

GROUNDPLAN STRUCTURE AND HOMOLOGY OF THE PLEURON IN HYMENOPTERA BASED ON A COMPARISON OF THE SKELETOMUSCULATURE OF XYELIDAE (HYMENOPTERA) AND RAPHIIDIIDAE (NEUROPTERA)

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Abstract

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The groundplan structure and homologies of the mesothoracic pleurosternum of Hymenoptera are postulated using the subcoxal theory of the origin of the pterothoracic pleura of insects, and the cryptosternite theory of an invaginated sternum in most holometabolous insects, based on a comparison of the skeletomusculature of Xyelidae (Hymenoptera) and Raphidiidae (Neuroptera). The following are hypothesized for Hymenoptera: (1) the mesosternum is invaginated except for the prepectus, which is a detached remnant of the presternum; (2) lines that delineate ventral regions on the mesepisternum of many Symphyta are secondarily evolved sulci and are not pleurosternal sutures; (3) a basalar cleft and an anepisternum are present in the groundplan structure; (4) in Hymenoptera other than Xyelidae the basalar cleft and anapleural cleft intersect so the anepisternum is detached as a separate sclerite, the postspiracular sclerite; (5) the preepisternum is enlarged secondarily at the expense of the katépisternum, resulting in the paracoxal suture and a narrow katépisternum closely paralleling the posteroventral margin of the episternum anterior to the mesocoxa; (6) the mesepimeron is not divided into an anepimeron and katépimeron by a paracoxal suture but in some taxa is divided secondarily into an upper and lower mesepimeron by marks that delineate the line of confluence between different sets of muscles; and (7) the trochantin is absent from the groundplan structure. Postulated homologies support the hypothesis that Xyelidae represent the basal lineage of Hymenoptera but do not support the hypothesis that the rest of Hymenoptera had a biphyletic origin from Xyelidae. The study exemplifies the positive feedback relationship between morphology and systematics and demonstrates the necessity of systematics and phylogenetic hypotheses for testing hypotheses of homology derived through comparative morphology. Schematic figures illustrate the subcoxal theory of pleuron origin and the postulated groundplan of the hymenopteran mesopleuron; mesothoracic muscles that were studied to help homologize pleurosternal features between Xyelidae and Raphidiidae are tabulated and skeletomusculature is documented by scanning electron photomicrographs.

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Résumé

L'hypothèse sur la structure de base et les homologies du pleurosternum mésothoracique des Hyménoptères formulée ici est fondée sur la théorie subcoxale de l'origine des pleures pterothoraciques des insectes et sur la théorie cryptosternale d'un sternum invaginé chez la plupart des insectes holométaboles, de même que sur la comparaison des musculatures squelettiques des Xyelidae (Hyménoptera) et des Raphidiidae (Neuroptera). Un certain nombre d'hypothèses sur les Hyménoptères sont avancées: (1) le mésosternum est invaginé, à l'exception du prépectus qui est un vestige détaché du présternum; (2) les lignes qui délimitent les régions ventrales du mésépisternum chez plusieurs Symphytes sont des sulcus apparus ultérieurement et non des sutures pleurosternales; (3) un sillon basalaire et un anépisternum font partie de la structure de base; (4) chez les Hyménoptères à l'exception des Xyelidae, le sillon basalaire et le sillon anapleural se croisent, ce qui entraîne le détachement de l'anépisternum en un sclérite distinct, le sclérite poststigmatique; (5) le préépisternum s'agrandit secondairement aux dépens du catépisternum, formant ainsi la suture paracoxale et le catépisternum étroit apposé parallèlement à la bordure postéroventrale de l'épisternum en avant de la mésocoxa; (6) le mésépimère n'est pas divisé en un anépimère et un catépimère par une

suture paracoxale, mais chez certains taxons, est divisé de façon secondaire en un mésépimère supérieur et un mésépimère inférieur par des marques qui indiquent la ligne de confluence entre différents groupes de muscles; (7) le trochantin est absent de la structure de base. Les homologues postulées appuient l'hypothèse selon laquelle les Xyelidae représentent la base de la lignée ancestrale des Hyménoptères, mais n'appuient pas l'hypothèse selon laquelle tous les autres Hyménoptères ont eu une origine biphylétiq ue à partir des Xyelidae. Cette étude constitue un exemple de la rétroaction entre la morphologie et la systématique et démontre l'importance de reposer sur la systématique et sur des hypothèses phylogénétiques les tests d'hypothèse sur les homologues élaborées à partir d'études morphologiques comparatives. Des figures schématiques illustrent la théorie subcoxale de l'origine du pleuron et la structure de base hypothétique du mésopleuron d'un Hyménoptère; des tableaux des muscles mésothoraciques étudiés pour établir les homologues des structures pleurosternales entre les Xyelidae et les Raphidiidae sont présentés et des photomicrographies au microscope électronique à balayage illustrent la musculature squelettique.

