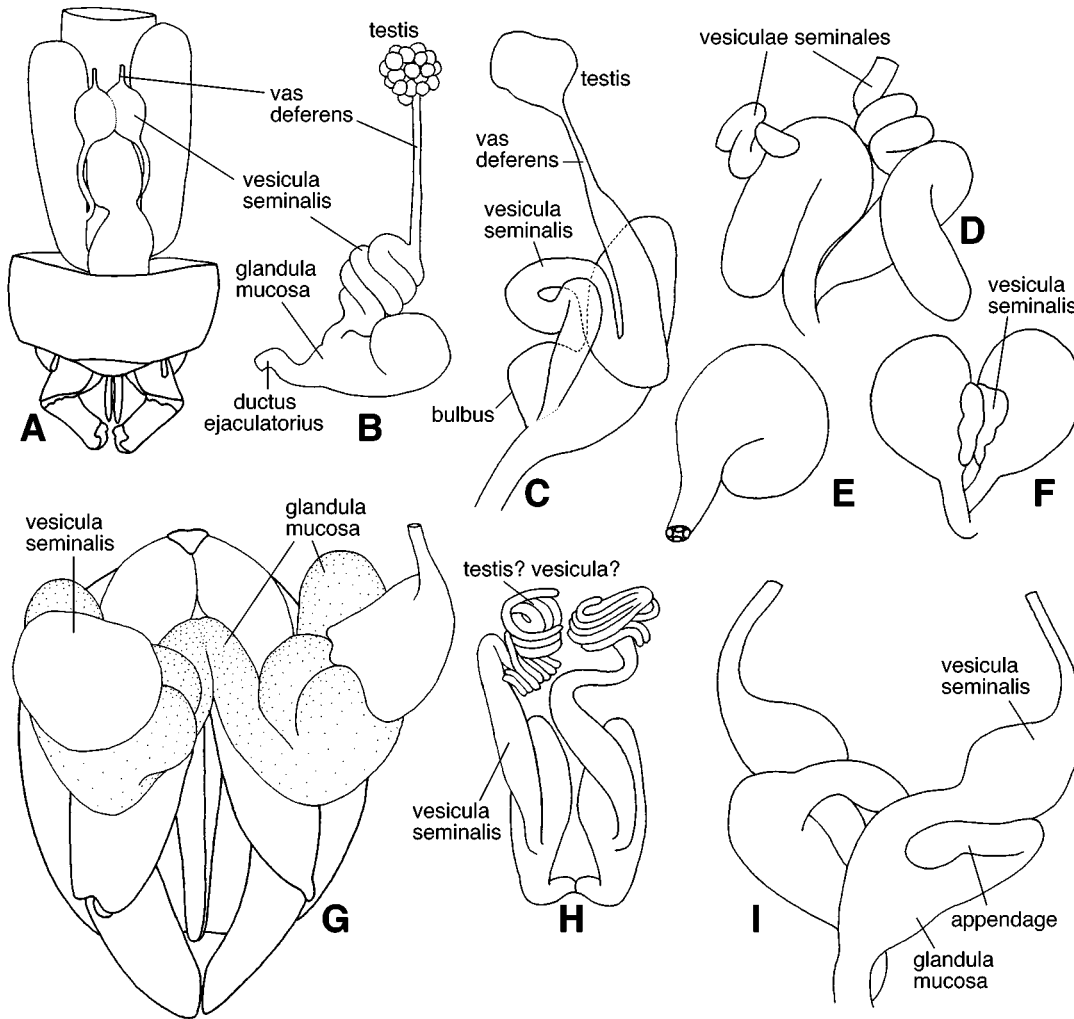


Fig. 13. Male internal reproductive organs of Hymenoptera (caudal ends oriented downward; in most cases the testes are not shown). A. *Macroxyela ferruginea* (Xyelidae). B. *Athalia rosae* (Tenthredinidae). C. *Aglaostigma lichtwardti* (Tenthredinidae). D. *Diprion* sp. (Diprionidae), glandulae and vesiculae. E. *Arge cyanocrocea* (Argidae), glandula mucosa. F. *Decameria* sp. (Pergidae). G. *Megalodontes cephalotes* (Megalodontesidae). H. *Cephus pygmeus* (Cephidae). I. *Dolichovespula adulterina* (Vespidae).

end of the harpe, the gonomacula (Figs. 1, 7, 9, 10). A muscle (v) leads from the middle of the gonomacula to the side of the harpe (Figs. 7C, 9E). It has been shown by Schulmeister (2001) that in *Macroxyela ferruginea* the gonomaculae serve as suction cups. In the present study it was discovered that in Xyelidae the harpe is closed off basally with a membrane, which separates the interior of the harpe from the interior of the rest of the external genitalia (Fig. 1G, H). This makes the harpe a 'closed chamber'. Muscle fibers run across this internal membrane (Fig. 1G, H). They likely serve to decrease the size of the chamber, thereby increasing the pressure within it. This, in turn, likely acts antagonistically to muscle v which pulls the gonomacula basally, respectively internally. Xyelidae are also able to 'hide' their gonomaculae (Fig. 1E, F).

Ability to open and close the copulatory apparatus

Some members of the Vespina, e.g. in *Orussus* and *Schlettererius*, were found to have the volsellae more or less hidden inside the external genitalia, as seen in Figs. 10C and 12A. This leads to the question how such males can make use of their volsellae. A potential answer was found when several pinned museum specimens of *Schlettererius cinctipes* were examined in the present study. Some were found to have the genitalia in the 'closed' fashion mentioned above, with the volsellae hidden inside, along the medio-sagittal plane (Fig. 12A). Others, however, had the copulatory apparatus 'opened' like a book, with the volsellae now exposed on the ventral side of the genitalia (Fig. 12B). Apparently, at least

