

Phylogenetic Implications of the Mesofurca and Mesopostnotum in Hymenoptera

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Abstract.—The skeleto-musculature of the mesofurca and the mesopostnotum is examined in Hymenoptera. Character systems based on internal structure of the mesothorax support recent hypotheses that suggest sawflies are paraphyletic with respect to Apocrita. Unique character states for Hymenoptera include the presence of two mesofurcal-laterophragmal muscles, a mesofurcal-third basalar muscle, and a scutellar-metanotal muscle. Other possible apomorphies include the medial emargination of the mesopostnotum and the formation of anterior furcal arms. The arrangement of mesofurcal muscles that attach to the profurca and the laterophragma are described and interpreted in light of recent phylogenetic hypotheses. Changes in attachment sites, fusion or loss of the anterior arms of the mesofurca and features of the laterophragma provide characters that are consistent with the monophyly of Tenthredinoidea + (Cephoidea + (Siricoidea (including Anaxyelidae) + (Xiphydriidae + Orussoidea + Apocrita))). Groundplan states for the Apocrita are proposed that include retention of a mesofurcal bridge, retention of an anterior process on the bridge that supports the interfurcal muscles, reduction of the mesofurcal-laterophragmal muscles from two to one, retention of the mesotergal-laterophragmal muscle, loss of the mesofurcal-third basalar muscle, and loss of the metafurcal-spina muscle. Within Apocrita the distribution of character state changes is less informative than in Symphyta, but provide evidence for relationships of some taxa. The mesofurcal bridge is lost convergently in Ceraphronoidea, Pelecinidae, Platygastroidea, Mymarommatoidea, Mymaridae and some Chalcidoidea. The tergal-laterophragmal muscle and associated posterior lobe of the laterophragma are postulated to have been lost independently in nine lineages of Apocrita. The development of the laterophragma into an axillary lever is a synapomorphy for Vespoidea and Apoidea, and in Apiformes the lever is an independent sclerite. The distribution of states for 12 characters is discussed for 62 families of Hymenoptera. Parsimony analysis of these data result in trees that generally agree with the current hypotheses for Symphyta but not for Apocrita.

INTRODUCTION

"Students of these [hymenopteran] parasites discover that the thorax presents valuable characters for the determination and classification of species, but they are handicapped by the lack of reliable studies on the structure of the thorax"

Snodgrass, 1910 p. 37

Since Snodgrass (1910) first attempted to expand our knowledge of the structure of the hymenopteran thorax, additional studies have described the skeleto-musculature of single species or single families (Weber 1925, 1927, Tulloch 1935, Maki 1938, Duncan 1939, Michener 1944, Bucher 1948, Alam 1951, Saini et al. 1982, Daly 1964, Gibson 1986, 1993). Fewer studies have compared thoracic structures among families of Hymenoptera (Snodgrass 1942, Daly 1963, Rasnitsyn

1969, 1980, Matsuda 1970, Shcherbakov 1980, 1981, Gibson 1985, Johnson 1988, Whitfield et al. 1989). The determination of homologous structures and polarity of characters in Hymenoptera are crucial for understanding phylogenetic relationships, a topic recently addressed by various authors (Rasnitsyn 1969, 1980, 1988, Brothers 1975, Königsmann 1977, 1978a 1978b, Carpenter 1986, Brothers and Carpenter 1993).

The mesofurca is an invagination of the sternum into the thorax that forms a central point of attachment for the ventral longitudinal muscles, the sterno-pleural muscles, the coxal and trochantal muscles, and the mesopostnotal muscles (Kelsey 1957, Matsuda 1970). The mesofurca is comprised of a basal plate (discrimenal lamella) that rises vertically from the discrimen, slopes posteriorly to the furcal base, and divides dorsally

into two lateral arms, termed the sternal apophyses (Snodgrass 1927, Chapman 1992, Lawrence et al. 1992). The mesopostnotum is one of the primary dorsal sclerites involved in flight through the posterior inflection of the antecosta (second phragma) which forms the posterior attachment of the longitudinal flight muscles. Recent studies involving skeleto-musculature of the hymenopteran thorax have focused on the pleural attachments (Shcherbakov 1980, 1981, Gibson 1985, 1993), the extrinsic musculature of the mesocoxa (Johnson 1988), and the development of the metapostnotum (Whitfield et al. 1992). Rasnitsyn (1969, figs. 187-194) was the first person to compare the different skeletal structures for the mesofurca of 8 families of Symphyta. His illustrations show the transformation series for Symphyta that are discussed in this paper. Rasnitsyn (1988) refers to the furca for features supporting Tenthredinoidea and for Cephioidea + Siricoidea + Apocrita. Similarly, Snodgrass (1942) presented a pictorial evolutionary history for development of the axillary lever of Apoidea. This work expands upon these initial studies and extends the comparative aspects of these works to include most families of Apocrita.

This study of the mesofurca and mesopostnotum began as an attempt to understand the polarity and homology of mesofurcal structures and muscles of Aphelinidae (Chalcidoidea) and the phylogenetic implications of these attributes within the Chalcidoidea. Eventually the entire Hymenoptera needed to be surveyed to resolve what we initially thought were relatively simple questions. In this study, all muscles attaching to the mesofurca and mesopostnotum are identified and compared to homologous muscle groups in Neuropterida and Mecopterida (*sensu* Kristensen 1992), as they are considered to be phylogenetically close to Hymenoptera (Kristensen 1992), and have a mesothorax which is structured similar to the Symphyta. Within Hymenoptera, we have concentrated our analysis on the skeletal structure of the mesofurca and mesopostnotum, and on the muscles attaching between the thoracic furcae and the laterophragma of the mesopostnotum. The evidence provided by the mesofurca and mesopostnotum for relationships within the Chalcidoidea will be discussed in a subsequent paper.

MATERIALS AND METHODS

Terms for structures and muscles generally follow Snodgrass (1910, 1942), Daly (1963), Gibson (1985, 1986, 1993) and Ronquist and Nordlander (1989). Muscles were identified using the systems proposed by Kelsey (1957) and Daly (1963) (Table 1). Figures 1 and 2 are used to place the skeleto-musculature within the context of the mesosoma. Muscles and structures are extensively labeled in Figs. 3 and 4. The Kelsey system uses a fixed set of numbers and is useful for comparisons across the Endopterygota. Daly's system is preferred for clarity because the insertion-origin of attachment sites are readily identified and new muscles can be added to the system; for example, the new muscle fu_2-ba_3 was given the abbreviation fb1 for the Kelsey system as it could not be assigned a numeric value that would signify its relative position to other muscles in the mesothorax. Terms proposed by Matsuda (1970) are comprehensive and may be referenced across orders of insects; however his abbreviated system is difficult to use and is not followed here.

Several new classifications of families within Hymenoptera have been proposed recently that differ largely in placement of certain families as separate superfamilies, families, or subfamilies. We follow the classification of Huber and Goulet (1993), as it represents the most current synthesis of information across the order.

Dissections were based on specimens preserved in 70% ethanol or initially fixed in Dietrich's or Kahle's solution and then transferred to ethanol. All specimens were critical point-dried prior to dissection. The mesosoma of *Monomachus* (Monomachidae) was rehydrated using Barber's solution, transferred through increasing concentrations of ethanol to 98% and then critical point-dried. For each dissection, the mesosoma was anchored onto a standard SEM stub using chloroform-based silver paint. Dissections were made using hooked minuten pins or fragments of razor blades. Dried haemolymph and extraneous tissues were removed from dissections using small amounts of glue obtained by dragging a hooked minuten pin across clear sticky tape (Gibson 1985).

Exemplar taxa were chosen to represent the maximum variation within taxa. In some groups (e.g. Apoidea), there was virtually no variation; whereas within some taxa (e.g. Diapriidae) both

structure and presence of muscles varied and more genera were dissected to characterize this variation. Our primary concern was for establishing groundplan states for higher taxa, although autapomorphies are discussed. The taxa examined for internal characters are listed in Table 2. Numerous Chalcidoidea were also dissected as part of a comprehensive study of the mesofurca in that superfamily. Representative dissections are housed at the Canadian National Collection (CNCI), Royal Ontario Museum (ROM) and Texas A&M University (TAMU). When possible, conspecific adults of the dissected specimens are deposited as voucher specimens in the above collections. The majority of specimens were obtained from the CNCI alcohol collection.

The mesofurcal-mesopostnotal complex was broken up into 12 characters with a total of 36 character states. Seventy hymenopteran taxa were scored (Appendix 2) based on the examination of internal characters for 119 species (Table 2). A single outgroup taxon was scored based on dissections of 5 families of Neuropterida and 3 families of Mecopterida. Characters 1, 3 and 9 are postulated as unique characters for Hymenoptera; in each of these cases, the outgroup is coded as a unique character state (state 0). The state value "?" was used to denote uncertain homology, not missing data.

Illustrations were made with a camera lucida. Outlines of muscles present but not illustrated are represented by dashed lines. Some muscles not central to this study were not consistently figured (e.g. muscle 180 for Symphyta) and caution should be exercised in deriving additional interpretation from the illustrations. Abbreviations referring to muscles are circled in all figures, skeletal characters are not. The mesofurcal-mesopostnotal complex is abbreviated as MF-MPN complex.

RESULTS AND DISCUSSION

Character Analysis

Character 1. Mesofurcal bridge

The most significant modification of the mesofurca in Hymenoptera is the fusion of the elongate anterior arms (af) into a mesofurcal bridge (fb) that characterizes virtually all Apocrita. In basal groups of Symphyta (excluding Cephioidea

+ remaining Hymenoptera), the anterior furcal arms are either absent, short, or elongate and well separated along their entire length. The anterior arms, or the equivalent region on the lateral arms of the mesofurca, form the posterior attachment sites for the ventral intersegmental muscles (muscle 124, fu_2 - fu_1 , and muscle 127, fu_2 - sps_1). With fusion of the anterior arms, the furca separates the gastric and nervous systems and the ventral nerve cord passes through the foramen bounded by the mesofurcal bridge and the lateral arms of the mesofurca.

In most Neuropterida and Mecopterida, the interfurcal muscles attach directly to the anterior face of the lateral arms of the mesofurca (**state 0**, no arms) (Snodgrass 1927, Kelsey 1957, Matsuda 1970). In Xyelidae (Fig. 3) and Pamphiliidae (Fig. 6) (and probably Megalodontidae, cf. fig. 187, Rasnitsyn 1969), the interfurcal muscles attach to anterior projections (af, anterior furcal arms) that are long, robust, and separated along their entire length (**state 1**). Of the outgroup taxa examined, only *Brachynemurus* (Myrmeleontidae) have anterior arms (state 1) similar to Xyelidae, and thus their presence could be plesiomorphic or apomorphic for Hymenoptera. Because anterior arms are present only in a derived member of the outgroup, we consider the presence of long anterior arms in Xyeloidea and Megalodontoidea to be apomorphic for Hymenoptera.

In Tenthredinoidea, the anterior arms (af) can be reduced in size (Cimbicidae Fig. 8, Blasticotomidae Fig. 20, and *Nematus* (Tenthredinidae) Fig. 21), modified into supporting cup-like structures (Diprionidae, Fig. 7), or lost entirely so that the interfurcal muscles attach to the anterior face of the lateral furcal arms (Argidae, Pergidae Fig. 5, and most Tenthredinidae). Rasnitsyn (1988) treated "fore arm short" as a character state (his 2-3d) supporting Tenthredinoidea and "fore arm reduced" (his 6-8a) for Argidae + Pergidae. Short arms, as in Blasticotomidae (Fig. 20), are probably plesiomorphic for Tenthredinoidea, and further modifications of the arms or complete loss are derived within Tenthredinidae. It is possible to code for several different character states within Tenthredinoidea (small, absent, cup-shaped, etc.), but this would only introduce unnecessary homoplasy into the analysis (i.e. "absence" derived 2 or more times) or a series of autapomorphic char-

Table 1. Homology and terms for muscles of the mesopostnotum and mesofurca examined in Neuroptera and Hymenoptera. Letter m added to distinguish metathoracic muscles. Muscle fb1 described in text.

Kelsey 1957— <i>Corydalus</i>		Hymenoptera				
No.	Name	Matsuda 1970	Daly 1964	Johnson 1988	Present designation	Notes
Mesothoracic dorsal indirect muscles						
112	internal [ventral] longitudinal	t14	1ph-2ph	-	1ph-2ph	longitudinal flight muscle. Kelsey (1957) recognized both ventral (internal, 112) and dorsal (external, 113) muscles. Recognition of the two muscles in Hymenoptera is unnecessary.
112m	metathoracic longitudinal	t14	2ph-3ph	-	2ph-3ph	reduced and attached laterally in most Hymenoptera.
114	scutellar-metanotal	t13	t ₂ -t ₃	-	t ₂ -t ₃	in Hymenoptera, paired medial muscles passing from metanotum (t ₃) to scutellum over mesopostnotum (PN ₂); external in some sawflies. From PN ₂ in Neuroptera.
116	second dorsal diagonal	t12	t ₂ -2ph	-	t ₂ -pn ₂	dorsomedial attachment on mesoscutum to anterior face of laterophragma (pn ₂); attachment to dorsal axillar surface where transscutal articulation present.
Mesothoracic ventral muscles						
124	mesothoracic interfurcal	s13	fu ₂ -fu ₁	-	fu ₂ -fu ₁	from lateral face of fu ₁ to anterior face or arms of fu ₂ . Kelsey (1957) treats as three muscles (124-126) and Matsuda (1970) as bundles of the same muscle. Hymenoptera have maximum of two bundles and homology of each is uncertain.
127	mesofurcal-spina	s14	fu ₂ -1sps	-	fu ₂ -sps ₁	spina of profurca to apex of lateral arm of fu ₂ .
181	metathoracic interfurcal	s13	fu ₃ -fu ₂	-	fu ₃ -fu ₂	posterior face of lateral arms of fu ₂ to fu ₃ . Kelsey (1957) treats as three muscles (181-183). Hymenoptera have maximum of two.
180	metafurcal-spina	s14	-	-	fu ₃ -sps ₂	spina of mesofurca to apex of lateral arm of fu ₃ .
Tergopleural muscles						
137	laterophragmal-basalare	t-p8?	-	-	t ₃ -ba ₃	posterior face of laterophragma (=t ₃) to apodeme of basalare (ba ₃). Synonymy with t-p8 is questionable.
Furcal muscles						
150a	posterior furcal-laterophragmal	t-s1	fu ₂ -2ph	-	fu ₂ -pn _{2a}	posterior attachment on lateral arm of fu ₂ to anterior process of laterophragma (ap).
150b	anterior furcal-laterophragmal	t-s1	-	-	fu ₂ -pn _{2p}	attachment anterior to 150a on anterior or lateral arm of fu ₂ to posterior lobe of laterophragma (pn ₂).
151	furcal-pleural arm	p-s1	pl ₂ -fu ₂	-	pl ₂ -fu _{2a}	lateral surface of fu ₂ to pleural ridge.
170	coxal articulation-furcal	s-cx2	-	-	pl ₂ -fu _{2b}	lateral surface of fu ₂ to coxal process on pleuron.
fb1	furcal-basalare	p-s3?	fu ₂ -pl ₃ ?	-	fu ₂ -ba ₃	apex of lateral arm of fu ₂ to basalare (ba ₃); may be homologous with pupal muscle of <i>Apis</i> (Daly 1964); well developed with dorsal cap and apodeme in <i>Diprion</i> (one preparation where ba ₃ dissected with fu ₂ -ba ₃ and pl ₃ -ba ₃ both attached). Possibly homologous with Matsuda's p-s3 from furca to anterior margin of succeeding episternum.
Walking and indirect flight muscles						
169	anterior furcal-coxal	s-cx6	fu ₂ -cx _{2a}	fu-cx ₃	fu ₂ -cx _{2a}	anterior base of fu ₂ to median rim of coxa.
173	posterior furcal-coxal	s-cx3	fu ₂ -cx _{2b/c}	fu-cx _p	fu ₂ -cx _{2p}	attachment on fu ₂ posterior to muscle 169 to posteromesal rim of coxa.
174	furcal depressor of trochanter	s-tr1	fu ₂ -tr ₂	-	fu ₂ -tr ₂	anterior base of fu ₂ (or arms) to trochanteral apodeme.

Table 2. Taxa dissected for study of the mesofurcal-mesopostnotal complex.

Section: NEUROPTERIDA

Mantispidae	<i>Mantispa</i> sp.
Chrysopidae	<i>Chrysopa</i> sp.
Corydalidae	<i>Corydalus</i> sp.
Myrmeleontidae	<i>Brachynemurus</i> sp.
Rhaphidiidae	<i>Rhaphidia</i> sp.

Section: MECOPTERIDA

Bittacidae	<i>Bittacus</i> sp.
Meropidae	<i>Merope tuber</i> Newman
Panorpidae	<i>Panorpa</i> sp.

Order: HYMENOPTERA**SYMPHYTA**

Xyeloidea	
Xyelidae	Macroxyelinae: <i>Macroxyela ferruginea</i> (Say); Xyelinae: <i>Pleuroneura</i> sp., <i>Xyela minor</i> Norton

Megalodontoidea

Pamphiliidae	Cephalciinae: <i>Acantholyda</i> sp., Pamphiliinae: <i>Pamphilius</i> sp.
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Tenthredinoidea

Blasticotomidae	<i>Blasticotoma</i> sp.
Tenthredinidae	Heteranthinae: <i>Profenusa canadensis</i> (Marlatt); Nematinae: <i>Nematus</i> sp.; Selandriinae: <i>Aneugmenus flavipes</i> (Norton), <i>Strongylogaster tacita</i> (Norton); Tenthredininae: <i>Filacus</i> sp., <i>Macrophya</i> sp.
Diprionidae	Diprioninae: <i>Diprion similis</i> (Hartig)
Cimbicidae	Cimbicinae: <i>Cimbex americana</i> Leach; Ambiinae: <i>Zaraea americana</i> Cresson
Pergidae	Acordulecerinae: <i>Acordulecera</i> sp., Syzygoninae: <i>Lagideus ?mexicana</i> Smith
Argidae	Arginae: <i>Arge</i> sp., <i>Durgoa matogrossensis</i> Mal.

Cephoidea

Cephidae	<i>Cephus cinctus</i> Norton, <i>Hartigia trimaculata</i> (Say)
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Siricoidea

Anaxyelidae	<i>Syntexis libocedrii</i> Rohwer
Siricidae	Siricinae: <i>Urocerus albicornis</i> (Fabricius); Tremicinae: <i>Tremex columba</i> (Linnaeus)

Xiphydriidea

Xiphydriidae	<i>Xiphydria abdominalis</i> Say
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Orussoidea

Orussidae	<i>Orussus terminalis</i> Newman
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APOCRITA**Stephanoidea**

Stephanidae	<i>Megischus bicolor</i> (Westwood)
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Trigonalyoidea

Trigonalyidae	<i>Orthogonalys pulchella</i> (Cresson)
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Ceraphronoidea

Megaspilidae	<i>Megaspilus fuscipennis</i> (Ashmead), <i>Trichosteresis</i> sp.
Ceraphronidae	<i>Ceraphron</i> sp.

Evanoidea

Aulacidae	<i>Pristaulacus strangaliae</i> (Rohwer)
Evaniidae	<i>Hyptia thoracica</i> (Blanchard), <i>Evania</i> sp.
Gasteruptiidae	<i>Gasteruption</i> sp.