[Traduit par la rédaction]

Introduction

Snodgrass (1910, p. 37) asserted that "there are always two classes of workers concerned in the scientific study of any group of animals who think that the work of the other class is properly but secondary to their own. These are the systematists and the morphologists." Yet systematics and morphology are inextricably interrelated because each is dependent upon the other for its own success. Systematics is necessarily dependent on morphology because interpretation of structural features is the fundamental, indispensable prerequisite for taxon recognition, phylogenetic reconstruction, and classification. However, morphology attempts to explain and relate structural diversity, which is a product of evolution. If comparative morphology is to be more than an exercise of imaginative scenario-making it must be within a theoretical framework of structural and evolutionary continuity. This theoretical framework is an hypothesis of evolutionary relationships, or reconstructed phylogeny, which is provided by systematics.

Since the pioneering work of Snodgrass (1910) there have been numerous attempts to deduce the groundplan structure of the pterothoracic pleurosterna of Hymenoptera and to homologize the regions with those of less modified insects (Weber 1927; Michener 1944; Arora 1956; Richards 1956; Matsuda 1960*a*, 1960*b*, 1970; Compere 1962; Rasnitsyn 1969; Saini and Dhillon 1980; Shcherbakov 1980; Saini 1985; Shinohara 1986). That these problems have remained fertile topics of research for 80 years and have yet to be resolved definitively is at least partly a consequence of insufficient phylogenetic knowledge of Hymenoptera. To differentiate homologous structures (similar or dissimilar structures derived from a common ancestor) from analogous structures (similar structures derived independently through separate transformation series), evolutionary continuity of structure has to be demonstrated, which requires knowledge of the groundplan structure and relationships of taxa. Explicit hypotheses of infraordinal relationships have been lacking for Hymenoptera until relatively recently. Consequently, comparative morphology necessarily was based on taxa selected simply because they exhibited structural features that could be interpreted variously as homologs of more generalized insects, i.e. because of coincidence of position. Coincidence of position is insufficient to demonstrate homology.

The relatively recent phylogenetic hypotheses of Rasnitsyn (1980, 1988) and Königsmann (1977) provide the evolutionary framework necessary to derive and to test morphological interpretations based on continuity of structure rather than coincidence of position. Although I do not support all aspects of the phylogeny proposed for Hymenoptera by Rasnitsyn (1980, 1988), I support his general pattern of symphytan-apocritan relationships as opposed to the phylogenetic concepts of Königsmann (1977). Rasnitsyn (1980, 1988) hypothesized Xyelidae (Symphyta: Xyeloidea) as the basal lineage of Hymenoptera.

If this hypothesis is valid then xyelid structure most likely, most closely resembles the groundplan structure of Hymenoptera. Any credible hypothesis of the groundplan structure and homologies of the pterothoracic pleurosterna of Hymenoptera therefore must include, explain, and relate xyelid structure. However, the reconstructed phylogenies postulated by Rasnitsyn (1980, 1988) establish that most previous hypotheses of pleurosternal groundplan structure and homologies were based on relatively derived Symphyta (usually Tenthredinoidea), or even such highly derived Apocrita as Chalcidoidea (Richards 1956; Compere 1962; Matsuda 1960*b*, 1970).

Though comparative morphology requires a phylogenetic framework to be testable, and thus scientific, accurate knowledge of evolutionary relationships is insufficient in itself to ensure correct interpretation of structure and homology. Most external features of an insect exoskeleton reflect internal musculature, either as sites of muscle attachment or as lines of cuticular strengthening or flexibility correlated with muscle placement and function. Knowledge of the sites of origin and insertion of muscles, of the morphogenesis of muscles, and of the functional relationships of muscles with sclerites is essential for understanding external structure. Knowledge of musculature can indicate homology of externally dissimilar structures as well as discrepancies in observation or interpretation of external structure.

Of the 14 different interpretations of the pterothoracic pleurosterna of Hymenoptera that have been published during the past 80 years (listed above), only Shcherbakov (1980) interpreted groundplan structure and homology based on Xyelidae representing the basal lineage of Hymenoptera. He was also the first to use musculature as evidence for homology of external structures. Shcherbakov's (1980) hypotheses of groundplan structure and homologies are considerably more accurate than are those of his predecessors largely because of these two differences in method. However, he made errors of interpretation as well. These errors resulted partly because Shcherbakov (1980) interpreted xyelid structure only on the basis of *Xyela* Dalman (Xyelinae) and did not include members of Macroxyelinae, and partly because he did not examine the complete complement of muscles originating from or inserting into the pterothoracic pleurosterna.

