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Before the wasp-waist: comparative anatomy and phylogenetic implications of the skeleto-musculature of the thoraco-abdominal boundary region in basal Hymenoptera (Insecta)

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Abstract The skeleto-musculature of the metathorax and first abdominal segment was studied in representatives from all ‘symphytan’ families. Forty-three informative characters were coded and scored. The distribution of character states are discussed with reference to recent cladistic treatments of the Hymenoptera. Previously unreported autapomorphies for the Hymenoptera are the separation of the metathoracic trochantins from the metepisterna and metacoxae, the position of the metafurca anteriorly on the discriminal lamella of the metathorax and the presence of second abdominal sternum (S2)-metacoxal muscles. The absence of metapleuro-S2 muscles is an autapomorphy for the non-xyelid Hymenoptera. Putative autapomorphies of the Tenthredinoidea are: (1) the presence of transverse metanotal muscles, (2) the subdivision of the second phragmo-third phragmal muscles, part of which arises from the metalaterophragmal lobes, (3) the posterior thoracic spiracle occlusor muscles arising from the mesepisterna, (4) the absence of trochantins and metanoto-trochantinal muscles and (5) the presence of elongate lateral metafurcal arms. Having the paracoxal sulci extending along the anterior margins of the metepisterna and the anterior metafurcal arms reduced are synapomorphies for all tenthredinoid families excluding Blasticotomidae. The presence of transversely extended cenchri with hooks on their entire surface is a putative synapomorphy for Diprionidae + Cimbicidae + Argidae + Pergidae. The clade Cimbicidae + Argidae + Pergidae is supported by the absence of metanoto-metabasalar muscles, the fusion of the first abdominal tergite (T1) with the metepimera and the absence of posterior metapleuro-metafurcal muscles. Autapomorphies of the Cimbicidae are the absence of the metalaterophragmal lobes and the metalaterophragmal-metafurcal muscles. Having the mesoscutello-metanotal muscle inserting on a projection from the anterior margin of the

metanotum, surrounding the tendon with sclerotised cuticle, is a synapomorphy for the Argidae and Pergidae. Autapomorphies of the Cephoidea are the absence of cenchri, the presence of distinct articulations between T1 and the metepimera, and having the paracoxal sulci extending subparallel with the metafurcal discrimen. The monophyly of the Siricidae is supported by the absence of the anapleural clefts and the presence of an elongate mesospina projecting posteriorly between the anterior metafurcal arms. The presence of a membranous pouch ventrally of T1 and of large T1-metafurcal muscles is unique to *Xiphydria camelus* among the taxa examined. The absence of hind wing tegulae, posterior metapleuro-metafurcal, metanoto-trochantinal and anterior metanoto-metacoxal muscles, and the presence of elongate lateral metafurcal arms are synapomorphies for Xiphydriidae + Orussidae + Apocrita. The Orussidae greatly resembles the Apocrita in the region studied, a synapomorphy for the two taxa being the presence of metepisternal depressions. An autapomorphy for the Apocrita is the fusion of T1 with the metapleural arms; these structures closely abut in Orussidae. The fusion of T1 with the metepimera was preceded by the reduction of the posterior parts of the metepimera, as observed in Anaxyelidae, Xiphydriidae, and Orussidae. This makes the lines of fusion between T1 and the metepimera confluent with the metapleural sulci in the Apocrita. There is no compelling evidence for considering the configuration of T1 and the metepimera in Cephoidea to be incipient in the formation of the propodeum in Apocrita. The close association between the meso- and metathorax and the integration of T1 in the metathorax evolved gradually twice within the basal hymenopteran lineages, culminating in the Apocrita and the Cimbicidae + Argidae + Pergidae clade.

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A. Introduction

The suborder Apocrita is by far the largest and most diverse part of the Hymenoptera. It is characterised by

having the first abdominal segment entirely incorporated into the thorax as the propodeum, and the formation of a constriction between the first and second abdominal segments (the 'wasp-waist'). The latter feature is one of the most striking modifications observed within the Insecta, and it has undoubtedly contributed substantially to the evolutionary success of the Apocrita. Most apocritans are parasitoids of other insect larvae, and the 'wasp-waist' is probably an adaptation to this life-style, enhancing the manoeuvrability of the abdomen and thus facilitating ovipositing in the host. Indeed, the 'wasp-waist' is one of the best examples of a putative 'key innovation' among insects (Kristensen 1999). The incorporation of the first abdominal segment in the thorax is no less remarkable, being in effect a transfer of a segment from one tagma to another. The terms 'mesosoma' (the thoracic segments and the first abdominal segment) and 'metasoma' (the remaining abdominal segments) (Goulet and Huber 1993) employed by hymenopteran systematists reflect this.

The remaining, non-apocritan Hymenoptera, also known as the 'Symphyta', are characterised only by the absence of the 'wasp-waist', and are thus not a natural group. Instead, they comprise the basal hymenopteran lineages, being paraphyletic relative to the Apocrita (Vilhelmsen 1997; Ronquist et al. 1999). Already Snodgrass (1910) realised that to elucidate the evolution of the propodeum and 'wasp-waist' in the Hymenoptera, one needs to examine representatives from the 'symphytan' families as well as apocritans. The earlier studies (Snodgrass 1910; Weber 1927; Dhillon 1966) dealing in detail with the anatomy of the thorax in basal Hymenoptera focused mainly on Tenthredinoidea and Siricidae. This was unfortunate, because the Tenthredinoidea are highly autapomorphic in many features of the thorax (see below and Vilhelmsen 1999); the Siricidae share a number of derived traits with the Apocrita, but are not the closest living relative of the latter taxon. The study of the skeleto-musculature of the anterior abdominal segments in Hymenoptera by Short (1959) was likewise deficient in taxon sampling.

The introduction of cladistic concepts to the study of Hymenoptera by Oeser (1961), Hennig (1969) and especially Königsman (1976, 1977, 1978a,b) made workers realise the importance of including crucial taxa such as the Xyelidae, Pamphiliidae and Orussidae in detailed comparative studies. The papers by Shcherbakov (1980, 1981), treating both the pterothoracic segments, were pioneering in this respect. However, the landmark study dealing with thoracic features in a cladistic context remains Gibson (1985). This, and some of the studies it inspired (Gibson 1986, 1993; Johnson 1988; Heraty 1989; Heraty et al. 1994, 1997), focused on the mesothorax, being the larger and most accessible of the pterothoracic segments. That the metathorax might also contain information of phylogenetic relevance was apparent from the papers by Daly (1963), Shcherbakov (1980, 1981) and Saini (1986), and was further demonstrated by Whitfield et al. (1989).

The constriction between the first and second abdominal segments observed in Cephoidea, while not as pronounced as that observed in Apocrita, led Ross (1937) to believe that the Apocrita had evolved from a cephoidean ancestor. This was translated into a sister-group relationship between the two taxa by Hennig (1969) and Königsman (1977). However, the majority of the evidence accumulated from other character systems indicates that the Orussoidea are the sister group of the Apocrita (Rasnitsyn 1988; Vilhelmsen 1997, 1999; Ronquist et al. 1999). This was corroborated by Shcherbakov (1981), who proposed an alternative transformation series, deriving the condition in Apocrita from that observed in Orussidae.

The present study deals with the skeleto-musculature of the metathorax and first abdominal segment of the basal hymenopteran lineages, including representatives from all the 'symphytan' families. It was undertaken to provide additional information for testing hypotheses about hymenopteran phylogeny proposed by Vilhelmsen (1997) and Ronquist et al. (1999). It is also intended to provide a platform for further investigations of the variation displayed by apocritan taxa, which it was not possible to examine here in sufficient detail. Furthermore, it will be attempted to decide between alternative hypotheses (Shcherbakov 1981; Ronquist and Nordlander 1989) regarding the exact location of the boundaries between the metathorax and the propodeum in Apocrita.

B. Materials and methods

I. Techniques

1. Whole mounts

Both ethanol-preserved and dried specimens were examined; the latter were used when the former could not be obtained. Specimens were dissected with scalpels and eyelens scissors, and some were macerated in KOH prior to examination. They were stored in glycerol and examined under a dissection microscope.

2. Scanning electron microscopy

The dissected specimens were macerated in KOH and transferred to 96% ethanol in an ethanol series. The specimens were then critical point-dried, mounted with double-sided adhesive tape on stubs and coated with gold prior to examination.

3. Histological sections

Only specimens preserved in ethanol, Pampel's fluid or Bouin's fluid were used. Specimens were dehydrated in butanol and embedded in Paraplast. Sagittal and transverse sections of 7–25 µm thickness, depending on the size of the specimen, were prepared using a microtome. The sections were stained with a trichrome stain (Weigert's haematoxylin–bluish erythrosin–fast green, preceded by phosphomolybdic acid) and embedded in Canada balsam.

4. Serial reconstructions

The skeloto-musculature of the region under study was reconstructed for selected taxa (see Figs. 8, 9, 10, 11, 12, 13, 14, 15).

Table 1 Material examined and techniques employed. (*Ana* Anaxyelidae, *Arg* Argidae, *Aul* Aulacidae, *Bla* Blasticotomidae, *Cep* Cephidae, *Cim* Cimbicidae, *COL* Coleoptera, *Dip* Diprionidae, *Iba* Ibalidae, *LEP* Lepidoptera, *MEC* Mecoptera, *Meg* Megalodontesidae, *Mly* Megalyridae, *NEU* Neuroptera, *Oru* Orussidae, *Pam* Pamphiliidae, *Per* Pergidae, *PSO* Psocodea, *RAP* Raphidioptera, *Sir* Siricidae, *Ste* Stephanidae, *Ten* Tenthredinidae, *Tri* Trigonalidae, *Ves* Vespidae, *Xip* Xiphydriidae, *Xye* Xyelidae, *B* Bouin's fluid, *E70* 70% ethanol, *P* pinned, *Pa* Pampel's fluid, *HS* histological sections, *SEM* scanning electron microscopy, *WM* whole mounts)

Taxon	Number of specimens	Preservation	Study techniques	Thickness of sections ^a
<i>Amphigerontia bifasciata</i> (PSO)	3	E70	WM	–
<i>Priacma serrata</i> (COL)	2	P	WM	–
<i>Chrysopa perla</i> (NEU)	3	E70	WM	–
<i>Raphidia</i> sp. (RAP)	2	E70	WM	–
<i>Panorpa</i> sp. (MEC)	3	E70	WM	–
<i>Micropterix calthella</i> (LEP)	2	Pa	WM	–
<i>Pleroneura californica</i> (Xye)	1	P	WM	–
<i>Xyela julii</i> (Xye)	11	E70, Pa	HS, SEM, WM	7/7 µm
<i>Macroxyela ferruginea</i> (Xye)	3	E70	WM	–
<i>Blasticotoma filiceti</i> (Bla)	1	P	WM	–
<i>Paremphtus flavipes</i> (Bla)	1	E70	WM	–
<i>Runaria reducta</i> (Bla)	1	E70	HS	–/8 µm
<i>Tenthredo arcuata</i> /sp. (Ten)	7	E70	SEM, WM	–
<i>Dolerus niger</i> (Ten)	2	E70	WM	–
<i>Athalia</i> sp. (Ten)	7	E70	HS, WM	10/10 µm
<i>Nematus</i> sp. (Ten)	5	E70	HS, WM	10/10 µm
<i>Diprion pini</i> (Dip)	1	P	WM	–
<i>Gilpinia</i> sp. (Dip)	5	E70	HS, WM	–/12 µm
<i>Monoctenus juniperi</i> /sp. (Dip)	3	E70, P	WM	–
<i>Cimbex</i> sp. (Cim)	1	E70	WM	–
<i>Abia sericea</i> (Cim)	2	P	WM	–
<i>Zaraea fasciata</i> /sp. (Cim)	4	E70, P	HS, WM	–/16 µm
<i>Corynis obscura</i> /sp. (Cim)	3	E70, P	WM	–
<i>Arge</i> spp. (Arg)	9	E70	HS, SEM, WM	12/12 µm
<i>Sterictiphora furcata</i> (Arg)	3	E70, P	WM	–
<i>Perga dorsalis/condei</i> (Per)	3	E70, P	WM	–
<i>Phylacteophaga frogatti</i> (Per)	4	E70	HS, WM	8/8 µm
<i>Lophytoma interrupta</i> (Per)	2	P	WM	–
<i>Syzygonia cyanocephala</i> (Per)	2	P	WM	–
<i>Euryinae</i> gen. sp. (Per)	1	E70	WM	–
<i>Pamphilius</i> sp. (Pam)	3	E70	WM	–
<i>Neurotoma nemoralis</i> (Pam)	2	P	WM	–
<i>Cephalcia arvensis</i> (Pam)	9	E70	HS, SEM, WM	12/12 µm
<i>Acantholyda erythrocephala</i> (Pam)	2	P	WM	–
<i>Megalodontes cephalotes</i> (Meg)	3	B, P	HS, WM	–/14 µm
<i>Cephus nigrinus</i> (Cep)	9	E70	HS, SEM, WM	10/10 µm
<i>Calameuta filiformis</i> (Cep)	2	E70	WM	–
<i>Hartigia linearis</i> (Cep)	2	E70	WM	–
<i>Syntexis libocedrii</i> (Ana)	4	E70, P	HS, WM	14/12 µm
<i>Sirex juvencus</i> (Sir)	7	B, E70, P	HS, SEM, WM	25/16 µm
<i>Urocerus gigas</i> (Sir)	4	E70	HS, WM	16 µm/–
<i>Tremex columba</i> (Sir)	2	P	WM	–
<i>Xiphydria camelus</i> (Xip)	10	E70, P	HS, SEM, WM	12/12 µm
<i>Orussus abietinus</i> /spp. (Oru)	11	E70, P	HS, SEM, WM	10/12 µm
<i>Schlettererius cinctipes</i> (Ste)	2	P	WM	–
<i>Megalyra fasciipennis</i> (Mly)	2	P	WM	–
<i>Aulacus striatus</i> (Aul)	3	P	WM	–
<i>Ibalia rufipes</i> (Iba)	2	E70	WM	–
<i>Orthogonalys pulchella</i> (Tri)	2	E70	WM	–
<i>Vespula rufa</i> (Ves)	2	E70	WM	–

^a Thickness of sections in transverse/longitudinal series, – series not made

Continuous series of sections (55–130 sections, depending on the size of the specimen) were photographed in a light microscope. Printouts were used as templates for tracing muscular and skeletal features. During reconstruction, features in the printouts were continuously cross-checked on the corresponding slide-mounted sections and on whole mounts of the taxon being examined.

5. Mapping of character evolution

The cladogram shown in Fig. 16 is a summary of one of the most parsimonious trees from Vilhelmsen (1999). It was derived by parsimony analysis of a comprehensive morphological data set, including the findings of the present study. In total, 233 characters were scored for 44 taxa (6 outgroup, 32 'symphytan', 6 apocritan). Character evolution was explored with the aid of MacClade 3.0. (Maddison and Maddison 1992).

II. Material examined

For further details, number of specimens examined, mode of preservation and techniques employed for each taxon, see Table 1.

1. Outgroup

- Psocodea. Psocidae: *Amphigerontia bifasciata* (Latreille, 1799)
- Coleoptera. Cupedidae: *Priacma serrata* Leconte, 1861
- Neuroptera. Chrysopidae: *Chrysopa perla* (Linné, 1758)
- Raphidioptera. Raphidiidae: *Raphidia* sp.
- Mecoptera. Panorpidae: *Panorpa* sp.
- Lepidoptera. Micropterigidae: *Micropterix calthella* (Linné, 1761)

2. Hymenoptera

- Xyeloidea. Xyelidae: *Xyela julii* (Brébisson, 1818), *Pleroneura californica* (Ashmead, 1898), *Macroxyela ferruginea* (Say, 1824)
- Tenthredinoidea. Blasticotomidae: *Blasticotoma filiceti* Klug, 1834, *Paremphtus flavipes* (Takeuchi, 1939), *Runaria reducta* (Malaise, 1931); Tenthredinidae: *Tenthredo arcuata* Forster, 1771, *Tenthredo* sp., *Dolerus niger* (Linné, 1767), *Nematus* sp., *Athalia* sp.; Diprionidae: *Gilpinia* sp., *Diprion pini* (Linné, 1758), *Monoctenus juniperi* (Linné, 1758), *Monoctenus* sp.; Cimbicidae: *Cimbex* sp., *Zaraea fasciata* (Linné, 1758), *Zaraea* spp., *Abia sericea* (Linné, 1767), *Corynis obscura* (Fabricius, 1775), *Corynis* sp.; Argidae: *Arge nigripes* (Retzius in Degeer, 1783), *A. gracilicornis* (Klug, 1812), *A. ustulata* (Linné, 1758), *Sterictiphora furcata* (Villers, 1789); Pergidae: *Perga dorsalis* Leach, 1817, *P. condei* (Benson, 1939), *Lophyrotoma interrupta* Klug, 1814, *Syzygonia cyanocephala* Klug, 1824, *Phylacteophaga frogatti* (Riek, 1955), Euryinae gen. sp.
- Pamphilioidea. Pamphiliidae: *Cephalcia arvensis* Panzer, 1805, *Acantholyda erythrocephala* (Linné, 1758), *Pamphilius* sp., *Neurotoma nemoralis* (Linné, 1758); Megalodontesidae: *Megalodontes cephalotes* (Fabricius, 1781)
- Cephioidea. Cephidae: *Cephus nigrinus* Thomson, 1871, *Calameuta filiformis* (Eversmann, 1847), *Hartigia linearis* (Schrank, 1781)
- ‘Siricoidea’. Anaxyelidae: *Syntexis libocedrii* Rohwer, 1915; Siricidae: *Sirex juvenis* (Linné, 1758), *Urocerus gigas* (Linné, 1758), *Tremex columba* (Linné, 1763); Xiphydriidae: *Xiphydria camelus* (Linné, 1758)
- Orussoidea. Orussidae: *Orussus abietinus* (Scopoli, 1763), *O. occidentalis* (Cresson, 1879), *Orussus* sp.; gen. sp.
- Stephanioidea. Stephanidae: *Schlettererius cinctipes* (Cresson, 1880)
- Megalyroidea. Megalyridae: *Megalyra fasciipennis* Westwood, 1832
- Evanoidea. Aulacidae: *Aulacus striatus* Jurine, 1807
- Cynipoidea. Ibalidae: *Ibalia rufipes* Cresson, 1879
- Trigonalyoidea. Trigonaliidae: *Orthogonalys pulchella* (Cresson, 1867)
- Vespoidea. Vespidae: *Vespa rufa* (Linné, 1758)

C. Results

The terminology of this section partly follows that of Ronquist and Nordlander (1989). The systematics are according to Gauld and Bolton (1988), except that Megalodontesidae has replaced Megalodontidae (Springate 1994; ICZN 1996) and Pamphilioidea has replaced Megalodontoida (Springate 1999). ‘Siricoidea’ is retained as an informal term for the families Anaxyelidae, Siricidae and Xiphydriidae, although it is not a natural group (Vilhelmsen 1997, 1999; Ronquist et al. 1999). The fam-

ilies Tenthredinidae, Diprionidae, Cimbicidae, Argidae and Pergidae (that is, the Tenthredinoidea exclusive of the Blasticotomidae) will be referred to collectively as the Tenthredinoidea *s. s.* This is in order avoid such unwieldy terms as ‘the non-blasticotomid Tenthredinoidea’. The muscle numbers are indicated in parentheses.

I. Xyeloidea, Xyelidae

The following somewhat detailed description will serve as a general account of the region under study as well as to introduce the terminology. The descriptions of the other superfamilies, especially when concerning musculature, will mainly emphasise the details where they differ from the Xyeloidea. The description is based on *Xyela julii* and *Macroxyela ferruginea*; *Pleroneura californica* does not differ significantly from *X. julii* judging from the limited number of observations that could be made.

1. Skeletal features (Figs. 1, 3C, 4A, 7A, 8)

The metathorax is considerably smaller than the mesothorax. It is obliquely slanted (Fig. 1) and the dorsal parts of the metathorax overlap the posteroventral parts of the mesothorax; the mesocoxae lie in line with the metanotum. The first abdominal tergite (T1) overlies the posterior parts of the metapleura, a first abdominal sternite being absent from all Hymenoptera examined. The metacoxae, which are larger than the mesocoxae, extend posteriorly and ventrally of the second abdominal sternite.

The metanotum (N3) is rectangular in dorsal view and broader than long. The anterior margin of the metanotum is continuous with the second phragma (*Ph2*; Fig. 8A), which projects posteriorly and ventrally of the metanotum, reaching the level of the posterior margin of the metanotum (Fig. 4A). The blunt lateral metanotal processes (*Imp*; not illustrated for Xyelidae, but see Figs. 10B, 12B) are situated at the anterolateral corners of the metanotum, separated from the rest of the metanotum by short sulci and internal ridges. The processes lie in unsclerotised cuticle just laterally of the second phragma; a few setae are present on their surfaces. A pair of lobes, the cenchri (*ce*), project from the anterior part of the metanotum; they are oval in outline and less than twice as broad as long. The anterior margins of the cenchri are continuous with the metanotum and laterally and posteriorly they are connected to the metanotum through membrane, their posterior margins being inflected and membranous (Fig. 3C). The dorsal surfaces of the cenchri are covered with sclerotised hooks. The lateral margins of the metanotum have distinct incisions close to their anterior corners and the slender median parts of the incisions extend towards the cenchri (Fig. 1A). A pair of anterior (*anwp*) and posterior (*pnwp*) metanotal wing processes are situated anteriorly and posteriorly of the incisions, respectively; these are most conspicuous in *M. ferruginea*. Medially on the pos-

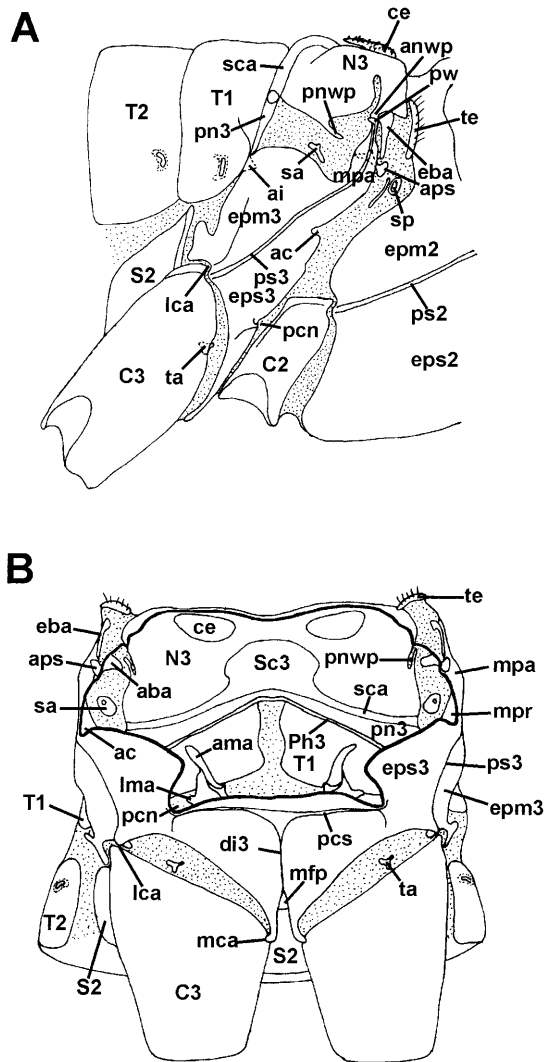


Fig. 1A,B *Macroxyela ferruginea* (Xyelidae), metathorax. **A** Lateral view. **B** Ventral view. Mesothorax removed to reveal the anterior parts of the metafurcal arms and the metanotum in ventral view; cuticle severed along the anterior margins of the metapleura, as indicated by heavy black line. *aba* Apodemal part of the basalare, *ac* anapleural cleft, *ai* articular inflection, *ama* anterior metafurcal arm, *anwp* anterior metanotal wing process, *aps* anapleural sclerite, *ce* cenchrus, *C2* mesocoxa, *C3* metacoxa, *di3* discrimen of the metathorax, *eba* external part of the basalare, *epm2* mesepimeron, *epm3* metepimeron, *eps2* mesepisternum, *eps3* metepisternum, *lca* lateral metacoxal articulation, *lma* lateral metafurcal arm, *mca* median metacoxal articulation, *mfp* metafurcal pit, *mpa* metapleural arm, *mpr* metapleural ridge, *N3* metanotum, *pcn* paracoxal notch, *pcs* paracoxal sulcus, *Ph3* third phragma, *pn3* metapostnotum, *pnwp* posterior metanotal wing process, *ps2* mesopleural sulcus, *ps3* metapleural sulcus, *pw* metapleural wing process, *sa* subalare, *sca* scutellar arm, *Sc3* metascutellum, *sp* posterior thoracic spiracle, *S2* second abdominal sternum, *ta* trochantal apodemes, *te* tegula, *T1* first abdominal tergum, *T2* second abdominal tergum

terior part of the metanotum is the metascutellum (*Sc3*); it is quadratic in outline in *X. julii* and more rounded in *M. ferruginea*. A pair of scutellar arms (*sca*) extend along the lateral parts of the posterior margin of the metanotum, connecting the metascutellum with the posterior margins of the hind wing bases.