Ichneumonoidea

Braconidae	Alysiinae: <i>Coelinus</i> sp.; Hybrizontinae: <i>Hybrizon</i> sp.; Macrocentrinae: <i>Macrocentrus</i> sp.; Miscogasterinae: <i>Apanteles</i> sp.; Rogadinae: genus ?.
Ichneumonidae	Ephialtinae: genus ?, <i>Scambus</i> sp., <i>Megarhyssa</i> sp.; Ophioninae: <i>Enicospilus</i> sp.

Chrysidoidea

Plumariidae	<i>Plumaria</i> sp.
Sclerogibbidae	<i>Probethylus</i> sp.
Embolemidae	<i>Embolemus nearcticus</i> (Brues)
Dryinidae	Anteoninae (female), Gonatopodinae (male)
Bethylidae	<i>Anisepyrus</i> sp., <i>Epyrus</i> sp.
Chrysididae	Amiseginae: <i>Adelphe anisomorphae</i> Krombein; Chrysidinae: <i>Chrysis</i> sp., <i>Parnope</i> sp.; Cleptinae: <i>Cleptes</i> sp.

Vespoidea

Tiphiidae	<i>Myzinum</i> sp.
Sapygidae	<i>Sapyga</i> sp.
Mutillidae	Sphaerophthalminae (males, 3 genera)
Sierolomorphidae	<i>Sierolomorpha canadensis</i> Provancher
Pompilidae	Pepsinae: <i>Calicurgus hyalinatus</i> Fabr.; Pompilinae: <i>Aporinella galapagensis</i> Rohwer, <i>Aporus</i> sp.
Rhopalosomatidae	<i>Rhopalosoma</i> sp.
Bradynobaenidae	<i>Bradynobaenus</i> sp.
Formicidae	Myrmicinae: <i>Solenopsis invicta</i> Buren (queen & worker); Formicinae: <i>Camponotus planus</i> F. Smith (queen), <i>Paratrechina</i> sp. (queen)
Scoliidae	<i>Scolia</i> sp.
Vespidae	Eumeninae: <i>Odynerus</i> sp., <i>Parancistrocerus</i> sp.; Vespinae: <i>Dolichovespula</i> sp., <i>Vespula</i> sp.

Apoidea

Crabronidae	<i>Ectemnius</i> sp., <i>Larra</i> sp.
Heterogynaeidae	<i>Heterogyna</i> sp.

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Table 2 continued

Andrenidae	<i>Andrena</i> sp.
Anthophoridae	<i>Nomada</i> sp., <i>Ceratina</i> sp.
Apidae	<i>Apis mellifera</i> L., <i>Bombus</i> sp., <i>Trigona</i> sp.
Halictidae	<i>Agapostemon</i> sp., <i>Lasioglossum</i> sp.
Megachilidae	<i>Megachile</i> sp.
Proctotrupeoidea	
Diapriidae	Ambositrinae: <i>Dissoxylabis</i> sp.; Belytinae: <i>Aclista</i> sp., <i>Acropiesta</i> sp., <i>Aneurynchus</i> sp., <i>Oxylabis</i> sp.; Diapriinae: <i>Coptera</i> sp., <i>Paramesius</i> sp., <i>Spilomicrus</i> sp., <i>Trichopria</i> sp.
Monomachidae	<i>Monomachus</i> sp.
Vanhorniidae	<i>Vanhornia eucnemidarum</i> Crawford
Heloridae	<i>Helorus</i> sp.
Roproniidae	<i>Ropronia</i> sp.
Proctotrupidae	<i>Exallonyx</i> sp., <i>Miota vera</i> (Fouts)
Peleciniidae	<i>Pelecinus polyturator</i> (Drury)
Cynipoidea	
Ibaliidae	<i>Ibalia</i> sp.
Eucoilidae	genus ?
Alloxystidae	<i>Alloxysta</i> sp.
Platygastridae	
Scelionidae	Scelioninae: <i>Anteris</i> sp., <i>Calotelea</i> sp., <i>Cremastobaeus</i> sp., <i>Gryon</i> sp. (wingless), <i>Macroteleia absona</i> Muesebeck, <i>Sparasion</i> sp., Teleasinae: <i>Trimorus</i> sp.
Platygastridae	Inostemmatinae: <i>Isocybus</i> sp., <i>Inostemma</i> sp.
Mymarommatoidea	
Mymarommatoidea	<i>Palaeomymar</i> sp.
Chalcidoidea (additional dissections for work in progress not listed)	
Mymaridae	<i>Gonatocerus</i> sp.
Pteromalidae	Cleonyminae: <i>Cleonymus</i> sp., <i>Oodera</i> sp.

acter states. Coding of character states must in part reflect the level of analysis. At a different level, for example in an analysis of the relationships of Tenthredinoidea that is associated with a more extensive survey of taxa, it might be appropriate to further partition the various shapes. These modifications are difficult to characterize and here we have combined them into one apomorphic state, the reduction of well-separated anterior arms (**state 2**).

A clear transformation series leading to the development of the mesofurcal bridge is found within the Symphyta beginning with the Cephidae. In Cephidae (Fig. 9), the anterior arms are narrow and elongate and only the extreme apices of each

arm are joined (**state 3**). The anterior arms are considered to be homologous with those of Xyeloidea and Megalodontoidea; therefore, state 3 is probably derived from state 1. Rasnitsyn (1988; his character 19b) includes Cephidae with Siricoidea + Vespina based on having the forearms of the mesofurca long and fused for some distance. Although true for Siricoidea + Vespina, the arms are only apically fused in Cephidae.

In Anaxyelidae (Fig. 10) and Siricidae (Fig. 11), the anterior arms are elongate and fused along most of their length (**state 4**). The anterior arms of Siricidae are laterally flattened (Fig. 11b) and in dorsal view each arm can be distinguished along its entire length (Fig. 11a). Anaxyelidae have a similar structure, including anterior placement of muscle 150b, but fusion of the arms is more complete (Fig. 10a). Posteriorly, the anterior furcal arms of Anaxyelidae are connected by a thin horizontal plate of cuticle.

In Xiphydriidae (Fig. 12), the anterior arms are completely fused and form a transverse mesofurcal bridge (**state 5**), and the entire dorsal and lateral surfaces form the posterior attachment for muscle 124. Displacement of muscles 150a and 150b to the lateral arms suggests that fusion of the arms in Xiphydriidae may be independent of the fusion in Siricidae and Anaxyelidae.

Orussidae (Fig. 13) exhibit complete fusion of the anterior arms into a smooth and bowed mesofurcal bridge (**state 6**) with a strong median anterior process that is the attachment site for muscles 150 and 124, as occurs in Anaxyelidae and Siricidae.

The groundplan states for the mesofurca of Apocrita consists of 1) a complete mesofurcal bridge (as in Xiphydriidae and Orussidae), 2) an anterior medial projection supporting muscle 124 (fu_2 - fu_1) (as in Xiphydriidae and Orussidae), and 3) lateral displacement of muscle 150a (fu_2 - pn_{2p}) (as in Xiphydriidae). No Apocrita have muscle 150 originating on the anterior projection of the mesofurca as in Orussidae. Because of the lateral displacement of muscle 150a, which is similar to Xiphydriidae (see character 2), Apocrita with a mesofurcal bridge are coded as character state 4.

The mesofurcal bridge is absent (**state 7**) in Ceraphronoidea (Fig. 25), Peleciniidae (Fig. 31), some Chalcidoidea (including all Mymaridae), Mymarommatoidea, and Platygastridae (Fig. 28). We consider that absence of the bridge is an

apomorphic loss of the type of bridge found in Xiphydriidae (state 5), which is similar to the type found in most Apocrita. Assuming that presence of a bridge is a groundplan state for Apocrita (whether states 4, 5 or 6), losses within each of these taxa are considered irreversible (unlikely that a bridge can be regained) and probably independent. In Ceraphronidae, Pelecinidae, Mymaromatidae, Platygastriidae, and some Mymaridae, the mesofurca is lyre-shaped with the lateral arm terminating in a cup-shaped process that supports muscle 150a. When the furcal bridge is lost in Chalcidoidea (Aphelinidae, Encyrtidae, Rotoitidae, Signiphoridae and Trichogrammatidae), the shape of the mesofurca and attachment of muscle 150a are considerably different.

Synonymy for mesofurcal bridge:

Siricidae & Vespidae: mesofurcal ring (Tenthredinidae, *Vespa*, Weber 1925). Ichneumonidae: mesofurcal bridge (*Stenobracon*, Alam 1951). Aculeata: mesofurcal bridge (ArF₂) (*Vespula*, Duncan 1939); supraneural bridge (*Apis*, Snodgrass 1942). Chalcidoidea: arch of the furca (*Monodontomerus*, Bucher 1948); tendinous arch of the mesofurca (*Tetramesa*, James 1926).

Character 2. Laterophragma of mesopostnotum (pn₂)

In Neuropterida, Mecopterida, Xyelidae and Pamphiliidae, the laterophragma of the mesopostnotum forms a lobe (pn₂, Figs. 4, 6) (state 0) that extends obliquely into the mesothorax from the lateral corners of the mesopostnotum, mediad of the lateral attachment to the upper mesepimeron and lateral to the second phragma. The laterophragma in all of these taxa forms the attachment site for muscle 150 (fu₂-pn₂, see Character 3), muscle 116 (t₂-pn₂, see Character 4) and muscle 137 (pn₂-ba₃). The posterior face of the laterophragma forms the attachment site for muscle 137 (pn₂-ba₃, Fig. 3). Muscle 137 is usually small and difficult to trace, but it is apparently lost in Pergidae and all Apocrita.

In Xyelidae (Figs. 3, 4) and most Symphyta (Figs. 6, 8, 9), an apodeme (ap) is present on the anterolateral margin of the lobe that serves as the attachment site for muscle 150a (fu₂-pn_{2a}). The laterophragma is functionally coupled with

muscles 150 and 116, and the loss of either of these muscles is associated with a corresponding change in structure of the laterophragma. To avoid duplication of character coding, the presence or absence of certain structures of the laterophragma are treated under other characters. For example, the anterior apodeme is lacking in Neuropterida and Mecopterida but this was not coded as a different state for this character because it is reflected in the differentiation of muscle 150a in Hymenoptera, which is dealt with as Character 3. A broad laterophragma with a small anterior apodeme (state 0) occurs in Xyelidae, Pamphiliidae (and probably Megalodontidae), Blasticotomidae, Tenthredinidae, Argidae, Diprionidae, and Cephidae.

The laterophragma of Cimbicidae (Fig. 8) possesses an exaggerated apodeme (ap) and an enlarged posterior lobe (pn₂), which is fused with the second phragma (2ph). The laterophragma is unique in form and apparently autapomorphic.

In Xiphydriidae (Fig. 12), Monomachidae (Fig. 14), Vanhorniidae (Fig. 15), Cynipoidea (Fig. 22), Ceraphronoidea (Fig. 25) and most Diapriidae (Fig. 29), the laterophragma is excised between the elongate apodeme (ap) and the posterior lobe (pn₂) (state 1). In most of these taxa the apodeme of the laterophragma extends medially and horizontally into the thoracic cavity, but in Cynipoidea (cf. Fig. 22), the apodeme is vertical. The posterior lobe is lost in most Apocrita (including some Diapriidae), but this was not coded as an additional state change for this character because it reflects the loss of the muscle 116 (Character 4). The anterior apodeme (=axillary lever) or associated attachment for muscle 150a is present in all Apocrita. Additional character state changes for the laterophragma in Apocrita are based only on changes in the shape of the anterior apodeme.

In Pergidae (Fig. 5) and Orussidae (Fig. 13), the laterophragma is reduced to a narrow triangular process that forms an attachment for the tendon of muscle 150 (state 2). This reduction is also associated with the loss of muscle 116. State 2 could be derived from either state 0 or state 1.

In Apocrita, the axillary lever (ap) occurs in a variety of shapes that probably have different effects on leverage of the laterophragma with respect to the fourth axillary sclerite and the second phragma. In all Apocrita the apex of the axillary lever maintains a connection with muscle 150a

(fu_2 - pn_{2a}). The plesiomorphic lever for Apocrita is narrow and inflected medially into the thorax as found in Xiphidriidae (**state 1**) and occurs either in association with a posterior lobe (most Diapriidae, Monomachidae (Fig. 14), Vanhorniidae (Fig. 15), Ceraphronoidea (Fig. 25) and Cynipoidea (Fig. 22) or without the posterior lobe (Trigonalyidae (Fig. 23), Stephanidae (Fig. 24), Diapriidae (Fig. 29), Proctotrupidae (Fig. 32), some Ichneumonidae, Mymarommatidae, and Chrysidoidea (Figs. 34-39) (except some Chrysididae). The axillary lever exists in a variety of forms in Apocrita but in shapes that are difficult to separate into discrete states, especially without a more thorough survey of the apocritan taxa. In all cases where the lever was narrow and inflected medially the character was coded as state 1.

In Platygastriidae (Fig. 28), some Scelionidae and most Chalcidoidea, the axillary lever is deflected ventrally (**state 3**). In Mymarommatidae, the lever is robust and inflected medially (**state 1**). In *Sparasion* (Scelionidae; Fig. 16), the lever is reduced to a small cup-shaped lobe on the laterophragma (autapomorphic and not coded). In other Scelionidae and Mymaridae the lever is short, narrow and medially inflected (**state 1**).

The axillary lever in Stephanidae (Fig. 24) and most Chrysidoidea (Figs. 35-38, also in Fig. 34 but this view is slightly different) is elongate and strongly inflected medially (**state 1**). This conformation of the lever is likely the precursor to the lever found in Apoidea and Vespoidea, discussed below. However, in Cleptinae and Chrysidinae (Chrysididae) the lever is reduced (**state 4**) forming a short, broad process attaching to a broad tendon of the shortened muscle 150a (Fig. 40).

In Apoidea (Figs. 45, 46, 54) and Vespoidea (Figs. 41, 42, 44) the axillary lever is robust and strongly appressed to the inner surface of the second phragma (**state 5**). This type of lever was found in all Apoidea examined and is associated with a robust muscle 150a. Except in Bradynobaenidae and Formicidae, muscle 150a is conical and attached to the lever by a narrow tendon or robust and nearly tubular (Mutillidae and Sapygidae). In Sierolomorphidae, the lever is not closely appressed to the second phragma (inflected medially about 30°), but this was not treated as a different state (intermediate between states 1 and 5). In Bradynobaenidae, the lever is reduced to a rounded knob (attaching to a narrow tendon of

muscle 150a) (**state 4?**). In Formicidae (Fig. 43), the lever forms a narrow, twisted apodeme (**state 1?**). Neither Bradynobaenidae and Formicidae were broadly surveyed and other forms may exist.

In Ichneumonidae the axillary lever is either closely appressed to the second phragma and similar to the lever found in Vespoidea and Apoidea (**state 5**), or rod-like and extending medially into the mesothorax (**state 1**), or inflected medially and dorsally (Fig. 17a). A robust lever is not found in Braconidae, including Hybrizontinae (Fig. 33), in which it was knob-like or short and slightly deflected ventrally (**state 1**), similar to Trigonalyidae and some Proctotrupoidea. The lever of Gasteruptiidae (Fig. 26) is similar to some Ichneumonidae but is oriented vertically with respect to the second phragma. In *Oodera* (Pteromalidae), the lever is robust, appressed to the second phragma and horizontal (**state 5**). This form of the lever appears to be convergent with Ichneumonidae and Aculeata, since in *Oodera* muscle 150a attaches to the entire ventral aspect of the apodeme as in other Chalcidoidea.

All Apiformes have the axillary lever separated (**state 6**) as an independent sclerite (Snodgrass 1942). This feature was verified in all of the Apiformes examined here. The apical connection of the mesopostnotum is weak and encased by the cup-shaped basal process of the axillary lever (Figs. 45, 54).

Synonymy for laterophragma:

Symphyla: lateral lobe of second phragma (2ph) (Daly 1963). Ichneumonoidea: muscle bearing process of mesopostphragma (*Stenobracon*, Alam 1951); axillary lever (Snodgrass 1942). Cynipoidea: mesopostnotal apodeme (*Ibalia*, Ronquist and Nordlander 1989); 2ph (Daly 1963). Aculeata: axillary lever (*Apis*, Snodgrass 1957; *Bombus*, Pringle, 1957, 1960, 1961); accessory sclerite of the fourth axillary sclerite (*Apis*, Snodgrass 1910); inner process of mesopostphragma (*Vespa*, Weber 1925 [states that lever turns apex of mesophragma and the connected axillary 4]); anterior process of mesopostphragma (MPPh₂) (*Vespula*, Duncan 1939). Hymenoptera: axillary lever (Matsuda 1970).

Character 3. Furcal-laterophragmal muscle

In Neuropterida and Mecopterida, only a

single muscle (150, fu_2 - pn_2) acts between the mesofurca and laterophragma of the mesopostnotum (**state 0**) (Kelsey 1957, Matsuda 1970). In the majority of Symphyta, including Xyelidae and Pamphiliidae, two distinct muscles (150a and 150b) operate antagonistically on the enlarged laterophragma (Figs. 2, 3, 4, 6). The presumed division of muscle 150 into two muscles is considered as an apomorphy for Hymenoptera (**state 1**). Muscle 150a (fu_2 - pn_{2a}) originates on the lateral arms of the mesofurca posterior or lateral to the origin of 150b and inserts onto an anterior apodeme or process of the laterophragmal lobe (Figs. 4, 6, 7, 9). Muscle 150b (fu_2 - pn_{2p}) originates anteriorly or medially on the lateral or anterior arms of the mesofurca and broadly attaches to the margin of the laterophragmal lobe (Figs. 4, 6, 7, 9). The fibres of muscle 150b are often arranged so that the anteriormost fibres attach to the posteriormost or innermost margin of the laterophragmal lobe, although this is dependent on the size of the muscle and lobe.

If both muscles are present, muscle 116 (t_2 - pn_2) is also present. Loss of muscle 150b (**state 2**) occurs in Cimbicidae, Monomachidae, Vanhorniidae, Diapriidae, Cynipoidea, and Ceraphronoidea, all of which have retained both the laterophragmal lobe (presumably the former point of insertion of muscle 150b) and muscle 116. All Apocrita have lost muscle 150b. In Anaxyelidae (Fig. 10), muscle 150b is attached to the posterior face of the posterior lobe (versus the margin) and muscle 150a is retained. Because of a similar placement and attachment of muscles in Siricidae (Fig. 11), it can be postulated that muscle 150a is lost and 150b remains (**state 3**). When both the laterophragmal lobe and muscle 116 are missing, as in Pergidae (Fig. 5) and Orussidae (Fig. 13), it is difficult to assess which muscle, 150a or 150b, has been lost. We could assume that muscle 150b is lost in both families. However, the forward attachment of muscle 150 to the mesofurca in Orussidae suggests that it is homologous with muscle 150b of Anaxyelidae and Siricidae. Therefore, the configuration in Pergidae and Orussidae could also be treated as a parallel loss of muscle 150a. Because of this uncertainty, we code the reduction to a single muscle in Pergidae and Orussidae as of questionable homology (**state ?**). Based on the presence of muscle 150a in the apocritan families mentioned above, we assume that muscle 150b is

lost in all Apocrita without a posterior laterophragmal lobe. Autapomorphic losses of muscle 150a occurs in workers of *Formica* and *Camponotus* (Märkl 1966, Saini et al. 1982).