The purpose of this paper is to resolve definitively the groundplan structure and homologies of the mesothoracic pleurosternum of Hymenoptera using the methods espoused above, and thereby demonstrate the necessity of phylogenetics and the study of musculature for successful comparative morphology.

Materials and Methods

Inference of the groundplan structure of the mesopleurosternum of Hymenoptera is based on skeletomusculature of members of Xyelidae compared with other Hymenoptera (see Gibson 1985), based on the hypothesis that Xyelidae represent the basal lineage of Hymenoptera (see Rasnitsyn 1988). Hypotheses of homology should be based on comparison of xyelid structure with that of the sister group of Hymenoptera, but relationships of Hymenoptera with other Holometabola remain unresolved (see Boudreaux 1979, 1981; Hennig 1981; Königsmann 1976; Kristensen 1975, 1981; Rasnitsyn 1969, 1980). Consequently, the outgroup I use for comparison with Hymenoptera is arbitrary and is based on perceived similarity. I use the suborder Raphidioidea (Raphidiidae and Inocelliidae) of Neuroptera as the outgroup for comparison because structure of the dorsal mesepisternum of members of this suborder appears very similar to that of xyelids. In particular, xyelids, raphidiids, and inocelliids share a well-delineated subspiracular interpleurite (= prepectus) at the apex of the anapleural cleft. All Neuroptera were not surveyed for presence or absence of a subspiracular interpleurite, though members of Corydalidae (suborder Megaloptera) have a much larger, less distinctly separated sclerite (see Crampton 1914*b*).

Study of the skeletomusculature of Raphidioidea is based on specimens of *Raphidia* (*Agulla*) spp. (Raphidiidae) collected into 70% ethanol from British Columbia, Wyoming,

and California. Interpretation of raphidiid external structure follows Ferris and Pennebaker (1939) and Matsuda (1956), but Kelsey's (1957) study of the skeletomusculature of *Corydalus cornutus* (L.) (Neuroptera: Corydalidae) was used to help interpret pterothoracic musculature. Dissections showed that except for muscle 144, relevant muscles are the same in *Raphidia* as those described by Kelsey (1957) for *Corydalus*, and Kelsey's (1957) study is more comprehensive and the descriptions and illustrations of muscles are superior to those of Matsuda (1956) for *Raphidia*.

Interpretation of external structure of Xyelidae is based on representatives of Xyelinae (*Xyela* Dalman and *Pleroneura* Konow) and Macroxyelinae (*Xyelecia* Ross, *Macroxyela* Kirby, and *Megaxyela* Ashmead), but study of mesothoracic musculature is based solely on dissections of females of *Xyela minor* Norton. Specimens of *X. minor* were collected on the Central Experimental Farm, Ottawa, Ontario, killed in Kahle's fluid, and stored in 70% ethanol prior to dissection. Daly (1963) was used to help interpret thoracic musculature.

Table 1 lists the mesothoracic muscles that were studied to homologize pleurosternal regions between *Raphidia* and *Xyela*. To facilitate comparison of muscles between these two taxa and across Pterygota, the muscles are designated by the numbering and naming systems used by Kelsey (1957) for *Corydalus*, by the system used by Matsuda (1970) for Pterygota, and by a modified version of the system used by Daly (1963, 1964) for Hymenoptera. The numbering system of Kelsey (1957) is used to denote muscles in the illustrations. Other abbreviations used to denote structures in the illustrations are listed in the Appendix. The terms "suture," "sulcus," and "line" are used according to Daly (1964).

Methods of dissection and study of musculature by scanning electron microscopy (SEM) follow Gibson (1985, 1986b). The methods, described below, are simple and more effective for determining accurately points of origin and insertion of muscles than is study with polarized light (except for minute insects that can be examined whole on microscope slides).

The head, appendages, and most of the abdomen were dissected from specimens in 70% ethanol using a knife with a razor blade edge. A further sagittal section of the thorax was made for study of interior muscles, but for exterior muscles (those adjacent to the pleural wall) the whole thorax was dried before dissecting the cuticle and attached muscles from the body. Dissected specimens were critical-point-dried to prevent shrinkage and distortion of muscles and cuticle and then positioned on SEM stubs by adhering each to a small piece of Scotch brand "flat stock liner double coated tape" (manufactured by the 3M Company). The dissection was affixed rigidly and grounded to the stub using silver paint. Once affixed, specimens were dissected further and cleaned for SEM under a binocular dissecting microscope. A piece of double coated tape was affixed to the stub next to the dissection and the end of a minuten pin, inserted into a thin wooden dowel, was scratched across the tape surface until a small piece of the adhesive adhered to the tip. This probe was then used to pick out unwanted muscles, dried hemolymph, tracheae, and other extraneous tissue without disturbing relevant structures. Once cleaned by this method dissections were gold coated with a sputter coater and photographed using an AMR 1000A scanning electron microscope.