The posterior margin of the metanotum is separated from the narrow metapostnotum (*pn3*) by a narrow membranous area medially; laterally, they are continuous. The metapostnotum and *T1* are continuous and are fused along an inflection, the third phragma (*Ph3*). The third phragma is very low medially (Fig. 4A) and sublaterally there are a pair of inconspicuous metalaterophragmal lobes (*lpl*). The lateral ends of the third phragma articulate with the posterodorsal parts of the metepimera. *T1* is subdivided medially from the metapostnotum to its posterior margin. The first abdominal spiracles are situated in the lateral parts of *T1*, which are weakly sclerotised in *X. julii*.

The posterior thoracic spiracles (*sp*) lie in the membranous areas between the mesopostnotum and the metapleural wing process (Fig. 1A). Posteriorly of the spiracles are a pair of small, slender sclerites which accommodate the origins of the spiracular occlusor muscles (*I*). Dorsally of the spiracles and anteriorly of the metapleural wing processes and the anterolateral corners of the metanotum are a pair of setose tegulae (*te*; not observed in *X. julii*, but present in *P. californica*). The external basalares (*eba*) are slender sclerites lying between the tegulae and the dorsal parts of the metapleural wing processes. The apodemal parts of the basalares (*aba*) are cup-shaped sclerites invaginated medially of the metapleural wing processes. In *M. ferruginea*, a pair of triangular anapleural sclerites (*aps*) lie in the integument just anterolaterally of the apodemal parts of the basalares, to which they are connected by narrow strips of sclerotised cuticle (Fig. 1B); these sclerites were not observed in *X. julii*.

The metapleura are subdivided into the dorsoposterior metepimera (*epm3*) and the anteroventral metepisterna (*eps3*) by the metapleural sulci (*ps3*), extending from the metapleural wing processes (*pw*) dorsally of the lateral metacoxal articulations (*lca*) ventrally. The metapleural wing processes are situated apically on the metapleural arms (*mpa*), the slender dorsal parts of the metapleura delimited dorsally by incurvations in the metepimera and ventrally by the anapleural clefts (Fig. 1A). The cup-shaped subalares (*sa*) are invaginated from the membranous areas posteriorly of the metapleural arms, lateroventrally of the metanotum and dorsomedially of the metepimera. The metepimera have dorsal projections extending to their articulation points with the lateral ends of the third phragma; the articular inflections (*ai*) project ventromedially from the metepimera at these points (Fig. 1A). The parts of the metepimera posteriorly of the articulations with the third phragma taper towards the lateral metacoxal articulations in *X. julii*; in *M. ferruginea*, the metepimera have weakly delimited small projections dorsally of the lateral metacoxal articulations. The metapleural sulci are deep grooves externally. Internally, they correspond to the narrow metapleural ridges (*mpr*) extending along the entire length of the sulci. Small apodemes for the posterior metapleuro-metafurcal muscles (24) are situated on the metapleural ridge just anteriorly of the lateral metacoxal articulations.

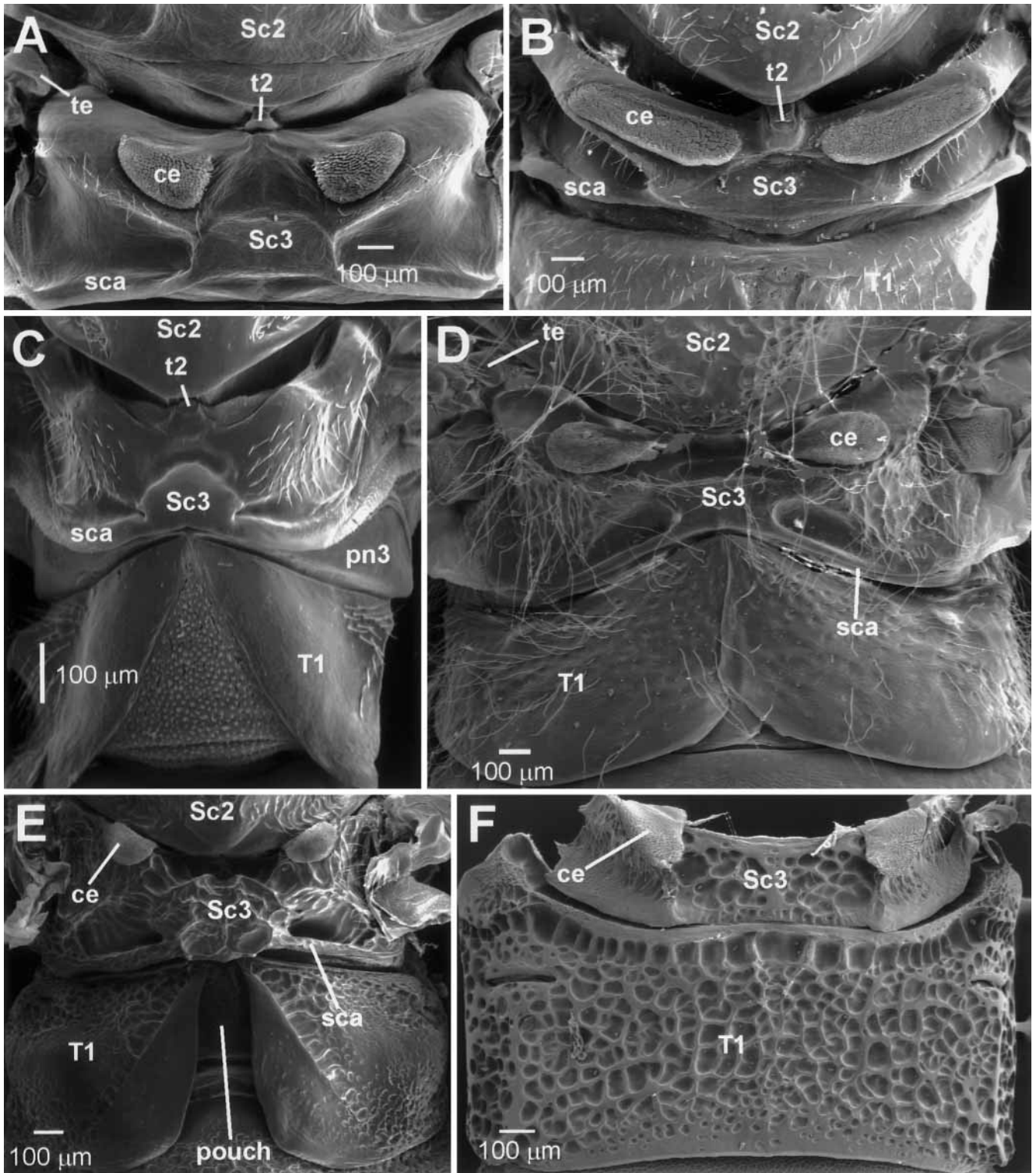


Fig. 2 A *Cephalcia arvensis* (Pamphiliidae). B *Arge ustulata* (Argidae). C *Cephus nigrinus* (Cephidae). D *Sirex juvenecus* (Siricidae). E *Xiphydria camelus* (Xiphydriidae). F *Orussus abietinus* (Orussidae). Metanotum and T1, dorsal view; mesothorax removed in F. Sc2 Mesoscutellum, t2 tendon 2

Two pairs of notches are present on the anterior margins of the metepisterna (Fig. 1B). The dorsal pair, the anapleural clefts (*ac*), delimit the metapleural arms ventrally. The ventral pair, the paracoxal notches (*pcn*), are at the lateral ends of the paracoxal sulci (*pcs*). These sulci arise medially from the anterior end of the discrimen of the metathorax and extend laterally on both sides in straight lines. In *X. julii*, the paracoxal sulci terminate in a pair of small incisions on the posterior margins of the metepisterna; in *M. ferruginea*, they bend a little posteriorly at their extreme lateral ends to terminate in darkened depressions on the posterior margins of the metepisterna (Fig. 1B). Internally, the paracoxal sulci correspond to the paracoxal ridges (*pcr*; Fig. 7A). The posterior margins of the metepisterna extend in concave curves between the lateral and the median metacoxal articulations (*mca*); the latter are situated on small projections just laterally of the metafurcal pit. The cup-shaped trochantal apodemes (*ta*) are invaginated from the membranous areas anteriorly of the metacoxae (*C3*), at the level of the paracoxal notches (Fig. 1B).

The metafurca (*F3*) is invaginated medially from the posterior margin of the metapleura at the metafurcal pit (*mfp*; Fig. 1B). The discrimen of the metathorax (*di3*) is a median line extending from the metafurcal pit to the paracoxal sulci. Internally, it corresponds to the discriminal lamella of the metathorax (*dl3*; Fig. 8A), a median vertical septum. The hollow metafurcal arms diverge laterally from the anterior end of the discriminal lamella. Distally, the metafurcal arms divide into a pair of short lateral metafurcal arms (*lma*; almost absent in *X. julii*; Fig. 7A) extending towards the metapleural ridges and receiving the insertion points of the anterior metapleuro-metafurcal muscles (23), and a pair of anterior metafurcal arms (*ama*) projecting towards the mesofurca and accommodating the origins of the metafurco-mesospinal muscles (28).

2. Musculature (Fig. 8)

Putative homologues with muscles described by Matsuda (1970)/Kelsey (1957) are in parentheses; – muscles not mentioned.

1. Occlusor muscle of the posterior thoracic spiracle (-/111). Small, paired muscles arising from the small sclerites posteriorly of the spiracles and inserting on the rims of the spiracles.
2. Mesoscutello-metanotal muscles (t13/114). Paired muscles arising from the posterior sides of the internal ridge delimiting the mesoscutellum anteriorly; they taper posteriorly to tendons which merge prior to extruding from the mesothorax between the posteroventral margin of the mesoscutellum and the dorsal margin of the second phragma in *M. ferruginea*; in *X. julii*, the tendon passes through an opening near the dorsal margin of the second phragma (Figs. 4A, 8A). In both taxa, the tendon inserts medially on the anteroventral margin of the metanotum.
3. Mesolaterophragmo-metabasalar muscles (t-p3/137). A pair of small muscles arising laterally from the outer side of the mesolaterophragma and inserting on the anterodorsal part of the apodemal parts of the metathoracic basalares.
4. Mesolaterophragmo-hind wing base muscles (tp4?/142?). A pair of small muscles arising just dorsally of the mesolaterophragmo-metabasalar muscles (3); their precise points of insertion could not be observed, but lie approximately on the anterior parts of the hind wing base.
5. Second phragmo-third phragmal muscles (t14/112, 113). Paired, tubular muscles arising dorsally on the second phragma and inserting submedially on the third phragma. These are the dorsal longitudinal indirect wing depressors.
6. Metanoto-metalaterophragmal muscles (t12/116). Paired muscles arising laterally about halfway between the anterior and posterior margins of the metanotum; they extend obliquely to insert on the metalaterophragmal lobes.
7. Metalaterophragmo-metafurcal muscles (t-s1/150). Paired muscles arising from the metalaterophragmal lobes and inserting dorsally on the apices of the anterior metafurcal arms.
8. T1-metafurcal muscles (t-s1/-). Paired muscles arising sublaterally on the anterior part of T1 just posteriorly of the metalaterophragmo-metafurcal muscles (7), with which they are continuous and share points of insertion.
9. Medial metanoto-metapleural muscles (t-p5, 6/128, 129). Paired, elongate muscles arising from the anterolateral parts of the metanotum and inserting medially on the anteroventral margins of the metapleura, just anteriorly of the paracoxal ridges. These are the dorsoventral indirect wing levators.
10. Lateral metanoto-metapleural muscles (t-p12/153). Paired, short muscles arising on the dorsal sides of the metapleural ridges, posteriorly of the metapleuro-hind wing muscles (12), and inserting medially on the lateral margins of the metanotum, posteriorly of the posterior metanotal wing processes.
11. Metanoto-metabasalar muscles (t-p7, 8/141). Small, paired muscles arising anteriorly on the lateral margins of the metanotum and inserting dorsally on the apodemal parts of the metathoracic basalares.
- 12a+b. Metapleuro-hind wing muscles (t-p13, 14/163, 164). Two pairs of short muscles, the first arising from the dorsal sides of the metapleural ridges, anteriorly of the lateral metanoto-metapleural muscles (10) and the second anteriorly on the metapleural arms. The first run dorsoventrally and the second run horizontally and laterally of the first; both insert on the third axillaries. These are the hind wing folding muscles.
13. Metabasalar-metapleural muscles (p3/154). Paired, elongate muscles arising anteriorly on the apodemal parts of the basalares and inserting on the anteroventral margins of the metapleura, anteriorly of the

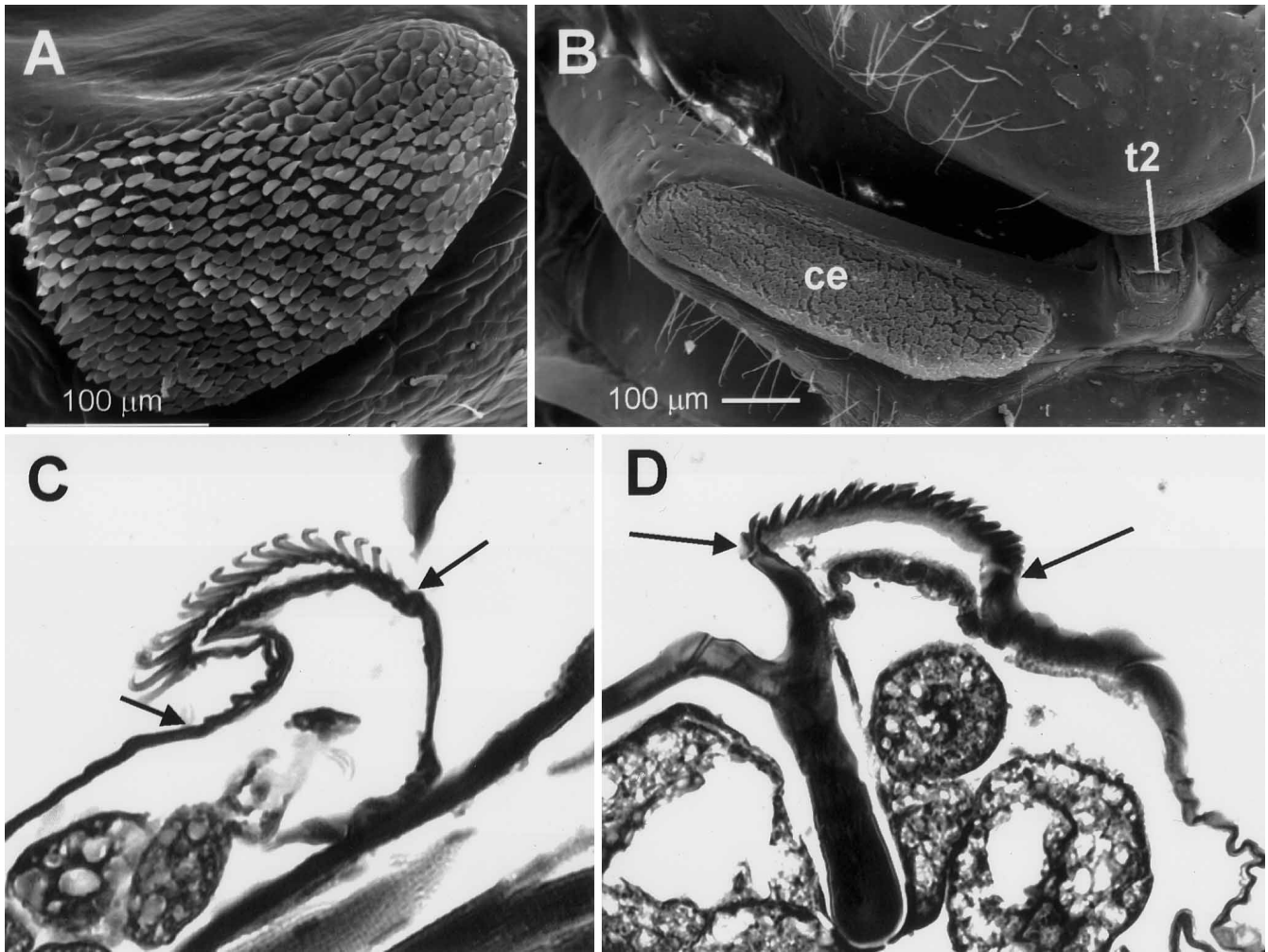


Fig. 3 **A** *C. arvensis* (Pamphiliidae). **B** *A. ustulata* (Argidae). **C** *Xyela julii* (Xyelidae). **D** *Gilpinia* sp. (Diprionidae). **A,B** Cenchrus, dorsal view; anterior upwards. **C,D** Cenchrus, transverse section; anterior to the right. *Arrows* indicate anterior and posterior boundaries of the cenchrus

paracoxal ridge and laterally of the median metanoto-metapleural muscles (9).

14. Intrinsic metapleural muscles (p1/145). Paired, spindle-shaped, slender muscles arising as tendons from the anterior margins of the metapleura just ventrally of the anapleural clefts and inserting, through tendons, ventrally on the anteroventral margins of the metapleural arms.
15. Metapleuro-metasubalar muscles (t-p16, 19/161). Paired, fan-shaped muscles arising from the dorsal projections of the metepimera and inserting in the membrane a little dorsoposteriorly of the subalares. (This is the condition in *X. julii*; in the other taxa examined, they insert on the subalares.)
16. T1-second abdominal sternum (S2)/metapleural muscles (-/-). Paired, slender muscles arising from the lateroposterior parts of T1 and, in *X. julii*, inserting on the anterolateral corners of S2.

17. Metanoto-trochantinal muscles (t-ti2, 3/130). Paired, elongate, slender muscles arising from the metanotum and inserting on the trochantinal apodemes. (They could not be traced all the way to their sites of origin in *X. julii*, but trochantinal apodemes with muscles inserting on them were clearly observed.)
18. Anterior metanoto-metacoxal muscles (t-cx5/158?). Paired, elongate muscles arising from the lateral parts of the metanotum posterolaterally of the median metanoto-metapleural muscles (9) and inserting on the lateral margins of the metacoxae, just anteriorly of the metasubalar-metacoxal muscles (22).
19. Posterior metanoto-metacoxal muscles (t-cx6/159b). Paired muscles arising from the posterolateral parts of the metanotum and inserting, through very long tendons, on the posterior margins of the metacoxae posteriorly of the metasubalar-metacoxal muscles (22).
20. Metanoto-trochanteral muscles (t-tr1/165). Paired, elongate muscles arising from the metanotum and inserting on the metatrochanteral apodemes (not observed in the present study, but reported from *Xyela minor* Norton by Daly 1963).
21. Metabasalar-metacoxal muscles (p-cx4?/156). Paired, elongate muscles arising from the posterior parts of

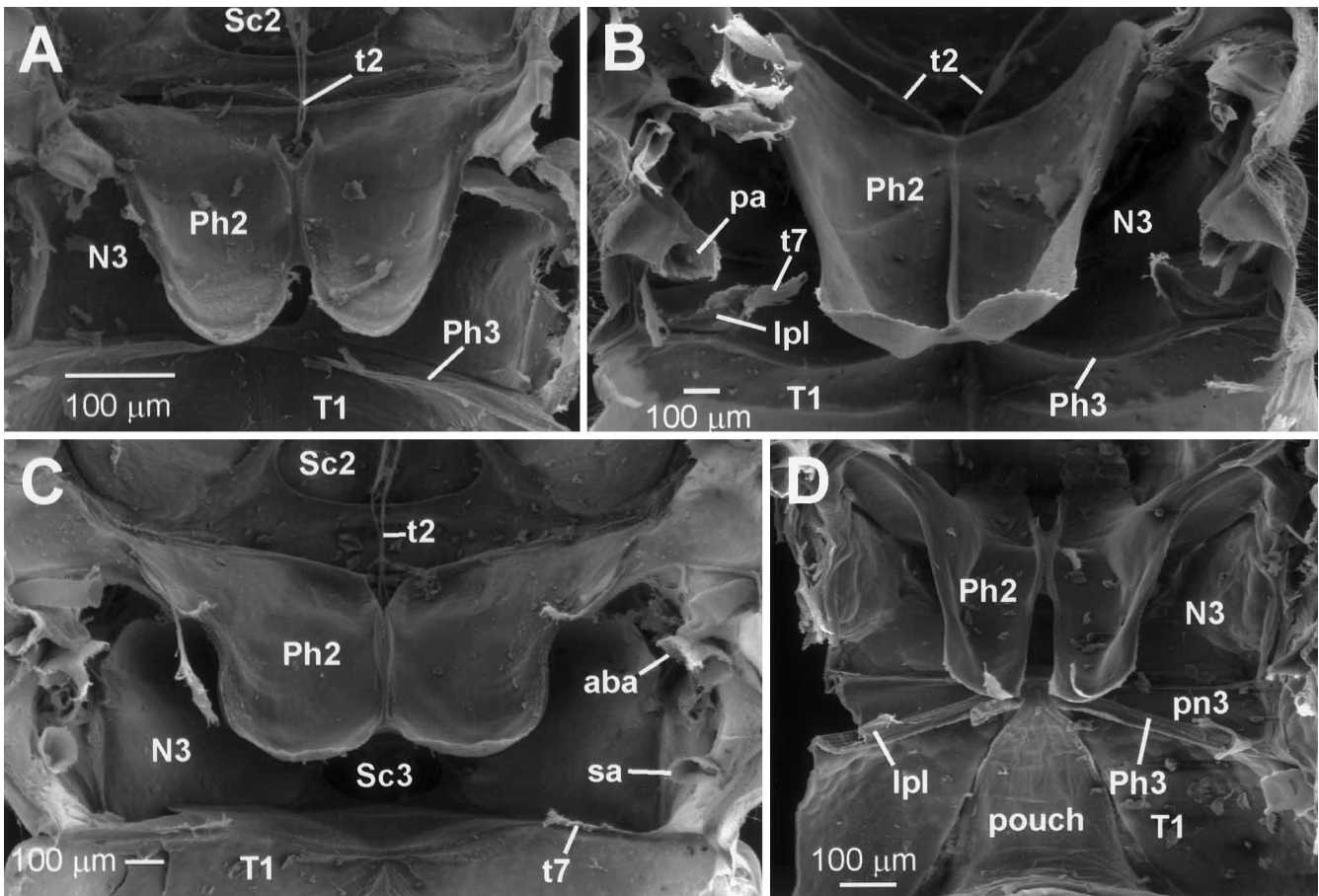


Fig. 4 A *X. julii* (Xyelidae). B *Tenthredo arcuata* (Tenthredinidae). C *C. arvensis* (Pamphiliidae). D *X. camelus* (Xiphophoridae). Second and third phragma, ventral view. *lpl* Laterophragmal lobe, *pa* pleural apodeme, *Ph2* second phragma, *t7* tendon 7

the apodemal parts of the basalares, inserting on the laterodorsal margins of the metacoxae, just anteriorly of the lateral metacoxal articulations.

22. Metasubalar-metacoxal muscles (t-cx8/160). Paired, elongate muscles, arising from the metasubalares and inserting on the laterodorsal margins of the metacoxae, just posteriorly of the lateral metacoxal articulations.
23. Anterior metapleuro-metafurcal muscles (p-s1/151). Paired, cone-shaped muscles, arising from the metapleural ridge midway along the latter, tapering to insert apically on the lateral metafurcal arms.
24. Posterior metapleuro-metafurcal muscles (s-cx2/170). Paired muscles arising from the metafurca medioventrally of the lateral metafurcal arms, tapering to insert posteriorly on the metafurcal ridge on small apodemes just anteriorly of the lateral metacoxal articulations.
25. Median metapleuro-metacoxal muscles (p-cx5/169?). Paired muscles arising from the metapleura posteriorly of the paracoxal ridges and the median parts of the metafurcal arms and inserting on the median margins of the metacoxae.