Synonymy for muscle 150:

Tenthredinidae: Ilism1 (*Dolerus*, *Schizocerus*, *Tenthredo*, Weber 1927), 25 & 26 (*Euthomostethus*, Maki 1938). Ichneumonidae: 25 (*Psilopsycha*, Maki 1938); 63 (*Stenobracon*, Alam 1951). Aculeata: 25 (*Vespa*, Maki 1938); 78 (*Formica*, Märkl 1966; *Apis*, Snodgrass 1942); Ildv2 (*Vespula*, Duncan 1939); Ilism (*Vespa*, Weber 1925); fu_2 -2ph (*Apis*, Daly 1964). Hymenoptera: t-s1 (Matsuda 1970).

Character 4. Second dorsal diagonal (=phragmal flexor) muscle

Muscle 116 (t_2 - pn_2) is found attaching between the mesonotum and the anterior face of the laterophragmal lobe in Neuropterida, Mecopterida and most Symphyta (Figs. 2, 3, 12, 14, 15, 20), and is therefore plesiomorphic for Hymenoptera (**state 0**). Muscle 116, and the associated posterior lobe of the laterophragma, is lost (**state 1**) in Pergidae, Orussidae and most Apocrita. It seems unlikely that a functional complex composed of both muscle 116 and the corresponding posterior lobe of the laterophragma could be regained, and we consider the apomorphic state (loss of muscle and lobe) to be irreversible. An assumption of irreversibility has obvious consequences for models of character state change which are discussed in the later section on parsimony analyses. Muscle 116 and the corresponding posterior lobe are present in Monomachidae, Vanhorniidae, Cynipoidea, Ceraphronoidea and most Diapriidae, and it is likely that this complex is the groundplan for Apocrita (Daly 1963; Gibson 1985). The loss of this complex in Pergidae and Orussidae is therefore convergent with the loss in most Apocrita.

Synonymy for muscle 116:

Symphyta: 21 (*Euthomostethus*, Maki 1938). Symphyta, Monomachidae, Diapriidae, Vanhorniidae, Ceraphronoidea, Cynipoidea: t_2 -2ph (Daly 1963; Gibson 1985). Hymenoptera: t12 (Matsuda 1970).

Character 5. Mesopostnotum and scutellar-metanotal muscle

In Neuropterida and Mecopterida, the mesopostnotum is broadly exposed medially; although in *Corydalus* (Megaloptera) the mesopostnotum is weakly sclerotized medially and appears to be split. The scutellar-postnotal muscle (muscle 114, t_2 - t_3 ; absent in *Bittacus*) passes internally from its origin on the scutellar area of the mesonotum to the anterior medial margin of the mesopostnotum (Kelsey 1957; Matsuda 1970). Within Hymenoptera, changes in the structure of the mesopostnotum and attachment of muscle 114 are correlated; however, the attachment of muscle 114 to the mesopostnotum is unique with respect to the outgroup, and the outgroup is scored as a separate state (**state 0**).

In Hymenoptera, muscle 114 (t_2 - t_3) arises dorsomedially from a fan-shaped attachment on the mesonotum and passes medially over the mesopostnotum (rarely under), to a narrow medial attachment on the anterior margin of the metanotum. In all Symphyta, our dissections indicate a posterior attachment of muscle 114 to the metanotum. Our observations are supported by illustrations of attachments to the metanotum in Weber (1925) for *Vespa* (his IIdm₂) and Märkl (1966) for *Apis* (his 70). In *Eutomostethus* (Tenthredinidae), muscle 114 was described as inserting on the median membrane that divides the mesopostnotum (Maki 1938, his 19 & 20), but in Tenthredinidae muscle 114 passes through the membrane to the metanotum. The attachment of muscle 114 to the metanotum is apomorphic for Hymenoptera.

Determination of the groundplan condition for Hymenoptera is complicated by the presence of different character states in the two extant subfamilies of Xyelidae. In Xyelinae (Xyelidae) (based on *Pleuroneura*, Fig. 47, and *Xyela*), the mesopostnotum (PN₂) is broadly exposed dorsally and the scutellar-metanotal muscle (114, t_2 - t_3) passes under the mesopostnotum through a small emargination of its posterior margin (**state 1**, broadly exposed and 114 internal). In Macroxyelinae (Xyelidae) (based on *Macroxyela ferrunginea* (Say), *Megaxyela tricolor* Norton, *Megaxyela aviingrata* (Dyar) and *Xyelicia nearctica* Ross), Megalodontoidea (Fig. 48), Tenthredinoidea and Cephioidea (Fig. 49), the mesopostnotum is exposed dorsally (depending on the contortion of

the mesosoma) and muscle 114 passes externally over the mesopostnotum as a tendon enclosed by a sheath of connective tissue (**state 2**, broadly exposed and 114 external). In groups with an external muscle and an exposed mesopostnotum (state 2), the anterior medial margin may be shallowly or deeply emarginate (appearing split) underneath muscle 114. In some genera of Tenthredinidae and Diprionidae, the mesopostnotum is obscured by posterior development of the scutellum, but otherwise conforms to state 2 (see Character 6).

In Anaxyelidae, the mesopostnotum and muscle 114 are the same as in Xyelinae (Fig. 47). Initially, we coded this as the same character state (**state 1**). However, this caused problems in developing an additive coding scheme that would force the anaxyelid state to be autapomorphic and not transitional between states 2 and 4. To resolve this problem, Anaxyelidae were assigned a new character state (**state 3**), which is treated as an autapomorphy. In all of the analyses, coding for Anaxyelidae and Xyelinae as state 1 or state 3 had no effect on tree topology.

In Siricidae, a median vertical process on the anterior margin of the metanotum forms the posterior attachment of muscle 114, which is internal and lacks any connective sheath. Although the process is unique for Hymenoptera, this conformation is considered to be a modification of state 2 even though the mesopostnotum is generally not exposed. The scutellum often extends over the metanotal process and, as in some Tenthredinoidea, the internalization of muscle 114 and mesopostnotum may be secondary. Snodgrass (1910) reported that the mesopostnotum of *Tremex columba* was exposed medially; however, we observed an exposed mesopostnotum only in some specimens of *Urocerus*. Some Cephidae (Fig. 49) also have a similar attachment to a peg-like process (mp) on the metanotum.

In Xiphydriidae (Fig. 50), Orussidae and Apocrita, muscle 114 (t_2 - t_3) and the mesopostnotum (medially) are completely internal and muscle 114 passes medially over the second phragma (**state 4**). An autapomorphic modification of state 4 is found in Xiphydriidae, in which the cuticle of the second phragma (between the lobes of the pseudophragma) encircles the muscle tendon as it passes through to the metanotum. Further development of the mesopostnotum and its associated

phragma in Apocrita is toward an even greater degree of internalization and a lateral shift of the points of articulation with the scutellum and metanotum (Snodgrass 1910) (see character 10). In Aculeata (Fig. 53), the second phragma is almost entirely disassociated mesally and the notal attachments are reduced to lateral lamellae along the extreme lateral margins (Snodgrass 1942).

Synonymy for muscle 114:

Tenthredinidae: 19 & 20 (*Euthomostethus*, Maki 1938). Ichneumonidae: 20 & 21 (*Psilopsyche*, Maki 1938). Aculeata: Ildlm₂ (*Vespa*, Weber 1925); 23 (*Vespa*, Maki 1938); IIs1 (*Vespula*, Duncan 1939); 70 (*Apis*, Märkl 1966); t₂-t₃ (*Apis*, Daly 1963). Hymenoptera: t13 (Matsuda 1970, Brodskiy 1992).

Character 6. Formation of pseudophragma

The postphragma (2ph) originates at the junction of the mesopostnotum and metanotum and forms the posterior attachment site for the longitudinal flight muscles (112, 1ph-2ph) (Snodgrass 1910). In Mecopterida, Neuropterida, Xyelidae (Fig. 47), Megalodontoidea (Fig. 48) and Tenthredinoidea, the anterior margin of the mesopostnotum is broadly attached to the posterior margin of the mesonotum (scutellum) by a narrow conjunctiva (60, term from Ronquist and Nordlander 1989) (**state 0**). In Cephidae (Fig. 9b), Anaxyelidae, Siricidae (Fig. 11b), Xiphydriidae and Apocrita, the anterior margin of the mesopostnotum is developed into a broad bilobed internal plate (pseudophragma) that extends anteriorly and dorsally beyond the dorsal attachment of the mesopostnotum to the mesonotum (**state 1**). The pseudophragma is an extension of the second phragma and both form the posterior attachment for the longitudinal flight muscles (1ph-2ph). A pseudophragma is not apparent in Orussidae (Fig. 13) and some Ichneumonidae and has probably been lost.

Characters 7-8. Furcal-spina muscles

In Xyeloidea (Fig. 3) and Pamphiliidae (Fig. 2, indicated by dashed line), muscles 127 (fu₂-sps₁) and 180 (fu₃-sps₂) connect the spina with the furca of the following segment (**state 0**). Muscle 127 is present in both Neuropterida and Mecopterida and muscle 180 is found only in Neuropterida (Maki 1938, Kelsey 1957, Matsuda 1970); we veri-

fied their presence only in *Corydalus*. Muscle 127 is lost (**state 1**, character 7) in all Hymenoptera except the Xyeloidea and Megalodontoidea. Rasnitsyn (1969, fig. 204) illustrates a muscle connection (127?) between sps₁ (his sst) and fu₂ in *Tremex* (Siricidae), but we did not observe this in either *Tremex* or *Urocerus*. The loss of muscle 180 (**state 1**, character 8) is a synapomorphy of Apocrita.

Synonymy for muscle 127:

Apidae: fu₂-1sps [pupal muscle only] (*Apis*, Daly 1964). Hymenoptera: s12 (Matsuda 1970; not listed by Matsuda for Hymenoptera).

Synonymy for muscle 180:

Symphyta: IIVlm₁ (*Dolerus*, *Schizocerus*, *Tenthredo*, Weber 1927).

Character 9. Furcal-basalare muscle

The furcal-basalare muscle (fb1, fu₂-ba₃) appears to be found only in Hymenoptera (**state 1**). The muscle is apparently absent in the outgroup (**state 0**). Muscle fb1 could be homologous with Matsuda's p-s3 which connects the furca to the anterior margin of the succeeding episternum. Muscle p-s3 is found in Neuropterida (IIPm17, Korn 1916 for *Myrmeleon*), but apparently not in other Neuropterida or Mecopterida (Matsuda 1970). In Symphyta (Figs. 2, 3, 5-13) muscle fb1 extends from the extreme lateral apex of the mesofurcal arm to the apodeme of the basalare of the hindwing (ba₃). This muscle was first illustrated, but not discussed, by Rasnitsyn (1969, fig. 204) for *Tremex*. In Diprionidae (Fig. 7), muscle fb1 ends in a sclerotized cap attached to the apodeme of the basalare, along with muscle 137 (t₃-ba₃) which originates from the posterior face of the laterophragma (t₃).

Muscle fb1 is absent (**state 0**) in most Apocrita. However, what appears to be the same muscle occurs in Mutillidae (Fig. 18), Rhopalosomatidae (Fig. 19) and Bradynobaenidae (**state 1**). The muscle in these taxa originates laterally on the mesofurcal arms (dorsal to the furcal-trochanteral muscle, muscle 174) and narrows to a fine tendon that enters the pleural area near the base of the hind wing. The dorsal point of insertion was not observed but the muscle enters the pleural area posterior to the subalar muscle of the mesothorax and may insert onto the basalare or axillary sclerites of the hind wing. No such muscle was observed in

other Apocrita. The loss of muscle fb1 in Apocrita could be the result of a shift of the muscle origin from the furca to the pleural wall. Gibson (1986) reported a unique muscle in Eupelmidae and Pteromalidae (pl_2-3ax_3a) that attached between the lower mesepimeron and possibly the metathoracic third axillary sclerite (of uncertain insertion; Gibson pers. comm. 1993). The homology of fb1 with the pleural muscles is beyond the scope of this study.

Character 10. Lateral articulation of mesopostnotum

In Xyeloidea, Megalodontoidea (Fig. 51) and Tenthredinoidea and the outgroup taxa, the mesopostnotum is broadly and evenly joined to the upper mesepimeron (state 0). In Cephidae (Fig. 52), Anaxyelidae and Siricidae, the juncture is invaginated and connected by weak cuticle within the invagination, but maintains a strong cuticular connection at the anteriormost point of attachment (state 1). In Xiphydriidae, Orussidae and Apocrita, the mesopostnotum is completely internal and the lateral connection of the mesopostnotum to the upper mesepimeron is reduced to the anteriormost point of attachment (state 2).

Character 11. Fusion of lateral arms of mesofurca and metafurca

In most Aculeata the lateral arms of the mesofurca and metafurca are closely appressed, but as in most other Hymenoptera and the outgroup taxa, they are broadly separated and joined by the interfurcal muscle 181 (state 0) (Fig. 3). In Apoidea (Figs. 46, 53), the lateral arms of both furcae are fused at the junction with the mesofurcal bridge and the interfurcal muscle is lost (state 1). The lower furcal arms form a four-cornered brace for the furcal complex, and the metafurcal arms are divided lateral to the furcal bridge. A similar fusion of the mesofurca and metafurca occurs in Amiseginae (Chrysididae; Fig. 39) and Gasteruptiidae (Fig. 26), but in both cases muscle 181 is retained and these are considered to be non-homologous and autapomorphic changes. Additional coding as autapomorphic states is unnecessary for this analysis but may be warranted in more extensive studies of related taxa.

Character 12. Furcal process for trochanteral muscle 174

In most Hymenoptera and the outgroup taxa, the furcal depressor of the trochanter (muscle 174, fu_2-tr_2) attaches to the lateral arms of the mesofurca (Fig. 3) (state 0). In Chrysididae (Cleptinae and Chrysidinae), muscle 174 attaches to anterior extensions of the lateral furcal arms (Fig. 40, vp) (state 1). In Pompilidae (Fig. 42), Sapygidae, Scoliidae, Sierolomorphidae and Vespidae (Fig. 41), muscle 174 attaches to similar extensions (vp) that arise instead from the furcal bridge (state 2). In Vespoidea, muscle 174 has two origins - the lateral furcal arms and the ventral process (= scoop shaped processes, schT, Weber 1925; anterior process of mesofurcal bridge, PF₂, Duncan 1939).

PHYLOGENETIC HYPOTHESIS FOR
HYMENOPTERA

Figs. 55, 56

The higher classification of Hymenoptera has come under increasing scrutiny following reviews published by Königsman (1977, 1978a) and Rasnitsyn (1969, 1980). Königsman (1978a) presented evidence that Hymenoptera was comprised of two monophyletic sister taxa, the Symphyta (excluding Cephoidea) and Cephoidea + Apocrita, with most apocritan families presented as a series of unresolved lineages. Although this more traditional concept of the Symphyta is still used (Zessin 1985), it has not been accepted in more recent papers except to present an alternate hypothesis of relationships (Gauld and Bolton 1988). Rasnitsyn (1980) presented evidence that Symphyta is paraphyletic relative to Apocrita with Cephoidea as the sister group of Apocrita. Studies subsequent to Rasnitsyn (1980) (Gibson 1985, 1986; Naumann and Masner 1985; Carpenter 1986) led Rasnitsyn to modify his original hypotheses in a later paper (Rasnitsyn 1988), in which Cephoidea were placed as a more basal lineage of Hymenoptera and Orussidae as the sister group of Apocrita. A far more resolved set of relationships among the parasitic Apocrita (Fig. 56) were presented by Rasnitsyn (1988). Some of Rasnitsyn's hypotheses have been corroborated in recent morphological or phylogenetic treatments (Johnson 1988; Whitfield et al. 1989), although Gibson (1993) presented evidence against the biphyletic origin of Hymenoptera from Xyelidae and Brothers and Carpenter (1993) sup-

ported a different hypothesis for Chrysidoidea and Aculeata. For our data, these modifications affect only the distribution of character 12 in the Aculeata, and have no effect on the parsimony arguments presented in a later section. Cladograms comparing the hypotheses of Rasnitsyn and Königsman are presented in Whitfield (1992).

Rasnitsyn (1980, 1988), Shcherbakov (1980, 1981) and Gibson (1993) have proposed Xyelidae as the most basal extant lineage of Hymenoptera. As well as possessing a branched Rs vein, Xyelidae retain the anepisternum as an integral part of the pleuron and retain the plesiomorphic condition of a relatively equally proportioned meso- and meta-thorax (Gibson 1993). Other than the structure of the antenna, which may be plesiomorphic, there are no features that support the monophyly of the Xyelidae, and Rasnitsyn (1988) proposed that the two subfamilies of Xyelidae belong to two lineages of Hymenoptera (Hymenoptera biphyletic with respect to the two subfamilies). Gibson (1993 and personal communication, 1993) argues that Hymenoptera excluding Xyelidae are monophyletic but that no characters support the monophyly of the Xyelidae. The mesofurcal-mesopostnotal complex of Pamphiliidae and both subfamilies of Xyelidae are basically the same and we consider them to represent the plesiomorphic condition for Hymenoptera.

Rasnitsyn (1988) classified the suborder Siricina into three infraorders that include the following extant families: Xyelomorpha (Xyelidae), Tenthredinomorpha (Argidae, Blasticotomidae, Cimbicidae, Pergidae and Tenthredinidae [including Diprionidae]), and Siricomorpha (including Megalodontoidea [=Pamphilioidea]: Pamphiliidae and Megalodontidae; Cephoidea: Cephidae; Siricoidea: Anaxyelidae, Siricidae and Xiphydriidae). Rasnitsyn (1988) treated Xyelidae as paraphyletic with respect to Tenthredinoidea and remaining Hymenoptera, and the three families of Siricoidea are paraphyletic with respect to the Orussidae + Apocrita (Suborder Vespina). Rasnitsyn (1988) placed Cephoidea as basal to the Siricoidea + Apocrita, rather than sister group to the Apocrita as in his earlier treatments (Rasnitsyn 1969, 1980).

As a framework for evaluating our results, we have compiled the results of Rasnitsyn (1988) and Gibson (1985, 1993) to derive the cladogram presented in Figure 55. Contrary to Rasnitsyn (1988), Hymenoptera excluding Xyeloidea are treated as monophyletic based on the presence of a postspiracular sclerite (=detached anepisternum) (Gibson 1985, 1993) and an apically simple Rs vein that is not bifurcate (Rasnitsyn 1988). Xyelidae are treated as paraphyletic to allow for discussion of Character 5. Tenthredinoidea are monophyletic and placed here as sister group to the remaining Hymenoptera, excluding Xyeloidea and Megalodontoidea, based on a reduction in the number of preapical tibial spurs (from 2-4 spurs on the hind legs in Xyeloidea and Megalodontoidea to less than 1 in Tenthredinoidea, 1-2 in Cephoidea and 0 in remaining Symphyta and Apocrita; H. Goulet and G. Gibson, pers. comm., 1993), and the loss of the ventral mesofurcal-spina muscle, fu_2 -sps₁, which is present only in Xyeloidea and Megalodontoidea (see Character Analysis).