Origin of Pterygote Thoracic Pleurosternum. Most recent interpretations of the thoracic pleurosternal regions of holometabolous insects have been based on two theories: the subcoxal theory of the origin of the pleuron in insects and the cryptosternite theory of an invaginated mesosternum in most holometabolous insects. The former theory was originated by Heymons (1899) and modified by such workers as Snodgrass (1927) and Matsuda (1960b, 1963, 1970). The latter theory was originated by Weber (1928) and advocated by Ferris (1940) and others in a series of papers that were reviewed by Matsuda (1960b, 1963, 1970).

It must be emphasized that the subcoxal and cryptosternite theories are but theories. The subcoxal theory postulates that the thoracic pleuron was formed through incorporation and subsequent subdivision of a solidly chitinized subcoxal segment into the body wall between the tergum and sternum. An alternate theory postulates that the thoracic pleuron was formed from separate plates that evolved secondarily through progressive sclerotization and pigmentation of an initially membranous lateral surface because of muscle attachment and mechanical stresses (Crampton 1914*a*, 1914*b*). It is beyond the scope of this paper to test the validity of different theories. Morphological terms based on the subcoxal and cryptosternite theories are in general use and for this reason these two theories were used to interpret the pleurosternal structures of raphidiids and xyelids.

Subcoxal theory (Fig. 1). The subcoxal theory of the origin of the thoracic pleuron in insects postulates that the pleuron developed from a leg segment basal to the coxa, the subcoxa, which became flattened and embedded in the membranous lateral wall of the thorax between the tergum and sternum. After the subcoxal segment was incorporated into the pleural wall as a ring around the coxa, in the pterothoracic segments of pterygote insects it was strengthened for support of the wing base by development of a dorsoventral apodeme, the **pleural ridge**. The pleural ridge terminates dorsally as the **pleural wing process** and externally is visible as the **pleural suture**, which divides the pleuron into an anterior **episternum** and posterior **epimeron**. The originally single subcoxal segment also was subdivided subsequently into an outer anapleural ring and inner katapleural ring by the **paracoxal suture**, so the pleuron was divided into an anterior **anepisternum** and **katepisternum** and a posterior **anepimeron** and **katepimeron**. The katepisternum was subdivided further when a separate sclerite, the **trochantin**, was detached. The trochantin formed a third, anterior articulation with the coxa in addition to the dorsal and ventral coxal articulations. Possibly a second sclerite, the **ventropleurite**, also was detached from the katepisternum to form the ventral articulation [see Matsuda (1970) for a discussion of the katapleural or sternal origin of the ventropleurite]. Similarly to the katepisternum, the anepisternum also was subdivided further. The **basalare** was detached from the anepisternum,¹ and in some pterygotes a vertical **basalar cleft** (= episternal longitudinal suture sensu Matsuda 1970) also secondarily subdivided the anepisternum below the basalare. The anepisternum was subdivided further by the **anapleural suture**, which distinguished a ventral **preepisternum** anterior to the katepisternum.

The pleuron was highly membranous primitively but with acquisition of the wings the pteropleura underwent increasing secondary sclerotization. Though the anapleural suture is persistent even in most holometabolous insects, most pterygotes lack a basalar cleft and the paracoxal suture often is lost or is visible only on the episternum (in some groups the epimeron is subdivided by a secondary horizontal line or sulcus, the **trans-epimeral line** or **sulcus**). The trochantin also is lost or is fused basally with the katepisternum in most pterygotes.

Cryptosternite theory. In apterygotes the sternum is composed of five subdivisions, the presternum, basisternum, furcasternum, spinasternum, and poststernum. Pterygotes lack the poststernum from the pterothoracic segments (Fig. 1) and in many groups the other original subdivisions are obscured. Further, under the cryptosternite theory, most holometabolous insects are hypothesized to have the sternum internally invaginated. The pleural elements are postulated to have been extended ventrally so that the originally lateral subcoxae meet along the ventral midline. As a consequence of the ventral extension of the pleura the sternal elements are invaginated and form the internal median longitudinal ridge, which is visible externally as the **discrimen** (Fig. 3).

Skeletomusculature of the Mesopleuron of Raphidiidae. External structure. If the insect pleuron was derived from a subcoxal segment of the leg, then there are probably

¹The **subalare** is hypothesized as tergal in origin.