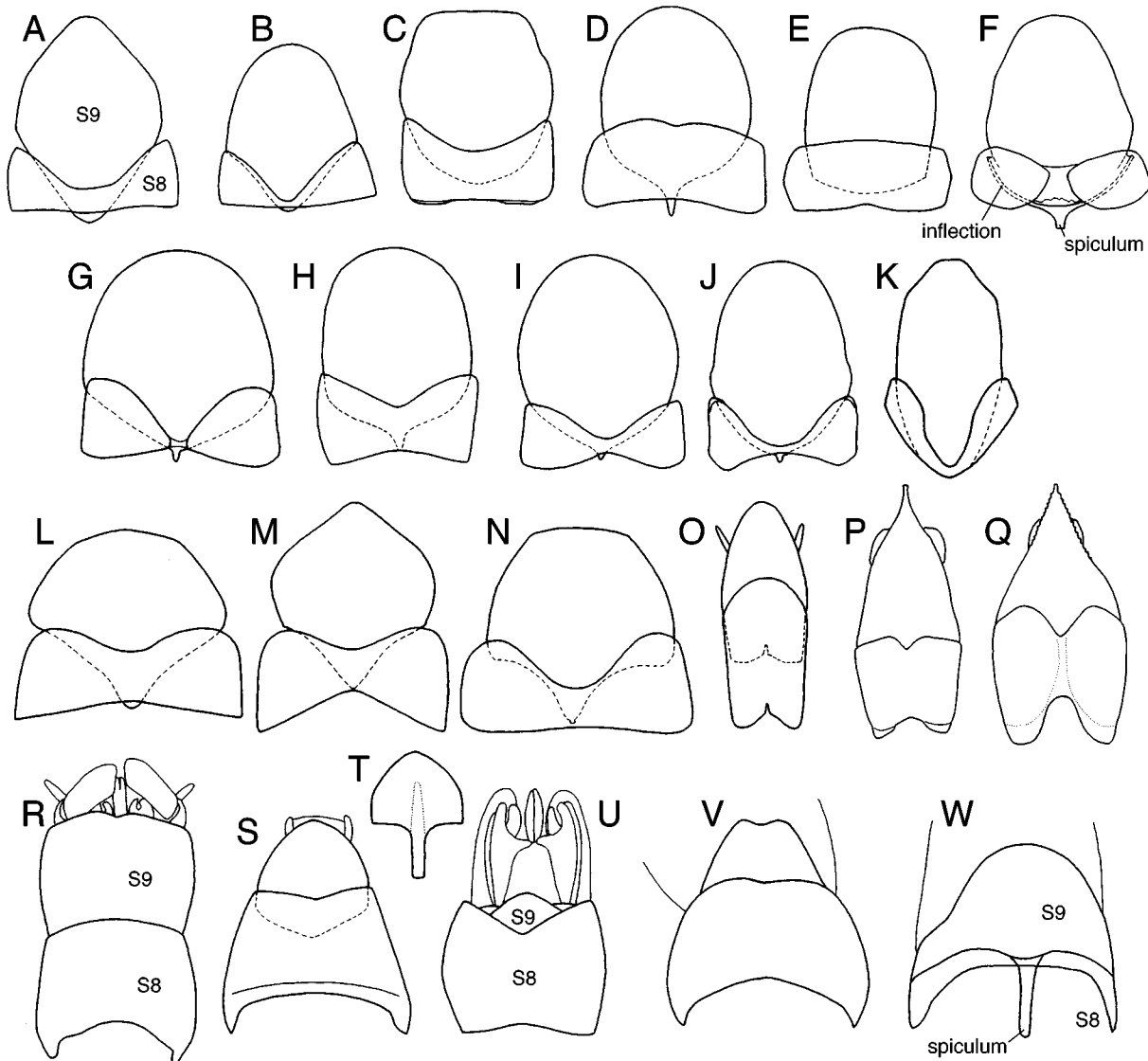


Fig. 14. Eighth and ninth sternites of Hymenoptera. A. *Macroxyela ferruginea* (Xyelidae). B. *Xyela* sp. (Xyelidae). C. *Runaria reducta* (Blasticotomidae). D. *Sterictiphora furcata* (Argidae). E. *Acordulecera dorsalis* (Pergidae). F. *Corynis crassicornis* (Cimbicidae). G. *Monoctenus juniperi* (Diprionidae). H. *Strongylogaster multifasciata* (Tenthredinidae). I. *Aglaostigma lichtwardti* (Tenthredinidae). J. *Dolerus* sp. (Tenthredinidae). K. *Cladius pectinicornis* (Tenthredinidae). L. *Onycholyda amplecta* (Pamphiliidae). M. *Cephalcia* sp. (Pamphiliidae). N. *Megalodontes skorniakowii* (Megalodontesidae). O. *Calameuta filiformis* (Cephidae). P. *Xeris spectrum* (Siricidae). Q. *Tremex columba* (Siricidae). R. *Xiphydria camelus* (Xiphydriidae). S. *Orussus abietinus* (Orussidae). T. *Stephanus serrator* (Stephanidae), ninth sternite. U. *S. serrator*, eighth and ninth sternite in situ. V. *Sceliphron caementarium* (Sphecidae). W. *Dolichovespula adulterina* (Vespidae).

Schlettererius cinctipes is able to fold up and unfold its copulatory apparatus, and it can be assumed that the open condition corresponds to the copulatory posture.

Characters

This section lists all 87 characters that were coded from the terminal abdominal segments of male Hymenoptera,

and the different states recognized for each character. Where necessary, the states are illustrated. The characters have been numbered consecutively from 267 to 353. This was done in order to match the character numbering of Vilhelmsen (2001) and of recent studies by Schulmeister (2003a, b) which use the characters from the present study in addition to the non-genital characters (236 from Vilhelmsen 2001 plus 30 from Schulmeister 2003a). In the character list below, numbers following

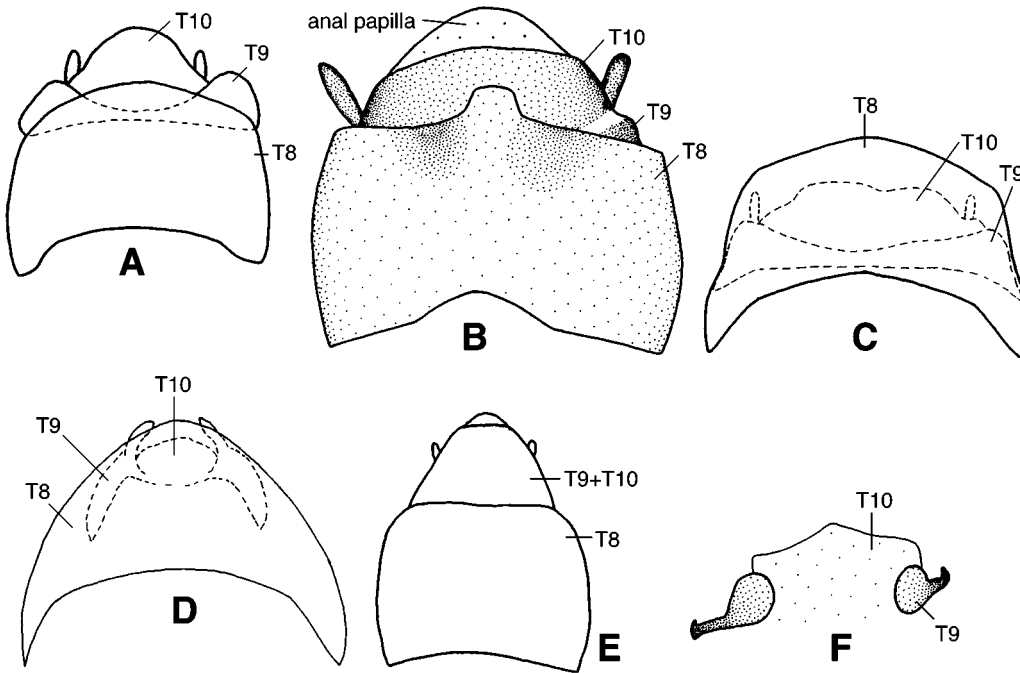


Fig. 15. Terminal dorsal sclerites of male Hymenoptera. A. *Runaria reducta* (Blasticotomidae). B. *Nematus* sp. (Tenthredinidae). C. *Monoctenus juniperi* (Diprionidae). D. *Orussus abietinus* (Orussidae). E. *Stephanus serrator* (Stephanidae). F. *Sceliphron caementarium* (Sphecidae).

citations refer to character numbers, not to pages. The coding of character states for the species listed in Appendix 1 is given in Appendix 2.