26. Lateral metapleuro-metacoxal muscles (p-cx6/157). Paired, fan-shaped muscles arising broadly from the ventral sides of the metapleural ridges and the metepisterna, tapering to insert on the anterodorsal margins of the metacoxae.
- 27a+b. Metafurco-mesofurcal muscles (s13/181–183). In *X. julii*, two pairs of muscles connect the meso- and metafurca. One pair arises from the anterior metafurcal arms just posteriorly of the metafurco-mesosplinal muscles (28) and the other from the medioventral parts of the metafurcal arms; both insert on the same points medially on the mesofurcal arms. In *M. ferruginea*, only one pair is present, arising from the median parts of the metafurcal arms.
28. Metafurco-mesosplinal muscles (s12/180). Paired muscles arising from the apices of the anterior metafurcal arms and extending medially of the metafurco-mesofurcal muscles (27) to insert jointly on the mesospina.
29. Mesofurco-metabasalar muscles (p-s3?/-). Paired muscles arising about halfway up the mesofurcal arms laterally of the metafurco-mesofurcal muscles (27) and inserting on the anterior margin of the apodemal parts of the basalares in *X. julii*; in *M. ferruginea*, they insert on the anapleural sclerites.
30. Metafurco-metacoxal muscles (s-cx3/173). Paired muscles arising from the medioposterior parts of the

Table 2 Occurrence of muscles among taxa examined. 0 present, 1 absent, ? unknown or uncertain. Muscles: 1 occlusor muscle of the posterior thoracic spiracle, 2 mesoscutello-metanotal muscles, 3 mesolaterophragmo-metabasalar muscles, 4 mesolaterophragmo-hind wing base muscles, 5 second phragmo-third phragmal muscles, 6 metanoto-metalaterophragmal muscles, 7 metalaterophragmo-metafurcal muscles, 8 T1-metafurcal muscles, 9 medial metanoto-metapleural muscles, 10 lateral metanoto-metapleural muscles, 11 metanoto-metabasalar muscles, 12 metapleuro-hind wing muscles, 13 metabasalar-metapleural muscles, 14 intrinsic metapleural muscles, 15 metapleuro-metasubalar muscles, 16 T1-second abdominal sternum (S2)/metapleural muscles, 17 meta-

noto-trochantal muscles, 18 anterior metanoto-metacoxal muscles, 19 posterior metanoto-metacoxal muscles, 21 metabasalar-metacoxal muscles, 22 metasubalar-metacoxal muscles, 23 anterior metapleuro-metafurcal muscles, 24 posterior metapleuro-metafurcal muscles, 25 median metapleuro-metacoxal muscles, 26 lateral metapleuro-metacoxal muscles, 27 metafurco-mesofurcal muscles, 28 metafurco-mesospinal muscles, 29 mesofurco-metabasalar muscles, 30 metafurco-metacoxal muscles, 31 metafurco-trochanteral muscles, 32 third phragma-second abdominal tergite (T2) muscles, 33 metapleuro-S2 muscles, 34 S2-metacoxal muscles, 35 metafurco-S2 muscles

Taxon	Muscles			
	1 1234567890	1111111112 1234567890	2222222223 1234567890	33333 12345
<i>Xyela julii</i> (Xye)	0000000000	000000000?	0000000000	00000
<i>Runaria reducta</i> (Bla)	0000000100	0001011101	0000000000	00100
<i>Athalia</i> sp. (Ten)	0010010100	0001001010	0000000100	00100
<i>Gilpinia</i> sp. (Dip)	0000010100	0001001111	0000000000	00100
<i>Zaraea fasciata</i> /sp. (Cim)	0011011110	1001011111	1001000110	00100
<i>Arge</i> spp. (Arg)	0010010100	1001011111	0001000100	00100
<i>Phylacteophaga frogatti</i> (Per)	0010010000	1001011100	1101000110	00110
<i>Cephalcia arvensis</i> (Pam)	0000000100	0000010100	0000000000	00100
<i>Megalodontes cephalotes</i> (Meg)	0010000100	1001111001	1000000000	00100
<i>Cephus nigrinus</i> (Cep)	0001000000	1000000001	0000000000	00100
<i>Syntexis libocedrii</i> (Ana)	00??000100	0000010100	0000000000	00100
<i>Sirex juvenus</i> (Sir)	00??100100	1001000000	1000000000	00100
<i>Xiphydria camelus</i> (Xip)	00??100000	100?001101	1001000000	00100
<i>Orussus abietinus</i> /spp. (Oru)	00??010110	1000001100	1001000000	00100

metafurcal arms and inserting on the posterior margins of the coxae.

31. Metafurco-trochanteral muscles (s-tr1/174). Paired muscles arising from the lateroventral parts of the metafurca and inserting on the metatrochanteral apodemes.
32. Third phragma-second abdominal tergite (T2) muscles (-/-). Paired, broad sheets of muscles arising from the posterior surface of the third phragma and inserting on the anterior margin of T2.
33. Metapleuro-S2 muscles (-/-). Paired, fan-shaped muscles arising from the dorsal projections of the metepimera and inserting on the anterodorsal corners of S2.
34. S2-metacoxal muscles (-/-). Paired muscles arising from the anterodorsal corners of S2 and inserting lateroposteriorly on the metacoxae.
35. Metafurco-S2 muscles (s20/-). Paired sheets of muscles arising from the posterior margins of the median parts of the metafurcal arms and inserting broadly on the median part of the anterior margin of S2.

For the occurrence of muscles in the taxa examined in detail for musculature, see Table 2.

II. Tenthredinoidea

The common tendon of the mesoscutello-metanotal muscles (2) passes dorsally of the second phragma and in-

serts medially on the anterior margin of the metanotum (Fig. 10A), as in *M. ferruginea*. The second phragma and the anterior margin of the metanotum are separated by an extended region of membranous cuticle. The lateral metanotal processes are slender in all taxa except Blasticotomidae and Cimbicidae and extend ventrally and/or medially towards the second phragma. In some taxa, the processes could be observed to be connected to the dorsal surface of the second phragma by thickened mesocuticular pads. Transverse metanotal-metapleural muscles (4) arise from the metapleural arms just ventrally of the pleural wing processes and insert on the mesocuticular pads at the points where they attach to the lateral metanotal processes (Figs. 9A, 10A). Mesolaterophragmo-metabasalar muscles (3) are absent except in *Runaria reducta* (Blasticotomidae) and Diprionidae. The metalaterophragmal lobes (Fig. 4B) are distinct in all taxa except Cimbicidae. The second phragmo-third phragmal muscles (5) are subdivided, part of them arising from the metalaterophragmal lobes (Figs. 9A, 10A); the metanoto-metalaterophragmal muscles (6) are absent from most taxa examined (but see below). The posterior thoracic spiracles are situated in distinct concavities of the mesepimera (Fig. 5A; exceptions are noted below) and the occlusor muscles (1) arise from the posterior margins of the mesepimera ventrally of the spiracles (Figs. 9A, 10A). The metapleuro-S2 muscles (33) are absent. The metapleural ridges have distinct pleural apodemes (*pa*; Figs. 4B, 7D, 9B, 10B) situated at varying distances along their length, usually about midway. These apode-

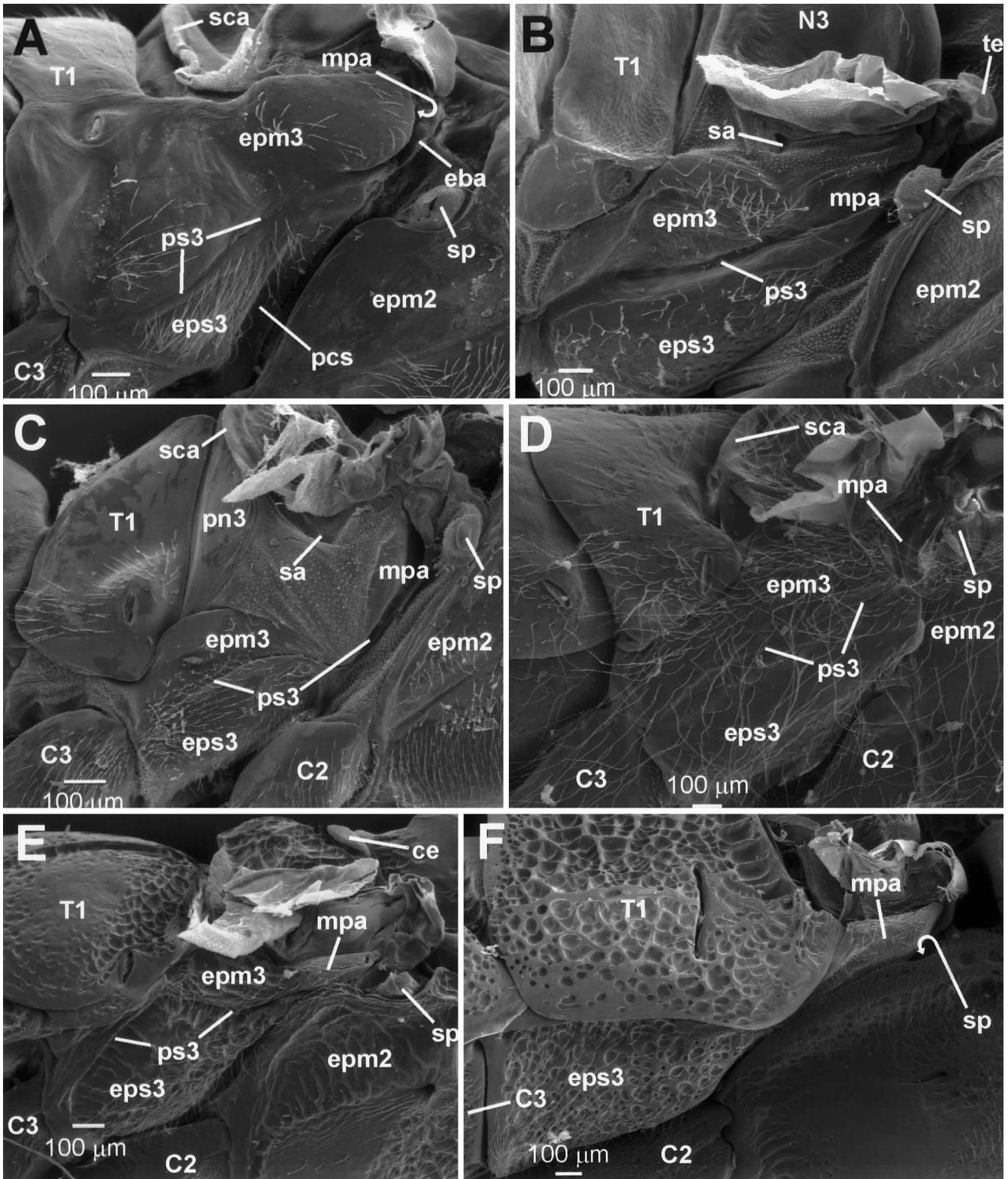


Fig. 5 A *A. ustulata* (Argidae). B *C. arvensis* (Pamphiliidae). C *C. nigrinus* (Cephiidae). D *S. juvenis* (Siricidae). E *X. camelus* (Xiphodriidae). F *O. abietinus* (Orussidae). Metapleura and T1, lateral view

mes accommodate the origins of the anterior metapleuro-metafurcal muscles (23) ventrally; dorsally they receive the insertions of the lateral metanoto-metapleural muscles (10). Externally, the positions of the metapleural apodemes are often indicated by pits or depressions in the otherwise shallow metapleural sulci. The anapleural clefts are small, but usually distinct. The intrinsic metapleural muscles (14) are absent, as are the paracoxal notches. The paracoxal sulci and ridges extend along the anterior margin of the metepisterna towards the metapleural sulci/ridges (Figs. 6A, 7D, 10B) in all taxa except Blasticotomidae. The trochantinal apodemes and metanoto-trochantinal muscles (17) are absent. The anterior metanoto-metacoxal muscles (18) were observed only in *Athalia* sp. (Tenthredinidae) and the posterior metanoto-metacoxal muscles (19) only in *R. reducta* and *Phylacteophaga frogatti* (Pergidae). The anterior metafurcal arms, as indicated by the points of origin of the metafurco-mesospinal muscles (28; when present), are short apodemes, except in Blasticotomidae (see below). They arise halfway along the main stem of the metafurcal arms, which continue laterally as elongate lateral metafurcal arms (Fig. 7C,D).

1. Blasticotomidae (Fig. 9)

In *R. reducta*, the metanotum and the second phragma are continuous for a short distance medially and the tendon of the mesoscutello-metanotal muscle (2) is attached both to the dorsal margin of the second phragma and the anterior margin of the metanotum (Fig. 9A). Laterally, the metanotum and the second phragma are separated by a considerable length of membrane. The posterior thoracic spiracles are not visible in lateral view, being hidden by a pair of dorsoposterior flanges projecting from the mesepimera. The spiracles are oriented dorsally and lie in concavities of the posterior margin of the mesepimera. The metalaterophragmal lobes are invaginated from the lateral parts of the third phragma as distinct apodemes and project anteriorly; in *R. reducta*, they receive a pair of metanoto-metalaterophragmal muscles (6; Fig. 9B). The anapleural sclerites are present. The apodemal parts of the basalares are elongate and irregularly shaped; in *R. reducta*, muscles from the mesolaterophragma (3), the metanotum (11), the metapleura (13), the metacoxae (21) and the metatrochanters (21a) attach to the basalares (Fig. 9). The posterior parts of the metepimera are expanded dorsally. They articulate with and cover the lateral margins of T1 laterally for the entire length of the latter, partly overlapping the first abdominal spiracles (Fig. 9B). The articular inflections are absent. The metabasalares are not visible externally; they are broad apodemes ventrally and, dorsally, they taper into elongate rods. The dorsal parts of the metapleural sulci and ridges are well developed, extending sinuously from the metapleural wing processes to the metapleural apodemes; the position of the apodemes are marked externally by

pits. Posteriorly of these pits, the metapleural sulci/ridges are weakly developed in *Blasticotoma filiceti* and well developed in *Paremphytus flavipes* and *R. reducta*; the apodemes of the posterior metapleuro-metafurcal muscles (24) were only observed in *P. flavipes* and *R. reducta*. The paracoxal sulci and ridges are weakly developed, bending posteriorly on the metepisterna and terminating some distance from the posterior margins of the latter; the condition in *R. reducta* could not be determined. A pair of weakly developed furrows extend along the anterior margins of the metepisterna. The anterior metafurcal arms are not as shortened as in other Tenthredinoidea (Fig. 9A), being almost as long as the well-developed lateral metafurcal arms.

2. Tenthredinidae (Figs. 4B, 7C)

In *Athalia* sp., the third phragma has a pair of lobes medially of the metalaterophragmal lobes, the former being larger than the latter; the medial lobes receive the insertions of the second phragmo-third phragmal muscles (5). The metanoto-metalaterophragmal muscles (6) are present in *Tenthredo* sp. and absent in the other taxa examined; they were reported to be present in *Athalia proxima* by Dhillon (1966; his muscle 83), but I have been unable to confirm this. The posterior thoracic spiracles are covered laterally by the posterior margins of the mesepimera in *Tenthredo* sp., *Dolerus niger* and *Athalia* sp., but not in *Nematus* sp. where they are situated in concavities of the posterior margin of the mesepimera. The apodemal parts of the basalares are cup-shaped in *Tenthredo* sp. and *Athalia* sp.; in *D. niger*, they are subdivided, the mesofurco-metabasalar muscles (29) inserting on separate internal sclerotisations. In *Nematus* sp., these muscles insert on the anapleural sclerites; these sclerites are absent from *Athalia* sp.. The anapleural clefts are absent from *Tenthredo* sp.. The subalares are well developed in *D. niger* and small and cup-shaped in *Athalia* sp.; they were not observed in *Nematus* sp. and *Tenthredo* sp. except for a pair of slender tendons in the latter taxon. In *Tenthredo* sp., the posterodorsal margins of the metepimera closely abut the lateral margins of the metapostnotum and the anterolateral parts of T1; in the other taxa, there is close contact between the metepimera and T1 only at the lateral ends of the third phragma. The articular inflections of the metepimera are absent from all taxa examined. In *Athalia* sp., the metepimera are larger than the metepisterna in lateral view, the metapleural sulci extending almost vertically close to the anterior margin of the metapleura before bending posteriorly in line with the lateral metacoxal articulations. The T1-S2/metapleural muscles (16) insert on small apodemes on the posterior margins of the metepimera in *Athalia* sp., some distance from the lateral metacoxal articulations. In the other taxa examined, the metapleural sulci extend obliquely in straight lines anteriorly of the lateral metacoxal articulations, making the metepimera smaller than the metepisterna in lateral view. The mesospina and the metafurco-mesospina

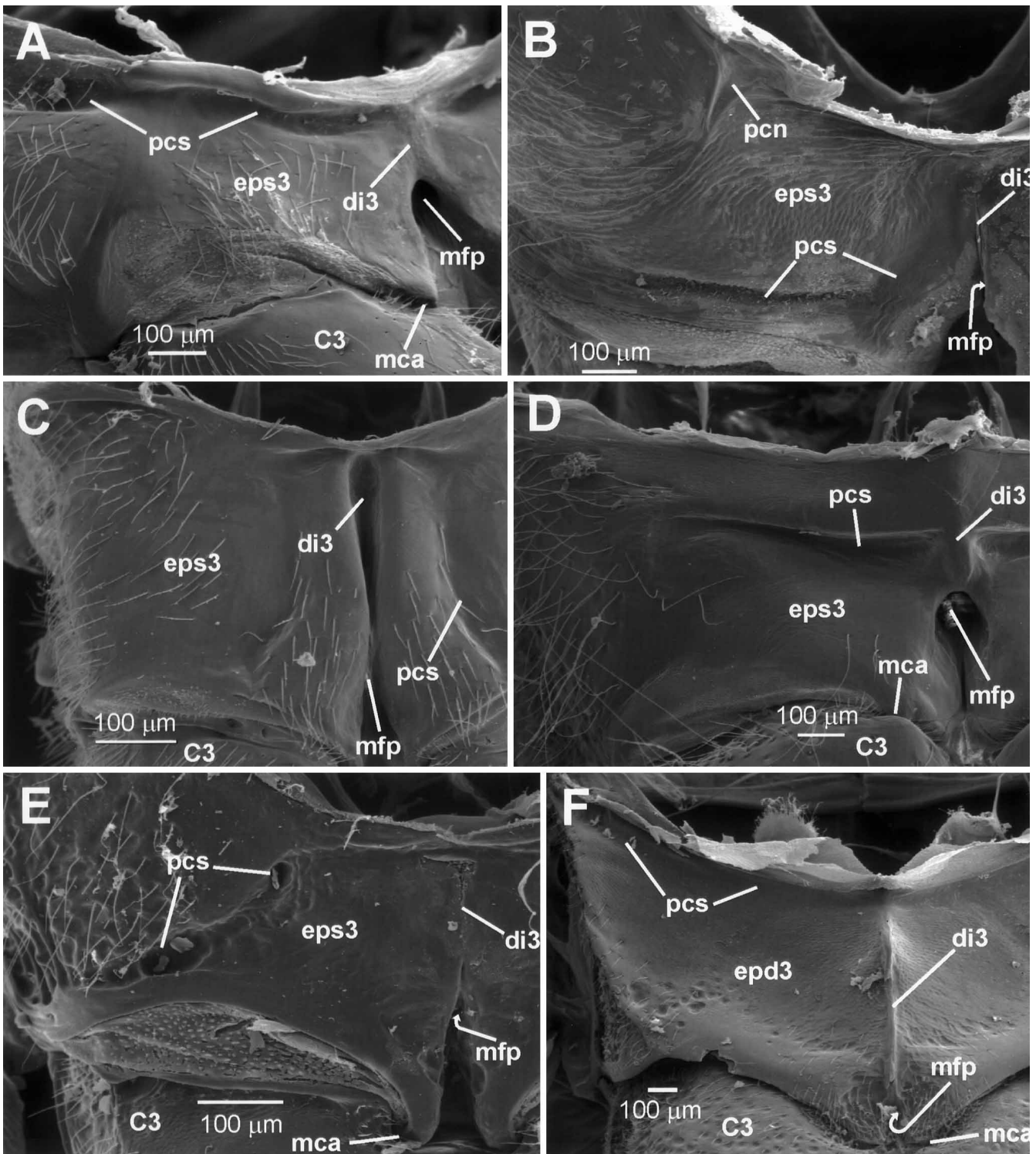


Fig. 6 **A** *A. ustulata* (Argidae). **B** *C. arvensis* (Pamphiliidae). **C** *C. nigrinus* (Cephalidae). **D** *S. juvenicus* (Siricidae). **E** *X. camelus* (Xiphydriidae). **F** *O. abietinus* (Orussidae). Right metepisternum, ventral view. *epd3* Metepisternal depressions

nal muscles (28) are absent from *Athalia* sp. and present in the other taxa (Fig. 7C).

3. *Diprionidae* (Fig. 3D)

The lateral metanotal processes extend medially. The cenchri are transversely extended, more than twice as broad as long and their posterior parts are not inflected or mem-

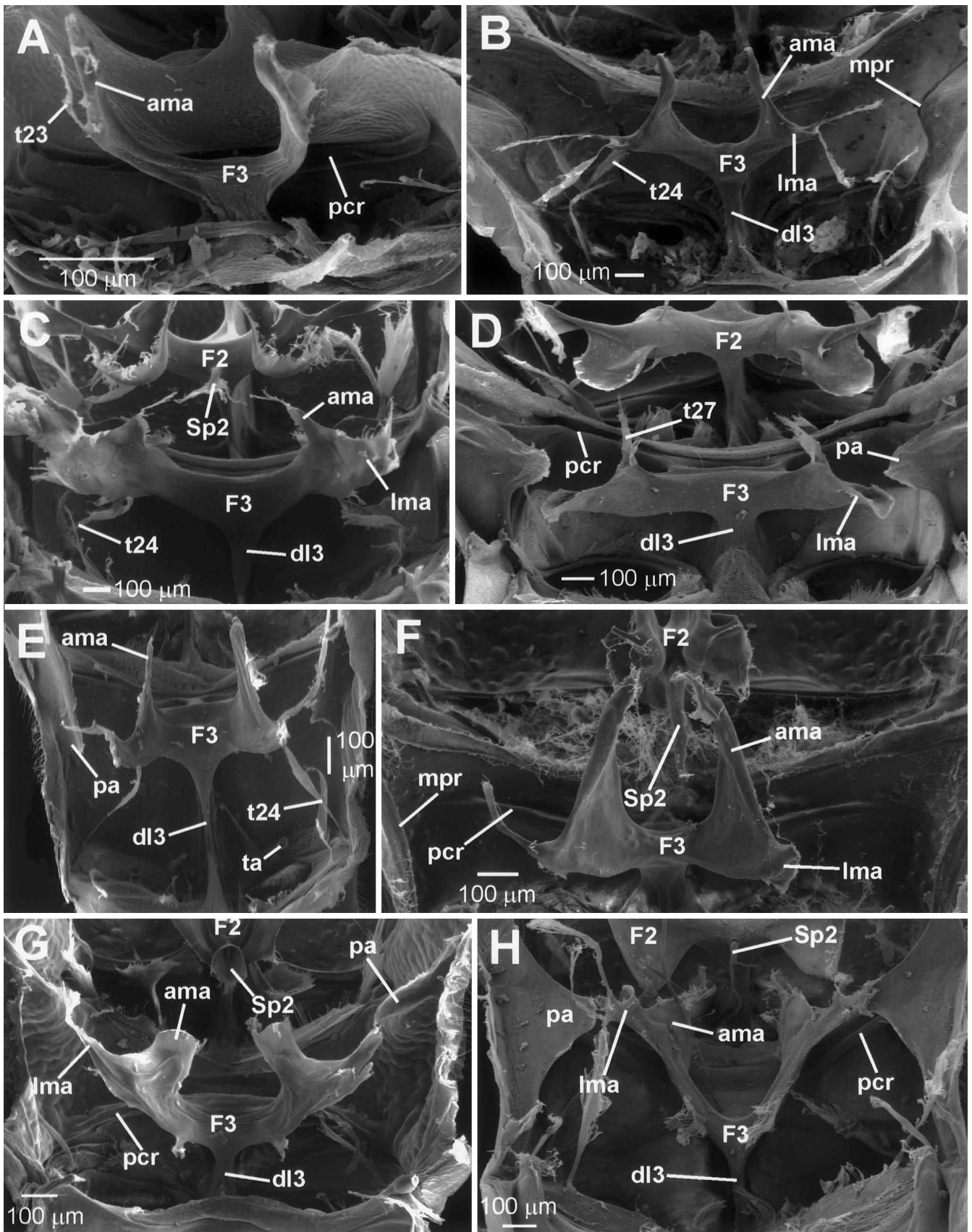


Fig. 7 **A** *X. julii* (Xyelidae). **B** *C. arvensis* (Pamphiliidae). **C** *T. arcuata* (Tenthredinidae). **D** *A. ustulata* (Argidae). **E** *C. nigrinus* (Cephalidae). **F** *S. juvenis* (Siricidae). **G** *X. camelus* (Xiphytri-

idae). **H** *O. abietinus* (Orussidae). Metafurca, dorsal view. *dl3* Discrimininal lamella of the metathorax, *F2* mesofurca, *F3* metafurca, *pcr* paracoxal ridge, *Sp2* mesospina, *t23*, *t24*, *t27* tendons 23, 24, 27