Table 1. Mesothoracic muscles examined in *Raphidia* and *Xyela* for homologizing pleural regions between Raphidioidea (Neuroptera) and Hymenoptera

		<i>Corydalus / Raphidia</i>		<i>Xyela</i>		Notes
		Kelsey 1957				
Number	Name	Matsuda 1970	Designation	Figures	(remarks refer to <i>Xyela</i> unless stated otherwise)	
110	dilator of spiracle	—	ism-sp ₂	32	— in <i>Raphidia</i> from membrane ventrad of spiracle (Fig. 34); in <i>Xyela</i> from intersegmental membrane ventrad of spiracle immediately anterior to anterior margin of prepectus; dilator muscle in <i>Corydalus</i> vide Kelsey (1957) but occlusor muscle in <i>Xyela</i> vide Tonapi (1958); site of origin in <i>Raphidia</i> incorrectly stated as preepisternum by Matsuda (1956)	
128/129	anterior scutal-preepisternal* (128) lateral scutal-preepisternal* (129)	t-p6 t-p5	t ₂ -prep ₂	24, 30	— dorsoventral indirect flight muscles; double muscle in <i>Raphidia</i> (Fig. 22) but single muscle in <i>Xyela</i> , from mesoscutum posterolaterad of notaulus to preepisternum [region designated as pseudosternum by Shcherbakov (1980)]	
130	tergal-trochantinal	t-ti(cx)2	—	—	— absent	
132	basalar-trochantinal	p-ti(cx)3	—	—	— absent	
137	laterophragmal-basalar	t-p3	ph ₂ -ba ₂	29, 31	— from extreme lateral region of mesophragma at antero-lateral margin of mesoscutum to dorsal surface of basalar	
141	scutal-basalar	t-p8	t ₂ -ba ₂	30, 31	— from lateral margin of mesoscutum to dorsal surface of basalar mesad of ligamentous attachment of basalar; listed as t-p18 for Hymenoptera by Matsuda (1970)	
142	prealary sclerite	t-p4	t ₂ -plr ₂	29, 31	— from anterolateral margin of mesoscutum posteriad of muscle 137 to mesopleural wing process	
143	scutal-pleural ridge	t-p15	—	—	— absent	
144	intersegmental pleurite-basalar	p2	ism-ba ₂	29	— not confirmed for <i>Raphidia</i> , but in <i>Xyela</i> from intersegmental membrane ventrad of muscle 110, to antero-mesal dorsal margin of basalar	
145	anepisternal-t-preepisternal*	p1	anep ₂ -prep ₂	29, 30, 32	— in <i>Raphidia</i> as small, tubular muscle across apex of pleural cleft (Fig. 34); in <i>Xyela</i> as broad, thin muscle band spanning prepectus between anteroventral margin of anepisternum and anterodorsal margin of preepisternum; mistakenly stated as basalar muscle "pl ₂ -ba _{2a} " by Daly (1963)	

151	furcal-pleural arm	p-s1	epm ₂ -fu ₂	27, 28	— from lower epimeron ventrad of pleural apophysis to mesofurca; juncture between muscles 151 and 161 externally visible as transepimeral line, which divides epimeron into upper and lower epimeron — fan-shaped muscle from posterior tergal lever of mesoscutum to epimeron at mesopleural apophysis (by slender ligamentous attachment); t-p15 <i>vide</i> Shcherbakov (1981) — from preepisternum laterad of muscle 128/129; "p ₂ -ba ₂ " of Daly (1963) — from anterior margin of coxa to basalar posteriad of muscle 154; reported absent from <i>Xyela</i> by Johnson (1988) — in <i>Raphidia</i> as broad, band-like muscle from ventral region of anepisternum to mesocoxa; in <i>Xyela</i> as long, slender muscle from preepisternum along mesopleural ridge, apparently not extended dorsally into reduced episternum — from mesoscutum posteriad of muscle 165, to posterior margin of mesocoxa — absent — absent — from posterior margin of mesocoxa to subalare — from upper epimeron along mesopleural ridge dorsad of pleural apophysis and muscle 151 (see 151); listed as t-p19 for Hymenoptera by Matsuda (1970) and Shcherbakov (1981) — very small muscle from upper margin of wing process, extended ventrally to insert into third axillary sclerite
153	tergal-pleural arm	t-p12	t ₂ -epm ₂	27, 28	
154	preepisternal*-basalar	p3	prep ₂ -ba ₂	24-27, 29-31	
156	basalar-coxal	p-cx4	ba ₂ -cx ₂	26, 31	
157	anepisternal†-coxal	p-cx5	prep ₂ -cx ₂	28, 33	
158	tergal-meral remotor of coxa	t-cx5	t ₂ -cx ₂	25, 26	
159a	1st posterior tergal lever-meron	t-cx6	—	—	
159b	2nd posterior tergal lever-meron	t-cx7	—	—	
160	meral-subalare	t-cx8	cx ₂ -sa ₂	27	
161	epimeral-subalare	t-p16	epm ₂ -sa ₂	28	
163	anepisternal†-3rd axillary sclerite	t-p13	plr ₂ -3ax ₂	28, 31	
164	pleural ridge-3rd axillary sclerite	t-p14	epm ₂ -3ax ₂	28	
165	scutal-trochanteral	t-tr1	t ₂ -tr ₂	24, 25	— from upper epimeron along mesopleural ridge dorsad of muscle 143, to third axillary sclerite; listed as t-p13 for Hymenoptera by Matsuda (1970)
166	basalare-trochanteral	p-tr2	—	—	— from mesoscutum posteriad and lateral of muscle 128/129 to mesotrochanter — absent

*Preepisternum = precoxal bridge of Kelsey (1957).