Remaining infraorders of extant Vespina proposed by Rasnitsyn (1988) include the Orussomorpha, Evaniomorpha (Stephanoidea, Evanioidea), Proctotrupomorpha (Proctotrupoidea, Cynipoidea, Chalcidoidea), Ichneumonomorpha (Ichneumonoidea), and Vespomorpha (Chrysidoidea, Sphecoidea, Pompiloidea, Scolioidea, Formicoidea and Vespoidea). Recent classifications (Naumann 1992; Huber and Goulet 1993) treat the five families of Rasnitsyn's Stephanoidea as higher taxa (Ceraphronoidea [Ceraphronidae and Megaspilidae], Megalyroidea, Stephanoidea and Trigonalynoidea). Following Brothers (1975) and Huber and Goulet (1993), the Aculeata are referred to only three superfamilies (Chrysidoidea, Apoidea and Vespoidea) and Mymarommatidae are placed as a superfamily.

GROUP ANALYSIS

Character states are referred to in brackets as [character:state]. Relationships are discussed according to the phylogenetic hypotheses illustrated in Figures 55 and 56. The distribution of character states for each taxon are listed in Appendix 2.

Xyeloidea + Megalodontoidea + remaining Hymenoptera

Figs. 1, 2, 3, 4, 6, 47, 48, 51

Four characters of the mesofurcal-mesopostnotal (MF-MPN) complex are not found in the outgroups and therefore support the monophyly of Hymenoptera: long anterior arms of the mesofurca [1:1]; two furcal laterophragmal muscles [3:1]; muscle 114 attaching to the metanotum (part of Character 5, see below); and furcal-basale muscle (fb1, fu_2 -ba₃) present [9:1].

Xyeloidea and Megalodontoidea are plesiomorphic for all characters postulated for Hymenoptera in the mesofurcal-mesopostnotal complex. Megalodontidae were verified for external characters only and the presence of anterior furcal arms [1:1] was based on fig. 189 in Rasnitsyn (1969). Rasnitsyn (1969) also refers to the mesofurco-metapre-episternal muscle as found only in *Xyela*. This muscle was not identified in our dissections, although it may be synonymous with muscle 127 (fu_2 -sps₁).

The mesopostnotum is external and broad medially in both Xyeloidea and Megalodontoidea. In extant Xyelinae (Xyelidae), the mesopostnotum is entire medially and muscle 114 is internal [5:1, Fig. 47]. A similar conformation is found in the outgroup, but the attachment of muscle 114 is different [5:0]. In Macroxyelinae (Xyelidae), Megalodontoidea and Tenthredinoidea, the mesopostnotum is almost completely separated medially and muscle 114 passes externally [5:2, Fig. 48]. The deep emargination of the mesopostnotum associated with state 5:2 is visible externally and can be interpreted from fossil Hymenoptera. Based on illustrations in Rasnitsyn (1969), external passage occurs in the fossil xyelids: Archexyelinae: *Asioxyela* (fig. 34), *Leioxyela* (fig. 41), *Triassoxyela* (fig. 32), *Xiphoxyela* (figs. 45, 46); Macroxyelinae: *Agaridyela* Rasn. (fig. 41), *Chaetoxyla* Rasn. (fig. 76), *Ceroxyela* Rasn. (fig. 77); and Xyelinae: *Eoxyela* Rasn. (fig. 59), *Lydoxyela* Rasn. (fig. 68), *Spathoxyela* Rasn. (fig. 42), *Xyelisca* Rasn. (fig. 61), and *Xyela mesozoica* Rasn. (fig. 62). If correctly interpreted in fossil Xyelinae, the internal passage of muscle 114 and an entire mesopostnotum are derived within extant Xyelinae, and the external passage of muscle 114 and an emarginate mesopostnotum are probably apomorphic for Hymenoptera.

Tenthredinoidea + remaining Hymenoptera

Monophyly of Tenthredinoidea and the remaining Hymenoptera is supported by the loss of muscle 127 (fu_2 -sps₁) [7:1].

Tenthredinoidea

Figs. 5, 7-8, 20, 21

The anterior mesofurcal arms are reduced or lost in all Tenthredinoidea [1:2].

Blasticotomidae (Fig. 20)

The plesiomorphic combination of muscles is present. Anterior furcal arms are present, but they are short and thin. As discussed earlier (analysis of character 1), because of uncertainties in the homology of reduced arms, we have scored both reduced and absent anterior furcal arms as the same character state (1:2). The anterior apodeme of the laterophragma is absent and both 150a and 150b attach to the apex of the posterior lobe (Fig. 20a). This is considered to be an autapomorphic development, but there is also a general similarity with the laterophragma of *Nematus* (Fig. 19), in which short anterior furcal arms are also present.

Tenthredinidae (Fig. 21)

The plesiomorphic combination of muscles is present in all taxa examined, and the structure of the laterophragma is the same as in Xyelidae and Pamphiliidae. The anterior arms of the mesofurca vary from narrow, elongate apodemes extending from the anterior face of the lateral arms (*Nematus*), to short cup-like structures similar to those found in Diprionidae, to completely absent (most Tenthredinidae). Muscle 180 (fu_3 -sps₂) was not found in *Eutomostethus* (Blennocampinae) (Maki 1938).

Diprionidae (Fig. 7)

The plesiomorphic combination of muscles and structures for Tenthredinoidea are present but with the following apomorphic features: anterior arms reduced to cup-like receptacles for muscle 124; anterior process of laterophragma expanded and forming a broad attachment for 150a; and muscle 150b originates medially to 150a on the lateral furcal arms.

Cimbicidae (Fig. 8)

The anterior arms are reduced to small spoon-shaped processes, the posterior lobe of mesopostnotum is fused to second phragma forming attachment for a large muscle 116, and muscle 150b is lost [3:2]. The anterior process of the laterophragma is enlarged and extends ventrally into the cup-shaped lateral arm of the mesofurca (autapomorphy).

Argidae + Pergidae

The lateral arms of mesofurca are tubular and hollow (apomorphic), the anterior arms of the mesofurca are absent, and the attachment site for muscle 124 (fu_1 - fu_1) is to the rounded surface of the lateral arms. Although they would suggest a sister group relationship for these two families, these characters were not surveyed throughout Hymenoptera and were not coded for the parsimony analysis.

Argidae

The laterophragma and its associated muscle attachments are as in Tenthredinidae.

Pergidae (Fig. 5)

This family displays a number of autapomorphies: loss of the tergal depressor muscle (116) [4:1] and the associated posterior lobe of the laterophragma [2:2], and loss of one of the furcal laterophragmal muscles (possibly 150b) [3:2]. The laterophragma is reduced to a small triangular lobe that ends in a narrow attachment to muscle 150. The lateral arms form a cup-shaped attachment for muscles 150 and fb1. A sclerotized apodeme, probably derived from the lateral arm and muscle 151 (pl_2 - fu_{2a}), extends laterally to the pleural ridge. Ventrolateral extensions of the lateral arms are developed as insertions for the enlarged muscle 170 (pl_2 - fu_{2b}).

Cephidae + remaining Hymenoptera

Figs. 9, 49, 52

Monophyly of the Cephidae and the remaining Hymenoptera is supported by a suite of characters: apical connection of the anterior mesofurcal arms [1:3], formation of a pseudophragma [6:1], and invagination of the mesopostnotum laterally [10:1]. The pseudophragma is not present in all Hymenoptera, but its complete absence in the

lower Hymenoptera and presence in Cephidae, Anaxyelidae, Siricidae, Xiphydriidae and most Apocrita suggest that it is a synapomorphy at this level. There are no published accounts which make reference to a pseudophragma occurring elsewhere within Endopterygota.

Cephidae are plesiomorphic for other characters of the mesofurcal-mesopostnotal complex: muscles 116, 150a, 150b, and fb1 are present, and the laterophragma is divided into a large posterior lobe and a small anterior process. The mesopostnotum is usually exposed medially but is sometimes concealed by the scutellum. Muscle 114 passes externally over the mesopostnotum in all genera (plesiomorphic) and may arise dorsomedially from a vertical process on the metatergum (*Calameuta* Konow, *Cephus* Latrille [mp, Fig. 49], *Monolopopus* Konow, *Syrista* Konow and *Trachelus* Jurine) as in Siricidae, or from an emargination of the metatergum (*Caenocephalus* Konow and *Janus* Stephens) as in Anaxyelidae.

Anaxyelidae + (Siricidae + (Xiphydriidae + (Orussidae + Apocrita)))

Fig. 10

Monophyly of the Anaxyelidae and remaining Hymenoptera is based on a more complete fusion of the anterior arms of the mesofurca [1:4]. Fusion of the anterior mesofurcal arms in Anaxyelidae (Fig. 10a) appears to be more complete than in Siricidae (Fig. 11a) in which the arms are fused in about the anterior half. The anterior arms of Anaxyelidae (Fig. 10a) are still traceable in dorsal view and they are connected posteriorly by a thin plate of cuticle. The greater degree of fusion of the arms is probably autapomorphic in Anaxyelidae; however, in Anaxyelidae and Siricidae the fusion is intermediate between the apical connection found in Cephidae and the complete fusion including a strong furcal bridge found in Xiphydriidae + Orussidae + Apocrita. In Anaxyelidae, Siricidae and Xiphydriidae, muscle 150b inserts onto the posterior face of the laterophragmal lobe rather than to the ventral margin as in Xyeloidea, Megalodontoidea, Tenthredinoidea and Cephoidea. As the muscle is absent in Orussidae and Apocrita, the importance of this unique attachment as a character for supporting monophyly of Siricoidea (including Anaxyelidae and Xiphydriidae) or Siricoidea +

Orussoidea + Apocrita cannot be assessed.

In Anaxyelidae, the presence of both furcal-laterophragmal muscles (150a & 150b) and anterior origin of muscle 150b on the furcal arms is plesiomorphic. The mesopostnotum is broadly exposed medially and muscle 114 (t_2 - t_3) passes under the mesopostnotum medially (autapomorphy; 5:3). The dorsal enclosure of muscle 114 in Anaxyelidae may result from the extension and medial fusion of the anterior margin of the mesopostnotum. Rasnitsyn (1969, fig. 99) illustrates a split mesopostnotum [5:2] for the fossil *Anaxyela gracilis* Martynov. This supports the contention that an internal muscle 114 is derived within Anaxyelidae.

Siricidae + (Xiphydriidae + (Orussidae + Apocrita))

Fig. 11

No characters of the mesofurcal-mesopostnotal complex demonstrate the monophyly of Siricidae and the remaining Hymenoptera. The anterior mesofurcal arms of Siricidae (Fig. 11) are vertically flattened and in dorsal view are distinct along their entire length. The degree of fusion of the anterior arms is intermediate between Cephidae and Xiphydriidae + Orussidae + Apocrita, but, as discussed above, is comparable to that found in Anaxyelidae. Siricidae are autapomorphic for the loss of muscle 150a (along with the anterior process of the laterophragma) [3:3]. The posterior attachment of muscle 114 (t_2 - t_3) to a vertical process of the metanotum is shared with some Cephidae but not with Xiphydriidae, Orussidae or Apocrita, which lack a process. Internal passage of muscle 114 in Siricidae may result from the posterior extension of the scutellum rather than internalization of the mesopostnotum as in Cephidae and Tenthredinoidea.

Rasnitsyn (1988) proposed that Siricidae + remaining Hymenoptera were monophyletic based on four synapomorphies: 1) compound third antennal segment reduced and subequal to the following segments, 2) head capsule with postgenae subcontiguous, divided with narrow hypostomal bridge, 3) transscutal articulation present, and 4) prepectus concealed. In Anaxyelidae, the primitive state of a compound third antennal segment is found only in the fossil anaxyelid genus *Sphenosyntexis* Rasnitsyn; the derived state is found

in the remaining genera of Anaxyelidae including the only extant species, *Syntexis libocedrii* Rohwer. However, the antennal flagellum is apomorphic (reduced and divided) in Xyeloidea, Megalodontoidea, Tenthredinoidea, Cephoidea and within Anaxyelidae, and thus its reduction in Siricidae and remaining Apocrita is not a reliable character. The postgenae meet broadly along the medial line to form a postgenal bridge (=genaponta *sensu* Ross 1937) in Anaxyelidae, Siricidae and Xiphydriidae; we agree with Ross (1937) that the postgenae of Anaxyelidae and Xiphydriidae are similar and thus Anaxyelidae cannot be excluded from Siricoidea based on this character. Gibson (1985) demonstrated that a transscutal articulation is absent in Cephidae, Anaxyelidae and Siricidae. The presence of a concealed prepectus is useful for supporting the monophyly of Siricidae + Xiphydriidae + Orussidae + Apocrita (Rasnitsyn 1988; Gibson 1985).

Xiphydriidae + (Orussidae + Apocrita)

Fig. 12

There is strong support in the MF-MPN complex for the monophyly of Xiphydriidae, Orussidae and Apocrita. The anterior mesofurcal arms are completely fused into an anterior furcal process (fp) and posteriorly strengthened to form a transverse mesofurcal bridge (fb) [1:4], with the exception of some Apocritan taxa in which the mesofurcal bridge is lost. In addition, the mesopostnotum is completely internal medially [5:4] and laterally [10:2], and the laterophragma is strongly incised with the anterior process (ap) developed into a strong apodeme [2:1]. The plesiomorphic combination of muscles in the MF-MPN complex is retained. Among the Cephoidea, Siricoidea and Orussoidea, Xiphydriidae are unique in having muscle 150b attached to the lateral arms of the mesofurca (versus the anterior arms or furcal process). Muscle 124 (fu_2 - fu_1) is broadly attached to the furcal process and bridge. In Xiphydriidae, the tendon of muscle 114 (t_2 - t_3) is enclosed medially, and internally, by the cuticle of the second phragma (autapomorphic).

Orussidae + Apocrita

Fig. 13

No synapomorphies were found in the

mesofurcal-mesopostnotal complex that support the monophyly of Orussidae + Apocrita without Xiphydriidae. It is possible that the loss of muscle 150a supports the monophyly of Orussidae + Apocrita [3:2 = 3:2]. However, the homology of the remaining muscle 150 in Orussidae is uncertain (see discussion of Character 3). Therefore, it is also possible that muscle 150b is lost in Orussidae and 150a is lost in Apocrita.

Orussidae have at least three apomorphic features in the MF-MPN complex, two of which are also found in Pergidae and Cimbicidae. The furcal bridge (fb) is rounded and bowed anteriorly with a distinct median process (fp) [1:6]. The attachment of muscle 150 to the furcal process is found only in Orussidae. In Apocrita, muscle 150a is usually attached to the furcal bridge or lateral arm. Otherwise the furcal bridge and process in Orussidae are similar to Xiphydriidae and other Apocrita. Muscle 116 is lost [4:1] in Orussidae, and there is an associated reduction of the laterophragma to a small triangular lobe that forms the attachment for muscle 150 [2:2]. Additional autapomorphies in Orussidae include loss of the pseudophragma [6:0] and the configuration of muscle 180 (fu_3 - sps_2) which arises from the spina as a single narrow tendon that bifurcates about half-way along its length to the metafurcal arms (the plesiomorphic configuration is completely separated along its entire length).

Apocrita

Figs. 14-19, 22-46, 53, 54

The loss of two muscles in the MF-MPN complex supports the monophyly of the Apocrita: the metafurcal-spina muscle (180, fu_3 - sps_2) [8:1] and the furcal-basalare muscle (fb1, fu_2 - ba_3) [9:0]. Muscle 150b (fu_2 - pn_{2a}) [3:2] is lost in all Apocrita including those that retain the posterior lobe of the laterophragma. However, as discussed above, the homology of the remaining muscle 150 in Orussidae is not clear, and therefore loss of 150a is either a synapomorphy of Orussidae + Apocrita or an autapomorphy of Apocrita. Loss of muscle 137 may also support the monophyly of Apocrita (see discussion for Character 2).

Shcherbakov (1981) stated that muscle 170 (pl_2 - fu_{2b} , s-cx2) is connected to the coxal process of the mesopleuron in all Hymenoptera. Based on our observations, it is well developed in all

Symphyta and attaches laterally to the mesofurcal arms (Figs. 3, 5, 9b, 12b, 13). In Apocrita, the position of muscle 170 shifts from the apex of the furcal arms to the base of the furca and is more nearly horizontal. This is most apparent in Vespoidea (cf. Duncan 1939, muscle II fp_{l2} (71)).

The laterophragma of Cynipoidea, some Diapriidae, Monomachidae (Fig. 14) and Vanhorniidae (Fig. 15a) are similar in structure with an anterior apodeme (ap) narrowly separated by a deep incision from the posterior lobe (pn_2) [1:5], which supports muscle 116 [4:0]. In Megaspilidae (Fig. 25), the apodeme and lobe may be broadly or narrowly separated. Muscle 116 [4:1] is present only in the families listed above and probably has been lost numerous times within Apocrita (Gibson 1985). It is unlikely that this muscle and associated posterior lobe could be regained once lost. Under the present hypothesis of relationships in Apocrita, muscle 116 and the lobe are lost at least 9 times (10 if also lost in Austroniidae) (Fig. 56). Of these, only in Diapriidae is the muscle lost within an entire family.

Groundplan states for the Apocrita are exemplified by Monomachidae (Fig. 14), Vanhorniidae (Fig. 15), most Diapriidae (Fig. 29) and Cynipoidea (Fig. 22), in which muscle 116 and the posterior lobe of the laterophragma are retained (Daly 1963; Gibson 1985). Plesiomorphic attributes of Apocrita include 1) presence of a median furcal process (fp) forming the attachment for muscle 124, 2) furcal bridge complete (fb) [1:4], 3) muscle 150a originating laterally on the bridge or the lateral arm of the mesofurca, 4) laterophragma divided into an anterior apodeme and posterior lobe [2:1], 5) presence of the tergal depressor muscle (116) [4:0], 6) mesopostnotum internal [10:2] and 7) prephragma present [6:1]. Ceraphronoidea (Fig. 25) have lost the mesofurcal bridge [1:7] but retain a divided laterophragma, and in some Diapriidae (Fig. 22) the posterior lobe of the laterophragma is lost [4:1].

Apart from changes in the laterophragma, apomorphic changes of the MF-MPN complex in Apocrita include loss of the mesofurcal bridge [1:7] and changes in the structure of the anterior apodeme (=axillary lever) of the laterophragma [2:3-6]. Changes in the shape of muscle 150a, lateral arms, furcal bridge and second phragma are homoplastic and probably related to changes in thoracic shape. Notable exceptions in Aculeata include development of an axillary lever [2:5] that

is separated in Apiformes [2:6], fusion of the lateral arms of the mesofurca and metafurca [11:1], development of processes on the mesofurca for the furcal-trochanteral muscle [12:1,2], and a medial reduction of the attachment points (60 & 61) between the second phragma and terga.