Male external genitalia

Muscles

267. Muscles a and b: 0 = a absent, b muscles close together, i.e. there are no muscle fibers coming from the spiculum that insert directly on the gonocondyle, but the b muscles are inserting very close to the gonocondyle; 1 = a absent, b muscles widely separated, i.e. there are no muscle fibers coming from the spiculum that insert on or near the gonocondyle; 2 = a and b present. Unordered. The unpaired muscle a and the two muscles b often are not separable and have therefore been treated as one character.
268. Form of muscle a: 0 = straight, inserting only on spiculum; 1 = fan-shaped, inserting on spiculum and to the left and right of the spiculum on the basal margin of the ninth sternite; – = not applicable because a is absent.
269. Muscle c: 0 = present, inserting near the margin of the ninth sternite; 1 = present, inserting away from the margin of the ninth sternite; 2 = absent. Unordered.
270. Muscle running from the left to the right edge of the ninth sternite, across the external genitalia: 0 = absent; 1 = present.
271. Muscle d: 0 = present, inserting on or near gonocondyle; 1 = present, not near gonocondyle; 2 = absent. Unordered. For a cladistic analysis, this and the next character should be coded as inapplicable in those taxa in which the cupula is completely absent or fused with the gonostipes ventrally, because the absence of muscles d and e is in these cases dependent on the absence or fusion of the cupula.
272. Muscle e: 0 = present; 1 = absent. See previous character.
273. Muscle f: 0 = present; 1 = absent. For a cladistic analysis, this and the next character should be coded as inapplicable in those taxa in which the cupula is absent, because the absence of muscles f and g is in these cases dependent on the absence of the cupula.
274. Muscle g: 0 = present; 1 = absent. See previous character.
275. Muscle h: 0 = present, straight, inserting on apex gonostipitis (Fig. 6D, E); 1 = present, fanned out; 2 = present, but inserting on the gonostipital arm instead of the apex gonostipitis. Unordered.
276. Muscle i: 0 = present (Fig. 6D, E); 1 = absent.
277. Muscle j: 0 = present. There is only one state for this character because muscle j was found in all ex-

amed hymenopteran species, with little morphological variation other than in size. The character is nonetheless included here to document which taxa this muscle was found in.

278. Muscle k: 0 = present, inserting on the valvura, the ergot, or at the base of the valviceps (Fig. 6E); 1 = present, inserting within the valviceps (in-between medial and lateral side of one valviceps) (Fig. 6D); 2 = present, long, directed distally, inserting within the valviceps; 3 = absent. Unordered.
279. Muscle l: 0 = present; 1 = absent.
280. Muscle m: 0 = present; 1 = absent.
281. Muscle n: 0 = only nl; 1 = completely absent; 2 = nb, nd, and nl present; 3 = nb and nd present (Fig. 6D); 4 = nb and nl present. Unordered.
282. Muscles connecting the two volsellae: 0 = absent; 1 = present, between the two digiurae; 2 = present, between the two basivolsellae (muscle y) (Fig. 3E). Unordered. The frayed-out muscle connecting the left and right digiurae (state 1) in *Arge* was assumed to be muscle nd; nd was hence coded as present for *Arge* in the previous character. The frayed-out muscle connecting the left and right basal ends of the basivolsella in some pergids (Fig. 3E) was assumed to be new and not identical to muscle nl.
283. Muscle o: 0 = one muscle present, narrow or broad; 1 = two separate muscles present; 2 = muscle entirely absent. Unordered. Muscle o is usually one narrow muscle extending from the basal end of the basivolsella to the distal end of the gonostipes. In some taxa, however, its insertion on the basivolsella is clearly extending, sometimes covering the lateral side of the entire basivolsella. In other taxa, muscle o can be split into a distal and a basal part, as depicted in Schulmeister (2001: Figs. 8D, 9C).
284. Muscle p: 0 = present; 1 = absent.
285. Muscle qr: 0 = present; 1 = absent.
286. Muscles s and si: 0 = only si present (or si inserts between ergot and digiura); 1 = only s present; 2 = both si and s present; 3 = both absent. Unordered.
287. Harpe and muscle t (which connects the harpe to the gonostipes) (Vilhelmsen 1997b: 83, 2001: 218): 0 = harpe present, t present (as one or two muscles); 1 = harpe fused to gonostipes or absent, muscle t absent (Figs. 8B, 10C, 11); 2 = harpe present, but without any muscles connecting it to the gonostipes. Unordered. Vilhelmsen (1997b, 2001) recognized only the first two states. However, I found *Gilpinia* and *Orthogonalys* to lack muscles t even though they do have harpes. Presence of the harpe and presence of muscle t are here coded together because if the harpe is lost, muscle t must also be lost. This means that muscle t and the harpe do not form independent

characters, and that coding them separately would assign too much weight to their concerted loss.

288. Parts of muscle u: 0 = two parts which start next to each other basally, but are separate distally (Fig. 9E); 1 = two completely separate parts (Fig. 7C); 2 = one part (Schulmeister 2001: Fig. 8F); 3 = u is absent even though harpe is present; – = not applicable because harpe is absent. Ordered. For a cladistic analysis, state 3 should be coded as inapplicable so that this character deals only with the configuration of muscle u, not its presence or absence, as these should not be mixed up.
289. Distal insertion point of muscle u: 0 = on medial face of harpe (Figs. 7C, 9E); 1 = on lateral face of harpe; – = not applicable.
290. Muscle v and gonomacula (Ronquist et al. 1999: 137; Vilhelmsen 1997b: 85, 2001: 219): 0 = both present and fully developed (e.g. Figs. 1F; 7C; 9A, E); 1 = gonomacula vestigial or absent, v absent. The two examined specimens of *Runaria reducta* were found to have tiny membranous areas at the tips of their harpes, which were interpreted as remnants of gonomaculae. For a cladistic analysis, the character should be coded as inapplicable in those taxa lacking a (separate) harpe, in order to avoid placing double weight on the reduction of the harpe.
291. Muscle w: 0 = absent; 1 = present.
292. Muscle x: 0 = absent; 1 = present.
293. Muscle z: 0 = absent; 1 = present.

General characters

294. Orientation of the male genitalia (Königsmann 1977: 22; Ronquist et al. 1999: 133; Vilhelmsen 1997b: 86, 2001: 216): 0 = not inverted at rest (orthandrous); 1 = rotated 180 degrees around the longitudinal axis when at rest (strophandrous). Contrary to Ronquist et al. (1999) and in agreement with Vilhelmsen (1997b, 2001), I coded strophandry as one state in Xyelidae and Tenthredinoidea s.str., in order to provide a stronger test for (non-)homology of this state in the two taxa.
295. Left and right parts of the genitalia: 0 = cannot be folded towards each other; 1 = can be folded towards each other to hide the volsellae (see Functional morphology above, and Fig. 12).
296. Position of foramen genitale: 0 = dorsal (Fig. 5B); 1 = basal (Fig. 1A, B); 2 = ventral (Fig. 11C). Ordered.
297. Apex gonostipitis: 0 = proximal of parapenis; 1 = distal of basal margin of parapenis (Fig. 11C, D).
298. Ectophallic membrane: 0 = without pockets; 1 = forms two flat pockets on ventral side of genitalia (Fig. 4A).