†Anepisternum = episternum of Kelsey (1957).

few pterygotes in which the original subdivisions are more readily homologized than in raphidiids. Both meso- and metapleura are very similar in structure (Fig. 7). Each pleuron is divided subequally into an episternum and epimeron by an almost vertical pleural suture (Figs. 5, 7). The episternum also is divided almost equally into a dorsal anepisternum (= episternum of Kelsey 1957) and a ventral episternal region (= precoxal bridge of Kelsey 1957) by an arcuate anapleural cleft, which extends to the pleural ridge pit (Figs. 5, 7). The anepisternum lacks a basalar cleft but is narrowed abruptly dorsally to form the episternal part of the pleural wing process (Figs. 5, 11). The ventral episternal region is subdivided into an anterodorsal preepisternum and a posteroventral katepisternum by a relatively obscure paracoxal suture (Figs. 5, 17) (= transverse groove of Kelsey 1957), which extends from the discrimen at the mesofurcal pit (Fig. 17) to the anapleural cleft near the pleural ridge pit (Fig. 5). The paracoxal suture is developed internally as an apodeme; it does not extend across the epimeron so that the epimeron is not divided into an anepimeron and katepimeron (Figs. 5, 7). The mesocoxa has three articulations with the pleuron: a dorsal articulation with the katepisternum and epimeron at the pleural ridge (Figs. 5, 19), an anteroventral articulation with a slender trochantin that posteriorly is fused with the katepisternum (Figs. 17, 19), and a ventromesal articulation with a lobe-like extension of the katepisternum (Fig. 17). This lobe-like articulatory process was hypothesized as a modified ventropleurite and was called the **ventral process** by Matsuda (1970).

Both Ferris and Pennebaker (1939: figs. 62, 63) and Matsuda (1956: figs. 1, 2) illustrate a "presternum" (= intersegmental pleurite of Kelsey 1957) anterior to the mesothoracic preepisternum, anepisternum, and spiracle in *R. (A.) adnixa*. Their illustrations imply that this ventral and lateral region is developed similarly to other illustrated sclerites, but though the region is melanized it is sclerotized only very weakly, as was noted by Ferris and Pennebaker (1939). Both studies also failed to mention a subcircular sclerotized region that is contiguous with the "presternum" immediately anterior to the anapleural cleft and ventral to the mesothoracic spiracle (Figs. 5, 11). This omission probably resulted because the sclerite is not very distinct in many specimens of *R. (A.) adnixa*. The pronotum typically collapses against the mesothorax with shrinkage of the intersegmental membrane in air-dried specimens, often partly concealing the subspiracular sclerite. Further, the subspiracular sclerite usually is the same color as the "presternum" or is demelanized to a greater or lesser extent and therefore is less noticeable using light microscopy than scanning electron microscopy. The subspiracular sclerite is an **interpleurite** sensu Matsuda (1970) (Fig. 1). Interpleurites probably represent isolated parts of the presternum anterior to the pleuron according to Matsuda (1970).

Musculature. Matsuda (1956) studied the thoracic musculature of *R. (A.) adnixa* and listed other such studies in the Neuroptera, including Kelsey's (1957) study of *Corydalus cornutus* (Corydalidae). Matsuda (1970) tabulated the thoracic musculature of four Neuroptera, including *C. cornutus* but not *R. (A.) adnixa*. Tabulation of the muscles in this work follows Kelsey (1957) for the reasons given under Materials and Methods.

Table 1 lists the 25 mesothoracic muscles described by Kelsey (1957) for *Corydalus* that are relevant for homologizing parts of the mesopleuron in xyelids. Matsuda (1956) erred in stating that in *Raphidia* muscle 110 originates from the preepisternum. The muscle originates from within a V-shaped fold of intersegmental membrane ventral to the spiracle and anterior to the subspiracular interpleurite (Fig. 34: 110). The membranous fold is part of the region that was termed the presternum by Ferris and Pennebaker (1939) and Matsuda (1956). Kelsey (1957) stated that this muscle originated posterior to the subspiracular plate in *Corydalus* and was the dilator of the spiracle. As for *Corydalus*, no muscles originate from the katepisternum in *Raphidia*.