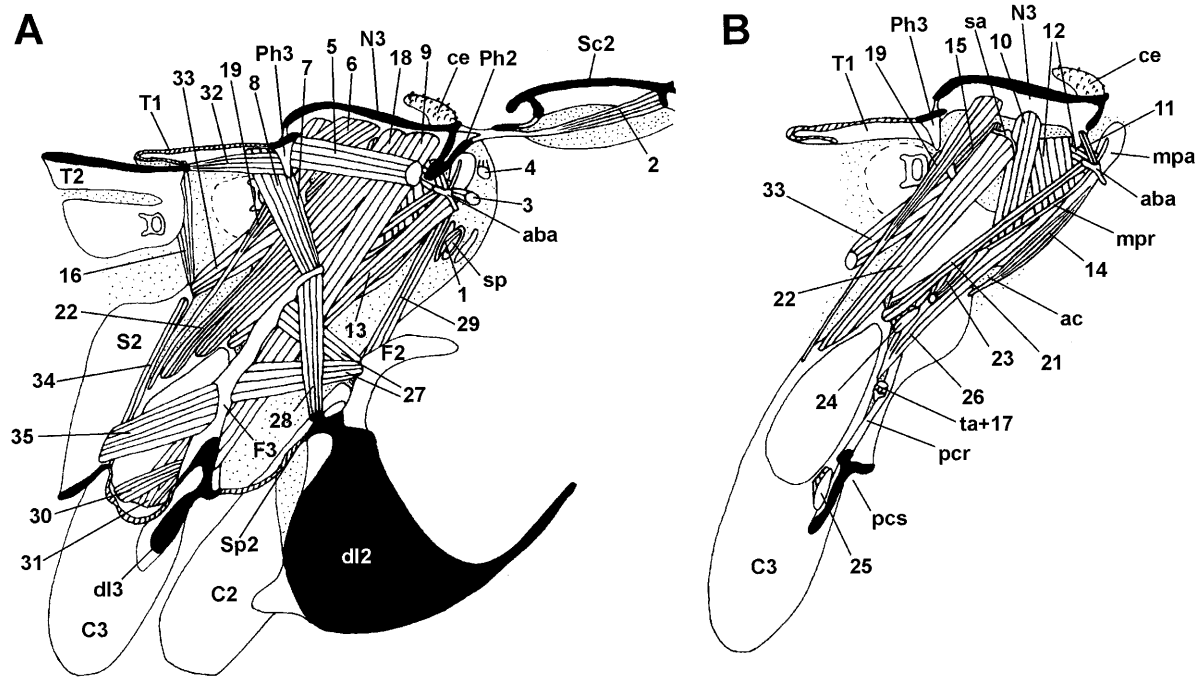


Fig. 8A,B *X. julii* (Xyelidae), metathoracic musculature. **A** Median sagittal view, most of second phragma removed. **B** Lateral sagittal view, metafurca and some muscles removed. *Black* Exocuticle, *hatched* mesocuticle, *white* endocuticle, *dl2* discriminial lamella of the mesothorax, *1* occlusor muscle of the posterior thoracic spiracle, *2* mesoscutello-metanotal muscles, *3* mesolaterophragmo-metabasalar muscles, *4* mesolaterophragmo-hind wing base muscles, *5* second phragmo-third phragmal muscles, *6* metanoto-metalerophragmal muscles, *7* metalaterophragmo-metafurcal muscles, *8* T1-metafurcal muscles, *9* medial metanoto-metapleural muscles, *10* lateral metanoto-metapleural muscles, *11* metanoto-metabasalar muscles, *12* metapleuro-hind wing muscles, *13* metabasalar-metapleural muscles, *14* intrinsic metapleural muscles, *15* metapleuro-metasubalar muscles, *16* T1-second abdominal sternum (S2)/metapleural muscles, *17* metanoto-trochantinal muscles, *18* anterior metanoto-metacoxal muscles, *19* posterior metanoto-metacoxal muscles, *21* metabasalar-metacoxal muscles, *22* metasubalar-metacoxal muscles, *23* anterior metapleuro-metafurcal muscles, *24* posterior metapleuro-metafurcal muscles, *25* median metapleuro-metacoxal muscles, *26* lateral metapleuro-metacoxal muscles, *27* metafurco-mesofurcal muscles, *28* metafurco-meso-spinal muscles, *29* mesofurco-metabasalar muscles, *30* metafurco-metacoxal muscles, *31* metafurco-trochanteral muscles, *32* third phragma-second abdominal tergite (T2) muscles, *33* metapleuro-S2 muscles, *34* S2-metacoxal muscles, *35* metafurco-S2 muscles

branous; minute hooks/scales cover their entire surface (Fig. 3D). The articular inflections of the metepimera are distinct and visible externally, not being covered by the anterolateral corners of T1. The T1-S2/metapleural muscles (*16*) insert on the posterodorsal margins of the metepimera a short distance dorsally of the lateral metacoxal articulations. The apodemal parts of the basalares are well developed and cup-shaped and only the mesolaterophragmo-metabasalar (*3*), metanoto-metabasalar (*11*) and mesofurco-metabasalar muscles (*29*) insert directly on them; the metabasalar-metapleural muscles (*13*) taper to insert on tendons continuous with the metanoto-metabasalar muscles (*11*). The metabasalar-metacoxal

muscles (*21*) have fibres arising from the metepisterna which all converge to insert in the membrane dorsal to the apodemal parts of the basalares. The anapleural sclerites are absent from all taxa and the anapleural clefts could not be observed in *Diprion pini* and *Gilpinia* sp. The metasubalares are small, but distinct in *D. pini* and *Gilpinia* sp., but they were not observed in *Monoctenus juniperi*. The metapleural apodemes are well developed with their positions indicated by pits externally; dorsally, they are reinforced by short, transverse rods. The anterior metanoto-metacoxal (*18*) and metanoto-trochanteral muscles (*20*) are absent.

4. Cimbicidae

Abia sericea is identical to *Zaraea fasciata*. The mesoscutello-metanotal muscle (*2*) insertion in *Z. fasciata* is flanked by small projections from the anterior margin of the metanotum, but these projections are not continuous ventrally of the insertion point; in *Cimbex* sp., the insertion point is entirely surrounded by sclerotised cuticle, being situated on a small projection. *Corynis* sp. does not have any modifications around the mesoscutello-metanotal muscle insertion point. The lateral metanotal processes are indistinct and the transverse metanoto-metapleural muscles (*4*) are absent from *Z. fasciata*, but present in the other taxa. The cenchri are transversely extended, without inflected membranous posterior parts, and minute hooks cover their entire surface. In *Cimbex* sp. and *Z. fasciata*, the points of origin of the large lateral metanoto-metapleural muscles (*10*) are distinct, plate-like apodemes on the lateral margins of the metanotum. The anterior (*18*) and posterior (*19*) metanoto-metacoxal, the metanoto-trochanteral (*20*) and the metabasalar-metacoxal muscles (*21*) are absent. The third phragma is

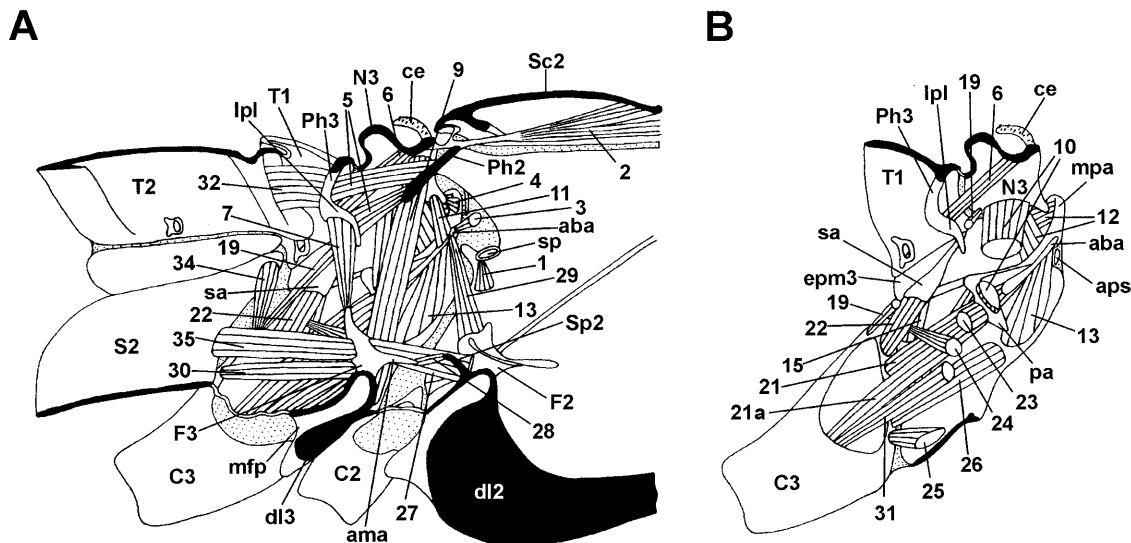


Fig. 9A,B *Runaria reducta* (Blasticotomidae), metathoracic musculature. **A** Median sagittal view, most of second phragma removed. **B** Lateral sagittal view, metafurca and some muscles removed. *Black* Exocuticle, *white* endocuticle, *21a* metabasalar-trochanteral muscle

well developed with one continuous sheet of muscle extending between the second and third phragma. Metalaterophragmal lobes and metalaterophragmo-metafurcal muscles (7) are absent from all taxa examined. In *Corynis* sp., the metanoto-metalaterophragmal muscles (6) are present. T1 is not medially subdivided and a distinct longitudinal crest is present medially on T1 in *Z. fasciata*. In *Cimbex* sp., the posterior margin of T1 is emarginate; the posterolateral corners of T1 articulate with the anterolateral parts of T2. The posterior thoracic spiracles are hidden from external view by the posterior margins of the mesepimera in *Corynis obscura*. The anapleural clefts are absent from *C. obscura*, and the anapleural sclerites are absent from all taxa examined. The apodemal parts of the basalars were not observed in *C. obscura*, but are well developed in *Z. fasciata* and *Cimbex* sp.; in the latter taxon, the mesofurco-metabasalar muscles (29) insert on small sclerites anteriorly of the rest of the apodemal parts of the basalars, whereas these muscles are absent from *Z. fasciata*. Metanoto-metabasalar (11) muscles are absent. The subalares are absent from all taxa examined. The metapleural arms are separated from the metepimera by distinct dorsal clefts. The posterodorsal margins of the metepimera are fused with the anterolateral parts of T1, obliterating the articular inflexions, and the T1-S2/metapleural muscles (16) are absent. The metapleural apodemes are large; in *Cimbex* sp. and *Z. fasciata*, their points of invagination are indicated by distinct pits which lie anteriorly in large depressions extending towards the first abdominal spiracles. The median metanoto-metapleural muscles (9) insert on oval apodemes projecting from the anterior margin of the metepisterna in *Cimbex* sp.; these muscles are absent from *Z. fasciata*. The paracoxal sulci and ridges are well

developed, extending to the pleural apodemes; in *Z. fasciata*, a pair of grooves extend posterolaterally from the paracoxal sulci towards the lateral metacoxal articulations. The posterior metapleuro-metafurcal muscles (24) and their apodemes at the lateral metacoxal articulations were not observed. The metafurco-mesospinal muscles (28) are absent from all taxa examined, but a median sclerotised rod is situated between the mesofurcal arms in *Cimbex* sp. and *Z. fasciata*.

5. Argidae (Figs. 2B, 3B, 5A, 6A, 7D, 10)

The mesoscutello-metanotal muscles (2) insert on a distinct projection medially on the anterior metanotal margin (Fig. 3B) and the point of insertion is entirely surrounded by sclerotised cuticle (Fig. 10A). The cenchri are transversely extended and are more than twice as broad as long (Fig. 3B). The anterior (18) and posterior metanoto-metacoxal muscles (19) and the metanoto-metatrochanteral muscles (20) are absent. In *Arge gracilicornis*, the lateral metanoto-metapleural muscles (10) arise from small apodemes just posteriorly of the posterior metanotal wing processes. T1 is continuous medially in *Sterictiphora furcata*, but medially subdivided in *Arge nigripes*. The anapleural sclerites are absent. The apodemal parts of the metabasalars are elongate in *A. gracilicornis* (this region could not be observed properly in *S. furcata*) and they receive a pair of muscles arising from the metatrochanteral apodemes (21a; Fig. 10A; see Discussion). The metanoto-metabasalar muscles (11) are absent. The mesofurco-metabasalar muscles (29) insert on a pair of small sclerites anteriorly of the apodemal parts of the metabasalars in *A. gracilicornis* (Fig. 10A). The metapleural arms are covered laterally by the bulbous anterodorsal parts of the metepimera (Fig. 5A); in *A. gracilicornis*, these parts of the metepimera are delimited by sulci and internal ridges from the metapleural ridge to the metalaterophragmal lobes. The metasubalares are absent; in *A. gracilicornis*,

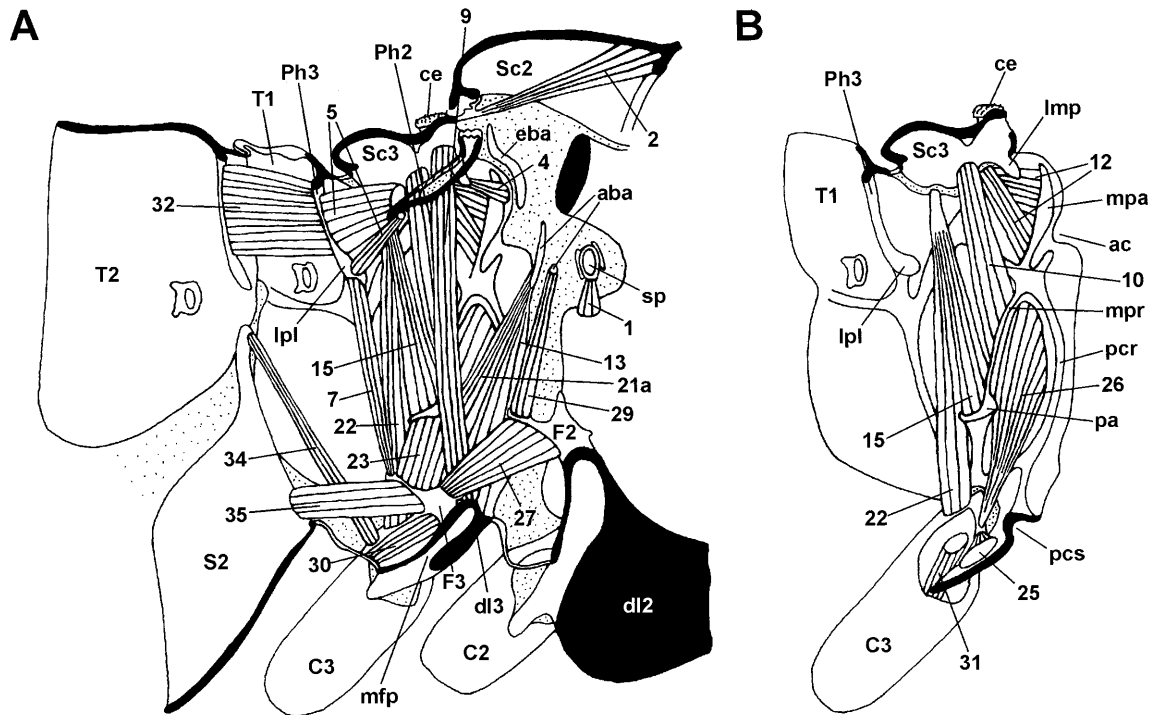


Fig. 10A,B *Arge gracilicornis* (Argidae), metathoracic musculature. **A** Median sagittal view, most of second phragma removed. **B** Lateral sagittal view, metafurca and some muscles removed. *Black* Exocuticle, *white* endocuticle, *Imp* lateral metanotal process

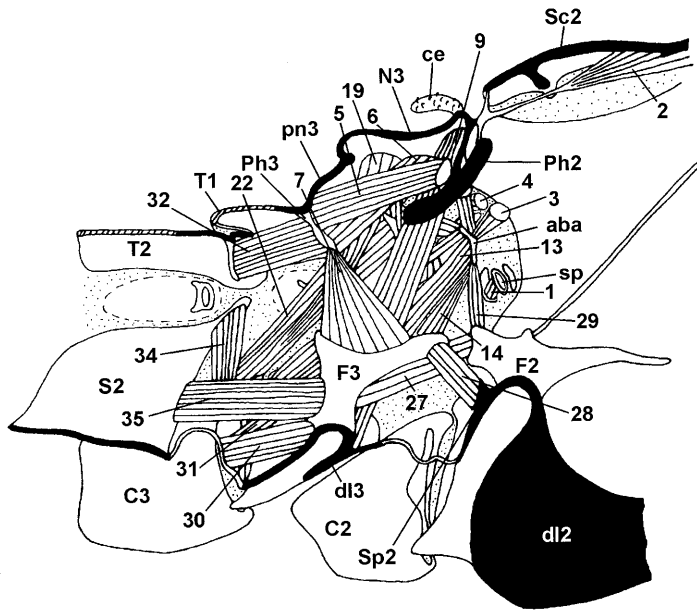
the metapleuro-metasubalar (15) and the metasubalar-metacoxal muscles (22) insert in membrane in the area where the metasubalares are usually observed (Fig. 10B). The dorsoposterior parts of the metepimera are fused with the anterolateral parts of T1 (Fig. 5A); in all of the *Arge* species, the lines of fusion are indicated by distinct sulci and internal ridges (Fig. 10B) extending from the metalaterophragmal lobes to the lateral metacoxal articulations. The T1-S2/metapleural muscles (16) are absent from *A. gracilicornis*. In *S. furcata*, a pair of small projections are invaginated from pits just antero-ventrally of the first abdominal spiracles; in *Arge* species, there is no trace of the articular inflections. The paracoxal sulci and ridges are well developed in the *Arge* species (Figs. 6A, 7D), especially their dorsal parts, which extend to the metapleural apodemes. The paracoxal and metapleural sulci are connected by a pair of short transverse sulci and ridges extending from half-way up the paracoxal sulci to the lateral metacoxal articulations. The posterior metapleuro-metafurcal muscles (24) are absent. The mesospina and metafurco-mesospinal muscles (28) are absent, and also from *Sterictiphora* sp. (Weber 1927; his '*Schizocerus*').

6. Pergidae

The mesoscutello-metanotal muscles (2) insert on a distinct projection medially on the anterior metanotal mar-

gin and the point of insertion is entirely surrounded by sclerotised cuticle. The cenchri are transversely extended and are more than twice as broad as long. They are weakly delimited and their posterior parts are not inflected; in *P. frogatti*, the hooks on the cenchri are weakly developed scales. The anterior metanoto-metacoxal muscles (18) are absent and the posterior metanoto-metacoxal muscles (19) are present. In *P. frogatti*, the metanoto-metatrochanteral muscles (20) arise as tendons from the anterolateral parts of the metanotum. T1 is only subdivided medially in *Lophyrotoma interrupta*; in the other taxa examined, T1 is continuous medially with little or no trace of the line of fusion. The posterior thoracic spiracles are covered by the posterior margins of the mesopleura in *P. frogatti*; in the other taxa examined, the spiracles are situated in distinct concavities in the posterior margins of the mesopleura. The anapleural sclerites are absent. The apodemal parts of the basalares were not observed in any of the taxa examined and the metabasalar-metapleural muscles (13) terminate in tendons connected to the membrane in the usual positions of the apodemal parts of the basalares; the metanoto-metabasalar (11) and the metabasalar-metacoxal muscles (21) are absent from *P. frogatti*. The mesofurco-metabasalar muscles (29) insert dorsally on the anterior margins of the metepisterna, just ventrally of the anapleural clefts, in all taxa except *P. frogatti*, from which these muscles are absent; in *Perga condei*, *L. interrupta* and *Syzygonia cyanocephala* they insert on distinct apodemes. The metapleural arms are covered laterally by the bulbous anterodorsal parts of the metepimera in *L. interrupta* and Euryinae gen. sp.; in *L. interrupta*, these parts of the metepimera are delimited by sulci and internal ridges from the metapleural ridge to the metalaterophragmal

A



B

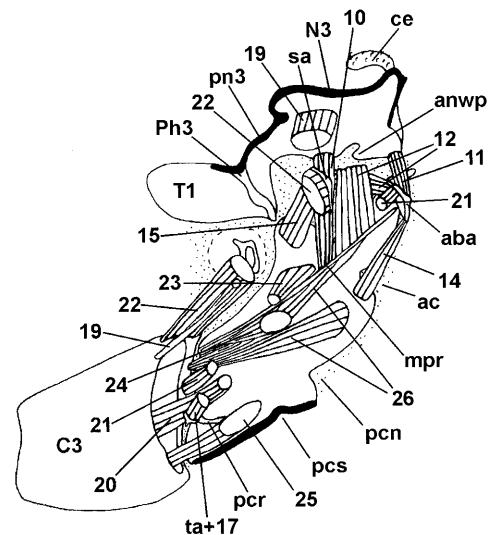


Fig. 11A,B *C. arvensis* (Pamphiliidae), metathoracic musculature. **A** Median sagittal view, most of second phragma removed. **B** Lateral sagittal view, metafurca and some muscles removed. *Black* Exocuticle, *hatched* mesocuticle, *white* endocuticle, 20 metanoto-trochanteral muscles

lobes. In the other taxa examined, the anterodorsal parts of the metepimera are less well developed and delimited, leaving the metepimeral arms visible in lateral view. The subalares are absent from all taxa examined except *L. interrupta*, where a pair of small sclerites were observed. The posterior parts of the metepimera are fused with the anterolateral margins of T1, obliterating the articular inflexions; in *L. interrupta*, the line of fusion is indicated by internal ridges extending from the metalaterophragmal lobes to the lateral metacoxal articulations. The T1-S2/metapleural muscles (16) are absent from *P. frogatti*, but could be observed in *P. condei*. The metapleural apodemes are not distinctly set apart from the broad metapleural ridges. In *L. interrupta*, the apodemes cannot be distinguished from the ridges, but even in this taxon, the anterior metapleuro-metafurcal muscles (23) arise from the pleural ridge. The apodemes for the posterior metapleuro-metafurcal muscles (24) are absent. The paracoxal sulci and ridges are weakly developed, lying very close to the anterior margins of the metepisterna, and the median metanoto-metapleural (9) and the metabasalar-metapleural muscles (13) attach posteriorly of the ridges. In *P. condei* and *Perga dorsalis*, a pair of grooves extend from the paracoxal sulci to the posterior margins of the metepisterna; the aforementioned muscles are attached anteriorly of these grooves. The metasubalar-metacoxal (22) and the S2-metacoxal muscles (34) are absent from *P. frogatti*, but were observed in some of the other taxa. The mesospina and metafurco-mesospinal muscles (28) are absent from all taxa examined.

III. Pamphilioidea

1. Pamphiliidae (Figs. 2A, 3A, 4C, 5B, 6B, 7B, 11)

The configuration of the region under study is very similar to that of Xyeloidea. The tendon of the mesoscutello-metanotal muscle (2) passes dorsally of the second phragma and inserts on an undifferentiated point on the anterior margin of the metanotum; the anterior margin of the metanotum is continuous with the second phragma ventrally. The anterior metanoto-metacoxal muscles (18) are absent and the posterior ones (19) present. The metapostnotum is not subdivided medially and continuous laterally with T1, which is entirely subdivided medially. The third phragma is low throughout and the metalaterophragmal lobes are weakly developed (Fig. 4C). In *Acantholyda erythrocephala*, there are distinct inflexions on the lateral parts of the anterior margins of T1 opposite the articular inflexions on the metepimera. The lateral parts of T1 surrounding the first abdominal spiracles are more or less separated from the median part by a weakly sclerotised line, at least anteriorly; in *Cephalcia arvensis*, the entire area around the first abdominal spiracles is weakly sclerotised. T1-S2/metapleural muscles (16) were not observed. The hind wing tegulae are large, but weakly sclerotised. The posterior thoracic spiracles protrude laterally and posteriorly to the mesepimera (Fig. 5B); the occlusor muscles (1) arise from small sclerites posteriorly of the spiracles (Fig. 11A). The anapleural sclerites are absent. The apodemal parts of the metabasales are well developed, receiving the insertions of the intrinsic metapleural muscles (14; Fig. 11B), and both the mesolaterophragmo-basalar (3) and the mesolaterophragmo-hind wing base muscles (4) are present (Fig. 11A). The metapleural sulci are deep (Fig. 5B) and the metapleural ridges are not very broad anywhere

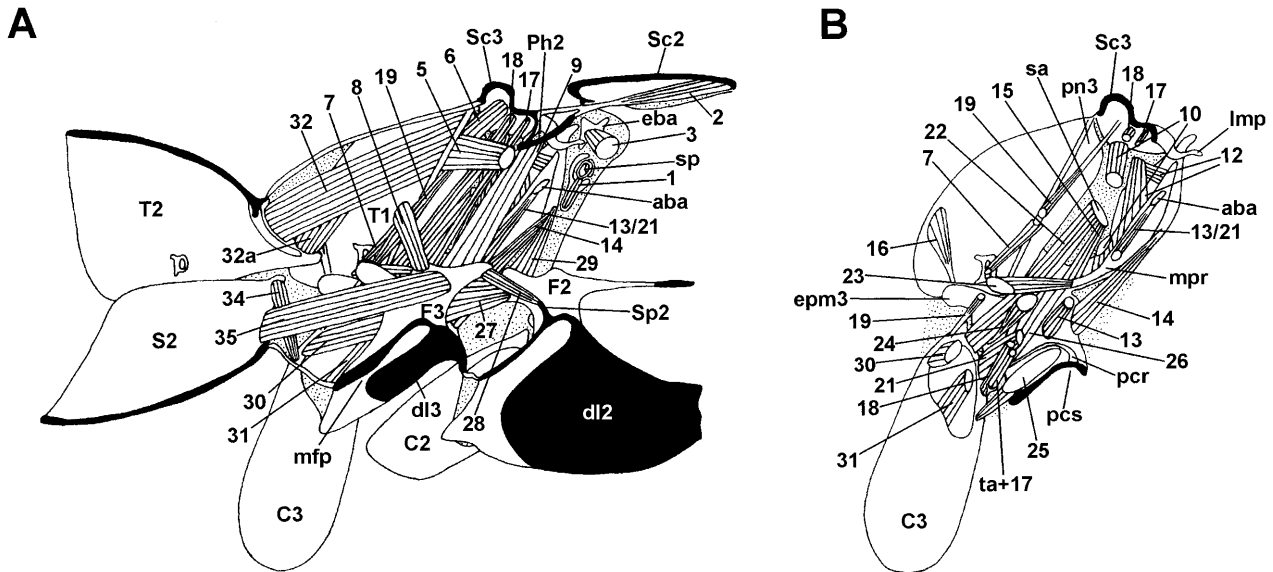


Fig. 12A,B *C. nigrinus* (Cephalidae), metathoracic musculature. **A** Median sagittal view, most of second phragma removed. **B** Lateral sagittal view, metafurca and some muscles removed. *Black* Exocuticle, *white* endocuticle, *32a* lateral T1–T2 muscle

(Fig. 7B) and absent posteriorly. The anterior metapleuro-metafurcal muscles (23) arise dorsally of the ridges (Fig. 11B). The metapleuro-metasubalar (15) muscles arise from the dorsal part of the metepimera, and the metapleuro-S2 muscles (33) are absent. The paracoxal notches are present. The paracoxal sulci and ridges bend posteriorly almost immediately after arising from the anterior end of the discrimen. They extend to the posterior margins of the metepisterna and continue along them (Fig. 6B) to terminate in the posterior parts of the metapleural sulci close to the lateral metacoxal articulations. The anteromedian parts of the paracoxal sulci and ridges are most conspicuous in *Pamphilius* sp., but only weakly developed in the other taxa examined. The metafurca have well-developed anterior arms, but comparatively short lateral arms (Fig. 7B), except in *A. erythrocephala*, where a pair of slender apodemes extends laterally towards the metapleural ridges; only one pair of metafurco-mesofurcal muscles (27) are present.