Cupula

299. Cupula (Vilhelmsen 2001: 217): 0 = cupula present and circular; 1 = cupula present, but complete-

ly reduced dorsally (Figs. 3B, 7E); 2 = cupula absent (Fig. 3C, D). Ordered. Vilhelmsen (2001) distinguished only the two states “absent” and “present” and assigned the latter state to all hymenopterans. However, many hymenopterans have the cupula partly or completely reduced. Therefore, an intermediate had to be introduced.

300. Fusion of cupula (Ronquist et al. 1999: 135): 0 = free; 1 = very closely connected to or fused with the gonostipites ventro-medially (Fig. 3A); 2 = fused with the gonostipites ventro-laterally (Fig. 5C); – = not applicable. Unordered.
301. Distally directed branch on lateral side of cupula: 0 = absent; 1 = present (Fig. 3B); – = not applicable.
302. Gonocondyle: 0 = basally directed (Fig. 1C); 1 = distally directed loop (Fig. 11C).

Gonostipes and harpe

303. Apices gonostipitum respectively gonostipital arms: 0 = pointing medially (Fig. 4D); 1 = pointing cranially (Fig. 9A, C).
304. Parapenis: 0 = antero-medial corner drawn out (Fig. 7B, E); 1 = not set off from the rest of the gonostipes (Figs. 1B, 3B); 2 = set off, but without constriction (Fig. 5B); 3 = with constriction, i.e. parapenisjugum narrowed (Figs. 4B, 6B). Ordered. The difference between states 0 and 2, which appear similar in Figs. 7B and 5B, is that in state 2 the entire parapenes, i.e. the entire insertion sites of muscles j, are slightly set off from the rest of the gonostipes and meet medially, whereas in state 0 only the antero-medial corners of the parapenes, containing maximally the insertion sites of muscles k, are drawn out to meet medially.
305. Basal margin of parapenis: 0 = more or less straight from left to right (Fig. 5B); 1 = drawn out basally (Fig. 5D). (The character is still applicable when the parapenes are fused to each other because if they are they can still be drawn out basally.)
306. Notch in the median margin of parapenis: 0 = absent; 1 = present (Fig. 2B, D).
307. Medial inflection of parapenis: 0 = absent; 1 = present. In state 1, the parapenis is inflected at the medial rim.
308. Basal inflection of gonostipes: 0 = absent; 1 = on gonostipital arm; 2 = on gonostipital arm and parapenis (Schulmeister 2001: Fig. 2D); 3 = on parapenis only. Unordered.
309. Inclination of parapenis: 0 = more or less parallel to the median axis of the genitalia (Fig. 6D); 1 = inclined (Fig. 6E).
310. Median fusion of parapenes: 0 = not fused basally (Fig. 8B); 1 = fused basally or completely (Fig. 3D).
311. Spine at the distal end of the gonoforceps (parameral spine (f) of Snodgrass 1941): 0 = absent; 1 = present.

312. Gonomacula: 0 = can be covered with a ‘lid’ (Fig. 1E, F); 1 = cannot be ‘hidden’; – = not applicable because gonomacula is lacking. Ronquist et al.’s (1999) character 138 distinguished gonomaculae situated either apically or subapically. I cannot see what was meant by this, but the distribution of states of their character 138 corresponds to the coding of my character 312.
313. Internal membrane between the harpe and the gonostipes (see above): 0 = present (Fig. 1G, H); 1 = absent; – = not applicable because harpe is lacking.
314. Harpe: 0 = rather straight, about as broad as the distal edge of the gonostipes, dorsal and ventral edge more or less parallel (Figs. 3B, 4E); 1 = rather triangular, with a dorsal flap which extends into the gap created by the constriction between the parapenis and the rest of the gonostipes (Figs. 4B; 5B, D; 6B); – = not applicable because harpe is lacking.
315. Ridge on distal edge of harpe: 0 = absent; 1 = present (Fig. 3A); – = not applicable because harpe is lacking.
316. Median face of harpe: 0 = extends about as far cranially as the lateral face; 1 = extends much farther cranially (Fig. 7D).

Penisvalvae and phallotrema

317. Penisvalvae: 0 = completely separate (Figs. 1D, 3B); 1 = fused dorsally (Figs. 2B; 7B; 8B; 9B, D).
318. Hairs on valviceps: 0 = absent; 1 = present (Fig. 1A–D).
319. Tip of valviceps/penisvalva (viewed from medial): 0 = rounded, not drawn out (Figs. 1B, 3B); 1 = drawn out into a pointed thread-like structure (Fig. 2A–D).
320. Pseudoceps and valvispina: 0 = absent (Figs. 4C, 7F); 1 = present (Fig. 6C). According to Ross (1945), who introduced these terms, a pseudoceps and valvispina are present in some Nematinae.
321. Row of teeth on valviceps: 0 = absent; 1 = present (Fig. 4C).
322. Ergot on penisvalva: 0 = absent; 1 = normal: short tip (Fig. 6C); 2 = scale-like (Fig. 4C); 3 = very long; 4 = wing-shaped (Fig. 7F). Unordered.
323. Valvura: 0 = not broader at apex (Fig. 4C); 1 = flattened and broadened at apex (not depicted).
324. Phallotrema (Vilhelmsen 1997b: 84): 0 = situated ventrally (Figs. 1C, 4D, 6A); 1 = situated apically (Figs. 3A, C; 8A; 9A, C). For a cladistic analysis, this character should be coded as inapplicable in those taxa that have a ventral sclerotized stylus, in order to avoid giving double weight to these correlated transformations.

Volsella

325. Volsella (Vilhelmsen 2001: 220): 0 = volsellae absent; 1 = volsellae present (Fig. 1A).

326. Digitus and basivolsella/parossiculus (includes Ronquist et al. 1999: 136): 0 = not fused (Fig. 3A); 1 = fused, but both digitus and cuspis are clearly present (Fig. 4A, D); 2 = either cuspis or digitus is missing, volsella ends in only one tip (Fig. 9C). Unordered.
327. Cranial end of basivolsella: 0 = not covering gonostipes; 1 = covering gonostipital arm (Figs. 4D, 11A).
328. Parossiculus/basivolsella: 0 = free (Fig. 3A); 1 = fused with gonostipes respectively gonoforceps (Figs. 8A, 9A); – = not applicable because volsella is missing.
329. Position of volsella: 0 = on medial face of gonostipes or gonoforceps (Figs. 1C, 10C, 11A, 12A); 1 = on ventral side of genitalia; – = not applicable because volsella is missing.
330. Basivolsellar apodeme: 0 = absent; 1 = present; – = not applicable because volsella is missing.
331. Gonossicular apodeme (Snodgrass 1941): 0 = absent; 1 = present; – = not applicable because volsella is missing. According to Snodgrass (1941), the gonossicular apodeme is a specialty of the Vespidae. However, I could not find a gonossicular apodeme in any of the examined specimens, including the vespids *Dolichovespula* and *Polistes*.
332. Basivolsellar bridge: 0 = absent; 1 = present (Fig. 11C); – = not applicable because volsella is missing. The basivolsellar bridge is a sclerotized bridge between the cranial ends of the basivolsellae (“j” in the figures of Snodgrass 1941).
333. Extension of volsella: 0 = not beyond gonoforceps; 1 = well beyond gonoforceps (Fig. 10C).
334. Thorns on basivolsella: 0 = absent; 1 = present (Fig. 10C).