Skeletomusculature of the Mesopleuron of Xyelidae and Hypotheses of the Groundplan Pleuron for Hymenoptera. Unlike Neuroptera, Hymenoptera have the metathorax

considerably reduced and simplified relative to the mesothorax (cf. Figs. 7, 8). This reduction is correlated with smaller hind wings and a reduced role for the metathorax in powering flight. The skeletomusculature of the mesothorax is considered to reflect more closely ancestral structure because it is less reduced. It forms the basis for the following hypothesis of the groundplan structure of the hymenopteran pleurosternum, which is illustrated schematically by Figure 2.

Dorsal episternum. Like raphidiids, xyelids have the mesopleuron divided into an episternum and epimeron by a distinct mesopleural suture, but the suture is angled much more obliquely and the epimeron is much smaller than the episternum (Figs. 8–10). Further, the anepisternum is partly detached from the rest of the episternum because of a longitudinal basal cleft (Figs. 12–14) dorsal to the more-or-less transversely arcuate anapleural cleft (Figs. 6, 12–14). The anepisternum is relatively large and subcircular in Macroxyelinae (Figs. 6, 8, 12) but it is much smaller and more slender in Xyelinae (Figs. 9, 10, 13, 14). The anapleural cleft is a less conspicuous pleural feature in xyelids than in raphidiids partly because anteriorly the margins are very widely divergent and the intervening region is occupied by a subrectangular sclerite (Figs. 8–10). This sclerite, called the **prepectus** in Hymenoptera, is in the same relative position as the subspiracular interpleurite of raphidiids, i.e. ventral to the mesothoracic spiracle at the apex of the anapleural cleft (cf. Figs. 5, 6). The anapleural cleft is also less conspicuous in xyelids because it is suture-like posterior to the prepectus and extends for only a very short distance across the episternum (Figs. 6, 12–14).

Comparison of external structure alone appears sufficient to justify proposed homologies between the dorsal mesopleural regions of xyelids and raphidiids (cf. Figs. 5, 6), but the homologies are supported further by musculature. The partly detached dorsal episternal region of xyelids is shown to be a part of the anepisternum by muscle 145. In *Raphidia* this short slender muscle spans the apex of the anapleural cleft posterior to the subspiracular interpleurite, connecting the anepisternum with the preepisternum (Fig. 34: 145). In *Xyela* the homologous muscle is a broad band of fibers that span the prepectus, connecting the incised margins of the mesopleuron above and below the prepectus (Figs. 29, 30: 145) and indicating the region above the prepectus as the anepisternum and the region below the prepectus as the preepisternum. Daly (1963) designated muscle 145 as muscle "pl₂-ba_{2a}" and incorrectly stated that it inserted into the basalare in *Xyela* (see Discussion).

Two muscles represent discrepancies in muscle origin for the anepisternum of *Xyela* compared with that of *Raphidia*. In *Raphidia*, muscle 157 is relatively broad and originates from the ventral margin of the anepisternum to insert into the anterolateral margin of the mesocoxa. Muscle 157 also inserts into the anterolateral margin of the mesocoxa in *Xyela* (Fig. 33: 157), but it is a slender muscle along the length of the mesopleural ridge ventral to the partly detached anepisternum (Fig. 28: 157). I consider this preepisternal site of origin for muscle 157 in *Xyela* to be secondary and correlated with the reduced size of the anepisternum and more obliquely angled pleuron and pleural ridge of Hymenoptera. Like muscle 157, muscle 163 has the same insertion but different sites of origin in *Raphidia* and *Xyela*. The muscle inserts into the third axillary sclerite in both taxa, but originates from the anepisternum in *Raphidia* and from within the pleural wing process in *Xyela* (Fig. 28). In *Raphidia*, muscle 163 is relatively large and spans diagonally the pleural ridge to insert into the third axillary sclerite from below, whereas it is a much smaller muscle in *Xyela*, extending almost vertically from the uppermost part of the pleural wing process to insert into the third axillary sclerite from above (Figs. 28, 31). As concluded for muscle 157, I consider this site as secondary for *Xyela*, derived for functional efficiency because of differences in the flight apparatus between xyelids and raphidiids.

Sites of muscle origin tend to be much less constant than are sites of insertion because with modification of the exoskeleton concomitant modifications of musculature are required

to maintain functional efficiency. Sites of muscle insertion are more stable because they remain constant unless function of the muscle itself changes (see Discussion). Consequently, the non-anepesternal sites of origin for muscles 157 and 163 in *Xyela* are not compelling evidence against the hypothesized anepisternum of xyelids, which is supported by the sites of origin and insertion for muscle 145.