2. Megalodontesidae

The cenchri are transversely extended, more than twice as broad as long and the posterior parts are inflected and devoid of hooks or scales. The metanoto-metatrochantal muscles (20) are absent. Only one pair of small, transverse muscles (4) extends between the anterolateral corners of the metanotum and the hind wing base. The metalaterophragmal lobes are very conspicuous, twisted structures and a pair of sulci and internal ridges run posteriorly from the lobes across T1 to the posterior margin of the latter. T1 is continuous, but narrow medially, being emarginated posteriorly between the aforementioned

sulci. The lateral parts of T1 surrounding the first abdominal spiracles are continuous with the median part of T1. The T1-metapleural muscles (16) are absent, as are the anapleural sclerites. The metanoto-metabasalar (11) and the metabasalar-metacoxal (21) muscles are absent. The metapleural arms are distinctly set off from the rest of the metapleura by the anapleural clefts ventrally and a pair of incisions dorsally. The dorsal parts of the metepimera are high, covering the well-developed subalares laterally; posteriorly, the articular inflections are represented by long ledges. The metapleuro-metasubalar muscles (15) could not be observed and the metapleuro-S2 (33) muscles are absent. The metapleural sulci are shallow, but distinct, extending as straight lines to the lateral metacoxal articulations; a pair of sulci extends dorsally from the posterior ends of the metapleural sulci to the articular inflections. The metapleural ridges are broad, extending medially towards the lateral metafurcal arms as large apodemes before tapering towards the lateral metacoxal articulations. The intrinsic metapleural muscles (14) are absent, as are the paracoxal notches. The paracoxal sulci and ridges extend for some distance along the anterior margins of the metepisterna, then bend posteriorly; the ridges terminate just after reaching the posterior margins of the metepisterna, whereas the sulci continue along the posterior margins towards the lateral metacoxal articulations. The trochantal apodemes and the metanoto-trochantal muscles (17) are absent. The metafurca have broad anterior and lateral arms, the latter being considerably shorter than the former.

IV. Cephoidea, Cephalidae (Figs. 2C, 5C, 6C, 7E, 12)

The second phragma and the anterior margin of the metanotum are separated by membranous cuticle except medially, where the mesoscutello-metanotal muscles (2) insert on a weakly sclerotised area (Fig. 12A); the sclerotisation lies in the middle of the cuticle, not on

the surface. The lateral metanotal processes are slender and project anteromedially towards the mesolaterophragmal lobes (Fig. 12B); the mesolaterophragmo-metabasalar muscles (3) arise from the latter and insert on the external parts of the basales (Fig. 12A). No other muscles arise from the mesolaterophragmal lobes. The apodemal parts of the basales are very small and the metanoto-metabasalar muscles (11) are absent. The cenchri are absent (Fig. 2C) as are the metanoto-metatrochanteral muscles (20). The metapostnotum is subdivided medially into two lateral triangular areas, being separated by the anteromedian parts of the two halves of T1. The metapostnotum and T1 closely abut, but there is no third phragma except for a pair of weakly developed metalaterophragmal lobes. In addition to the slender metalaterophragmo-metafurcal muscles (7), which insert on the apices of the lateral metafurcal arms, a larger pair of T1-metafurcal muscles (8) arise just posteriorly of the metalaterophragmal lobes and insert at the base of the anterior metafurcal arms (Fig. 12A). The membranous area subdividing T1 widens considerably posteriorly (Fig. 2C). The T1-S2/metapleural muscles (16) insert in membrane dorsally of the posterodorsal corners of the metepimera. Apart from the broad sheets of the third phragmo-T2 muscles (32), T1 and T2 are also connected by a pair of smaller, fan-shaped muscles arising from the posterolateral parts of T1 and inserting on apodemes on the anterolateral corners of T2 (Fig. 12A; 32a). The sclerites posteriorly of the posterior thoracic spiracles are large and sickle-shaped and the oclucor muscles (1) arise from the stalks of the sickle-shaped sclerites. The anapleural sclerites are absent. The metapleural arms are large (Fig. 5C), and the metapleural ridges are broad ledges in this area (Fig. 12B). The metabasalar-metapleural (13) and -metacoxal (21) muscles arise jointly from the basales (Fig. 12B). The mesofurco-metabasalar (29) and the intrinsic metapleural muscles (14) insert closely together on the anteroventral margins of the metapleural arms (Fig. 12A). The subalares are well developed and lie exposed in large membranous areas posteriorly of the metapleural arms. The posterodorsal parts of the metepimera articulate with the lateral margins of T1 (Fig. 5C); the latter extend obliquely across the metepimera in short, shallow grooves in the dorsal margins of the metepimera, which slightly overlap the anterolateral corners of T1 laterally. The posterodorsal corners of the metepimera are expanded into distinct projections, which are overlapped laterally by the posterolateral parts of T1 (Fig. 12B); articular inflexions and metapleuro-S2 muscles (33) are absent. The anapleural clefts are distinct. The metapleural sulci bend at the anapleural clefts before continuing in straight lines to the lateral metacoxal articulations. The metapleural ridges extend into small apodemes accommodating the origins of the anterior metapleuro-metafurcal muscles (23) before tapering to slender ledges posteroventrally. The paracoxal notches are absent. A pair of elongate depressions lie close to the anterior margins of the

metepisterna laterally; these depressions are not connected to the discrimen. The paracoxal sulci bend sharply posteriorly shortly after arising from the anterior end of the discrimen to extend subparallel with the latter for most of their length before bending a little laterally to terminate in the posterior margins of the metepisterna opposite the trochantal apodemes (Fig. 6C). The anterior metafurcal arms are elongate (Fig. 7E) and only one pair of metafurco-mesofurcal muscles (27) are present. The lateral metafurcal arms are short.

V. 'Siricoidea'

1. *Anaxyelidae*

The tendon of the mesoscutello-metanotal muscle (2) passes through an opening just ventrally of the dorsal margin of the second phragma before inserting on an undifferentiated area on the anterior margin of the metanotum. The anterior margin of the metanotum is separated from the second phragma by a region of membranous cuticle. The anterior metanoto-metacoxal muscles (18) are absent. The metapostnotum is subdivided medially and closely abuts the two halves of T1, but there is no third phragma or metalaterophragmal lobes. The anterolateral corners of T1 have distinct protuberances opposite the metepimeral articular inflexions. T1-metafurcal (8) and -metapleural muscles (16) were not observed. The posterior thoracic spiracles lie between a pair of small sclerites anteriorly and a pair of large, rectangular sclerites posteriorly; the latter sclerites accommodate the origins of the oclucor muscles (1). The anapleural sclerites are absent. The hind wing tegulae are represented by narrow, sclerotised strips with a few setae. One pair of muscles (3/4?) extends between membranous pads connected to the second phragma and the metapleural arms. The lateral metanoto-metapleural muscles (10) are attached to the metanotum through tendons. The metepimera are weakly developed posteriorly of the elongate metapleural arms, except for dorsal projections extending to the anterolateral corners of T1; the well-developed articular inflexions are situated at the dorsal ends of these projections. Posteriorly of the projections, the metepimera taper considerably so that only narrow strips remain dorsally of the metapleural sulci. The metapleural sulci are well developed and more or less straight throughout, becoming deeper posteriorly. The metapleural ridges are well developed anteriorly, but taper posteriorly, and a pair of small apodemes receiving the insertions of the intrinsic metapleural muscles (14) are situated on the ridges about halfway along the metapleural arms. The metapleuro-S2 muscles (33) are absent, as are the paracoxal notches. The paracoxal sulci and ridges extend laterally along the anterior margins of the metepisterna for some distance before curving posteriorly to terminate at the lateral metacoxal articulations. The anterior metafurcal arms curve dorsally to assume vertical positions for most of their lengths.

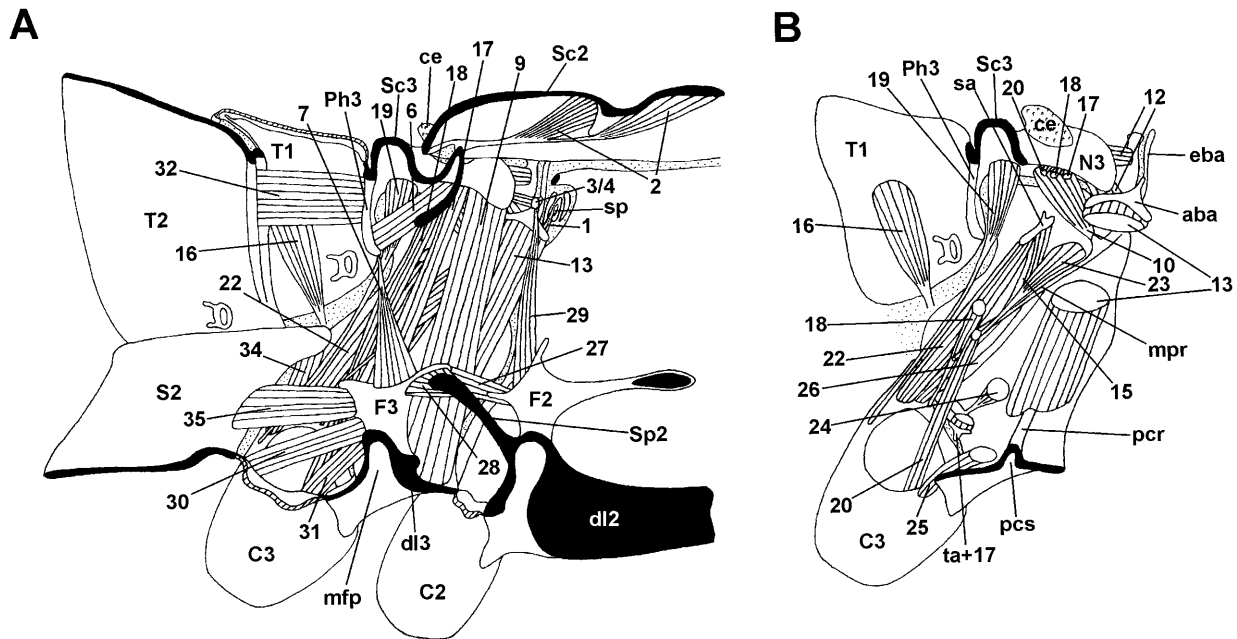


Fig. 13A,B *S. juvenus* (Siricidae), metathoracic musculature. **A** Median sagittal view, most of second phragma removed. **B** Lateral sagittal view, metafurca and some muscles removed. *Black* Exocuticle, *hatched* mesocuticle, *white* endocuticle

2. Siricidae (Figs. 2D, 5D, 6D, 7F, 13)

The mesoscutello-metanotal muscles (2) insert via a tendon on a sclerotised area on the anterior margin of the metanotum. The area around the insertion point is weakly sclerotised, but laterally the anterior margin of the metanotum is continuous with the second phragma. The lateral metanotal processes are reduced. The metanoto-metabasalar muscles (11) are absent. The metapostnotum is divided medially. The third phragma is very low, except for the well-developed metalaterophragmal lobes. The second phragmo-third phragmal muscles (5) are absent. The T1-S2/metapleural muscles (16) insert in membrane dorsally of the posterodorsal margins of the metepimera. The hind wing tegulae are large (Fig. 2D), and the anapleural sclerites are absent. The apodemal parts of the metabasales are large and receive the insertions of the mesofurco-metabasalar muscles (29) on small apodemes on the stalks dorsally of the main apodemes receiving the metabasalar-metapleural muscles (13; Fig. 13A). The metabasalar-metacoxal muscles (21) are absent. The metapleural arms are slender and extend directly dorsally (Fig. 5D). A pair of muscles arise from the mesolaterophragmal lobes and insert on the metapleural arms (Fig. 13A; 3/4; see discussion). The metepimera are well developed posteriorly, lying close to the lateral margins of the metanotum and covering the subalares laterally. The subalares are slender rods in *Urocerus gigas*, but cup-shaped in the other taxa examined. The articular inflexions are represented by narrow ledges. The metapleuro-S2 muscles (33) are absent. After descending from the metapleural arms, the metapleural sulci continue as

straight lines to the lateral metacoxal articulations (Fig. 5D). The metapleural ridges are ledges of moderate breadth throughout, tapering a bit posteriorly before the very conspicuous apodemes for the posterior metapleuro-metafurcal muscles (24). A pair of small apodemes for the lateral metanoto-metapleural muscles (10) are present on the dorsal side of the anterior part of the metapleural ridges (Fig. 13B). The intrinsic metapleural muscles (14) are absent, as are the anapleural clefts and the paracoxal notches. The paracoxal sulci (Fig. 6D) and ridges (Fig. 7F) extend laterally in straight lines, terminating before reaching the metapleural sulci. The very elongate mesospina projects posteriorly between the anterior metafurcal arms (Figs. 7F, 13A), the metafurco-mesospinal muscles (28) extending transversely from the latter to the former. Only one pair of metafurca-mesofurcal muscles (27) are present.

3. Xiphidriidae (Figs. 2E, 4D, 5E, 6E, 7G, 14)

The tendon of the mesoscutello-metanotal muscle (2) is attached medially on the dorsal margin of the second phragma (Fig. 14A). The lateral metanotal processes are inconspicuous. The metanoto-trochantinal (17), anterior metanoto-metacoxal (18) and metanoto-metatrochanteral (20) muscles are absent. The metapostnotum is subdivided medially, comprising two triangular sclerites. The third phragma is low, except for the distinct metalaterophragmal lobes (Fig. 4D), and the second phragmo-third phragmal muscles (5) are absent. The anteromedian corners of the two rectangular halves of T1 closely abut the posterior margin of the metanotum. From these points, a pair of crenulated furrows extend posterolaterally (Fig. 2E); they terminate before reaching the posterior margins of the T1 sclerites. The two halves of T1 closely abut medially, with parallel median margins; they

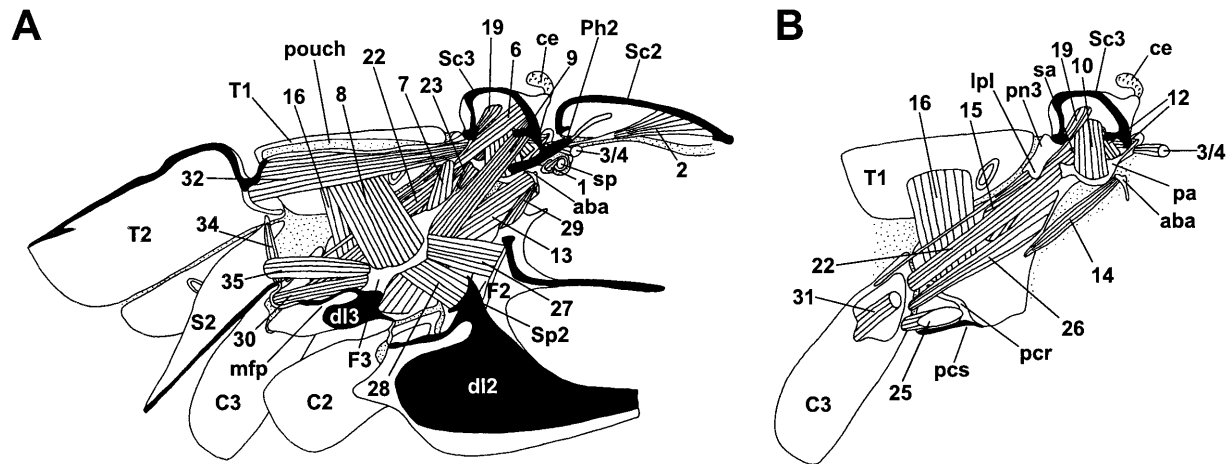


Fig. 14A,B *X. camelus* (Xiphidiidae), metathoracic musculature. **A** Median sagittal view, most of second phragma removed. **B** Lateral sagittal view, metafurca and some muscles removed. *Black* exocuticle, *white* endocuticle

are separated by an expanded region of membranous cuticle that is invaginated ventrally of them to form a pouch which widens posteriorly (Figs. 4D, 14A). A pair of large T1-metafurcal muscles (8) arise from the two halves of T1 some distance posteriorly of the third phragma and insert broadly on the metafurcal arms (Fig. 14A). The T1-S2/metapleural muscles (16) are also conspicuous and they insert broadly on the lateral parts of the metepisterna (Fig. 14B). The posterior thoracic spiracles lie in distinct concavities of the mesepimera, but are visible laterally (Fig. 5E), and the ocluser muscles (1) arise from separate sclerites posteriorly of the spiracles (Fig. 14A). The hind wing tegulae are absent and the apodemal parts of the metabasales are small. The metanoto-metabasalar (11) and metabasalar-metacoxal (21) muscles are absent, and the metabasalar-metapleural muscles (13) are subdivided into a large median pair and a smaller, lateral pair (Fig. 14B; 14; see Discussion). A pair of muscles arise from the mesolaterophragmal lobes and insert on the slender metapleural arms (Fig. 14B; 3/4; see Discussion). The metasubasales are small and covered laterally by the dorsal parts of the metepimera. The metapleuro-S2 muscles (33) are absent. The metapleural sulci curve moderately posteriorly of the articular inflexions. The metapleural ridges are well developed anteriorly, terminating in distinct metapleural apodemes (Fig. 7G), whose presence is indicated externally by pits. The metapleural apodemes are bent ventrally and their dorsal parts receive the insertions of the lateral metanoto-metapleural muscles (10; Fig. 14B). Posteriorly, the metapleural sulci bend ventrally to extend along the posterodorsal margins of the metapleura (Fig. 5E); the metapleural ridges are absent from this part. The metepimera are practically absent posteriorly of the indistinct articular inflexions. The posterior metapleuro-metafurcal muscles (24) and their corresponding apodemes are absent. The anapleural sclerites are absent and the anapleural clefts small. The paracoxal notches are absent. The

paracoxal sulci and ridges extend laterally for some distance before bending posteriorly to extend along the posterior margins of the metepisterna (Figs. 6E, 7G), terminating at the lateral metacoxal articulations. The metafurca has broad anterior arms and slender lateral arms extending towards the metapleural apodemes (Fig. 7G). Only one pair of metafurco-mesofurcal muscles (27) are present.

VI. Orussoidea, Orussidae (Figs. 2F, 5F, 6F, 7H, 15)

The second phragma is not attached to the anterior margin of the metanotum medially, and laterally it is connected to it by narrow strips of unsclerotised cuticle. The lateral metanotal processes are reduced. Two pairs of small muscles extend between the lateral margins of the metanotum and the metapleural arms; the anterior pair (Fig. 15A; 3/4) arise from the anterolateral corners of the metanotum and insert medially of the metapleuro-hind wing muscles (12) and the other pair (Fig. 15B; 10) arise more posteriorly and insert posteriorly of the metapleuro-hind wing muscles (for homologies of these muscles, see Discussion). The medial metanoto-metapleural (9), metanoto-metabasalar (11), metanoto-trochantal (17) and anterior metanoto-metacoxal muscles (18) are absent. The metascutellum is weakly delimited (Fig. 2F), and the scutellar arms are solid. The metapostnotum is separated from the posterior margin of the metanotum by a narrow strip of unsclerotised cuticle; it is continuous medially and fused with T1 posteriorly. The second phragmo-third phragmal muscles (5) arise laterally on the second phragma and extend transversely to insert on the median parts of the metapostnotum close to the midline anteriorly of the third phragma. The third phragma is indicated externally by a distinct crenulated furrow (Fig. 2F) and is well developed throughout. Ventrally, it is expanded into a smooth ledge projecting posteriorly and closely abutting the second phragma ventrally (Fig. 15A). The metalaterophragmal lobes and the metanoto-metalaterophragmal muscles (6) are absent. The metalaterophragmo-metafurcal muscles (7) arise from the posterior parts of the metanotum and insert on

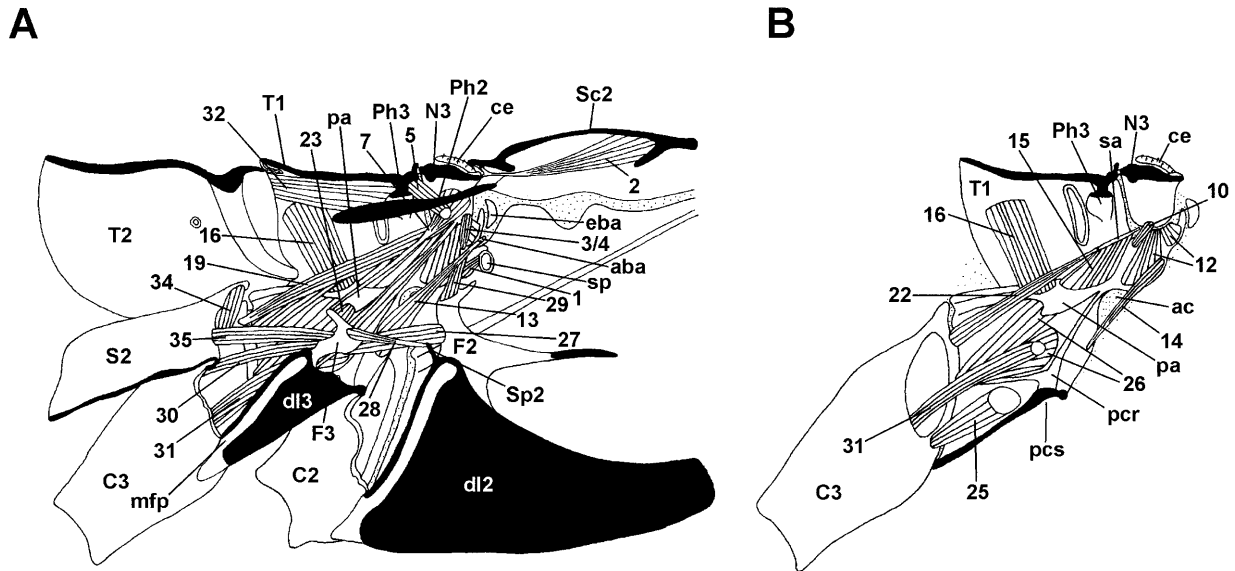


Fig. 15A,B Orussidae gen. sp., metathoracic musculature. **A** Median sagittal view, most of second phragma removed. **B** Lateral sagittal view, metafurca and some muscles removed. *Black* Exocuticle, *white* endocuticle

the lateral metafurcal arms through elongate tendons (Fig. 15A). T1 is entire medially (Fig. 2F) and its lateral margins cover the dorsal margins of the metapleura laterally from the connection between the metapleural arms and the rest of the metapleura to the lateral metacoxal articulations (Fig. 5F). Large T1-S2/metapleural muscles (16) arise laterally on T1 and insert dorsally on the metapleural ridges (Fig. 15B) posteriorly of the metapleural apodemes. The posterior thoracic spiracles are covered laterally by the posterior margins of the mesepimera (Fig. 5F); the latter also partly cover the metapleural arms. The hind wing tegulae were not observed. The apodemal parts of the metabasales are small and only the metabasalar-metapleural muscles (13) attach to them; the mesofurco-metabasalar muscles (29) insert on the ventral margins of the metapleural arms and the metabasalar-metacoxal muscles (21) are absent. The metapleural arms are strongly constricted at the base by the anapleural clefts ventrally with only narrow strips connecting them to the rest of the metapleura; they abut the anterolateral margins of T1 posterodorsally. The subalares are elongate strips (Fig. 15B). The metapleural sulci extend horizontally along the dorsal margin of the metapleura to the lateral metacoxal articulations, which lie at the posterodorsal corners of the metapleura. The posterior parts of the metepimera, including the articular inflections and the metapleuro-S2 muscles (33), are absent. Large metapleural apodemes are present (Figs. 7H, 15B) and, posteriorly of these, the metapleural ridges are reduced. The anapleural sclerites and paracoxal notches are absent. The metepisterna have a pair of shallow concavities, the metepisternal depressions (Fig. 6F; *epd3*), ventrally accommodating the mesocoxae. The depressions are separated medially by the discrimen, which is raised into a

median carina, and delimited laterally by a pair of carinae dividing the metepisterna into vertical, dorsolateral and horizontal ventromedian parts. The paracoxal sulci and ridges (Figs. 6F, 7H, 15B) extend laterally for a short distance and then divide. Anterior branches extend laterally along the anterior margins of the metepisterna to terminate in the metapleural ridges just posteriorly of the anapleural clefts, and short posterior branches (not visible externally) extend towards the posterior margins of the metapleura without reaching them. The trochantinal apodemes are absent. The anterior metafurcal arms are elongate. The lateral metafurcal arms extend towards the metapleural apodemes and the former are displaced anteriorly along the anterior metafurcal arms (Fig. 7H). Only one pair of metafurco-mesofurcal muscles (27) are present. The metafurco-mesospinal muscles (28) insert on the short mesospina through elongate tendons.