Additional sclerites

335. Fibula ducti: 0 = absent or small; 1 = large, on surface of ductus (Fig. 3B, D).
336. Ventral median sclerotized style: 0 = absent; 1 = present, separate from the gonostipites, unipartite (Figs. 8A; 9A, C); 2 = present, separate from the gonostipites, split into left and right parts; 3 = present, proximally fused with the gonostipites. Unordered. For a cladistic analysis, it should be considered to code this character in only two states (absent/present).
337. Dorsal rod: 0 = absent; 1 = present (Fig. 11D). The dorsal rod is a sclerotization of the aedeagus (Snodgrass 1941).

Male internal reproductive organs

338. Glandulae mucosae: 0 = left and right; 1 = more or less dorsal and ventral, or distal and basal, of each other.

339. Form of glandula mucosa: 0 = more or less round, oval, or straight, or slightly curved (Fig. 13A, F, H); 1 = with a ‘bulbus’ at the side (Fig. 13C); 2 = U-shaped (Fig. 13D); 3 = sigma-shaped (Fig. 13E); 4 = with three blind ends (Fig. 13G); 5 = with a distal appendage (Fig. 13I). Unordered.
340. Ductus ejaculatorius: 0 = short; 1 = extremely long so that the glandulae mucosae are far away from the genitalia.
341. Coiling of the part of the vas deferens that forms the vesicula seminalis: 0 = coiled (Fig. 13B); 1 = zigzagging, but not coiled (Fig. 13C); 2 = straight (at least basally) (Fig. 13H). Unordered.
342. Relative size of vesiculae seminales: 0 = normal; 1 = very small, lumped together, squeezed between the glandulae mucosae (Fig. 13F).

Sclerites of the terminal segments of the male abdomen

Sternites

343. Constriction of eighth sternite (after Ronquist et al. 1999: 124): 0 = not constricted, almost rectangular, but in some cases distal margin concave (Fig. 14C, D, E, L, M, O, P, R, S, V); 1 = somewhat constricted medially (Fig. 14A, H, I, N, P, Q, U); 2 = strongly constricted, with sclerotized bridge in the middle (Fig. 14B, J); 3 = separated in two sclerites connected only by membrane (Fig. 14F, G); 4 = very narrow throughout (Fig. 14W); 5 = V-shaped and rather narrow throughout (Fig. 14K). Ordered. For a cladistic analysis, states 1, 4 and 5 can be summarized as state 1, because the narrowness of the eighth sternite is also a kind of constriction. Ronquist et al. (1999) – based on Rasnitsyn (1988) – coded the form of the eighth sternite in only two states: excised apically or not. Their state 1 was interpreted as a synapomorphy of Cimbicidae plus Tenthredinidae including Diprionidae. Here, the character is divided into more character states, but treating this multistate character as ordered means that states 1 (including 4 and 5), 2 and 3 still provide a potential synapomorphy for the group in question, because all other members of the Tenthredinoidea s.l. included in the present analysis have state 0.
344. Eighth and ninth sternite: 0 = separate, only connected by membrane (Figs. 14A–V); 1 = closely connected or fused (Fig. 14W).
345. Basal margin of ninth sternite seen from above: 0 = convex or triangular; 1 = rather straight from left to right, but each half concave; 2 = triangular, but clearly concave left and right (Fig. 14L–N); 3 = straight from left to right as in Cephidae and Siricidae (Fig. 14O). Unordered.

346. Distal margin of ninth sternite (ventral view): 0 = convex or triangular; 1 = drawn out into a long, pointed tip (Fig. 14P, Q); 2 = more or less straight from the right to the left side, as if cut off (Fig. 14C, R); 3 = concave. Unordered.
347. Spiculum: 0 = not prominent; 1 = drawn out (Fig. 14F); 2 = extremely long and directed cranially (Fig. 14T, W). Ordered.
348. Strengthened line on ninth sternite parallel to its basal margin: 0 = absent; 1 = present.
349. Strengthening of basal margin of ninth sternite: 0 = not strengthened; 1 = thickened; 2 = with inflection ventrally; 3 = with protruding inflection ventrally (Fig. 14F). Ordered.

Tergites and cerci

350. Eighth tergite: 0 = more or less rectangular (Fig. 15A); 1 = apically extended to cover anus; 2 = apically extended to cover male genitalia; 3 = with apical excision; 4 = with apical appendage (Fig. 15B). Unordered.
351. Ninth tergite: 0 = largely sclerotized (Fig. 15A); 1 = largely membranous, only very little sclerotized; 2 = sclerotized, but split into two widely separated lateral parts, which are connected only to the tenth tergite but not to each other (Fig. 15F). Unordered. (State 2 should not be coded as a separate character because the division into two lateral sclerites is caused by the middle part not being sclerotized. State 2 is hence similar to state 1.)
352. Tenth tergite: 0 = largely sclerotized (Fig. 15B); 1 = largely or completely membranous, but clearly distinct from ninth tergite; 2 = sclerite completely absent or indistinguishable due to fusion with ninth tergite (Fig. 15E). Unordered.
353. Cerci of male: 0 = present; 1 = absent.

Discussion

The 87 characters presented here have been analyzed together with 256 other morphological characters (see Schulmeister 2003a) and DNA sequences from five genes (Schulmeister 2003b). The final hypothesis of Schulmeister (2003b) is shown in Fig. 16.

The characters of the male reproductive organs provide support for some of the nodes in the tree, particularly at lower levels. The lines across the lineages in Fig. 16 indicate the number of unambiguous changes provided by the characters of the male reproductive organs. The nodes Xyelidae, Hymenoptera minus Xyelidae, Unicalcarida, Unicalcarida minus Cephidae, Xiphydriidae + Vespina, and Apocrita are not supported by any unambiguous changes from the characters presented here.

In the discussion, numbers in parentheses refer to the nodes in Fig. 16, if they are not followed by a colon. If they are, they refer to characters.

Groundplan of Hymenoptera

The male reproductive organs of Hymenoptera differ significantly from those of other holometabolans. For this reason, most characters have been coded as unknown for outgroup taxa. In these cases, the state of a certain character in the last common ancestor of all Hymenoptera can only be inferred unambiguously if the stem lineage of Xyelidae and the stem lineage of the non-xyelid Hymenoptera are inferred to have had the same state. If they differ and no outgroup information is available, the groundplan state for the character is ambiguous. Fortunately, this is hardly ever the case for the present data.

Since the genitalia of *Xyela* and *Macroxyela* hardly ever depart from the inferred groundplan of Xyelidae, this means that in the majority of the characters, the inferred groundplan of Hymenoptera (1) shows the same character states as the Xyelidae. Exceptions are the constriction of the eighth sternite, the presence of muscle m (if m is assumed to be absent in the outgroup), and the presence of hairs on the valvices in Xyelidae and the strophandry in *Xyela*. Whether the separate penisvalvae, the internal membrane between harpe and gonostipes, and the ability to close the gonomaculae in Xyelidae were already present in the groundplan of Hymenoptera is unclear. Other than that, the male genitalia of the hymenopteran ancestor probably looked very similar to those of the Xyelidae (Fig. 1).