The cladogram presented in Figure 56 is consistent with the relationships proposed by Rasnitsyn (1988) and Brothers and Carpenter (1993) for extant Apocrita, and is used as the model for examination of character state change within Apocrita. Apart from the modifications in Aculeata, the MF-MPN complex offers little support for phylogenetic relationships proposed for Apocrita. Within Apocrita a total of 22 steps are required to explain the distribution of character states as modelled on Figure 56 (excluding changes in the Chalcidoidea + Platygastroidea + Mymarommatoida trichotomy, Austroniidae and Peradeniidae). Given that the tergal depressor muscle and posterior lobe of the laterophragma are present [4:0] in what are assumed to be relatively derived groups (e.g., Cynipoidea, Diapriidae and Monomachidae), this complex must be lost a minimum of 9 times (or 10 times if it is absent in Austroniidae). Only 8 losses are required if Pelecinidae and Vanhorniidae are monophyletic (Fig. 56). An additional 3 losses of muscle 116 [4:1] are required using Königsmann's (1978a) hypothesis for Apocrita. Obviously, loss of this muscle does not offer strong evidence for the monophyly of Megalyroidea, Stephanoidea and Trigonalyoidea (Fig. 56).

Among the parasitic families of Apocrita, the mesofurcal complex of Gasteruptiidae (Fig. 26) and Evaniidae (Fig. 27) were very different from each other. However, the mesofurcal bridge of Aulacidae and Evaniidae are similar in shape (broad and flattened with muscle 124 attaching under the anterior margin of the bridge). In all three families the axillary lever is strongly inflected and perpendicular to the lateral wall of the mesosoma (Figs. 26, 27), and the lever is connected by a long thin tendon to muscle 150a. Scelionidae and Chalcidoidea both have a similar mesofurcal bridge (bowed with the median process virtually absent) which may indicate a sister-group relationship between Chalcidoidea and Platygastroidea. However, given that the bridge is lost in Platygastriidae, Mymarommatidae, Mymaridae and some Chalcidoidea [1:7], it is not clear what

the groundplan state of this character is in either superfamily. Also, the axillary lever is deflected [2:3] in Platygastriidae, some Scelionidae and most Chalcidoidea. Almost all Chalcidoidea including Mymaridae are unique in that muscle 150a attaches to the entire length of the deflected axillary lever (versus only apical attachment). Mymarommatidae have a medially inflected lever [2:1] and muscle 150a is conical and attaches only to the apex of the lever (plesiomorphic). Proctotrupidae (Fig. 32) have a similar axillary lever to that of Platygastriidae (Fig. 28), although it is shorter and not as strongly deflected (Figs. 29-32). In Heloridae (Fig. 30) and Pelecinidae (Fig. 31), the lever is followed by a short spine (pn_2 ?) that has no muscle connection and may be the remnant of the posterior lobe of the laterophragma. Some Proctotrupidae have a blunt triangular lobe in a homologous position. Heloridae, Pelecinidae and Proctotrupidae are the only Hymenoptera with a vestigial posterior lobe of the mesopostnotum. Roproniidae were identical to Heloridae internally except for the lack of a vestigial posterior lobe.

Most Ichneumonoidea (Fig. 17) have a mesofurca consisting of a broad mesofurcal bridge and a strong medial projection. The furcal bridge of Hybrizontinae (Braconidae) (Fig. 33) lacks a median process but this could be autapomorphic. The axillary lever in Ichneumonidae is similar to Vespoidea and Apoidea [2:5]. This may be evidence for the close relationships to Aculeata that have been proposed (Rasnitsyn 1988, Sharkey and Wahl 1992), but a similar lever has not been found in Braconidae or Chrysidoidea.

Chrysidoidea do not have any defining apomorphies of the mesofurca or axillary lever. The arched bridge of Plumariidae (Fig. 34), Sclerogibbidae (Fig. 35) and Embolemidae (Fig. 36) are similar but this feature may be plesiomorphic, as this shape is similar to Stephanidae. The furcal bridge of the single female dryinid examined (Anteoninae) was similar to Bethylinidae (Fig. 38) (relatively straight with a strong apical projection), and the bridge of the male dryinid (Fig. 35) was reduced to a straight bar. Obviously more taxa need to be surveyed to understand the importance of furcal shape in Chrysidoidea. Chrysididae have apomorphies that distinguish taxa at the subfamily level: the fusion of the lateral arms of the mesofurca and metafurca

in Amiseginae (Fig. 39), and extensions of the furca that support the furcal depressor of the trochanter [12:1] in Chrysidinae (Fig. 40) and Cleptinae. These latter two subfamilies also share a reduction of the axillary lever [2:4]. Reduction of the axillary lever and presence of ventral processes in Cleptinae and Chrysidinae do not support the hypothesis of relationships among Chrysididae proposed by Kimsey and Bohart (1990) of Cleptinae + (Amiseginae + Chrysidinae). Based on relationships for Chrysidoidea proposed by Brothers and Carpenter (1993), Carpenter (1986) and Rasnitsyn (1988), the plumariid type of bridge is plesiomorphic, Dryinidae have an independently derived bridge, and Chrysididae + Bethyridae have a relatively broad, straight furcal bridge with a strong medial projection.

Monophyly of the Vespoidea and Apoidea is supported by the development of an axillary lever [2:6], which is subsequently reduced in Bradynobaenidae [2:4] and modified in Formicidae [2:1]. Most Aculeata also have a broad, flattened furcal bridge with muscle 124 attaching to the dorsal and lateral surfaces (Fig. 18), although the bridge is not as well developed in Rhopalosomatidae (Fig. 19), Sierolomorphidae and some Sphecidae (Fig. 46). In Tiphidae (Fig. 44), the furca is convoluted and broadly excavated dorsally. The furcal bridge has several shapes in Vespoidea but their importance for assessing relationships will require a much broader survey of taxa. A strong ventral process (vp) for the furcal depressor of the trochanter (fu_2 - tr_2) confluent with the furcal bridge [12:2] is present in Sapygidae, Sierolomorphidae, Pompilidae (Fig. 42), Scoliidae and Vespidae (Fig. 41). Under the most recent hypothesis of relationships for Vespoidea (Brothers and Carpenter 1993), the ventral process is derived independently in Sapygidae, Pompilidae and Scoliidae + Vespidae, although several models of state change are possible. Mutillidae (Fig. 18), Rhopalosomatidae (Fig. 19) and Bradynobaenidae have apparently retained muscle fb1 (fu_2 - ba_3) [9:1] and have a characteristically shaped mesofurca, however these families are not regarded as sister taxa (Brothers 1975, Carpenter and Brothers 1993).

Apoidea have been separated into two groups, the Apiformes and the Spheciformes (Goulet and Huber 1993). Heterogynidae have been included either within the Spheciformes (see Goulet and

Huber 1993) or as the sister group of Spheciformes + Apiformes (Carpenter and Brothers 1993). Apoidea (Figs. 45, 53), including Heterogynidae, have the arms of the mesofurca and metafurca fused at the junction with the mesofurcal bridge and muscle 181 (fu_3 - fu_2) is lost [11:1]. This feature is unique in Hymenoptera. In Vespoidea (Figs. 41, 42, 44), Spheciformes (Fig. 46) and Heterogynidae, the base of the axillary lever is broadly fused to the lateral arm of the mesopostnotum. All Apiformes have the axillary lever separated from the mesopostnotum as an independent sclerite [2:6] (Fig. 45) (Snodgrass 1942).

PARSIMONY ANALYSIS

The mesofurcal-mesopostnotal complex represents a single system of inter-related characters, and it should not be used alone to form new hypotheses of relationships. However, it is of interest to determine if our interpretations of character state evolution are in fact the most parsimonious for these data. We tried two approaches to explore this question. First, we superimposed the data in Appendix 2 on existing hypotheses of relationships. PAUP Version 3.0s (Swofford 1985) was used to optimize the character state data in Appendix 2 on Figure 55 for Symphyta and Figures 55 and 56 for the entire Hymenoptera (using one fully resolved tree for Apocrita based on Rasnitsyn (1988) and Brothers and Carpenter (1993)). Ibaliidae was used to represent the groundplan of Apocrita in the former case, and each matrix included the outgroup (Appendix 2). All most parsimonious models of character state evolution were examined on these tree topologies.

Characters 1 and 4 are sensitive to assumptions about transformation series. As discussed above (Character Analysis), it seems most reasonable to assume that character 1 can evolve from state 0 to state 1 (unique for Hymenoptera), from state 1 to state 2 or state 3, from state 3 to state 4 and from state 4 to state 5; states 6 and 7 are independent derivations from state 5. Character 1 was ordered using a character state tree (or "stepmatrix" in PAUP) that specified the above transformation series. As discussed earlier, character 4 is treated as irreversible. The assumptions of additive coding for characters 1 and 4 are referred to as the Ordered Characters. Other characters were always treated as nonadditive (unordered).

For Symphyta, the models of character state change shown in Figure 55 are in fact the most parsimonious for that tree topology. 27 steps are required to explain the data (indices of homoplasy are not possible for characters ordered using step matrices). Different models of state change are possible for character 3 (because it is scored as missing in Pergidae and Orussidae) and character 5 (unknown polarity for ingroup). For character 5, the presence of state 2 in fossil Xyelinae argues that this condition is groundplan for Hymenoptera, but it is equally parsimonious (at least for extant taxa) to assume that state 1 is groundplan and state 2 arises in the interval below Macroxyelinae and remaining Hymenoptera (dashed line, Fig. 55). The latter solution would make Xyelidae paraphyletic. Treating all characters as nonadditive (unordered) does not change the tree length (27 steps, consistency index 0.81, retention index 0.77). In fact, the only effect is to allow for a number of alternate models of state change for character 1. In this case, it is equally parsimonious to assume any of states 0, 1, 2 or 3 in the nodes below Tenthredinoidea + remaining Hymenoptera and Cephidae + remaining Hymenoptera, a result that essentially discards the information in the transformation series. Optimizing the ordered data onto alternate hypotheses of Symphyta resulted in longer trees. Rasnitsyn's (1988) tree, with Macroxyelinae as sister group to Tenthredinoidea, is one step longer, because of the parallel loss of muscle 127 [7:1]. Königsman's (1977) tree, with Symphyta monophyletic and Cephidae as sister group to Apocrita, requires 37 steps (character 3 optimized).

For Hymenoptera, similar results were obtained for optimizing the Ordered Character data onto one tree, which is summarized for Apocrita in Figure 56. 58 steps were required to explain the data. Different optimizations were possible for Character 1 for Chalcidoidea + Mymarommatoidea + Platygastroidea (if parallel loss of mesofurcal bridge [1:7] is preferred), and Character 9 in Vespoidea. In the former case, although it is equally parsimonious to assume loss of the mesofurcal bridge (1:7) followed by a gain [1:6], parallel loss of the bridge seems more likely. Likewise, it seems more likely to postulate a parallel loss of the furcal-basalare muscle [9:0] in Vespoidea. Treating all characters as nonadditive decreases the length of the hymenopteran tree by 5 steps because of a

different optimization for Character 4 (treated as irreversible in the ordered analysis) and reversals (4:1 to 4:0) are favoured. For this result, the loss of the posterior lobe of the laterophragma and associated muscle 116 (4:1) would be a synapomorphy of Orussidae and Apocrita and then the presence of both structures (4:0) would have to be regained at least 4 times within Apocrita. Although this may be a more parsimonious solution in terms of the number of steps, we feel it is an unacceptable model of character evolution and the assumption of irreversibility should be invoked.

Parsimony analysis using the branch and bound algorithm (Symphyta) or branch-swapping (Hymenoptera) was then performed on these data to determine if another tree topology would result in a more parsimonious solution. When characters are ordered as above, for Symphyta, 24 trees of 27 steps result (after derooting, condensing and rerooting the resulting trees in PAUP, which is necessary when using directed characters). Coding Anaxyelidae as state 1 (homoplastic) or state 3 (autapomorphic) had no effect on the number of steps or resulting trees. As should be apparent from Figure 55, the basal taxa (Xyelinae, Macroxyelinae and Pamphiliidae) are unresolved in each of the 24 trees. Tenthredinoidea is always resolved as monophyletic but with little or no further resolution and Cephidae is consistently placed as sister group to remaining Hymenoptera, as in Figure 55. Anaxyelidae and Siricidae form a trifurcation with Xiphydriidae + Orussidae + Apocrita while the latter three taxa are essentially unresolved. In other words, there is no more parsimonious interpretation of these data and the most parsimonious solutions are congruent with the data shown on Figure 55. When characters are unordered for Symphyta, 138 trees of 26 steps result. The strict consensus solution for these trees is almost completely unresolved. For Hymenoptera, the lack of character support in Apocrita resulted in a considerably shorter tree (40 steps for the Ordered Characters) but also provided no resolution of Apocritan relationships; the structure of the Symphyta portion remained unchanged.

CONCLUSIONS

The mesofurcal-mesopostnotal complex is a conservative character system that generally ex-

hibits few changes within families of Hymenoptera but undergoes considerable change at higher taxonomic levels. The most significant changes occur in the Symphyta, but additional characteristics of the mesofurcal-mesopostnotal complex provide characters that are useful in inferring relationships within Apocrita.

Of the competing hypotheses for relationships of Symphyta, those in Figure 55 are the most parsimonious using the hypotheses of character state transformation discussed in this paper. Exact search methods using additive (ordered) characters reproduce these relationships with the same number of steps and identical indices of character homoplasy and fit. Siricoidea are recognized as a paraphyletic group with respect to Apocrita. If Xyelidae are paraphyletic with the rest of Hymenoptera (Rasnitsyn 1980, 1988) and Macroxyelinae + Tenthredinoidea are monophyletic, then a minimum of one extra step is required for character 7 (loss of fu_2 - sps_1). In sharp contrast, a monophyletic grouping for Symphyta with Cephidae as sister group to the Apocrita (Königsmann 1977) requires 11 additional steps for the same data. The phylogenetic hypothesis for Apocrita proposed by Rasnitsyn (1988; Fig. 56) was shorter than Königsmann's by only three steps (for character 4). Hypotheses based on parsimony are much shorter for Apocrita, even when characters are ordered, but these hypotheses should not be accepted until they can be included in a larger data set with other character systems.

Monophyly of Orussidae + Apocrita (*Vespina sensu* Rasnitsyn) is supported by 10 external characters of adults (Rasnitsyn 1988) and a shift of the furcal-coxal muscles from a posterior to an anterior attachment on the discriminial lamella of the mesosoma (Johnson 1988). No features of the mesofurcal-mesopostnotal complex discussed here provide support for the monophyly of Orussidae + Apocrita, without Xiphydriidae. The mesofurca and laterophragma of Orussidae is highly derived and the only potential synapomorphy for *Vespina* (Character 3: loss of muscle 150b, fu_2 - pn_{2p}) is probably not homologous. The lack of 2ph-3ph in Siricidae and Xiphydriidae has been proposed as a potential synapomorphy for Xiphydriidae + Siricidae (Whitfield et al. 1992), but this muscle has also been lost independently in *Goniozus* (Bethyridae), *Cleptes* (Chrysididae), Formicidae and *Ampulex* (Sphecidae) (Daly 1963). Monophyly of

Xiphydriidae, Orussidae and Apocrita is supported by four synapomorphies. No evidence in the mesofurcal-mesopostnotal complex supports the inclusion of Xiphydriidae or Orussidae within Siricoidea or the monophyly of Anaxyelidae + Siricidae.

The monophyly of Apocrita is supported based on losses of the muscles fu_2 - pn_{2p} , fu_3 - sps_2 , fu_2 - ba_3 , pl_2 - fu_{2b} , and probably t_3 - ba_3 . Using the evolutionary scheme proposed by Rasnitsyn (1988), characters of the mesofurca and mesopostnotum were less useful for demonstrating relationships within Apocrita. Taxa which have retained the posterior lobe of the laterophragma and the associated muscle 116 are treated by Rasnitsyn (1988) as relatively derived taxa (especially Diapriidae and Cynipoidea). Rasnitsyn's hypothesis requires at least nine independent losses of character 4, if loss of both lobe and muscle is irreversible. This appears to be a poor character for postulating relationships. Loss of the mesofurcal bridge [1:7] could indicate support for the monophyly of Ceraphronoidea, but it is homoplastic within both Chalcidoidea and Platygastroidea. Some changes in shape of the axillary lever or mesofurcal bridge within Apocrita are difficult to categorize or to place into distinct transition series. Distinctive features such as the vestigial posterior laterophragmal lobe of Pelecinidae, Heloridae and Proctotrupidae are reductions and possibly convergent. The development and separation of the axillary lever, fusion of the mesofurca and metafurca, and the retention (or redevelopment) of muscle fb1 provide strong support for relationships within the Aculeata.

Changes in the mesofurcal-mesopostnotal complex probably result from an increased emphasis on the fore wings for flight, reduction of the metathorax and fusion of the first abdominal segment. Although the indirect flight muscles are the main wing depressors, the direct muscles of the mesothorax control flight through modifications of the pronation and rotation of the wings during the downstroke and by controlling the tension of the longitudinal flight muscles, thereby affecting the amplitude of the wing beat (Pringle 1957, 1960, 1961). In Apocrita, the axillary lever acts to turn the apex of the mesophragma and the associated fourth axillary sclerite (Weber 1925). This is a shift in function from the lower Hymenoptera where muscles 150a and 150b twist the posterior lobe of

the laterophragma, initiating a greater force upon the indirect phragmal flexor (muscle 116, $t_2\text{-pn}_2$). The excision of the laterophragma in Xiphydriidae would reduce the effect of the anterior apodeme (= axillary lever) on the posterior lobe. Pringle (1960, 1961) proposed that the pleurosternal and axillary lever muscles control the power generated by the indirect flight muscles and thus the amplitude of the wing beat. The flexibility of the axillary lever reaches a maximum in the Apiformes in which complete separation from the laterophragma results in more powerful leverage upon the associated axillary sclerites of the forewing (Snodgrass 1942).

Homologies may not be clear in taxa from opposite ends of a phylogenetic tree. For example, Weber (1925) discusses the mesofurcal ring (=mesofurcal bridge) of Siricidae and Vespidae as non-homologous. Superficially they do look different, but by examining the intermediate stages the homologies can be verified. Changes in the mesofurca and mesopostnotum provide a number of characters that show informative transitions from the plesiomorphic states in Xyelidae, but only by comparing a large number of taxa do these transformation series become apparent. Nonadditive multistate characters are not as useful in building a classification because unlinked character states support only their inclusive members. However, *a priori* ordering of transformation series are dependent on previous classifications or on the presumed homology of sometimes very divergent character states. For example, placement of Cephidae as sister group to the Apocrita led to a misinterpretation of the hypostomal bridge by Ross (1937) and the mesofurcal bridge was not discussed as an important character by Rasnitsyn (1969, 1980, 1988). Present interpretations of changes in the mesofurca and mesopostnotum would have made little sense without the direction provided from new classifications for Symphyta proposed by Gibson (1985) and Rasnitsyn (1988). The current distribution of character states of the mesofurca and mesopostnotum within Apocrita seems incongruent with other character information. Perhaps as more characters are used to construct improved classifications of Apocrita, this will also change.