D. Discussion

The phylogenetic aspects of the findings in this study will be discussed with reference to the recent cladistic treatments of the Hymenoptera by Vilhelmsen (1997, 1999) and Ronquist et al. (1999). The definition and distribution of character states are given in Table 3, and hypotheses of character evolution are shown in Fig. 16.

I. Ground plan of the hymenopteran metathorax and first abdominal segment

The considerable size difference between the meso- and metathorax was emphasised by Kristensen (1991). However, this condition is not unique to the Hymenoptera, being even more pronounced in Diptera, where there is also a considerable reduction of the musculature (Bonhag 1949; Mickoleit 1962), which is not observed in the ground plan of the Hymenoptera.

1. The metanotum and the first abdominal tergite

The insertion of the mesoscutello-metanotal muscles (2) through a tendon on the anterior margin of the metanotum is a hymenopteran autapomorphy (Heraty et al. 1994; their muscle 114); in Neuropterida and Mecoptera, it inserts on the mesopostnotum. Heraty et al. (1994) were unable to decide whether it is the ground plan state for Hymenoptera to have the tendon passing dorsally or ventrally of the mesopostnotum. The former condition is

Table 3 Distribution of character states. ? not known/uncertain, – not applicable. Character 1, insertion point of mesoscutello-metanotal muscles (2): not on any conspicuous structure on the anterior margin of the metanotum (Figs. 2A, 11A)=0; flanked by small projections from the anterior margin of the metanotum, projections not continuous ventrally=1; on distinct projections from the anterior margin of the metanotum, forming entire ring of sclerotised cuticle around the insertion point (Figs. 3B, 10A)=2; dorsally on second phragma (Fig. 14A)=3. Character 2, connection between second phragma and anterior margin of metanotum: totally fused or at most connected by narrow strip of unsclerotised cuticle (Figs. 8A, 11A)=0; separated by membranous area of considerable length (Fig. 10A)=1. Character 3, lateral metanotal processes: blunt or inconspicuous=0; slender, projecting ventrally and/or medially (Fig. 12B)=1. Character 4, transverse metanoto-metapleural muscles (4): absent, homologues attached to the mesolaterophragma and the hind wing bases (Fig. 8A)=0; present (Figs. 9A, 10A)=1. Character 5, structure of cenchri: oval in outline, less than twice as broad as long, with posterior part membranous and inflected, devoid of hooks (Fig. 3A,C)=0; transversely extended, at least twice as broad as long, no inflected posterior part, hooks on entire surface (Fig. 3B,D)=1; transversely extended, at least twice as broad as long, with posterior part membranous and inflected, devoid of hooks=2; absent (Fig. 2C)=3. Character 6, second phragmo-third phragmal muscles (5): present, undivided (Fig. 8A)=0; present, subdivided, lateral parts arise from the metalaterophragmal lobes (Figs. 9A, 10A)=1; absent (Figs. 13A, 14A)=2. Character 7, metanoto-metalaterophragmal muscles (6): present (Figs. 8A, 9A)=0; absent (Fig. 10A)=1. Character 8, apodemes for the lateral metanoto-metapleural muscles (10): at most weakly developed=0; distinct, plate-like apodemes set off from the lateral margins of the metanotum=1. Character 9, hind wing tegulae: present (Fig. 2A,D)=0; absent=1. Character 10, metanoto-metabasalar muscles (11): present (Figs. 8B, 9A)=0; absent (Figs. 10A, 13A)=1. Character 11, third phragma: present (Fig. 4A,B,D)=0; absent (Fig. 12A)=1. Character 12, metalaterophragmal lobes: well developed, project away from the third phragma as distinct apodemes (Figs. 4B, 9)=0; at most slightly raised lobes present laterally on third phragma (Fig. 4C)=1. Character 13, metalaterophragmo-metafurcal muscles (7): present (Fig. 8A)=0; absent=1. Character 14, metapostnotum: continuous medially=0; divided medially=1. Character 15, T1: divided medially (Fig. 2C,E)=0; continuous medially (Fig. 2F)=1. Character 16, T1-S2/metapleural muscles (16): present (Figs. 14B, 15B)=0; absent (Fig. 10A)=1. Character 17, posterior thoracic spiracles: concavities in posterior margins of mesepimera opposite spiracles at most shallow (Fig. 5B,C)=0; spiracles accommodated in distinct concavities of the mesepimera (Fig. 5A,E)=1; spiracles covered laterally by mesepimera (Fig. 5F)=2 (ordered). Character 18, occlusor muscles (1) of the posterior thoracic spiracles: arise from separate sclerites posteriorly of the spiracles (Figs. 8A, 12A)=0; arise from the posterior margin of the mesepimera ventrally of the spiracles (Figs. 9A, 10A)=1. Character 19, metapleural arms: not covered laterally by metepimera (Fig. 1A)=0; covered laterally by posterodorsal parts of metepimera (Fig. 5A)=1. Character 20, association between metapleural arms and T1: not abutting T1 (Figs. 1A, 5E)=0; abutting T1 (Fig. 5F)=1; fused with T1=2 (ordered). Character 21, anapleural sclerites: present (Figs. 1, 9B)=0; absent=1. Character 22, anapleural clefts: present (Fig. 1)=0; absent=1. Character 23, mesofurco-metabasalar muscles (29): present, do not

observed in Macroxyelinae, Tenthredinoidea, Pamphilioidea, Cephoidea and Siricidae, and I therefore consider this to be plesiomorphic. Having the tendon passing through an opening in the upper margin of the mesopostnotum/second phragma occurs only in Xyelinae and Anaxyelidae and is clearly derived.

The anterior margin of the metanotum is fused to the second phragma in all the outgroup taxa examined. Having a region of membranous cuticle between these two regions (character 2, state 1), as is the case in Tenthre-

insert on anterior margins of the metapleura (Fig. 11A)=0; present, insert on anterior margins of the metapleura (Fig. 12A)=1; absent=2. Character 24, metasubalares: present, receiving metapleuro-metasubalar (15) and metasubalar-metacoxal muscles (22) (Figs. 12B, 13B)=0; absent, muscles insert on membrane (Fig. 10B)=1. Character 25, metepimera: well developed, but without specialised articulation with T1 (Fig. 1A)=0; well developed, with specialised articulations with T1 at the anteroventral corners of the latter (Fig. 5C)=1; well developed, articulating with the lateral margins of T1 for the entire length of the latter, partly overlapping the first abdominal spiracles=2; posterior parts reduced (Fig. 5E)=3. Character 26, association between T1 and metepimera: may be closely abutting or articulating, but never fused (Figs. 1A, 5B)=0; fused (Fig. 5A)=1. Character 27, articular inflections on the metepimera: present (Fig. 1A)=0; absent=1. Character 28, metapleuro-S2 muscles (33): present (Fig. 8A)=0; absent (Figs. 9A, 11A)=1. Character 29, metapleural apodemes: at most shallow ridges present (Fig. 7B)=0; distinct apodemes projecting towards lateral metafurcal arms present (Fig. 7D,G,H)=1. Character 30, apodemes/tendons receiving the insertions of the posterior metapleuro-metafurcal muscles (24): present (Figs. 7E, 13B)=0; absent (Fig. 14B)=1. Character 31, metepisternal depressions: at most shallow, weakly demarcated concavities present (Fig. 6C,E)=0; well-developed depressions accommodating the mesocoxae present, separated medially by the raised metafurcal discrimen, delimited laterally by distinct carinae (Fig. 6F)=1. Character 32, paracoxal notches: present (Figs. 1, 6B)=0; absent (Fig. 6A,C,D)=1. Character 33, paracoxal sulci and ridges: straight or curving slightly anteriorly, if curving posteriorly then only for a short distance at the extreme lateral ends (Figs. 1B, 6A,D,F)=0; curved posteriorly (Fig. 6E)=1; strongly curved posteriorly, extending subparallel to metafurcal discrimen (Fig. 6C)=2 (ordered). Character 34, termination points of paracoxal sulci: in the posterior margins of the metepisterna (Figs. 1B, 6C,E)=0; in or close to the metapleural sulci at the anterior margins of the metepisterna (Fig. 5A)=1; in the metepisterna some distance from both the anterior and posterior margins (Fig. 6D)=2. Character 35, metathoracic trochantins: present, connected to the metapleura and anterior margins of metacoxae=0; present, invaginated as an apodeme not connected to the metapleura and metacoxae (Figs. 8B, 13B)=1; absent (Figs. 10B, 14B)=2. Character 36, anterior metanoto-metacoxal muscles (18): present (Figs. 8A, 13A)=0; absent (Fig. 9A)=1. Character 37, posterior metanoto-metacoxal muscles (19): present (Figs. 8B, 13B)=0; absent (Fig. 10B)=1. Character 38, metanoto-metatrochanteral muscles (20): present (Figs. 11B, 13B)=0; absent (Fig. 10B)=1. Character 39, metabasalar-metacoxal muscles (21): present (Fig. 8B)=0; absent (Fig. 13B)=1. Character 40, anterior metafurcal arms: elongate, at most only slighter shorter than the lateral metafurcal arms (Fig. 7A,B,F)=0; reduced, considerably shorter than the lateral metafurcal arms (Fig. 7C,D)=1. Character 41, lateral metafurcal arms: short (Fig. 7A,E,F)=0; elongate, extend towards the metapleural apodemes (Fig. 7C,D,G,H)=1, fused with the metapleural apodemes=2 (ordered). Character 42, mesospina: small, do not project posteriorly between the anterior metafurcal arms (Fig. 7C,G,H)=0; elongate, project posteriorly between the anterior metafurcal arms (Figs. 7F, 13A)=1; absent (Figs. 7D, 10A)=2. Character 43, metafurco-mesospinal muscles (28): present (Figs. 8A, 9A)=0; absent (Fig. 10A)=1

Taxon	Characters				
	1	1111111112	222222223	333333334	444
	1234567890	1234567890	1234567890	1234567890	123
<i>Amphigerontia bifasciata</i> (PSO) ^a	?00?3000??	01001?0?00	10?0301?01	01--0?0?00	020
<i>Priacma serrata</i> (COL) ^b	?000300010	0000100?00	1000001?00	1102000000	020
<i>Chrysopa perla</i> (NEU) ^c	-00?300010	00010?0?00	?010000?10	0101000001	021
<i>Raphidia</i> sp. (RAP) ^d	-00?30001?	0101000?00	10?0011010	01010?0??1	12?
<i>Panorpa</i> sp. (MEC) ^e	-00?300000	0110?0?000	10?0001010	0102001001	021
<i>Micropterix calthella</i> (LEP) ^f	?01?3000??	111101??00	?0?030100?	01--0010?1	02?
<i>Xyela julii</i> (Xye)	00000000?0	0100000000	1000000000	0000100000	000
<i>Macroxyela ferruginea</i> (Xye)	000000000?	01000?0?00	0000000000	00001????0	000
<i>Blasticotoma filiceti</i> (Bla)	01??01?00?	00000?2?00	000?201?1?	01122????0	100
<i>Paremphtus flavipes</i> (Bla)	010101?000	00000?2?00	00?0201?10	01122????0	100
<i>Runaria reducta</i> (Bla)	01?1010000	0000012100	0000201110	?1??210100	?00
<i>Tenthredo arcuata</i> /sp. (Ten)	011?01000?	00000?2?00	0101001?10	01012????1	100
<i>Dolerus niger</i> (Ten)	0111011000	00000?2?00	0000001?1?	01012????1	100
<i>Athalia</i> sp. (Ten)	0111011000	0000002100	1000001110	0101201001	121
<i>Nematus</i> sp. (Ten)	011101100?	00000?1?00	0001001?10	01012????1	100
<i>Diprion pini</i> (Dip)	01111??00?	00000?1?00	??00000?10	01012????1	10?
<i>Gilpinia</i> sp. (Dip)	0111111000	0000001100	1100000110	0101211101	100
<i>Monoctenus juniperi</i> /sp. (Dip)	011111100?	0000001?00	1001000?1?	01012????1	100
<i>Cimbex</i> sp. (Cim)	2101101101	0110111100	1001-1111	0101211111	101
<i>Zaraea fasciata</i> /sp. (Cim)	1100101101	0110111100	1021-11111	0101211111	101
<i>Corynis obscura</i> /sp. (Cim)	010110000?	01101?2?00	11?1-11?11	01012????1	121
<i>Arge</i> spp. (Arg)	2111111001	0000011110	1001011111	0101211101	121
<i>Sterictiphora furcata</i> (Arg)	211?11?00?	00001?1?10	?0?1-1??11	01012????1	121
<i>Perga dorsalis/condiei</i> (Per)	211111100?	0000101100	1011-11?11	01012????1	121
<i>Phylacteophaga frogatti</i> (Per)	21111110?1	0000112100	1021-11111	0101210011	121
<i>Lophyrotoma interrupta</i> (Per)	21111??00?	00000?1110	1010011?01	01012????1	12?
<i>Syzygonia cyanocephala</i> (Per)	21111??00?	00001?1100	1011-11?11	01012?0??1	12?
<i>Euryinae</i> gen. sp. (Per)	211111100?	00001?1?10	101?-11?1?	01012????1	121
<i>Pamphilus</i> sp. (Pam)	0000000000	01000?0000	10?0000?00	00101?0??0	000
<i>Neurotoma nemoralis</i> (Pam)	000?00?00?	01000?0?00	10?0000?00	00101????0	000
<i>Cephalcia arvensis</i> (Pam)	0000000000	0100010000	1000000100	0010110000	000
<i>Acantholyda erythrocephala</i> (Pam)	?00?00000?	01000?0?00	10?0000?00	00101????0	10?
<i>Megalodontes cephalotes</i> (Meg)	0000200001	0000110000	1000000110	0110200110	000
<i>Cephus nigrinus</i> (Cep)	0110300001	1101000000	1010101110	0120100100	000
<i>Calameuta filiformis</i> (Cep)	011030?00?	11010?0?00	1010101?10	01201????0	00?
<i>Hartigia linearis</i> (Cep)	0?1?30?00?	11010?0?00	10?0101?10	01201????0	00?
<i>Syntexis libocedrii</i> (Ana)	0100000000	1101010000	1000300100	0110110000	000
<i>Sirex juvencus</i> (Sir)	0000020001	0001000000	1100000100	0102100010	010
<i>Urocerus gigas</i> (Sir)	000?020001	0001000?00	1100000?00	01021????0	010
<i>Tremex columba</i> (Sir)	000?0??00?	00?10?0?00	11?0000?00	01021????0	01?
<i>Xiphydria camelus</i> (Xip)	3000020011	0001001000	1000300111	0110210110	100
<i>Orussus abietinus</i> /spp. (Oru)	0000001011	0100102001	1010301111	1101210010	100
<i>Schlettererius cinctipes</i> (Ste)	000?3??01?	01?01?2?02	11?0311?11	11012????0	00?
<i>Megalyra fasciipennis</i> (Mly)	000?3??01?	01?11??02	11??311?11	11012????1	22?
<i>Aulacus striatus</i> (Aul)	000?30?01?	00?01??02	11??311?1?	11012????1	22?
<i>Ibalia rufipes</i> (Iba) ^g	000?30?01?	00001?2?02	1020311?11	11012????1	121
<i>Orthogonalys pulchella</i> (Tri) ^h	000?30?01?	01?11?1?02	112?311?11	11??2????1	221
<i>Vespa rufa</i> (Ves) ⁱ	0000301011	011-110102	1120311111	1101211111	221

^a Additional information from Badonnel (1934)

^b Additional information from Baehr (1975)

^c Additional information from Korn (1943), Czihak (1956) and Heraty et al. (1994)

^d Additional information from Mickoleit (1966), Achtelig (1975) and Heraty et al. (1994)

^e Additional information from Hasken (1939), Mickoleit (1966), Hepburn (1970) and Heraty et al. (1994)

^f Additional information from Kristensen (1984) and Mickoleit (1966)

^g Additional information from Ronquist and Nordlander (1989) and Heraty et al. (1994)

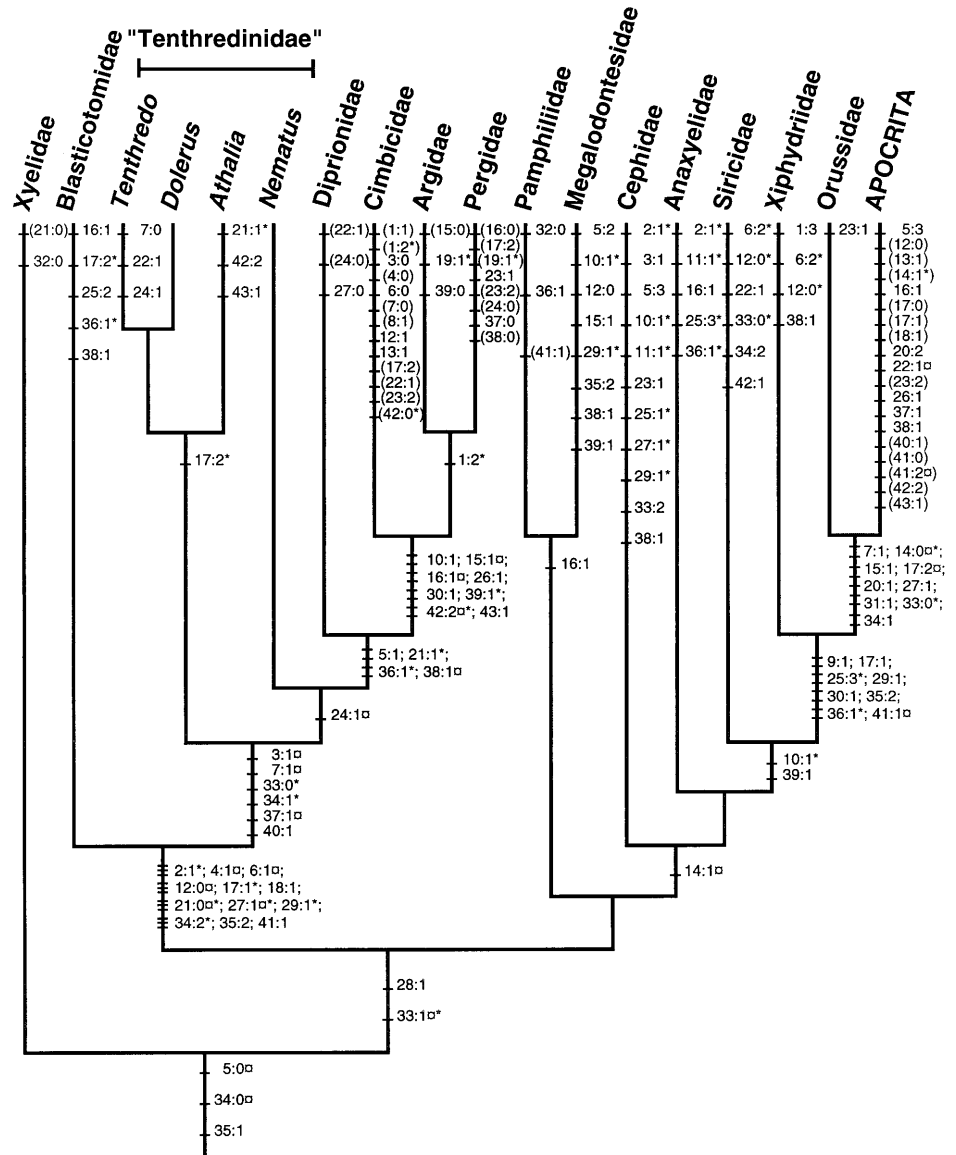
^h Additional information from Whitfield et al. (1989) and Heraty et al. (1994)

ⁱ Additional information from Duncan (1939)

dinoidea, Cephoidea and Anaxyelidae, is thus apparently secondary. This also goes for the occurrence of slender lateral metanotal processes (character 3, state 1) in the Tenthredinoidea s. s. and Cephoidea; putatively homologous structures occur only in *Micropterix calthella* (Lepidoptera) among the outgroup taxa.

The ultrastructure of the cenchri was studied by Schrott (1986), who stated them to be membranous lobes continuous with the haemolymph cavity of the metathorax and with sclerotised hooks on their dorsal surface. Failing to observe any cellular derivatives inside the cenchri, she concluded that their function is solely to keep

Fig. 16 Cladogram of the basal hymenopteran lineages (after Vilhelmsen 1999), with hypotheses of character evolution mapped onto it. * Equally parsimonious alternative optimisation(s) possible, □ character subsequently experiencing reversal, () character changes within clade. Characters 1, 2, 6, 10, 11, 12, 17, 25, 29 and 36 were optimised using delayed transformation; characters 14, 16, 21, 27, 33, 34 and 42 were optimised using accelerated transformation



the fore wings in place when at rest by attaching to the specialised 'area aspera', patches of cuticular spines in the anal areas of the fore wings. Rasnitsyn (1988) stated that the presence of cenchri is a hymenopteran autapomorphy. Putatively homologous structures occur outside the Hymenoptera (see Vilhelmsen 1997), but none the less, the configuration of the cenchri within the order seems to be unique. Königsmann (1977) argued for the monophyly of all 'symphytan' superfamilies except Cephioidea (his 'Symphyta s. s. '), based on the presence of cenchri. This has been effectively refuted by recent cladistic treatments of the basal hymenopteran lineages (Vilhelmsen 1997, 1999; Ronquist et al. 1999).

The full complement of muscles between the metanotum and the hind leg in the ground plan of the Hymenoptera comprises the metanoto-trochantinal (17), anterior (18) and posterior metanoto-metacoxal (19) and metanoto-metatrochanteral (20) muscles. Only in *X. julii* (Xyelidae)

and *Sirex juvencus* (Siricidae) were all these muscles observed. *C. arvensis* (Pamphiliidae) and *Syntexis libocedrii* (Anaxyelidae) do not have the anterior metanoto-metacoxal muscles (18), and the posterior metanoto-metacoxal muscles (19) are absent from *Cephus nigrinus* (Cephidae). This is largely in accordance with Daly (1963), who stated that the metanoto-trochantinal muscles (17; his $t_3\text{-cx}_{3a}$; these are evidently the metanoto-trochantinal muscles, inserting on the cup-shaped trochantinal apodemes as can be observed in his Figs. 1–4) are absent from *Cephus clavatus*. Furthermore, he did not treat the posterior metanoto-metacoxal muscles (19).

Kristensen (1991) suggested that the absence of demarcated mera on the coxae and of notocoxal muscles (inner tergo-coxal muscles of Mickoleit 1966) inserting on these areas is an autapomorphy for the Hymenoptera. However, these muscles could be identical with the anterior metanoto-metacoxal muscles (18). This implies that

at least for the metathorax, the absence of notocoxal muscles can no longer be upheld as a hymenopteran autapomorphy, although the absence of mera probably is. Alternatively, the anterior metanoto-metacoxal muscles could be homologous with the tergo-coxal muscles t-cx5 of Matsuda (1970). This is corroborated by their origins anteriorly on the metanotum and their insertions anteriorly of the metasubalar-metacoxal muscles (22) on the coxae. The inner tergo-coxal muscles (t-cx7 of Matsuda 1970) arise posteriorly on the notum and insert posteriorly of the metasubalar-metacoxal muscles (Matsuda 1970). This corresponds to the topology of the posterior metanoto-metacoxal muscles (19) in Hymenoptera. However, the connection of these muscles to the metacoxae through long tendons makes it more likely that they are homologous with the outer tergo-coxal muscles (t-cx6 of Matsuda 1970), which have a similar configuration in *Priacma serrata* (Coleoptera; Baehr 1975, his muscle 71). If this interpretation is correct, the inner tergo-coxal muscles are indeed absent from the Hymenoptera, as stated by Kristensen (1991).