The following muscles are inferred to have been present in the most recent common ancestor of all Hymenoptera (1): muscles b (inserting close together) (267: 0), muscles c (inserting at the margin of the ninth sternite) (269: 0), muscles d (inserting on or near gonocondyle) (271: 0), muscles e (272: 0), f (273: 0), g (274: 0), h (275: 0), i (276: 0), j (277: 0), k (278: 0), l (279: 0), o (one on each side) (283: 0), muscles p (284: 0), qr (285: 0), si (but not s) (286: 0), muscles t (287: 0), and u (with two completely separate parts in each harpe (288: 1), inserting on the medial side (289: 0)). The following muscles are inferred to have been absent from the most recent common ancestor of all Hymenoptera (1): muscles a (267: 0), m (if m is assumed to be absent in the outgroups) (280: 1), s (286: 0), w (291: 0), x (292: 0), y (282: 0), and z (293: 0). The optimization of muscle n is ambiguous at the base of the hymenopteran tree (281: ?).

The presence of a gonomacula with attached muscle v (290: 0) is assumed for the hymenopteran ancestor (1) if convergent reduction is preferred over convergent origin. The preference for convergent reduction and the assumption of the presence of a gonomacula and attached

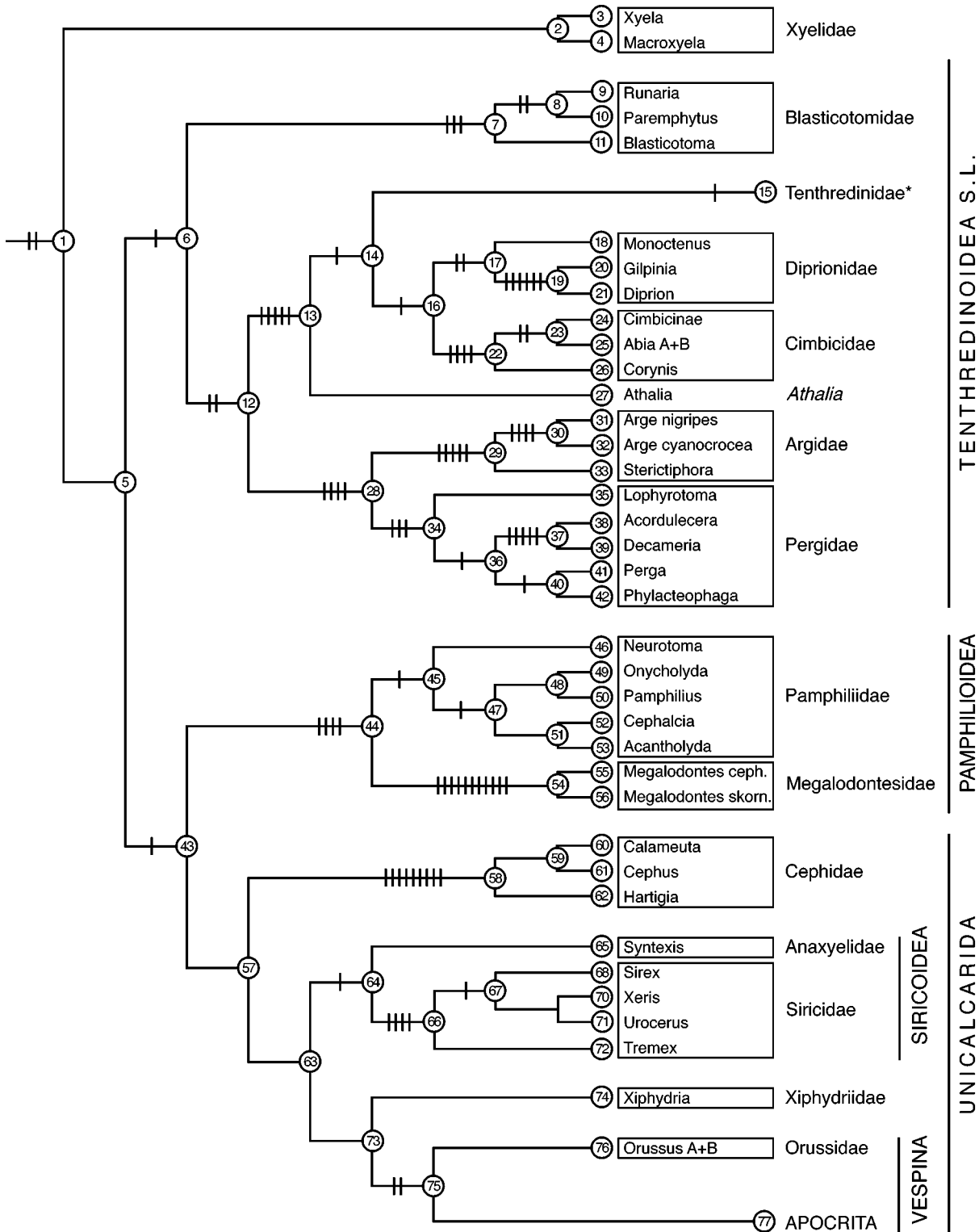


Fig. 16. Cladogram of Hymenoptera from Schulmeister (2003b), based on simultaneous analyses of 343 morphological characters and DNA sequences from five genes. Tenthredinidae* = Tenthredinidae minus *Athalia*. Lines across lineages (leading to nodes containing at least two terminals) indicate the number of unambiguous changes found within the characters presented here.

muscle in the groundplan of all Hymenoptera is supported by the presence of similar structures in basal Mecoptera that are assumed to have been present in the ancestor of all Mecoptera (Willmann 1989).

The male of the most recent ancestor of all Hymenoptera (1) is inferred to have had orthandrous genitalia (294: 0), with the harpes delimited from the gonostipites (287: 0), apices gonostipitum proximal of the parapenes (297: 0) and pointing medially (303: 0), a free and circular cupula (299: 0, 300: 0) with a basally directed gonocondyle (302: 0), a parapenis which is not set off from the rest of the gonostipes (304: 1), the basal margin of the parapenis being straight (305: 0), no notch in the medial margin of the parapenis (306: 0), a basal inflection on the gonostipital arm (308: 1), the parapenes more or less parallel to the median axis of the genitalia (309: 0) and fused to each other (310: 1), the harpe without a dorsal flap (314: 0), median face of harpe extending as far as lateral face (316: 0), no hairs on valvices (318: 0), penisvalvae simple and spoon-shaped (pseudoceps and valvispina absent) (319: 0, 320: 0) and without a row of teeth (321: 0), ergot present on penisvalva (322: 1 or 2), valvura slim (not broadened at the apex) (323: 0), phallotrema situated ventrally (324: 0), no median sclerotized style (336: 0), dorsal rod (337: 0) or sclerotic bridge between the basivolsellae (332: 0), volsellae present (325: 1) and not fused to the gonostipites (328: 0), digitus and parossiculus both present and separate from each other (326: 0), cranial end of basivolsella not covering gonostipes (327: 0), volsella not extending beyond the gonoforceps (333: 0) and not equipped with thorns (334: 0), fibula ducti absent or small (335: 0). It is uncertain whether the penisvalvae were fused (317: ?) in the hymenopteran ancestor, and whether the volsellae were situated on the medial side of the gonostipites as in Xyelidae or on the ventral side of the genitalia as in most sawflies (329: ?).