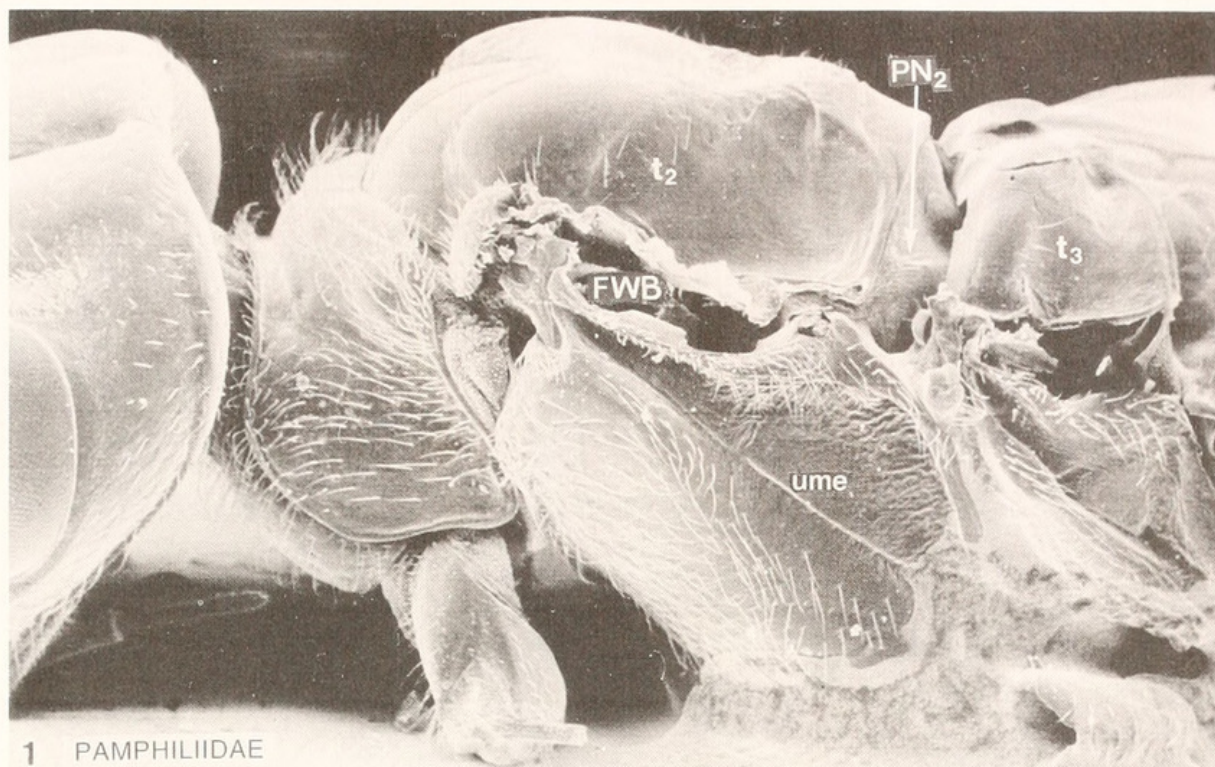
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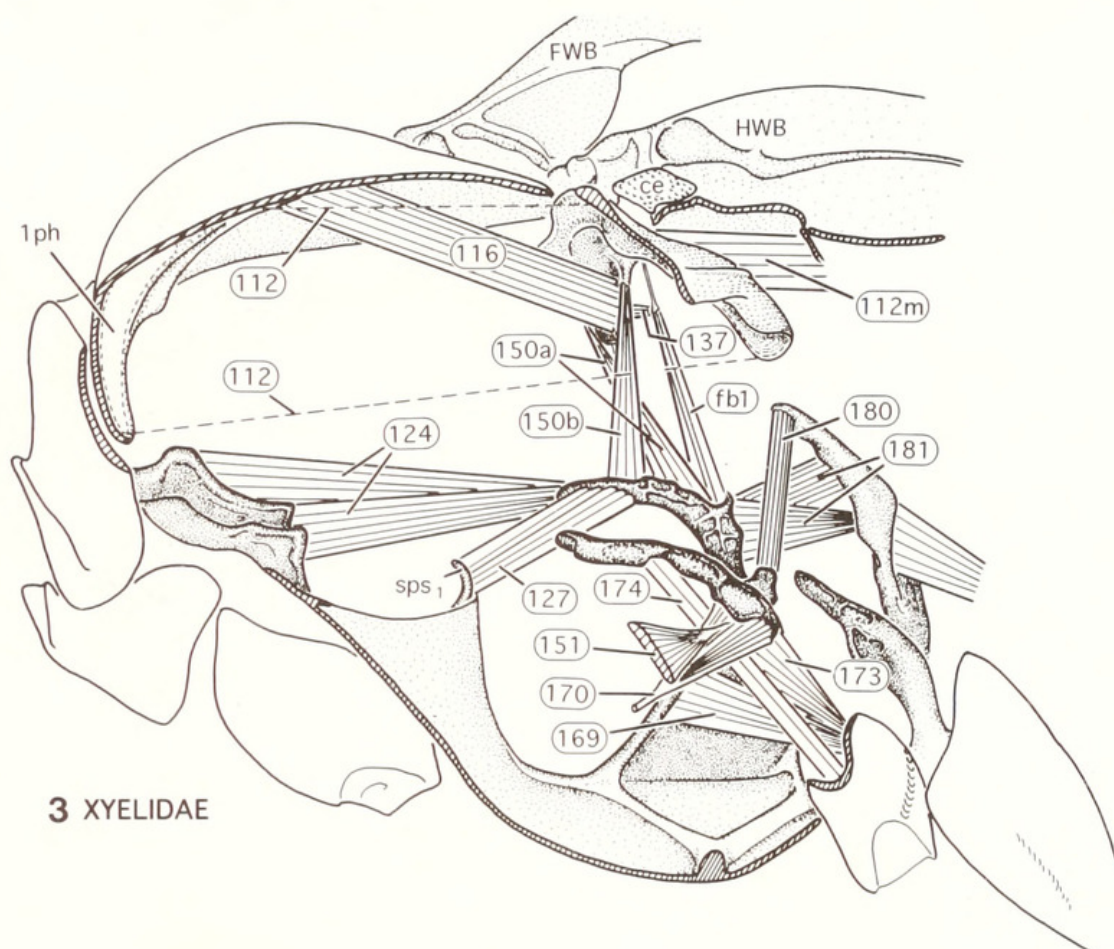


1 PAMPHILIIDAE

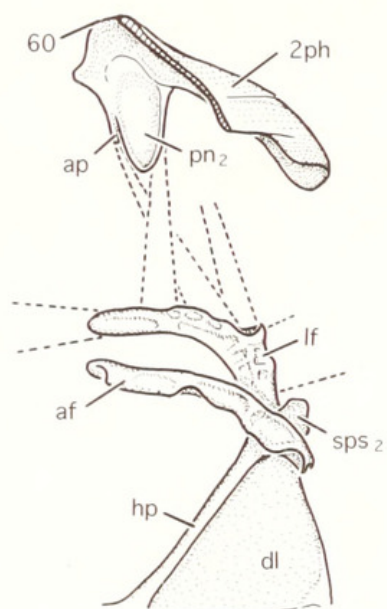


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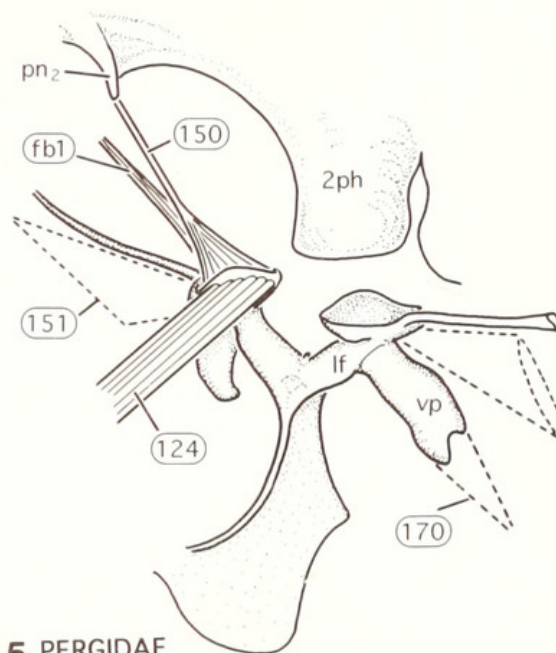
Figs. 1-2. Pamphiliidae. 1, *Pamphilius* sp., lateral habitus of mesosoma; 2, *Acantholyda* sp., sagittal section of mesosoma. Muscle 127 removed and location indicated by dashed line. Abbreviations as listed in Table 1 and Appendix 1.



3 XYELIDAE

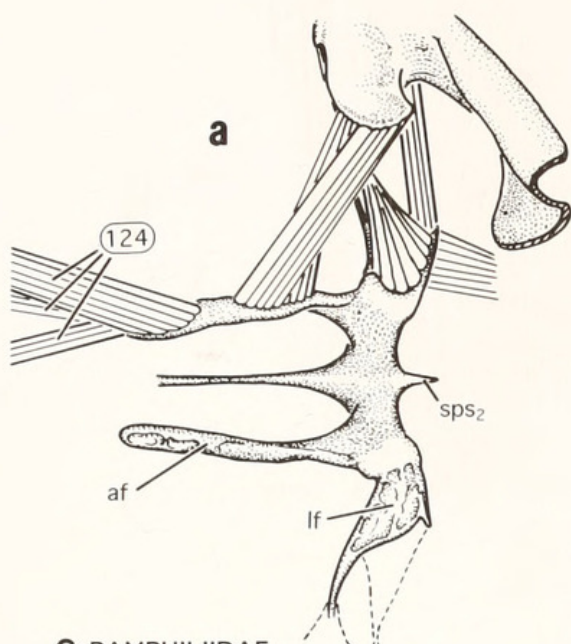
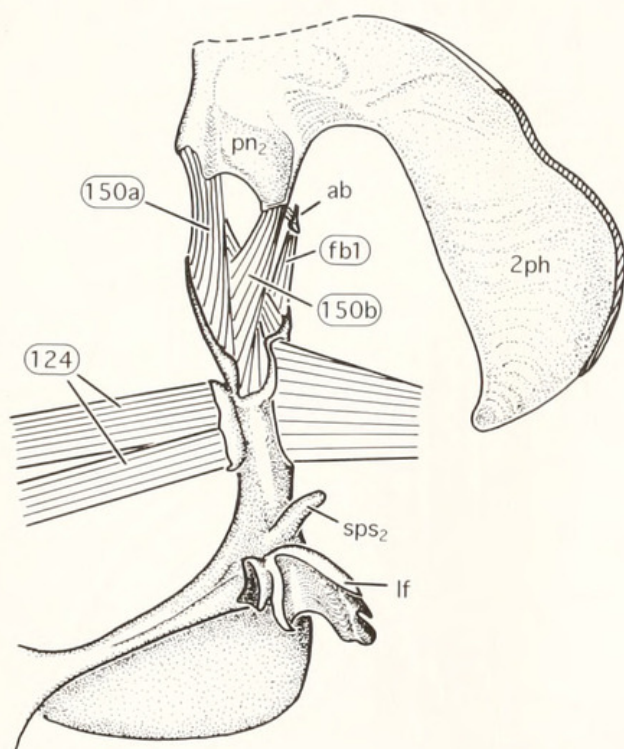
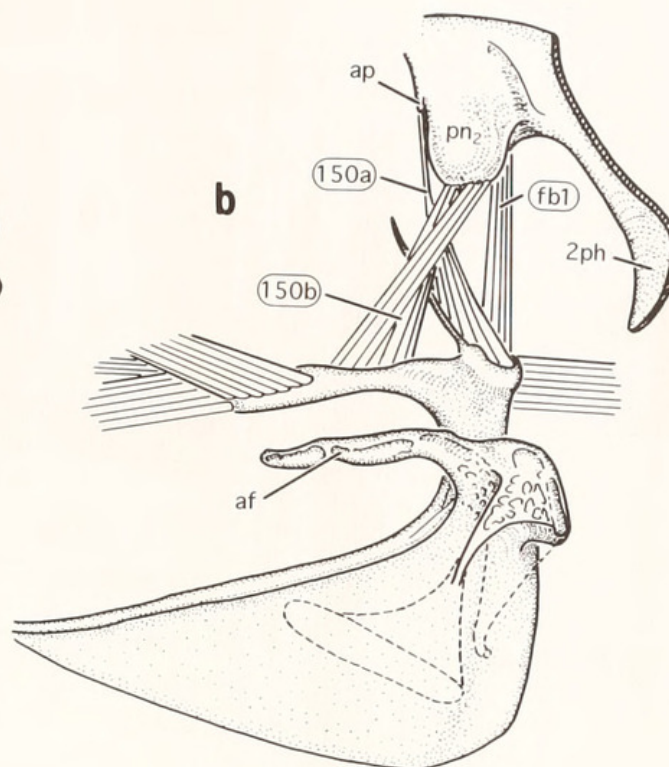
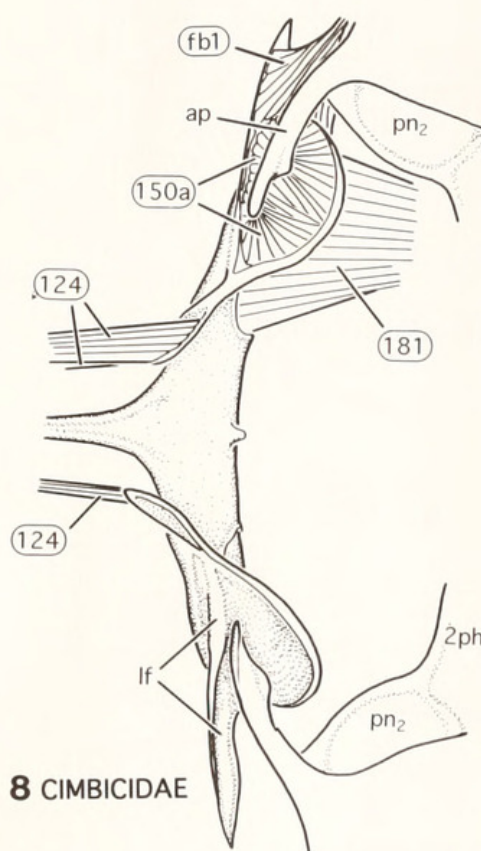