The metapostnotum is undivided in the hymenopteran ground plan. This is also the condition in several outgroup taxa: Psocodea (Badonnel 1934), *P. serrata* (Coleoptera; Baehr 1975), *Panorpa communis* and *Notiothauma reedi* (both Mecoptera; Hasken 1939; Mickoleit 1971), whereas others have the metapostnotum subdivided: *M. calthella* (Lepidoptera; Kristensen 1984), Neuroptera and Raphidioptera (Achtelig 1975). Laterally, the metapostnotum is fused with the metepimera in *Amphigerontia bifasciata* (Psocodea), *M. calthella*, *P. communis*, and *N. reedi*, like the mesopostnotum and the mesepimera in the Hymenoptera (Heraty et al. 1994), while the Neuropterida and *P. serrata* resemble the Hymenoptera in not having any contact between these two regions in the metathorax. The metapostnotum is in close contact with the anterior margin of T1 along the third phragma, a condition inferred to be an autapomorphy of the Hymenoptera by Königsmann (1976), but which is also observed in *P. serrata* (L. Vilhelmsen personal observations), several Neuropterida (Achtelig 1975) and Mecoptera (Hasken 1939; Mickoleit 1967, 1968, 1971); it is a rather vaguely defined condition at any rate. The mesolaterophragmal lobes are weakly developed in the hymenopteran ground plan. A condition resembling the ground plan state in Hymenoptera, as observed in Xyeloidea, Pamphilioidea and 'Siricoidea', with the anterolateral corners of T1 closely abutting the dorsal parts of the metepimera and with articular inflexions on the latter is only found in *Chrysopa perla* (Neuroptera). Other outgroup taxa have T1 fused with the metepimera in this area (*Raphidia* sp., Raphidioptera) or not in contact at all. The subdivision of T1 medially is definitely a ground plan feature of the Hymenoptera, but probably not an autapomorphy, as a partly or fully subdivided T1 is also found in *M. calthella*, *P. communis*, *Raphidia* sp. and *C. perla*.

2. The hind wing bases and the posterior thoracic spiracles

The hind wing tegulae are present in the ground plan of the Hymenoptera, being observed in Xyeloidea, Tenthredinoidea, Pamphilioidea, Cephoidea, Anaxyelidae and Siricidae; they are also present in *P. communis* (Mecoptera; Hasken 1939). The absence of hind wing tegulae (character 9, state 1) is a synapomorphy for Xiphydriidae + Orussidae + Apocrita. The occurrence of the mesolaterophragmo-metabasalar (3) and mesolaterophragmo-hind wing muscles (4) in Hymenoptera is difficult to interpret. The former pair is present in *P. serrata* (Coleoptera; 56 of Baehr 1975) and *Corydalus cornutus* (Megaloptera; 137 of Kelsey 1957), and the latter pair could not be homologised with certainty with any muscles reported in the literature for any outgroup taxa. Both pairs are present in *X. julii* (Xyelidae) and *C. arvensis* (Pamphiliidae). Most Tenthredinoidea have only one pair of muscles, the transverse metanoto-metapleural muscles (character 4, state 1). Given that *R. reducta* (Blasticotomidae) and *Gilpinia* sp. (Diprionidae) have a pair of mesolaterophragmo-metabasalar muscles (3) in addition to the transverse metanoto-metapleural muscles, it seems reasonable to homologise the latter with the mesolaterophragmo-hind wing base muscles (4). The shifts in attachment sites of these muscles can be interpreted as an autapomorphy of the Tenthredinoidea. In *Megalodontes cephalotes* (Megalodontesidae), the muscles arising from the anterolateral corners of the metanotum and inserting on the hind wing bases must be homologous with the mesolaterophragmo-hind wing base muscles (4). *C. nigrinus* (Cephidae), *Syntexis libocedrii* (Anaxyelidae), *S. juvenis* (Siricidae) and *Xiphydria camelus* (Xiphydriidae) have only one pair of muscles arising from the mesolaterophragmal lobes. In the former taxon, they insert on the external part of the metabasales and, in the other taxa, they insert on the ventral margin of the metapleural arms. Similar points of insertion are also observed for a pair of putatively homologous muscles arising from the anterolateral corners of the metanotum in *Orussus* sp. (Orussidae). Given the considerable variability in topology and consequent difficulty in establishing homologies (see Table 2), it has been decided not to code the occurrence of these muscles as characters.

In the hymenopteran ground plan, the apodemal parts of the metathoracic basales are cup-shaped sclerites separate from the upper parts of the metepisterna. Among the outgroup taxa, only *P. serrata* (Coleoptera) has the same condition; outside the Endopterygota, free apodemal parts of the metathoracic basales are observed in *Dissosteira carolina* (Orthoptera; Snodgrass 1929). All other endopterygotans examined, as well as Psocodea (Badonnel 1934), have them fused with the upper parts of the metepisterna, so the condition observed in *P. serrata* and Hymenoptera is probably derived. Indeed, it has been suggested that the basales are derived from the anepisterna (Matsuda 1970). Given the current hypotheses about the phylogeny of the holometabolans

orders (Kristensen 1991; Whiting et al. 1997), it is most parsimonious to assume that the separation of the apodemal parts of the metathoracic basalares from the metepisterna occurred independently in Hymenoptera and Coleoptera.

The metathoracic basalares have the following muscles attached to them in the hymenopteran ground plan: the mesolaterophragmo-metabasalar (3; see above), the mesofurco-metabasalar (29), the metanoto-metabasalar (11), the metabasalar-metapleural (13) and the metabasalar-metacoxal muscles (21). These muscles are also present in most of the outgroup taxa. The metanoto-metabasalar muscles (11) were not found by Mickoleit (1969; his muscle 2) in any of the hymenopteran taxa he examined, but he covered only a small sample of the order. In addition, a pair of metabasalar-trochanteral muscles are widespread among other Endopterygota [*P. serrata* (Coleoptera), 74 of Baehr 1975; *C. cornutus* (Megaloptera), 166 of Kelsey 1957; *Myrmeleon europaea* (Neuroptera), IIIpm₃ of Korn 1943; *Limnephilus marmoratus* (Trichoptera), 8.03 of Tindall 1965; *P. communis* (Mecoptera), IIIpm₃ of Hasken 1939] and also observed in some Thysanoptera (*Thrips physapus*, M. depr. troch. pl. of Mickoleit 1961); they are absent from *D. carolina* (Orthoptera, Snodgrass 1929). Metabasalar-trochanteral muscles (21a) were only observed in *R. reducta* (Blasticotomidae) and *A. gracilicornis* (Argidae) among the hymenopteran taxa examined here; in addition, they were reported from *P. dorsalis* (Pergidae) by Tait (1962; his 17a). However, in the two latter taxa, the metabasalar-metacoxal muscles (21) are absent. It seems reasonable to assume that the muscles extending between the apodemal parts of the metabasalares and the trochanteral apodemes in *A. gracilicornis* and *P. dorsalis* are the metabasalar-metacoxal muscles (21) with shifted points of attachment; this cannot be the case in *R. reducta*, as metabasalar-metacoxal muscles (21) are present in this taxon. If the absence of metabasalar-trochanteral muscles (21a) is a hymenopteran autapomorphy, their occurrence in *R. reducta* must be explained as secondarily having arisen by subdivision of the metabasalar-metacoxal muscles (21).

The small sclerites accommodating the origins of the occlusor muscles (1) of the posterior thoracic spiracles might be interpreted as serial homologues of the prepecti on the anterior margins of the mesopleura, from which the occlusor muscles (1) of the anterior thoracic spiracles arise (Gibson 1985, 1993). However, no observations in the outgroup taxa could be made to support this. Even more dubious would be to homologise the anapleural sclerites with the postspiracular sclerites in the mesothorax. The anapleural sclerites are only observed in *M. ferruginea* (Xyelidae), Blasticotomidae and some Tenthredinidae (character 21, state 0). The occurrence of these as independent sclerites in *M. ferruginea* is evidence against them being homologous with the postspiracular sclerites, as the corresponding regions in the mesothorax, the anepisterna, are not detached from the mesopleura in Xyelidae (Gibson 1993); the anepisterna of the metatho-

rax appear to be reduced to narrow strips on the ventral parts of the metapleural arms in all Hymenoptera examined. The anapleural sclerites are probably anatomically part of the metabasalares, considering that they are continuous with the apodemal parts of the basalares in *M. ferruginea* and receive the insertions of the mesofurco-metabasalar muscles (29) in *Nematus* sp. (Tenthredinidae).

3. The metapleura and the metathoracic trochantins

The metapleuro-S2 muscles (33) are observed only in the Xyelidae among the Hymenoptera examined. Among the outgroup taxa, putative homologues are reported from *P. communis* (Mecoptera; Iaism₂ of Hasken 1939) and *Raphidia flavipes* (Raphidioptera; 14 of Achtelig 1975). More doubtful homologues are present in *M. calthella* (Lepidoptera; 13 of Kristensen 1984), where they arise from the 'secondary metafurcal arms' lying in the integument; however, the latter structures are inseparable from the posterior margins of the metepimera (N.P. Kristensen, personal communication). These muscles might be of more widespread occurrence than this, as most of the studies consulted for outgroup information do not treat the musculature connecting the metathorax with the anterior abdominal segments. Therefore, it is a putative synapomorphy for the non-xyelid Hymenoptera to have the metapleuro-S2 muscles (33) absent (character 28, state 1).

The homology of the anapleural clefts is established by the occurrence of the intrinsic metapleural muscles (14), which in *X. julii* (Xyelidae) arise ventrally of the clefts and insert on the ventral margins of the metapleural arms. They are serially homologous with the anepisternal-preepisternal muscles (Gibson 1993; his muscle 145) spanning the anapleural clefts in the mesothorax. *C. nigrinus* (Cephidae), *S. libocedrii* (Anaxyelidae), and *Orussus* sp. (Orussidae) have intrinsic metapleural muscles (14) inserting on the ventral margins of the metapleural arms. They were not observed in the Tenthredinoidea or in *S. juvenicus* (Siricidae). In *C. arvensis* (Pamphiliidae), the putative homologues insert on the apodemal parts of the metabasalares and, in *X. camelus* (Xiphidriidae), they lie adjacent to the metabasalar-metapleural muscles (13) as slender bundles laterally. Due to the difficulties in identifying and homologising the intrinsic metapleural muscles (14) correctly in the different taxa, their occurrence has not been scored as a character.

According to Shcherbakov (1980), the paracoxal notches are homologous with the anapleural clefts in both the meso- and metathorax of Hymenoptera, and the anapleural clefts, as understood in the present paper, he termed the postspiracular incisures. Gibson (1993) refuted this hypothesis for the mesothorax, basing his interpretation on the topology of the anepisternal-preepisternal muscles, and the same case is argued here for the metathorax (see above). The paracoxal notches (character

32, state 0) were observed only in the Xyeloidea and the Pamphiliidae among the Hymenoptera, and not in any of the outgroup taxa. This makes it most parsimonious to assume that they have evolved independently in these two families.

The homology of the paracoxal sulci and ridges can be established by comparison with the mesothorax. In *X. julii* (Xyelidae), the median mesonoto-mesopleural and the mesobasalar-mesopleural muscles arise anteriorly of the paracoxal sulci (Gibson 1993; his muscles 128/129 and 154). The serial homologues in the metathorax, the median metanoto-metapleural (9) and metabasalar-metapleural muscles (13), also arise side by side anteriorly of the paracoxal sulci in most taxa, corroborating the homology. Serial homologues of the pseudosternal sulci in the mesothorax, which separate the attachments of the median mesonoto-mesopleural muscles medially from the mesobasalar-mesopleural muscles laterally on the episternum (Gibson 1993), do not occur in the metathorax. Having straight or slightly anteriorly curved paracoxal sulci and ridges (character 33, state 0) seems to be the ground plan state in Hymenoptera, occurring in Xyeloidea and all Tenthredinoidea except Blasticotomidae, as well as in the outgroup taxa where paracoxal sulci could be identified. The condition in Blasticotomidae is difficult to interpret. According to Shcherbakov (1981), two sulci extend laterally on the metepisterna in this family, an anterior pair close to the anterior margin and a posterior pair bending posteriorly to terminate in the metepisterna some distance from the posterior margins. He homologises the latter with the paracoxal sulci and I concur with his interpretation. This makes the ground plan configuration of the paracoxal sulcus in the Tenthredinoidea difficult to interpret. Either it is as observed in the Blasticotomidae, making posteriorly curved paracoxal sulci (character 33, state 1; reversed in Siricidae) a putative synapomorphy for the non-xyelid Hymenoptera (Fig. 16), but being reversed in the Tenthredinoidea *s.s.*, or the condition in Blasticotomidae is a parallelism with the condition seen in Pamphilioidea, Cephioidea, Anaxyelidae and Xiphydriidae. It could be an autapomorphy of the Hymenoptera to have the paracoxal sulci terminating in the posterior margins of the metepisterna close to the lateral metacoxal articulations (character 34, state 0). Outside the Hymenoptera, the paracoxal sulci terminate in, or close to, the anapleural clefts (*P. serrata*, Coleoptera; Baehr 1975; Neuropterida) or in the metapleural sulci a considerable distance from the lateral metacoxal articulations (*Bittacus pilicornis*; Mecoptera, Mickoleit 1968); only in *Merope tuber* and *N. reedi* (Mecoptera; Mickoleit 1967, 1971) do they terminate close to the lateral metacoxal articulations, but this is secondary according to Shcherbakov (1980). The paracoxal sulci terminating close to the anterior margin of the metepisterna (character 34, state 1) is a synapomorphy of the Tenthredinoidea *s.s.*

In the outgroup taxa, the trochantins of the metathorax connect at one end with the posterior margins of the metepisterna through narrow strips of sclerotised cuticle

and at the other end with the anterior margins of the metacoxae (character 35, state 0); only in *N. reedi* (Mecoptera; Mickoleit 1971) is the former connection absent. In the Xyeloidea, Pamphiliidae, Cephioidea, Anaxyelidae and Siricidae, the trochantins are represented by cup-shaped apodemes connected neither with the metepisterna nor with the metacoxae, being invaginated from the membranous areas between them (state 1). This condition is an hymenopteran autapomorphy. The loss of the trochantinal apodemes (state 2) and the metanoto-trochantinal muscles (17) has occurred three times independently within the Hymenoptera: in the Tenthredinoidea, in the Megalodontesidae and in the common ancestor of Xiphydriidae + Orussidae + Apocrita.

4. The metafurca and the ventral abdominal base

The position of the metafurca anteriorly on the discrimen is unique to the Hymenoptera. In all the outgroup taxa the metafurcal arms arise posteriorly on the discriminal lamella immediately dorsally of the metafurcal pit, as they also do in the mesothorax of the Hymenoptera. In the Hymenoptera, the base of the metafurca is displaced anteriorly and the metafurcal arms diverge at the anterior ends of the discrimen. Well-developed anterior metafurcal arms might be an additional hymenopteran autapomorphy. They could be interpreted as serial homologues of the anterior mesofurcal arms, also a hymenopteran autapomorphy (Heraty et al. 1994). However, elongate anterior metafurcal arms are also present in *A. bifasciata* (Psocodea) and *P. serrata* (Coleoptera; Baehr 1975).

The S2-metacoxal muscles (34), which were observed in all Hymenoptera where the musculature was examined except *P. frogatti* (Pergidae), have not been reported for any other taxa in the literature surveyed, not even in those studies where the musculature of the anterior abdominal segments is treated in detail (Achtelig 1975; Kristensen 1984). The presence of these muscles is thus a probable further hymenopteran autapomorphy.

The absence of the first abdominal sternite (S1) is not unique to the Hymenoptera. This sclerite has a scattered occurrence within the Holometabola, being present in *M. calthella* (Lepidoptera; Kristensen 1984), *Tipula vernalis* (Diptera; Mickoleit 1962) and Neuropterida (Achtelig 1975) but very reduced in *P. serrata* (Coleoptera; L. Vilhelmsen personal observation) and *N. reedi* (Mickoleit 1971), and absent from Trichoptera (Kristensen 1984), *P. communis* (Mecoptera) and *M. tuber* (Mecoptera; Mickoleit 1967). Outside the Holometabola, it has been reported from Thysanoptera (Mickoleit 1961), Psocodea (Badonnel 1934) and *D. carolina* (Orthoptera; Snodgrass 1929). Even in the cases where S1 is present, it is not connected to the metathorax by any muscles, the metafurca-S2 muscles (35) always extending across S1 to insert on the anterior margin of S2.

II. Variation among the Tenthredinoidea

The Tenthredinoidea have a highly autapomorphic metathorax, possessing derived states in several characters. Although there is considerable homoplasy, with many states occurring here and there in other hymenopteran taxa, the support for the monophyly of the Tenthredinoidea provided by this character system is very convincing.

A suite of modifications is associated with the connection between the second phragma and the anterior margin of the metanotum in the Tenthredinoidea. There is a region of unsclerotised cuticle separating these two regions (character 2, state 1), and transverse metanotal muscles (4) are present (character 4, state 1; see above). Furthermore, in the Tenthredinoidea *s.s.*, the lateral metanotal processes are slender and project towards the second phragma (character 3, state 1; reversed in the Cimbicidae). The functional significance of these modifications might be to facilitate bending the abdomen anteriorly during oviposition (Vilhelmsen 1999).

The subdivision of the second phragmo-third phragmal muscles (character 6, state 1) is a further tenthredinoid autapomorphy. This condition was illustrated by Daly (1963) for *Neodiprion fulviceps* (Diprionidae; 2ph-3ph_b in his Fig. 5). Of more doubtful significance is the presence of well-developed metalaterophragmal lobes (character 12, state 0). This condition is also present in the Megalodontesidae, Siricidae and Xiphydriidae. Furthermore, Cimbicidae have no conspicuous metalaterophragmal lobes (see below). The metanoto-metalaterophragmal muscles (6) are absent (character 7, state 1) from most taxa for which the musculature could be examined, but present in *R. reducta* (Blasticotomidae), *Tenthredo* sp. (Tenthredinidae) and *Corynis* sp. (Cimbicidae). This distribution indicates that the muscles probably were present in the ground plan of the Tenthredinoidea. It is most parsimonious, given the topology in Fig. 16, to assume that they were lost in the common ancestor of the Tenthredinoidea *s.s.*, but have secondarily reappeared in *Tenthredo* sp. and *Corynis* sp.

The posterior thoracic spiracles are closely associated with the posterior margins of the mesepimera in all Tenthredinoidea, being either accommodated in distinct concavities of the mesepimera (character 17, state 1) or covered laterally by the mesepimera (character 17, state 2). Which of these conditions represents the ground plan state of the superfamily is difficult to decide as both occur in several of the families. Intuitively, one might expect state 2 to be derived from state 1, as illustrated in Fig. 16. However, it is equally parsimonious for state 2 to be the ground plan state for the Tenthredinoidea. The oclucosor muscles (1) of the posterior thoracic spiracles arise from the posterior margins of the mesepimera (character 18, state 1) in all the tenthredinoid taxa that could be examined for this character. This was also observed by Tonapi (1958), and is another autapomorphy of the Tenthredinoidea. The articulation between the posterior parts of the metepimera and the entire lateral mar-

gins of T1, with the former overlapping the latter and covering the ventral halves of the first abdominal spiracles (character 25, state 2), is a putative autapomorphy of the Blasticotomidae.

The presence of elongate lateral metafurcal arms (character 41, state 1) is an autapomorphy of the Tenthredinoidea. Short anterior metafurcal arms (character 40, state 1) is a synapomorphy of the Tenthredinoidea *s.s.* Ronquist et al. (1999) considered the anterior metafurcal arms in the Blasticotomidae to be short as well; I observed them to be almost the length of the lateral metafurcal arms and consequently have assigned state 0 to this taxon. I do not concur with their assignment of a separate state ('very short'; Ronquist et al. 1999) for this character in Pergidae and Argidae either. These differences might stem from difficulties in defining discrete character states or from Ronquist et al. (1999) treating the meso- and metafurcae together as one character. However, also in contrast with the scorings of Ronquist et al. (1999) and Heraty et al. (1994), I consider the anterior mesofurcal arms in the Blasticotomidae to be distinctly longer than in other Tenthredinoidea, making the modifications in both meso- and metafurcae occur at the same node. It seems that these changes are strongly correlated, perhaps being caused by the same genetic event in both meso- and metathorax. The presence of elongate lateral metafurcal arms might be correlated with the presence of distinct metapleural apodemes accommodating the origins of the anterior metapleuro-metafurcal muscles (23; character 29, state 1; occurring in all Tenthredinoidea except *L. interrupta*), which insert on the lateral metafurcal arms.

Rasnitsyn (1988) proposed a sister-group relationship between two major clades within the Tenthredinoidea *s.s.*: the Argidae + Pergidae (his Pterygophoridae) and the Tenthredinidae (including the Diprionidae) + Cimbicidae. This hypothesis was corroborated by the analyses of Vilhelmsen (1997) and Ronquist et al. (1999), but many of the characters in these were scored from Rasnitsyn (1988). In contrast, Vilhelmsen (1999; Fig. 16) only partly support Rasnitsyn's hypothesis; the Tenthredinidae did not come out as a monophyletic group, not even if the Diprionidae were included, and the Cimbicidae consistently came out as the sister group of the Argida + Pergidae. A clade comprising *Tenthredo* sp. + *D. niger* + *Athalia* sp. (all Tenthredinidae) is supported by the posterior thoracic spiracles being covered laterally by the mesepisterna (character 17, state 2; but see above). *Nematus* sp. (Tenthredinidae) + the remaining Tenthredinoidea *s. s.* are supported by the absence of the metasubalares (character 24, state 1). None of these characters are very convincing, being paralleled or reversed in other taxa (Fig. 16).

The occurrence of transversely extended cenchri (character 5, state 1) is a putative synapomorphy of the Diprionidae + Cimbicidae + Argidae + Pergidae. The distinct shape of the cenchri in these taxa was realised by Schrott (1986), and Rasnitsyn (1969) correctly inferred the condition to be derived. However, both failed to ap-

preciate the specialised cenchral structure as revealed in sections. It is evident that the posterior inflected parts of the cenchri are reduced in the derived state, so that the sclerotised hooks cover almost the entire cenchral surface. This is different from the condition in *M. cephalotes* (Megalodontesidae), which also have transversely extended cenchri, but with the posterior parts still inflected and devoid of hooks (character 5, state 2). The absence of anterior metanoto-metacoxal muscles (18; character 36, state 1) and metanoto-metatrochanteral muscles (20; character 38, state 1) might be additional synapomorphies for the Diprionidae + Cimbicidae + Argidae + Pergidae. However, the latter muscles are present in *P. froggatti* (Pergidae), and both muscles need to be surveyed for a larger sample of taxa, especially from the Tenthredinidae. The absence of the anapleural sclerites (character 21, state 1) does not appear to provide strong support for the Diprionidae + Cimbicidae + Argidae + Pergidae either.

Substantial evidence in support of the Cimbicidae + Argidae + Pergidae was revealed by the present study. The metanoto-metabasalar muscles (11) are absent (character 10, state 1) from these taxa. T1 is continuous medially [character 15, state 1; reversed in *Arge* spp. (Argidae) and *L. interrupta* (Pergidae), however] and fused with the metepimera (character 26, state 1), which was noted by Goulet (1993) and is of course paralleled in the Apocrita (Snodgrass 1910). Perhaps correlated with this character is the absence of the T1-S2/metapleural muscles (16; character 16, state 1), which was observed in *P. condei* (Pergidae), however. The absence of the posterior metapleuro-metafurcal muscles (24) and their corresponding apodemes (character 30, state 1) is an additional synapomorphy of these taxa. The absence of metabasalar-metacoxal muscles (21; character 39, state 1) as a synapomorphy at this level is somewhat compromised by the presence of these muscles in *A. gracilicornis* (Argidae). The occurrence of the mesospina and the associated metafurco-mesospinal muscles (28) is somewhat confusing. Heraty et al. (1994) stated that these muscles are present in all Tenthredinoidea (their character 8), whereas they are apparently absent from *Sterictiphora* sp. (Argidae; Weber 1927, his *Schizocerus*). I was unable to observe them and consequently have scored them as absent (character 43, state 1) in *Athalia* sp. (Tenthredinidae), Cimbicidae, Argidae and Pergidae. In *Cimbex* sp. and *Zaraea fasciata* (both Cimbicidae), a mesospina was observed (character 42, state 0; this might be a reversal) without the occurrence of the metafurco-mesospinal muscles (28), and in some of the outgroup taxa (for example *P. serrata*; Coleoptera, Baehr 1975), the muscles are present but the mesospina is absent. This cautions against inferring the presence/absence of the metafurco-mesospinal muscles (28) from the presence/absence of the mesospina, as these are apparently not strictly correlated.