The glandulae mucosae are inferred to have been of oval shape (339: 0) and in positions left and right of each other (338: 0), the ducti ejaculatorii were short (340: 0), the vesiculae seminales coiled (341: 0) and of normal size (342: 0). The eighth sternite was not constricted (343: 0) and separate from the ninth sternite (344: 0). The ninth sternite was round (345: 0, 346: 0), its basal margin was thickened (349: 0), and the spiculum not prominent (347: 0). The eighth tergite was more or less rectangular (350: 0), the ninth and tenth tergites largely sclerotized (351: 0, 352: 0), and cerci were present (353: 0).

Evolution within Hymenoptera

Not surprisingly, the inferred groundplan of Hymenoptera (1) is largely identical with the configuration found in the Xyelidae (see above). Character states inferred for the ancestor of Xyelidae (2) that differ from the groundplan of Hymenoptera are the presence of

muscle m (if it was not present in the outgroups) (280: 0), the presence of hairs on the valvices (318: 1), and the eighth sternite being somewhat constricted (343: 1). It is also likely that the internal membrane separating the harpe from the rest of the genitalia was developed (313: 0) in the ancestor of the Xyelidae (2). *Xyela* (and *Pleroneura*; Snodgrass 1941) differ from the last common ancestor of Hymenoptera and that of Xyelidae in having strophandrous genitalia (294: 1).

Following what was said above, it is almost impossible to infer the state in the ancestor of the **Hymenoptera minus Xyelidae** (5) as different from that present in the ancestor of all Hymenoptera.

In the lineage leading to the **Tenthredinoidea s.l.** (6), the two parts of muscle u in each harpe fused to become one fan-shaped muscle (288: 2). In addition, the gonomacula and muscle v disappeared (if convergent reduction is preferred over convergent origin) (290: 1). In the stem lineage of **Blasticotomidae** (7), the basal inflection on the gonostipital arms disappeared (308: 0), the parapenes separated (310: 0), and the tip of the valvices developed a thread-like appendage (319: 1), whereas in the sister lineage, the one leading to **Tenthredinoidea s.str.** (12), strophandry evolved (294: 1), and a spiculum evolved on the ninth sternite (347: 1). In the lineage leading to **Tenthredinidae + Cimbicidae + Diprionidae** (13), muscle a evolved (267: 2), the insertion site of muscle k wandered inside the valvices (278: 1), the parapenis was set off from the rest of the gonostipes but still without a constriction (304: 2), and the harpe developed a dorsal flap (314: 1). Somewhere in the lineage leading to *Athalia* (27), the basal margin of the ninth sternite became rather straight (345: 1), whereas in the sister lineage, leading to the **Tenthredinidae* + Cimbicidae + Diprionidae** (14), the basal margin of the ninth sternite developed a ventral inflection (349: 2), and muscle a appeared (267: 2). In the stem lineage of the **Tenthredinidae*** (15), the insertion of muscle u switched from the medial to the lateral face of the harpe (289: 1). Possibly in the ancestor of the Diprionidae + Cimbicidae (16), the digitus fused with the basivolsella (326: 1). The ancestor of **Diprionidae** (17) evolved an inclination of the parapenes (309: 1) and a row of teeth on each valvices (321: 1), whereas in that of the **Cimbicidae** (22) muscle n (nb and nd) appeared (281: 3), the cranial end of the basivolsella came to cover the gonostipes (327: 1), and the inflection on the basal margin of the ninth sternite became prominent and protruding (349: 3). In the lineage leading to the **Argidae + Pergidae** (28), muscle si switched from the penisvalva to the digiura to become muscle s (286: 1), the phallotrema became closed basally (324: 1), the fibula ducti became unusually large (335: 1), and the vesiculae seminales very small (342: 1). In the **Argidae** (or *Arge* + *Sterictiphora*) (29), muscle n (nb and nd) appeared (281: 3), the basal inflection of the

gonostipital arms disappeared (308: 0), a ridge evolved on the harpe (315: 1), the glandulae mucosae became sigma-shaped (339: 3) and came to lie dorsally and ventrally (or distally and basally) of each other (338: 1). In the **Pergidae** (= Pterygophoridae) (36), muscle y evolved between the bases of the basivolsellae (282: 2), the cupula disappeared (299: 2), and the basal margin of the ninth sternite became straight (345: 3).

In the lineage leading to the **Unicalcarida + Pamphilioidea** (43), the muscles b came to insert away from each other on the cupula (267: 1). In the stem lineage of **Pamphilioidea** (44), muscle e disappeared (272: 1), muscle n (nb and nd) appeared (281: 3), the antero-medial corner of the parapenis was drawn out (304: 0), and the medial face of the harpe came to extend more basally than the lateral face (316: 1). In the lineage leading to the **Pamphiliidae** (45), muscle m evolved (280: 0). In the sister lineage, which leads to the **Megalodontesidae** (54), muscles l (279: 1), p (284: 1) and qr (285: 1) disappeared, the cupula was dorsally reduced (299: 1), the digitus fused with the parossiculus (326: 1), the eighth sternite became constricted (343: 1), a long spiculum evolved on the ninth sternite (347: 1), and a ventral inflection appeared on the basal margin of ninth sternite (349: 2).

The character states inferred to have been present in the last common ancestor of the **Unicalcarida** (57) do not differ from those inferred for the last common ancestor of Pamphilioidea + Unicalcarida. In the lineage leading to the **Cephidae** (58), muscle k switched its insertion site from the valvura to within the valviceps (278: 2), muscles qr disappeared (285: 1), muscle si switched from the penisvalva to the digiura to become muscle s (286: 1), the harpes with muscles t, gonomacula, and muscles v disappeared (287: 1), the basal inflection on the gonostipital arms disappeared (308:0), the parapenes separated (310: 0), the phallorema was closed basally with the median sclerotized style (336: 1) and muscle z evolved between the style and the valvura (293: 1), the parossiculus fused with the gonostipes (328: 1), and the vas deferens/vesicula seminalis became straight (341: 2), probably due to the slimness of the abdomen.

The ancestor of the **Unicalcarida minus Cephidae** (63) is inferred to have had the same character states as the ancestor of all Unicalcarida (57), just like that of **Xiphydriidae + Vespina** (73). In the ancestor of **Siricoidea** (64), muscle n (nb and nd) appeared (281: 3). In the ancestral lineage of **Siricidae** (66), muscle h was strongly fanned out (275: 1), the apices gonostipitum pointed cranially instead of medially (303: 1), the phallorema was closed basally with a median sclerotized style (336: 1), and the ninth sternite was drawn out into a pointed tip (346: 1). Somewhere in the lineage leading to **Xiphydria**, the distal margin of the ninth sternite became straight (346: 2). In the last common ancestor of the **Vespina**, i.e. Orussidae + Apocrita (75), the harpes with

muscles t, gonomacula, and muscles v disappeared (287: 1), and a spiculum appeared on the ninth sternite (347: 1). Somewhere in the lineage leading to **Orussus** (76), a unique muscle appeared which runs from one side of the ninth sternite to the other across the male genitalia (270: 1), the gonoforceps shortened so that the volsella extends beyond it (333: 1), thorns developed on the basivolsella (334: 1), and a strengthened line appeared on the ninth sternite, parallel to its basal margin (348: 1). In the last common ancestor of **Apocrita** (77), no new features can be detected compared to the ancestor of the Vespina.