4 XYELIDAE

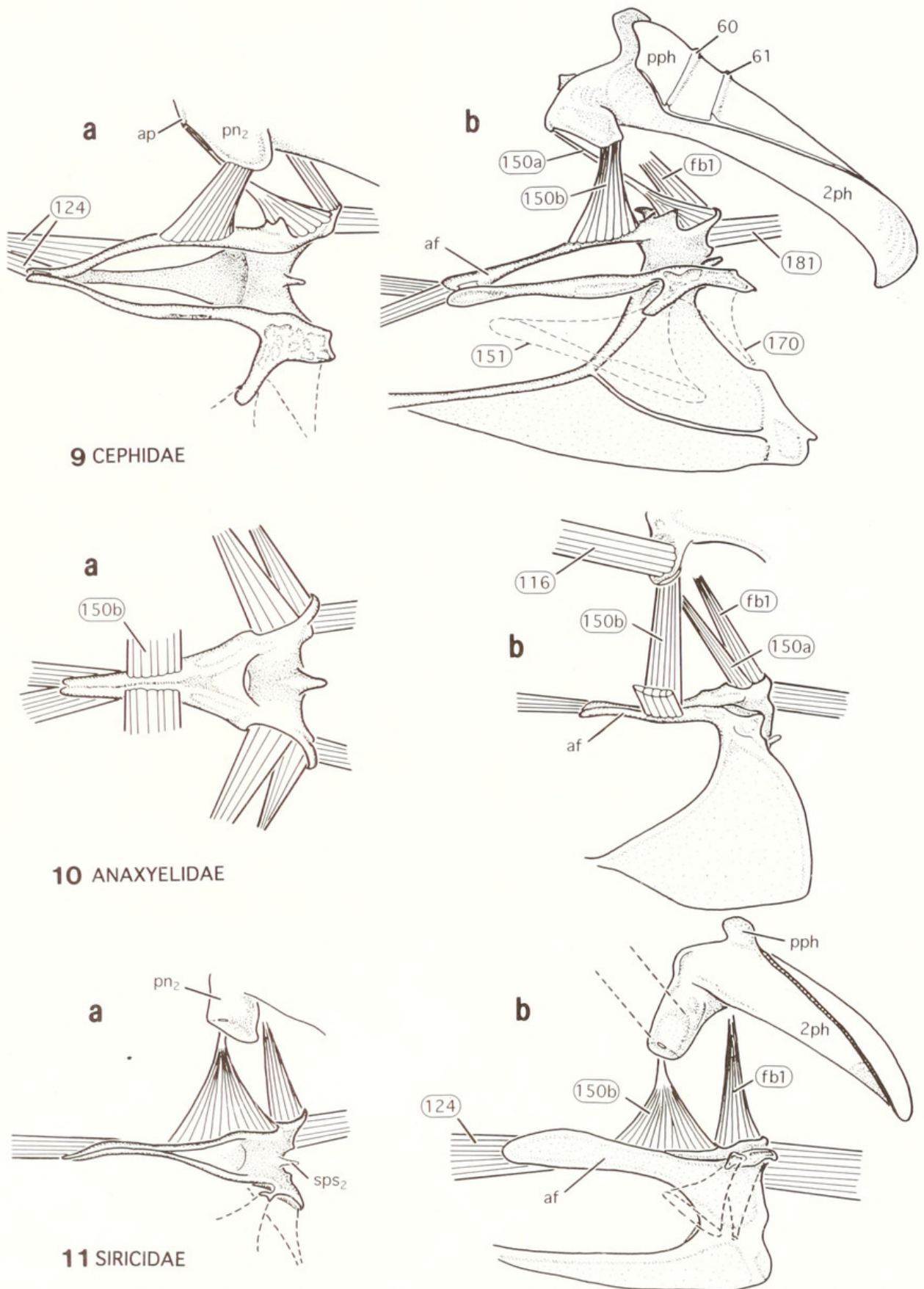


5 PERGIDAE

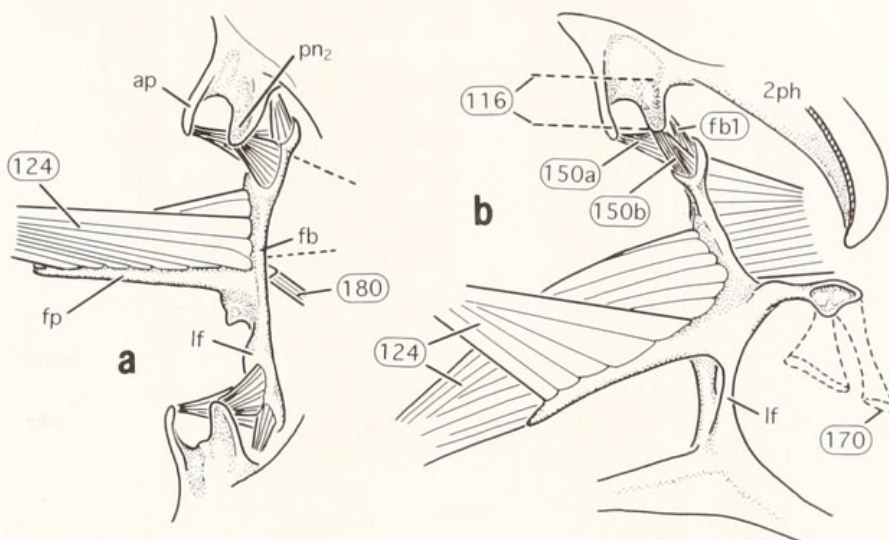
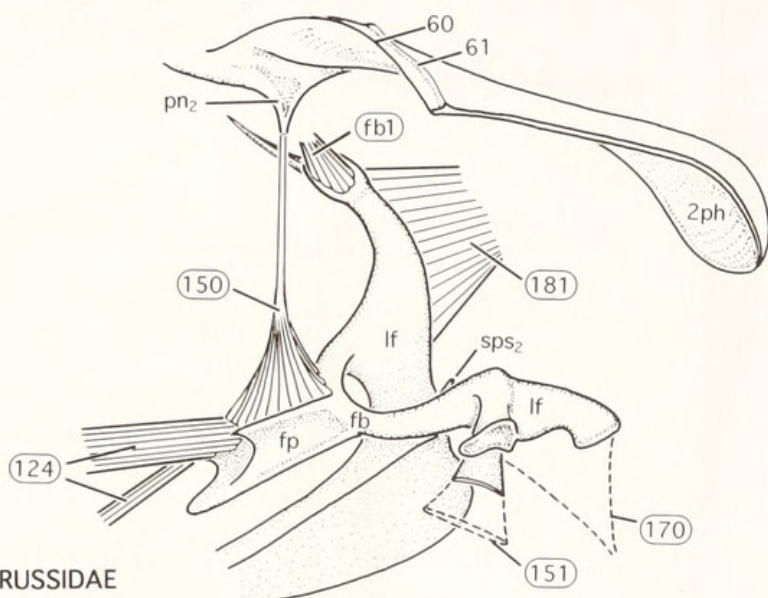
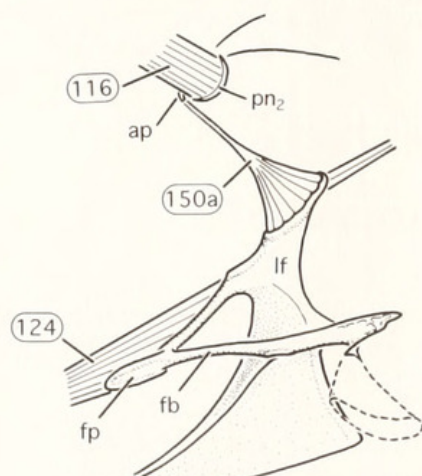
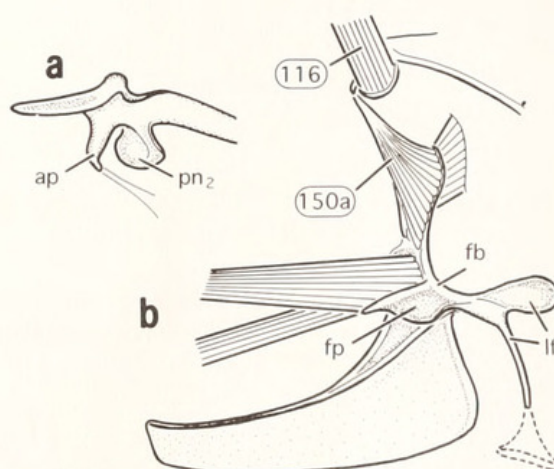
Figs. 3-5. 3, *Xyela minor*, oblique subsagittal section of mesothorax. 4, *Xyela minor*, skeletal components of Fig. 3, musculature removed. 5, *Acordulecera* sp., frontolateral view of MF-MPN complex. Abbreviations as listed in Table 1 and Appendix 1.

**6** PAMPHILIIDAE**7** DIPRIONIDAE**8** CIMBICIDAE

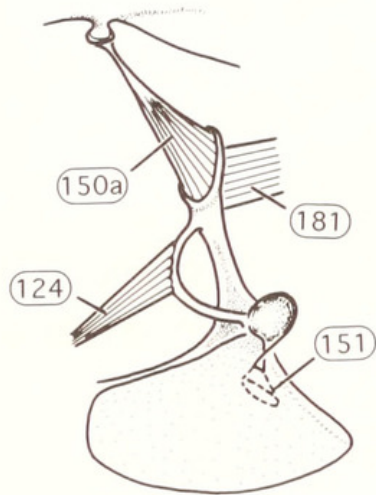
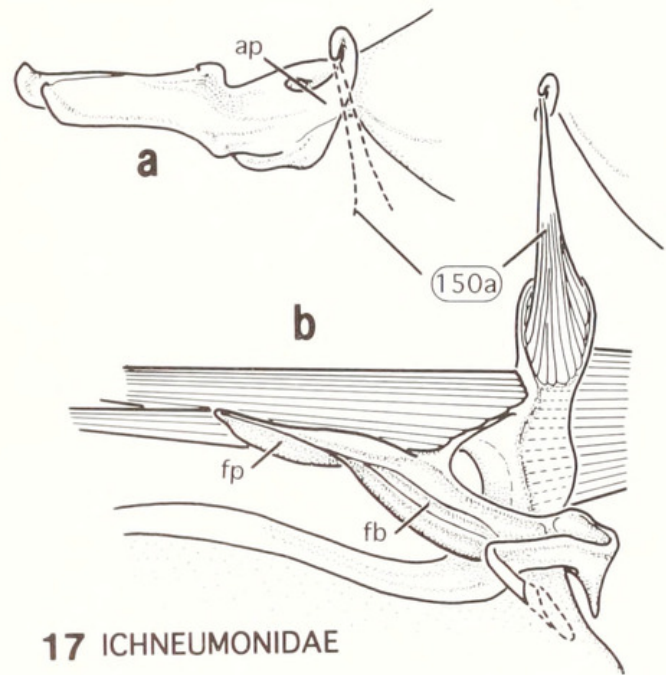
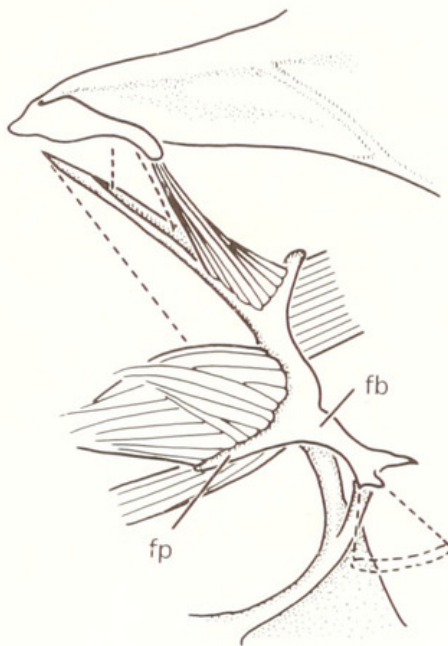
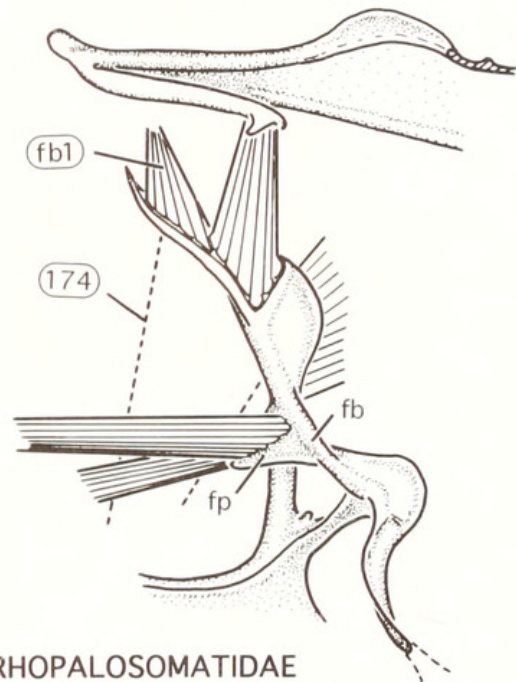
Figs. 6-8. 6, *Pamphilius* sp.: a, dorsal view of MF-MPN complex; b, lateral view of MF-MPN complex. 7, *Diprion* sp., supralateral view of MF-MPN complex. 8, *Zarea* sp., dorsal view of MF-MPN complex. Abbreviations as listed in Table 1 and Appendix 1.



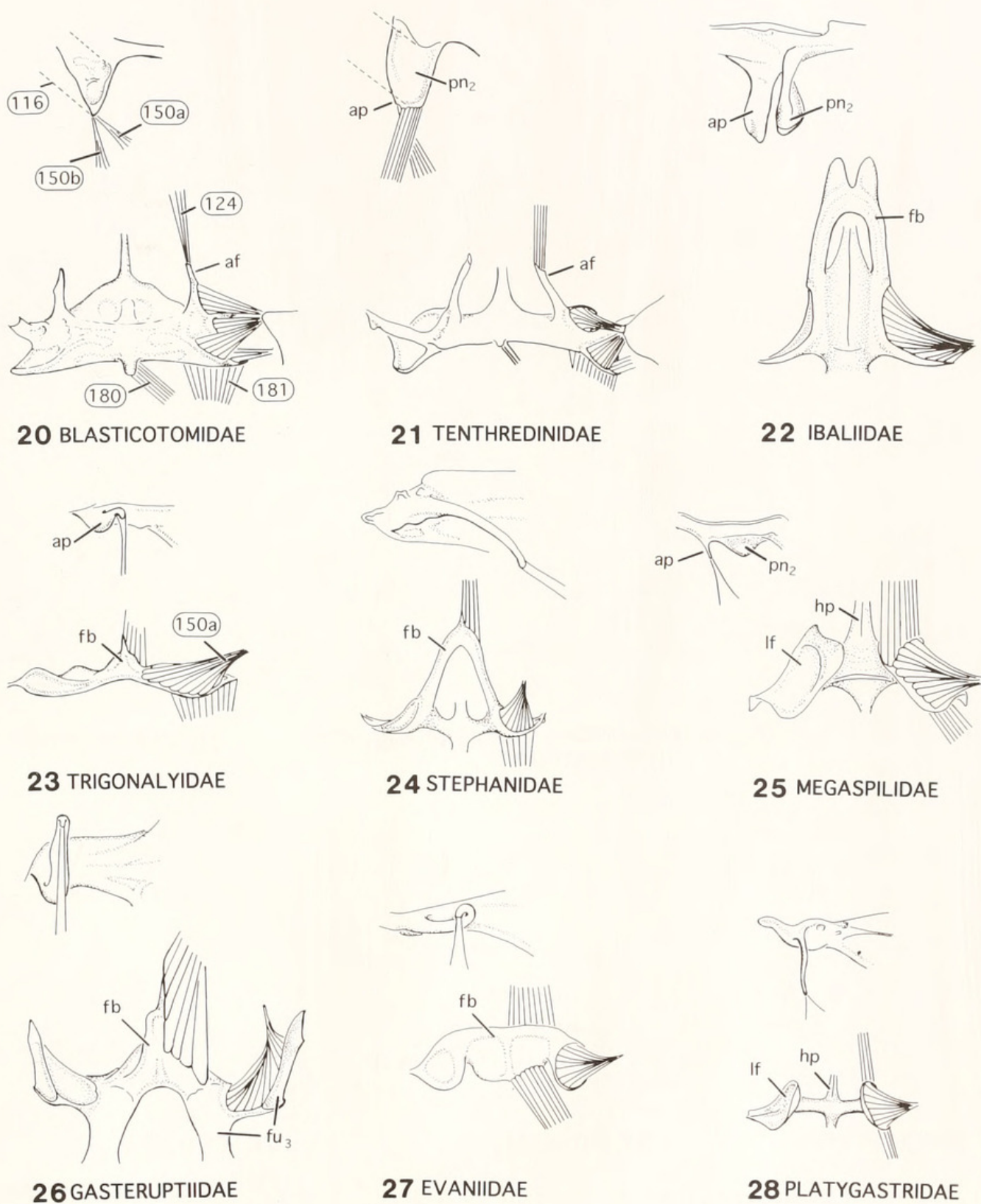
Figs. 9-11. MF-MPN complex. 9, *Cephus cinctus*: a, dorsal view; b, supralateral view. 10, *Syntexis libocedrii*: a, dorsal view; b, supralateral view. 11, *Tremex* sp.: a, dorsal view; b, lateral view. Abbreviations as listed in Table 1 and Appendix 1.

**12 XIPHYDRIIDAE****13 ORUSSIDAE****14 MONOMACHIDAE****15 VANHORNIIDAE**

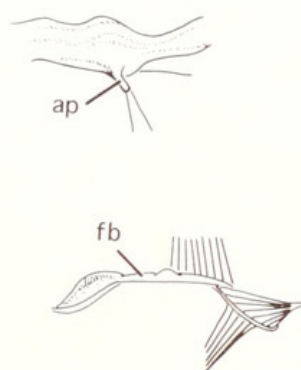
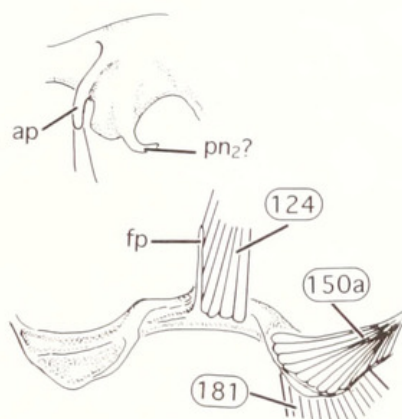
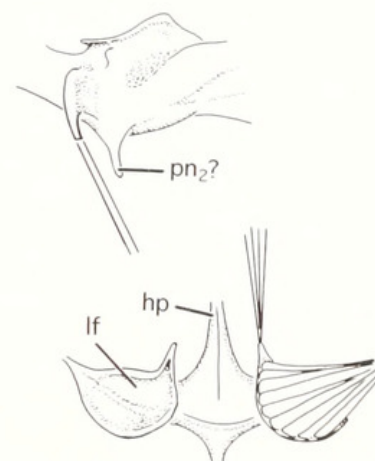
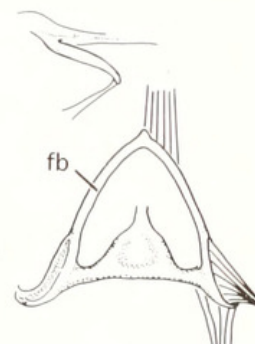
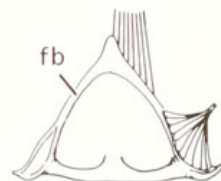
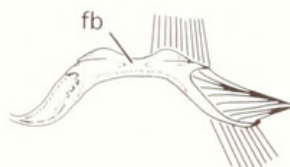
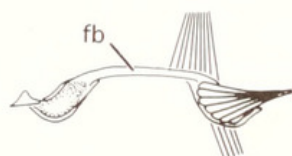
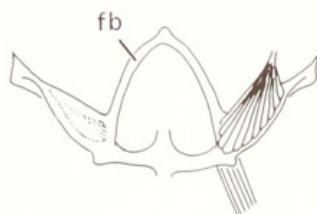
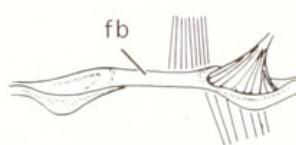
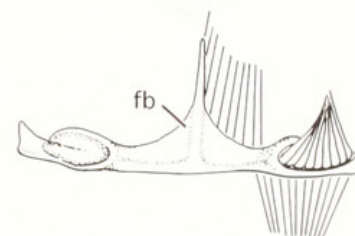
Figs. 12-15. MF-MPN complex. 12, *Xiphydria abdominalis*: a, dorsal view; b, supralateral view. 13, *Orussus sayii*, supralateral view. 14, *Monomachus* sp., supralateral view. 15, *Vanhornia eucnemidarum*: a, laterophragma; b, supralateral view. Abbreviations as listed in Table 1 and Appendix 1.

**16** SCELIONIDAE**17** ICHNEUMONIDAE**18** MUTILLIDAE**19** RHOPALOSOMATIDAE

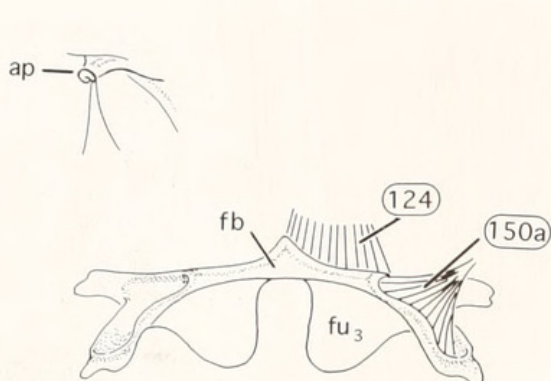
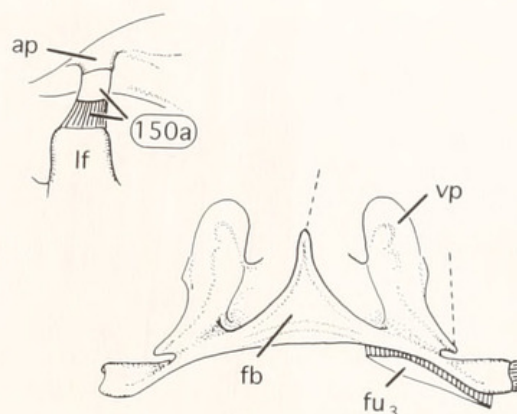
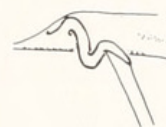
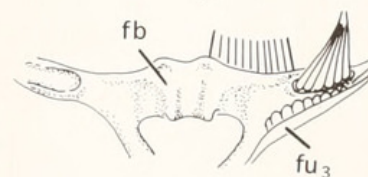
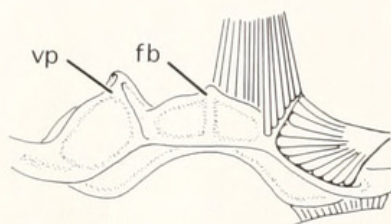
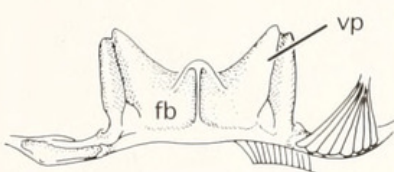
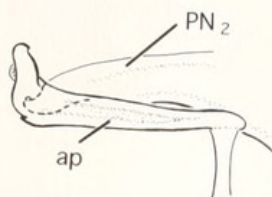
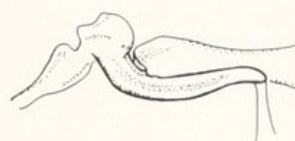
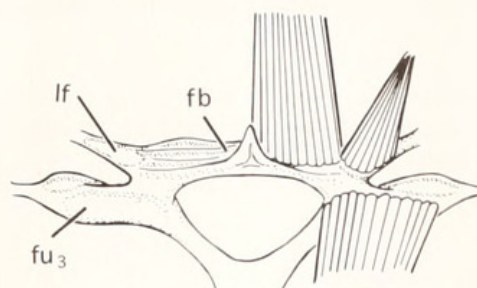
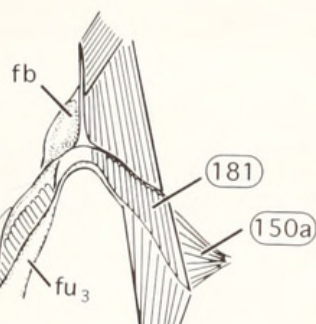
Figs. 16-19. MF-MPN complex. 16, *Sparasion* sp., supralateral view. 17, *Megarhyssa* sp. (Ichneumonidae): a, laterophragma (inner view); b, supralateral view. 18, Mutillidae (male), supralateral view. 19, *Rhopalosoma* sp., supralateral view. Abbreviations as listed in Table 1 and Appendix 1.