Putative autapomorphies for the Cimbicidae are the reduction of the lateral metanotal processes (character 3, state 0), the second phragmo-third phragmal muscles be-

ing undivided (5; character 6, state 0), the absence of the metalaterophragmal lobes (character 12, state 1) and the metalaterophragmo-metafurcal muscles (7; character 13, state 1). It seems reasonable to assume that the absence of the two latter features are strongly correlated, as these muscles arise from the metalaterophragmal lobes in the taxa possessing them. Within the Cimbicidae, a synapomorphy for *Cimbex* sp. and *Z. fasciata* is the presence of large apodemes on the lateral parts of the metanotum accommodating the sites of origin of the lateral metanoto-metapleural muscles (10; character 8, state 1).

The insertion point on the anterior margin of the metanotum for the mesoscutello-metanotal muscle (2; character 1, state 2) is a putative synapomorphy of the Argidae and Pergidae. The presence of small projections from the anterior margin of the metanotum lateral to the insertion point of the mesoscutello-metanotal muscle (2; character 1, state 1) in *Z. fasciata*, and in *Cimbex* sp. (both Cimbicidae) of a small projection in the same position receiving the insertions of the same muscle (character 1, state 2), probably evolved independently, as the configuration is different. Argidae, *L. interrupta* (Pergidae) and Euryinae gen. sp. (Pergidae) have the metapleural arms covered laterally by the anterodorsal parts of the metepimera (character 19, state 1). It is unclear whether this is parallelism, a trait of the common ancestor of the two families undergoing secondary reversal, or perhaps indicates paraphyly of the Pergidae. However, the mesofurco-metabasalar muscles (29) insert on the anterior margins of the metepisterna (character 23, state 1) in all the members of the Pergidae examined except *P. froggatti*, from which the muscles are absent, supporting the monophyly of the family. This might also be the case with the presence of posterior metanoto-metacoxal muscles (19; character 37, state 0), observed in *P. condei*, *P. froggatti* and *Syzygonia cyanocephala*, if this is a reversal and the absence of these muscles in other Tenthredinoidea s.s. not the result of parallel loss.

III. Variation among the Pamphilioidea, Cephoidea and 'Siricoidea'

The Pamphiliidae, among the Hymenoptera, retains the largest number of plesiomorphic traits in the metathorax apart from the Xyelidae. *M. cephalotes* (Megalodontesidae) differs from the Pamphiliidae in several characters: cenchri transversely extended, but with inflected posterior parts devoid of hooks (character 5, state 2), absence of metanoto-metabasalar muscles (11; character 10, state 1), metalaterophragmal lobes well developed (character 12, state 0), T1 continuous medially (character 15, state 1), metapleural apodemes present (character 29, state 1), absence of paracoxal notches (character 32, state 1), metathoracic trochantins absent (character 35, state 2), metanoto-metatrochanteral (20; character 38, state 1) and metabasalar-metacoxal (21; character 39, state 1) muscles absent. In the case of characters 5, 10, 15, 35, 38 and 39, the condition in *M. cephalotes* is probably derived. This

is more difficult to decide for the rest, considering the variation outside the Pamphilioidea.

Whitfield et al. (1989) stated that in the Pamphiliidae “the metapostnotum is a transverse strip *separate from T1* and the metanotum. It is *continuous medially anterior to the third phragma* but *divided into two lateral wedge-shaped sclerites posterior to the phragma*” (my italics). According to this description, this family has the metapostnotum extending posteriorly of the third phragma, which would be unique within the Hymenoptera, where the boundary between the metapostnotum and T1 is indicated by the third phragma. Evidently, Whitfield et al. (1989) misidentified the area posteriorly of the third phragma, which is actually T1. This is confirmed by the position of the first abdominal spiracles in the lateral areas of the “two lateral wedge-shaped sclerites”. Whitfield et al. (1989) were probably misled by the longitudinal subdivision of the second abdominal tergite, an autapomorphy of the Pamphiliidae (Königsmann 1977), which they confused with T1.

The subdivision of the metapostnotum (character 14, state 1) is a putative synapomorphy for the Cephoidea + ‘Siricoidea’ + Orussoidea + Apocrita, provided that the condition in the two latter taxa (state 0) is interpreted as a reversal. Königsmann (1977) proposed a sister-group relationship between the Cephoidea and the Apocrita, inferring that the constriction between the first and second abdominal segments in the former taxon represented an incipient state in the formation of the articulation between the meso- and metasoma in the latter. The close association in Cephoidea between the metepimera and T1 could be interpreted as incipient in the fusion between them in Apocrita. Considering the overwhelming amount of evidence against the sister-group relationship between these two taxa, both from this and other character systems (Vilhelmsen 1997, 1999; Ronquist et al. 1999), such a transformation seems highly improbable. The articulation between T1 and the metepimera in Cephoidea (character 25, state 1) is more likely an autapomorphy of the superfamily. Additional autapomorphies of the superfamily are the absence of the cenchri (character 5, state 3) and the presence of strongly posteriorly curved paracoxal sulci (character 33, state 2). The constriction between the first and second abdominal segments in Cephoidea is only apparent in the dorsoventral dimension, whereas in Apocrita it is also pronounced laterally (Ronquist et al. 1999). Furthermore, there are distinct modifications around the articulation between the two segments in Apocrita (Duncan 1939; Ronquist and Nordlander 1989) which have no counterpart in the Cephoidea. I therefore consider the resemblance in this region between Cephoidea and Apocrita to be entirely superficial and independently derived.

The absence of the metanoto-metabasalar (11; character 10, state 1) and metabasalar-metacoxal muscles (21; character 39, state 1) are possible synapomorphies for the Siricidae + Xiphydriidae + Orussidae + Apocrita; however, these muscles have been lost repeatedly among the basal hymenopteran lineages. The monophyly of the

Siricidae is supported by the absence of the anapleural clefts (character 22, state 1), the paracoxal sulci terminating in the middle of the metepisterna (character 34, state 2) and the presence of an elongate mesospina projecting posteriorly between the anterior metafurcal arms (character 42, state 1). Putative autapomorphies of the Xiphydriidae are the insertion of the mesoscutello-metanotal muscles (2) dorsally on the second phragma (character 1, state 3), the presence of a large membranous pouch ventrally of the two halves of T1 and the presence of very large T1-metafurcal muscles (8). The modifications of T1 and the associated musculature are probably correlated functionally, perhaps increasing the manoeuvrability of the abdomen. This would be a different mechanism from that observed in Apocrita (see below), and certainly independently derived. Additional xiphydriid genera need to be examined to establish whether these features can be ascribed to the ground plan of the family.

IV. The formation of the propodeum and the ground plan of the Apocrita

1. *The fusion of the metapleura with T1, and the association between the meso- and the metathorax in the Apocrita*

The Orussoidea closely resemble the Apocrita in several characters of the metathorax, which is to be expected as the sister-group relationship between these two taxa is the best supported node in recent cladistic treatments of the higher level phylogeny of the order (Vilhelmsen 1997, 1999; Ronquist et al. 1999). The main difference between Orussidae and Apocrita in the region studied here is the integration of T1 in the metathorax as the propodeum. This raises the question of whether it is possible to infer a transformation series from the conditions observed in ‘Siricoidea’ through Orussidae to the Apocrita and, if so, how to establish homologies between the areas involved.

Ronquist and Nordlander (1989) attempted this in their study of the skeletal morphology of *Ibalia rufipes* (Ibaliidae). They suggested that the lines of fusion between the metepimera and T1 are located just anteriorly of the propodeal spiracle (their carina 118). According to their interpretation, the posterior parts of the metepimera (their area 98) are of considerable size in *I. rufipes* and the lines of fusion not confluent with the metapleural sulci. An alternative hypothesis was suggested by Shcherbakov (1981). Contrary to Ronquist and Nordlander (1989), he also investigated *Orussus abietinus* (Orussidae), observing the reduction of the posterior parts of the metepimera in this taxon. This condition is also observed in Xiphydriidae and Anaxyelidae (character 25, state 3). Scherbakov (1981) inferred that the fusion of T1 with the metapleura took place along the metapleural sulci, making the lines of fusion indistinguishable from them. Bucher (1948), examining *Mono-*

dontomerus dentipes (Chalcidoidea), placed the lines of fusion in the same positions, but considered the epimera to be incorporated in the propodeum. In *I. rufipes*, the anteroventral corners of 'area(s) 98' actually project anterolaterally (L. Vilhelmsen personal observation), separating the dorsal 'area(s) 97' (Ronquist and Nordlander 1989) from the rest of the metapleura. 'Area(s) 97' has the pleural wing processes dorsally (L. Vilhelmsen personal observation), making them homologous with the metapleural arms. This closely resembles the condition in *O. abietinus*, where the metapleural arms are separated from the rest of the metapleura by the anterolateral corners of T1. In this interpretation, 'area(s) 98' of *I. rufipes* becomes homologous with the lateral parts of T1, which are secondarily set off from the median parts of T1 by carinae and fused with the metapleural arms anteriorly. I thus concur with the interpretation of Shcherbakov (1981). This might be further corroborated by studies of the musculature in the Apocrita. Mapping the topology of muscles attached dorsally [lateral metanoto-metapleural (10), metapleuro-hind wing (12) and metapleuro-metasubalar muscles (15)], on [anterior metapleuro-metafurcal muscles (23)] or ventrally of [lateral metapleuro-metacoxal muscles (26)] the metapleural sulci could be used to establish the course of the latter, even in cases where the sulci have been lost (Snodgrass 1910). The propodeal spiracles are probably not reliable as anatomic landmarks, as their positions on T1 seem to vary (Shcherbakov 1981). The fusion of the metapleural arms with the anterolateral parts of T1 (character 20, state 2) is a putative autapomorphy of the Apocrita; the condition in Orussidae, where the metapleural arms abut the anterolateral parts of T1 (character 20, state 1), might be interpreted as incipient to the state possessed by the Apocrita.

Another tendency of Apocrita, which can be traced back to the Orussidae and Xiphydriidae, is towards close association between the meso- and metathorax. This is exemplified by the integration of the posterior thoracic spiracles into the mesopleura (character 17, states 1 and 2, in Xiphydriidae and Orussidae, respectively). The condition in *Schlettererius cincipes* (Stephanidae) closely resembles that of Orussidae. The posterior thoracic spiracles could not be observed in *Megalyra fasciipennis* (Megalyridae) and *Aulacus striatus* (Aulacidae). In *I. rufipes* (Ibaliidae; Ronquist and Nordlander 1989), they are situated on processes (their structure 89) projecting from the mesepimera and, in *Orthogonalys pulchella* (Trigonidae) and *Vespula pensylvanica* (Vespidae; Duncan 1939), they are covered by sclerites attached to the mesepimera. In *V. pensylvanica*, the occlusor muscles (1) arise from the mesepimera (Duncan 1939). Tonapi (1958) stated that the posterior thoracic spiracles are concealed by the posterior margins of the mesepimera in many taxa, which apparently also accommodates the origins of the occlusor muscles (1). Not including *I. rufipes*, he reported the absence of the spiracles from Cynipoidea and Chalcidoidea. A more extensive survey of the Apocrita is needed to clarify the configuration of the mes-

epimera around the posterior thoracic spiracles, as Tonapi (1958) focused primarily on the anatomy of the spiracles themselves. Another feature that can be correlated with the close association between the meso- and metathorax is the presence of metepisternal depressions accommodating the posterior parts of the mesocoxae (character 31, state 1) in the Orussidae and Apocrita.

2. *The metascutellum, paracoxal sulci, metafurca and mesospina in the Orussidae and the Apocrita*

The metascutellum and the scutellar arms are not as well demarcated externally in Orussidae as in other 'Symphyta'. In most Hymenoptera, as well as in other winged insects, the meso- and metascutellum accommodate circulatory organs connected to the posterior wing veins via the hollow scutellar arms, facilitating circulation of haemolymph through the wings (Krenn and Pass 1994, 1994/1995). These wing circulatory organs are connected to the dorsal vessel in many insect orders, including representatives of all 'symphytan' families (Krenn and Pass 1994/1995; original observations) except Orussidae. This condition can be regarded as plesiomorphic, the more so because the circulatory organs are probably derived from specialised regions of the dorsal vessel (Krenn and Pass 1994). In the metathorax of Orussidae, the dorsal vessel does not extend into the metascutellum, and the scutellar arms are solid. The circulatory organ is thus apparently non-functional, a condition that can be correlated with the reduced hind wing venation in this family. It would be interesting to know the condition in more apocritan taxa, especially the Stephanidae, which have no externally visible metascutellum (original observation).

The paracoxal sulci and ridges in Orussidae are difficult to interpret, subdivided into anterior branches projecting laterally and posterior branches terminating in the metepisterna. The metabasalar-metapleural muscles (13) attach anteriorly of the anterior branches, indicating that these are the paracoxal ridges proper. This is in accordance with Shcherbakov (1981), who homologised the posterior branches with the paracoxal notches. However, the posterior branches have a configuration resembling the paracoxal ridges in Xiphydriidae, although they do not reach the posterior margins of the metepisterna. Using the criteria of muscle attachment, I consider the anterior branches of the paracoxal sulci/ridges in Orussidae to be the homologues of the structures observed in other 'Symphyta', and the posterior branches to be secondary formations; they have been scored accordingly (character 33, state 0; character 34, state 1). Within the Apocrita, putative homologues of the paracoxal sulci and ridges are observed in *M. dentipes* (Chalcidoidea; inflection of the metapectus of Bucher 1948), *I. rufipes* (Ibaliidae; intercoxal lamella of Ronquist and Nordlander 1989) and *V. pensylvanica* (Vespidae; transverse plate of the metasternal apophysis of Duncan 1939) as well as the taxa examined in the present study. In all cases, these struc-

Table 4 Muscle homologies between 'Symphyta' and Apocrita. – absent, ? unknown. When the muscles are absent from the Apocrita, the abbreviations used for other Hymenoptera are shown in parentheses

Present study	Apocrita in general ^{a-c}	<i>Vespula pennsylvanica</i> (Duncan 1939)	<i>Apis mellifera</i> (Snodgrass 1942)	<i>Stenobracon deesae</i> (Alam 1951, 1953)
1	?	3osp	–	?
2	114 ^c	IIIs1	70	70
3	?	–?	–?	–?
4	?	–?	–?	–?
5	2ph–3ph ^a	IIIId1	96	–
6	t3–3ph ^a	–	–	–
7	pl3–fu3 ^b	–	–	–
8	?	–	–	–
9	t3–pl3 ^a	IIIpm4	97–98–99?	84
10	pl3–t3 ^b	IIIpm4	97–98–99?	85, 86
11	?	–	–	–
12a+b	pl3–3ax3 ^b	IIIpm2a+b	100	88, 89
13	pl3–ba3 ^{a,b}	IIIpm1	101	87
14	?	–	–	–
15	pl3–sa3 ^{a,b}	IIIpm3a+b	102	82
16	?	–	–	–
17	–(t3–cx3a) ^a	–	–	–
18	–(t3–cx3b) ^a	–	–	–
19	?	–	–	–
20	t3–tr3 ^a	–	–	–
21	cx3–ba3 ^a	–	–	–
22	cx3–sa3 ^{a,b}	IIIpm5	105	81
23	fu3–pl3 ^b	–	–	–
24	?	–	–	–
25	?	IIIIm1	104	78, 80
26	pl3–cx3 ^b	IIIIm4	103	77a+b
27	fu2–fu3 ^{b,c}	IIIs2	–	71
28	–(180) ^c	–	–	–
29	fb1 ^c	–	–	–?
30	?	IIIIm2	106	79
31	?	IIIIm3	109	83
32	?	Iadl2	121	155, 156, 159
33	?	–	–	–
34	?	–	–	–
35	?	IIIIs1–3	118+119	157, 158

^a Compiled from Daly (1963)^b Compiled from Ronquist and Nordlander (1989)^c Compiled from Heraty et al. (1994)

tures are situated on the anterior margins of the metepisterna. *O. pulchella* (Trigonalidae) has a pair of posterior branches in addition to the anterior ones, resembling the condition in Orussidae. The median metanoto-metapleural muscles (9) are absent from *Orussus* sp. This corresponds with the absence of their serial homologues from the mesothorax in Orussidae (Gibson 1985).

The metafurca of Apocrita differs from that of most 'Symphyta'. In the apocritan taxa examined except *S. cinctipes* (Stephanidae), the lateral metafurcal arms are well developed, extending towards the metapleural apodemes in *I. rufipes* (Ibaliidae; Ronquist and Nordlander 1989) or even fusing with them as observed in *M. fasciipennis* (Megalyridae), *A. striatus* (Aulacidae), *O. pulchella* (Trigonalidae) and *V. pennsylvanica* (Vespidae; Duncan 1939); the latter condition (character 41, state 2) was also observed in *Apis mellifera* (Apidae; Snodgrass 1942) and *M. dentipes* (Chalcidoidea; Bucher 1948). The anterior metafurcal arms are less conspicuous (except in *S. cinctipes*), as the metafurca lies close to the mesofurca

(Duncan 1939); in Apoidea, the meso- and metafurcal arms are actually fused and the metafurco-mesofurcal muscles (27) are absent (Snodgrass 1942; Heraty et al. 1994). In Xiphydriidae and Orussidae, the metapleural apodemes and the lateral metafurcal arms are also conspicuous (character 29, state 1; character 41 state 1). The anterior metafurcal arms are still of considerable length (character 40, state 0). In Orussidae, the lateral metafurcal arms are displaced anteriorly on the anterior arms; this condition might be intermediate between that of Xiphydriidae and that of the Apocrita described in literature.

The mesospina is present only in *S. cinctipes* (Stephanidae) among the apocritans included in the present study; it was not possible to decide whether the metafurco-mesospinal muscles (28) are present or not. Heraty et al. (1994) did not observe any in *Megischus bicolor* (Stephanidae) and suggested that the absence of these muscles is a putative apocritan autapomorphy.

3. Modifications of the metathoracic musculature in the Apocrita

The musculature of the metathorax in Apocrita has only been investigated in detail for a few representatives, most of which belong to the Aculeata (Weber 1925; Duncan 1939; Snodgrass 1942; Markl 1966). The exception to this is the studies of *Stenobracon deesae* (Braconidae) by Alam (1951, 1953). Additional information for non-aculeate Apocrita has been supplied by Daly (1963), Ronquist and Nordlander (1989) and Heraty et al. (1994). Table 4 summarises the occurrence of muscles in Apocrita, compiled from these studies. A few comments, justifying homologies and emphasizing features of possible phylogenetic significance, are needed:

- Ronquist and Nordlander (1989) stated that two pairs of metapleuro-metafurcal muscles are present in *I. rufipes* (Ibaliidae), one pair connecting the metapleural apodeme (their structure 103) with the lateral metapleural arms (their structure 115), evidently the homologue of the anterior metapleuro-metafurcal muscles (23) and the second pair extending from the lateral metafurcal arms to ‘apophyses 116’ situated at the lateral ends of the third phragma. These apophyses are probably homologous with the metalaterophragmal lobes, and the muscles arising from them are consequently the metalaterophragmo-metafurcal muscles (7). The absence of the posterior metapleuro-metafurcal muscles (24; character 30, state 1) might then be a synapomorphy of the Xiphydriidae + Orussidae + Apocrita.
- In *V. pensylvanica* (Vespidae; Duncan 1939) and *A. mellifera* (Apidae; Snodgrass 1942), several bundles of muscles connect the lateral margins of the metanotum with the lateral metafurcal arms and the adjacent parts of the metapleura. The fusion of the lateral metafurcal arms with the metapleura and the absence of the anterior metapleuro-metafurcal muscles (23) makes homologising these muscles difficult, as they have secondarily shifted their points of attachment to the metafurca. However, it seems reasonable to assume that they are derived from components of both the median (9) and lateral (10) metanoto-metapleural muscles.
- Only one pair of fan-shaped muscles inserting on the third axillary has been observed in Apocrita (Duncan 1939; Snodgrass 1942; Ronquist and Nordlander 1989), whereas in ‘Symphyta’ two pairs of muscles are present. Alam (1951) described two pairs in *S. deesae* (Braconidae), but one arises from the metapleural apodeme and the other posteriorly of the first, so the homologues of the anteriormost pair, arising from the anterior parts of the metapleural arms in ‘Symphyta’, are apparently absent from this taxon also. A more thorough survey within the Apocrita is needed to decide whether this is an apocritan ground plan feature.
- A considerable number of extrinsic hind leg muscles are absent from the ground plan of the Apocrita. Most of the muscles lost are those arising from the metanotum and S2, whereas those arising from the metapleura and metafurca are retained. Absent from the apocritan ground plan are possibly the metanoto-trochantinal (17; character 35, state 2, synapomorphy for Xiphydriidae + Orussidae + Apocrita), the anterior (18; character 36, state 1, synapomorphy for Xiphydriidae + Orussidae + Apocrita) and posterior metanoto-metacoxal (19), the metabasalar-metacoxal (21) and the S2-metacoxal (34; but see below) muscles. Daly (1963) reported the presence of metabasalar-metacoxal muscles (21) from some aculeates, but apparently considered them to be secondarily derived from the metabasalar-metapleural muscles (13) in these taxa. These muscles have been lost progressively at different nodes during the early evolutionary history of the Hymenoptera.

The musculature connecting the metasoma with the mesosoma has been treated for apocritan taxa by Weber (1925), Duncan (1939), Snodgrass (1942), Alam (1953), Short (1959) and Markl (1966); of these, only Alam (1953) and Short (1959) treated non-aculeate taxa. The metasoma is moved by muscles arising from the mesosoma and inserting on the second abdominal segment through tendons. Two pairs of muscles arise from the propodeum (Iad1 and Iad2 of Duncan 1939; 120 and 121 of Snodgrass 1942; 155+156 and 159 of Alam 1953; 2 and 3 of Short 1959) to insert medially and laterally on T2, respectively. The former is homologous with the third phragmo-T2 muscles (32) in ‘Symphyta’. The homologues of the latter are a pair of muscles (32a) arising from the lateral parts of T1 to insert on the anterolateral corners of T2. These muscles were not extensively surveyed in the present study (but see Cephoidea above), but were identified in *U. gigas* (Siricidae) by Short (1959; his muscle 3). Another two pairs of muscles insert on the second abdominal sternum, which arise from the metafurca (IIIis2 of Duncan 1939; 118 of Snodgrass 1942; 157+158b of Alam 1953; 7 of Short 1959) and the discrimenal lamella of the metathorax (IIIis3 of Duncan 1939; 119 of Snodgrass 1942; 158a of Alam 1953; 8 of Short 1959), respectively. The former correspond to the metafurco-S2 muscles (35) in ‘Symphyta’ and the latter have no obvious homologues, but might have evolved by subdivision of the metafurco-S2 muscles (35). Short (1959) suggested them to be homologous with the S2-metacoxal muscles (34; his 8) in *U. gigas*, which are absent from Apocrita. This seems improbable, as this would have required changes in attachment at both ends of the muscles. Alternatively, the S2-metacoxal muscles (34) could have been lost from the Apocrita as a result of the modification of S2 during the formation of the petiole. *V. pensylvanica* (Vespidae; IIIis1; Duncan 1939) has an additional pair of muscles arising from the metapleural apodemes and inserting separately on S2. These might also be homologous with parts of the metafurco-

S2 muscles (35). This hypothetical fission of the metafurco-S2 muscles (35) might have evolved to enhance the manoeuvrability of the metasoma in Apocrita.

V. Conclusion

The present study has revealed the metathorax and T1 to be a rich source of phylogenetically relevant information among the basal hymenopteran lineages. Judging just from the few detailed studies undertaken so far (Weber 1925; Duncan 1939; Snodgrass 1942; Alam 1951, 1953; Ronquist and Nordlander 1989) from different representatives, there appears to be considerable variation within the Apocrita in the metathorax as well. An extensive survey within the Apocrita of the skeleto-musculature of the metathorax and anterior abdominal segments would probably prove highly rewarding.

The highly derived conditions of most features of the metathorax displayed by the Apocrita has evidently been acquired by gradual evolution in the early evolutionary history of the Hymenoptera, the Xiphydriidae and especially the Orussidae being the 'symphytan' lineages that most resemble the Apocrita. However, it is intriguing that many of the transformation series in the characters studied here can also be inferred to have occurred within the Tenthredinoidea. This applies to the fusion of T1 with the metepisterna, the integration of the posterior thoracic spiracles in the mesepimera, the loss of some extrinsic hind leg muscles, the configuration of the paracoxal sulci and the configuration of the metafurca. However, there can be no doubt that this is the result of convergent evolution, considering the amount of evidence supporting the monophyly of the Tenthredinoidea presented by this and other studies (Vilhelmsen 1999).

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