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Appendix 1. Species examined in the present study.

Higher taxon	Species used in the present study	Preservation method	OTU
Raphidioptera	Raphidioptera sp.	Fixation + Alc.	Raphidioptera
Coleoptera	<i>Priacma serrata</i> Leconte	Fixation + Alc.	Priacma
Lepidoptera	<i>Micropterix calthella</i> (Linnaeus)	Fixation + Alc.	Micropterix
Mecoptera	<i>Panorpa</i> sp.	Fixation + Alc.	Panorpa
Xyelidae	<i>Xyela</i> sp.	Fixation + Alc.	Xyela
	<i>Macroxyela ferruginea</i> (Say)	Fixation + Alc.	Macroxyela
Blasticotomidae	<i>Runaria reducta</i> (Malaise)	Fixation + Alc.	Runaria
	<i>Paremphtytus flavipes</i> (Takeuchi)	Fixation + Alc.	Paremphtytus
	<i>Blasticotoma nipponica</i> Takeuchi*	Pinned + Dried	Blasticotoma*

Appendix 1. continued

Higher taxon	Species used in the present study	Preservation method	OTU
Tenthredinidae	<i>Tenthredo campestris</i> Linnaeus	Fixation + Alc.	Tenthredo
	<i>Aglaostigma lichtwardti</i> (Konow)	Fixation + Alc.	Aglaostigma
	<i>Dolerus</i> sp.	Fixation + Alc.	Dolerus
	<i>Selandria serva</i> (Fabricius)	Fixation + Alc.	Selandria
	<i>Strongylogaster multifasciata</i> (Geoffroy)	Fixation + Alc.	Strongylogaster
	<i>Monophadnoides</i> sp.	Fixation + Alc.	Monophadnoides
	<i>Metallus</i> sp.	Fixation + Alc.	Metallus
	<i>Athalia rosae</i> (Linnaeus)	Fixation + Alc.	Athalia
	<i>Taxonus agrorum</i> (Fallén)	Fixation + Alc.	Taxonus
	<i>Hoplocampa fulvicornis</i> (Panzer)	Fixation + Alc.	Hoplocampa
	<i>Nematinus luteus</i> (Panzer)	Fixation + Alc.	Nematinus
	<i>Nematus</i> sp.1 + <i>Nematus</i> sp.2	Fixation + Alc.	Nematus
	<i>Cladius pectinicornis</i> (Geoffroy)	Fixation + Alc.	Cladius
Diprionidae	<i>Monoctenus juniperi</i> (Linnaeus)	Fixation + Alc.	Monoctenus
	<i>Gilpinia</i> sp.	Fixation + Alc.	Gilpinia
	<i>Diprion</i> sp. (<i>pini</i> or <i>similis</i>)	Fixation + Alc.	Diprion
Cimbicidae	<i>Cimbex</i> sp.	Pinned + Dried	Cimbex
	<i>Trichiosoma</i> sp.	Pure alcohol	Trichiosoma
	<i>Abia</i> sp.	Pure alcohol	Abia
Argidae	<i>Corynis crassicornis</i> (Rossi)	Fixation + Alc.	Corynis
	<i>Arge nigripes</i> (Retzius) or <i>berberidis</i> Schrank	Fixation + Alc.	Arge nigripes
	<i>Arge cyanocrocea</i> (Forster)	Fixation + Alc.	Arge cyanocrocea
Pergidae	<i>Sterictiphora furcata</i> (Villers)	Fixation + Alc.	Sterictiphora
	<i>Perga</i> sp.	Pinned + Dried	Perga
	<i>Phylacteophaga froggatti</i> (Riek)	Fixation + Alc.	Phylacteophaga
Pamphiliidae	<i>Lophyrotoma analis</i> (Costa)	Fixation + Alc.	Lophyrotoma
	<i>Acordulecera</i> sp.	Fixation + Alc.	Acordulecera
	<i>Decameria</i> sp.	Fixation + Alc.	Decameria
Megalodontesidae	<i>Neurotoma fasciata</i> (Norton)	Pinned + Dried	Neurotoma
	<i>Onycholyda amplexa</i> (Fabricius)	Fixation + Alc.	Onycholyda
	<i>Pamphilius middlekauffi</i> Shinohara & Smith	Pinned + Dried	Pamphilius
	<i>Cephalcia</i> sp. (<i>abietis</i> or <i>arvensis</i>)	Fixation + Alc.	Cephalcia
	<i>Acantholyda</i> sp. (<i>erythrocephala</i> or <i>flavipes</i>)	Fixation + Alc.	Acantholyda
Megalodontesidae	<i>Megalodontes cephalotes</i> (Fabricius)	Fixation + Alc.	Megalodontes c.
	<i>Megalodontes skorniakowii</i> (Freymuth)	Pinned + Dried	Megalodontes sk.
Cephalidae	<i>Cephus pygmeus</i> (Linnaeus)	Fixation + Alc.	Cephus
	<i>Calameuta filliformis</i> (Eversmann)	Fixation + Alc.	Calameuta
	<i>Hartigia trimaculata</i> (Say)	Fixation + Alc.	Hartigia
Anaxyelidae	<i>Syntexis libocedrii</i> (Rohwer)	Pinned + Dried	Syntexis
Siricidae	<i>Sirex juvencus</i> (Linnaeus) (coded after Boulangé 1924)		
	<i>Sirex</i> sp.	Pinned + Dried	Sirex
	<i>Xeris spectrum</i> (Linnaeus)	Fixation + Alc.	Xeris
	<i>Urocerus gigas</i> (Linnaeus)	Fixation + Alc.	Urocerus
	<i>Tremex columba</i> (Linnaeus)	Pinned + Dried	Tremex
	<i>Xiphydria camelus</i> (Linnaeus)	Fixation + Alc.	Xiphydria
Xiphydriidae	<i>Xiphydria camelus</i> (Linnaeus)	Fixation + Alc.	Xiphydria
Orussidae	<i>Orussus abietinus</i> (Scopoli)	Fixation + Alc.	Orussus
Stephanidae	<i>Stephanus serrator</i> (Fabricius)	Fixation + Alc.	Stephanidae
Megalyridae	<i>Megalyra fasciipennis</i> Westwood	Pinned + Dried	MegalyraA
Trigonalidae	<i>Orthogonalys pulchellus</i> (Cresson)	Pinned + Dried	Trigonalidae
Aulacidae	<i>Pristaulacus erythrocephalus</i> (Cameron)	Pinned + Dried	Aulacidae
Ichneumonidae	Ichneumonidae sp.1	Fixation + Alc.	IchneumonidaeA
	Ichneumonidae sp.2	Fixation + Alc.	IchneumonidaeB
Ibaliidae	<i>Ibalia rufipes</i> Cresson (coded after Ronquist & Nordlander 1989)		IbaliaA
Apoidea	<i>Sceliphron caementarium</i> (Drury)	Fixation + Alc.	ApoideaA
Vespidae	<i>Dolichovespula adulterina</i> (du Buysson) (= <i>D. arctica</i> Rohwer)	Fixation + Alc.	VespidaeA

* Coding also based on Shinohara (1983) and Togashi (1970).