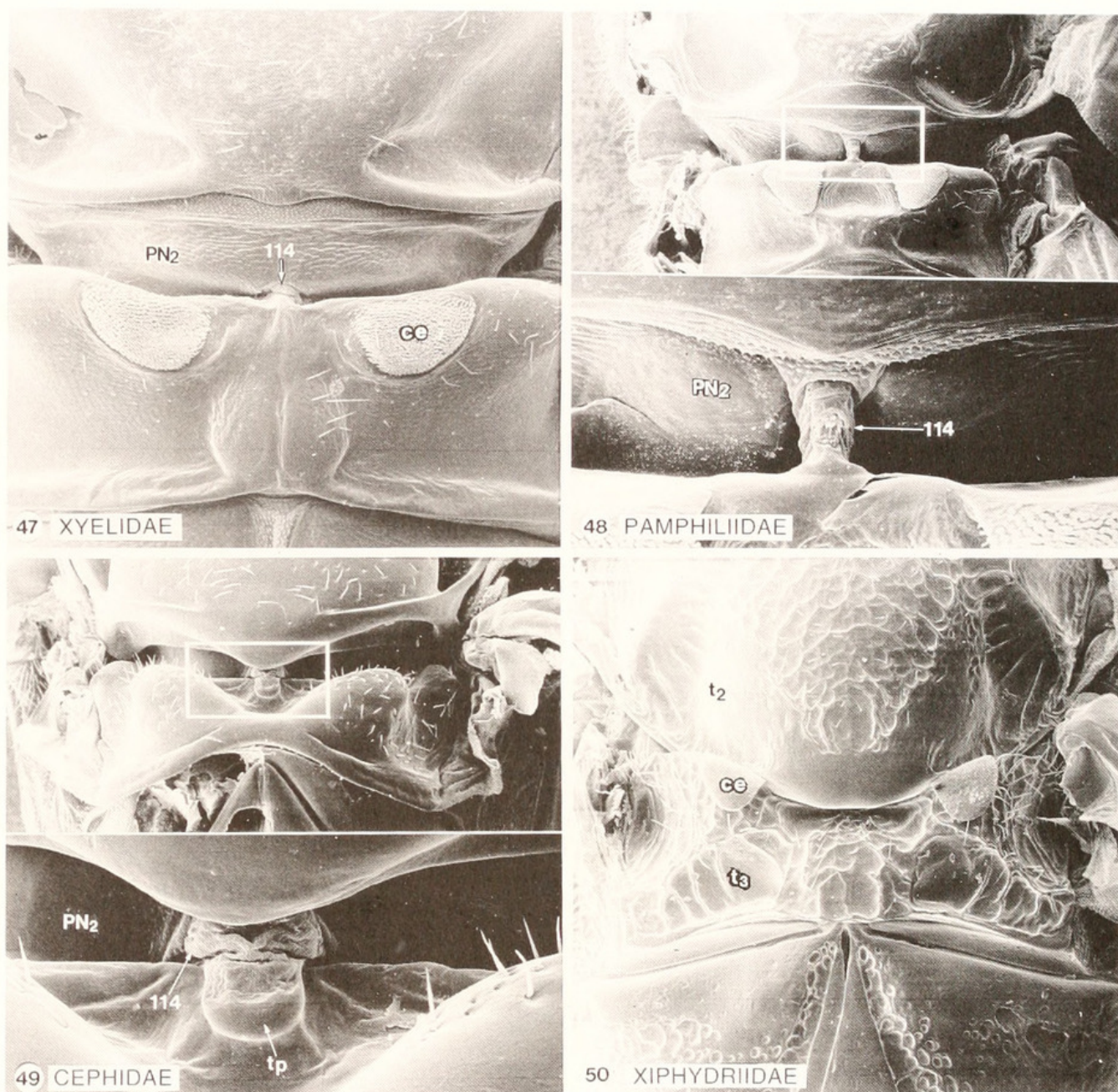
Figs. 20-28. MF-MPN complex of Apocrita: right laterophragma (upper figure); mesofurca in dorsal view (lower figure). 20, *Blasticotoma* sp.; 21, *Nematus* sp.; 22, *Ibalia* sp.; 23, *Orthogonalys pulchella*; 24, *Megischus* sp.; 25, *Megaspilus* sp.; 26, *Gasteruption* sp.; 27, *Hyptia* sp.; 28, *Isocybus* sp.

**29** DIAPRIIDAE**30** HELORIDAE**31** PELECINIDAE**32** PROCTOTRUPIDAE**33** BRACONIDAE,
HYBRIZONTINAE**34** PLUMARIIDAE**35** SCLEROGIBBIDAE**36** EMBOLEMIDAE**37** DRYINIDAE**38** BETHYLIDAE

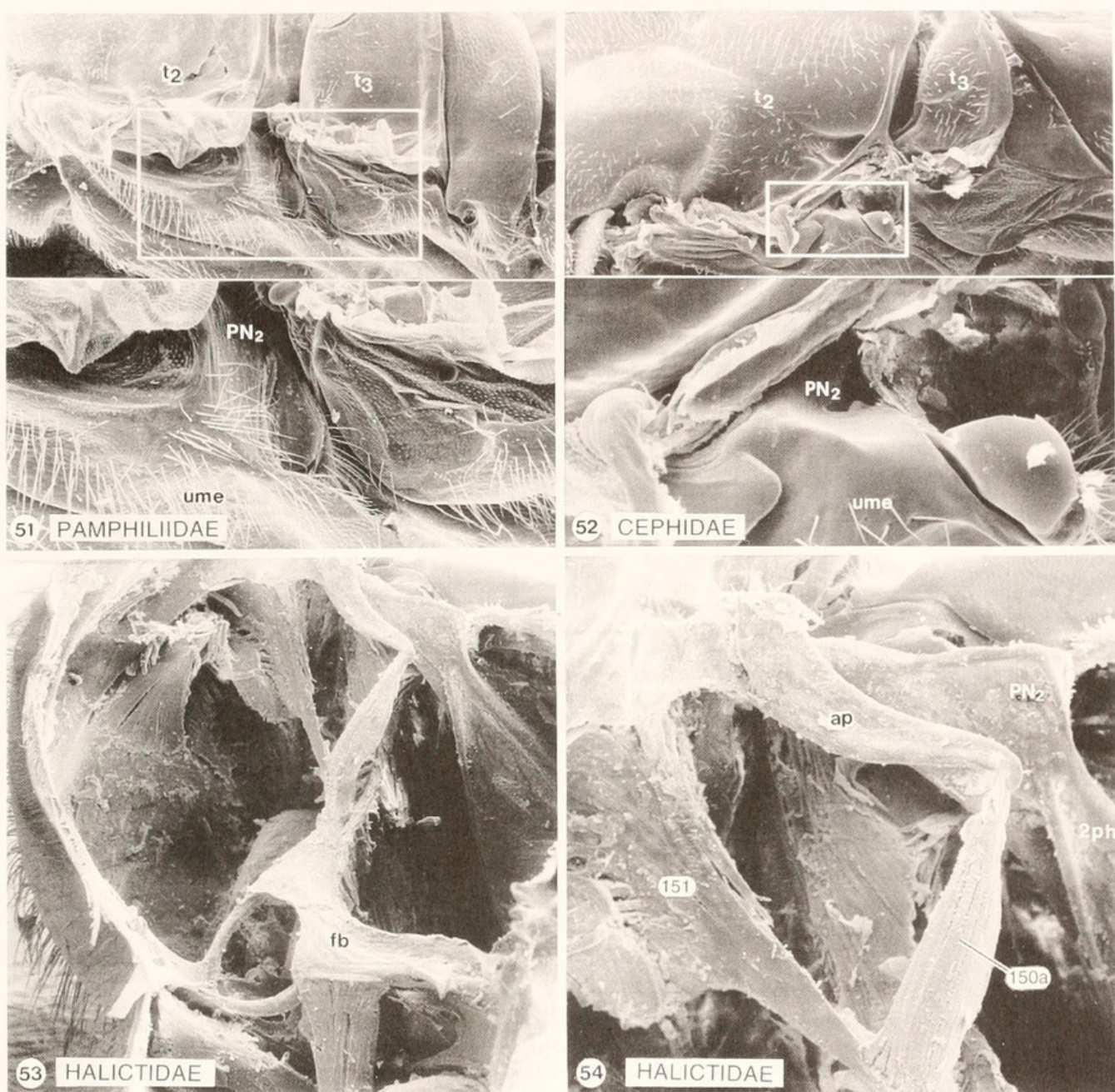
Figs. 29-38. MF-MPN complex of Apocrita: right laterophragma (upper figure); mesofurca in dorsal view (lower figure). 29, *Oxylabis* sp.; 30, *Helorus* sp.; 31, *Pelecinius polyturator*; 32, Proctotrupidae; 33, *Hybrizon* sp.; 34, *Plumaria* sp.; 35, Sclerogibbidae; 36, *Embolemus* sp.; 37, Gonatopodinae (male); 38, *Goniozus* sp.

**39** CHRYSIDIDAE, AMISEGINAE**40** CHRYSIDIDAE, CHRYSIDINAE**41** VESPIDAE**42** POMPILIDAE**43** FORMICIDAE**44** TIPHIIDAE**45** APIDAE**46** LARRIDAE

Figs. 39-46. MF-MPN complex of Apocrita: right laterophragma (upper figure); mesofurca in dorsal view (lower figure). 39, Amiseginae; 40, *Chrysis* sp.; 41, *Vespula* sp.; 42, *Aporinella galapagoensis*; 43, *Camponotus planus*; 44, *Myzinum* sp.; 45, *Trigona* sp.; 46, *Larra* sp.



Figs. 47-50. Mesopostnotum, dorsal view. 47, *Pleuroneura* sp.; 48, *Pamphilius* sp.; 49, *Cephus cinctus*; 50, *Xiphydria abdominalis*. Abbreviations as listed in Appendix 1. Split figures are magnifications of highlighted area in upper figure.



Figs. 51-54. 51-52, Mesopostnotum in lateral view with magnification of connection to upper mesepimeron. 51, *Pamphilius* sp.; 52, *Cephus cinctus*. Arrow indicates articulation of laterophragma with upper mesepimeron. 53-54, MF-MPN complex of *Lasioglossum*, dorsolateral view. 53, fused meso- and metafurca; 54, magnification of axillary lever (ap). Other abbreviations as listed in Table 1 and Appendix 1. Split figures are magnifications of highlighted area in upper figure.

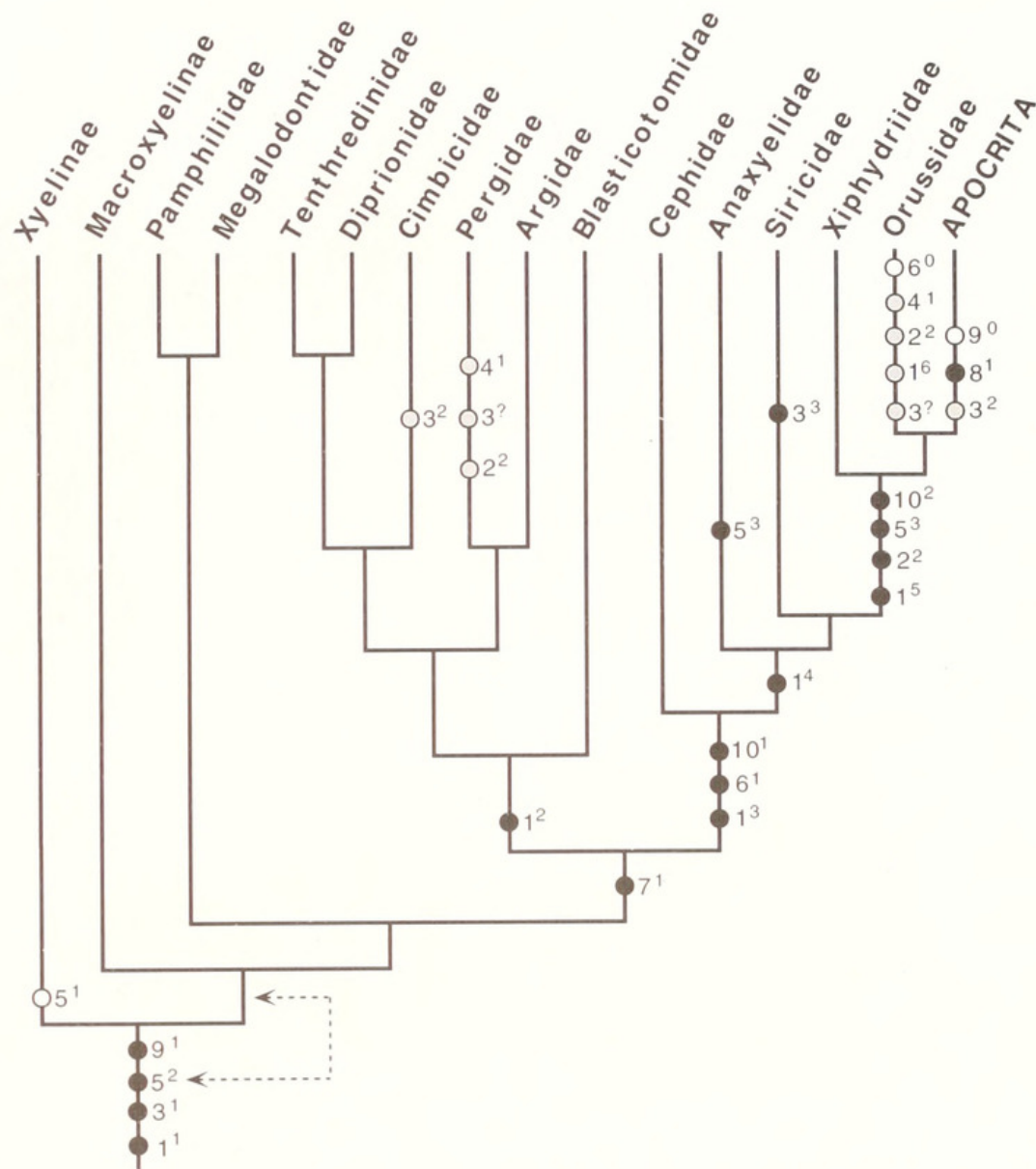


Fig. 55. Phylogenetic hypothesis for extant Hymenoptera based on Rasnitsyn (1988) and Gibson (1985, 1993), with characters of the MF-MPN complex superimposed. Characters and states discussed in text. Solid circles are unique apomorphies; shaded circles indicate convergence; open circle indicates reversal. Xyelidae are not demonstrably paraphyletic, but under some optimizations character 5:2 is treated as a synapomorphy of Macroxyelinae and the remaining Hymenoptera (dotted line to alternate placement, see text for discussion). Character 3:2 was not optimized, and this tree is two steps longer than found in the parsimony analyses (see text).

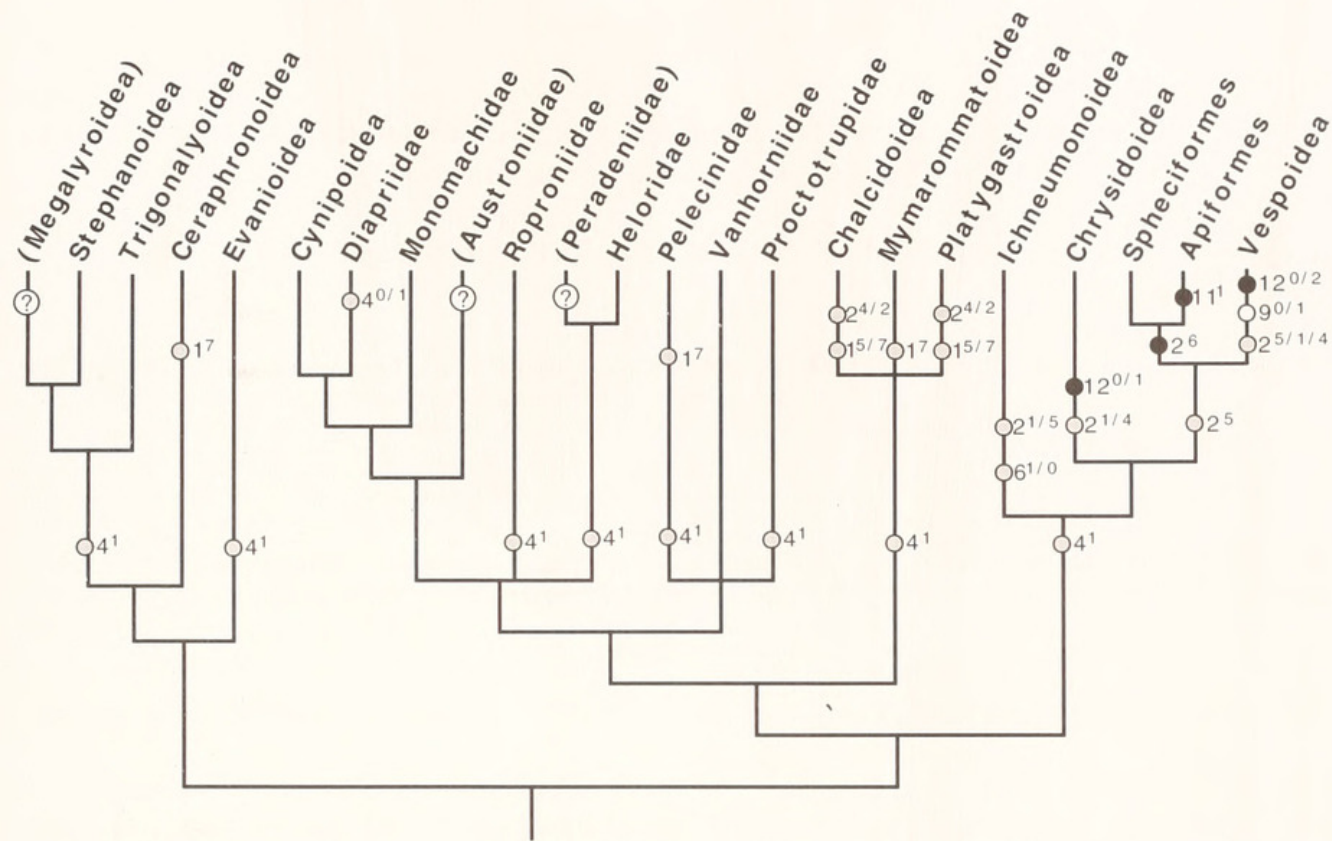


Fig. 56. Phylogenetic hypothesis for Apocrita based on Rasnitsyn (1988), with characters of the MF-MPN complex superimposed. Characters and states discussed in text. Placement of Peradeniidae and Vanhorniidae by Masner (pers. comm., 1993). Superfamily names follow Huber and Goulet (1993), those names in parentheses were not examined for internal characters and question marks indicate unknown character states. Solid circles are unique apomorphies; shaded circles indicate convergence; open circle indicates reversal. Multiple states indicate groundplan first followed by proposed derived state changes; changes listed in Appendix 2.



Heraty, J M, Woolley, James Braden, and Darling, D. Christopher. 1994.
"Phylogenetic implications of the mesofurca and mesopostnotum in
Hymenoptera." *Journal of Hymenoptera research* 3, 241–277.

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