Muscle 110 also helps substantiate that the prepectus of Hymenoptera most likely is homologous with the subspiracular interpleurite of raphidiids. The muscle originates ventral to the spiracle in *Raphidia*, from intersegmental membrane anterior to the interpleurite (Fig. 34: 110). In *Xyela*, the homologous muscle also originates ventral to the spiracle from intersegmental membrane immediately anterior to the prepectus, though the muscle is composed of two bands, one originating slightly above the other (Fig. 32: 110).

The proposed homologies for the anepisternum and prepectus are new. In Symphyta other than Xyelidae the basalar cleft and anapleural cleft intersect to detach the anepisternum as an independent sclerite posterior to the spiracle (= **postspiracular sclerite** sensu Michener 1944) (cf. Figs. 13, 14 with 15, 16). This transformation series was not recognized by most workers because most previous hypotheses of the hymenopteran pleurosternum were based on non-xyelid symphytes. Shcherbakov (1980) recognized that the independent sclerite of most symphytes evolved through separation of the partly detached dorsal episternal region characteristic of xyelids, but he did not associate the region with the anepisternum and instead called it the "first basalar" (Fig. 3). Often the sclerite was not taken into consideration when postulating homologies (Weber 1927; Arora 1956; Matsuda 1960a, 1960b, 1970), or if included was considered to be of secondary origin and variously called the "first parapteron" (Snodgrass 1910; Saini and Dhillon 1980), "first basalar" (Rasnitsyn 1969; Shcherbakov 1980), or "postspiracular sclerite" (Michener 1944; Richards 1956). Further, the prepectus has not been postulated previously as an interpleurite, i.e. an isolated part of the presternum. Snodgrass (1910) introduced the term prepectus but proposed that it was a secondarily detached part of the episternum. Arora (1956) incorrectly homologized the prepectus with the anepisternum, and Shcherbakov (1980) called it the "postspiracular sclerite" (Fig. 3) without indicating homology. Gibson (1985) described transformation of both the prepectus and postspiracular sclerite throughout Hymenoptera, discussed their phylogenetic significance, and more fully reviewed terms used for the sclerites.

Ventral episternum. Two sets of grooves delineate three regions on the episternum ventral to the anapleural cleft. A large dorsal region is distinguished from a smaller, triangular, ventromesal region by an oblique groove extending between the lateral posteroventral margin of the episternum and the discrimen (Figs. 4, 6, 18). A third, much smaller and narrower region is segregated partly from the large dorsal region by a sinuate groove near the lateral posteroventral margin of the episternum (Figs. 4, 20, 21). The oblique grooves that delineate triangular regions on either side of the discrimen (Fig. 18) have been interpreted variously as the sternopleural sutures (which delineate the sternum from the pleuron) (Snodgrass 1910, 1927; Weber 1927; Arora 1956; Richards 1956), as the anapleural sutures (which delineate a dorsal anepisternum from one or both of the preepisternum + katepisternum) (Matsuda 1960a, 1960b, 1970; Shinohara 1986), or as secondary sulci (Shcherbakov 1980; Saini and Dhillon 1980). I agree with Shcherbakov (1980) that the oblique grooves (Fig. 3) are secondary features of Hymenoptera which evolved to strengthen relatively thin cuticle against the antagonistic pull of two very large muscles, the "dorsoventral indirect flight muscles" (Fig. 24: 128/129) originating from within each triangular region (cf. Figs. 24, 25), and the "pleural-basalar muscles" originating lateral to each region (Figs. 25, 26: 154). The single pair of dorsoventral indirect flight muscles of xyelids can only be homologized with, and probably are a composite of, muscles 128 (interior scutal-preepisternal) and 129 (lateral scutal-preepisternal) of raphidiids (Fig. 22). This homology indicates that the triangular region represents a part of the preepisternum

in xyelids. If this is so, then the pleural-basalar muscle (Figs. 25, 26: 154) must be homologous with muscle 154 (preepisternal-basalar) of raphidiids (Figs. 23: 154). Because muscle 154 is also of preepisternal origin, the external sulcus and internal apodeme that separates it from muscles 128/129 must be secondary. Following Shcherbakov (1980), I refer to the grooves as the **pseudosternal sulci** and the triangular region as the **pseudosternum** (Figs. 6, 18).

Origin and homology are less certain for the second episternal groove, which partly segregates a narrow region near the lateral posteroventral angle of the episternum (Figs. 4, 20, 21). This groove could be a secondarily derived sulcus or a remnant of either the paracoxal suture or the trochantinal suture. The groove is developed as an apodeme internally (Fig. 33), and is a sinuate continuation of an apodeme that forms the posterior margin of each pseudosternum (cf. Figs. 18, 21, 33). Only the posterior-most fibers of muscle 154 (preepisternal-basalar) originate from the sinuate apodeme (Fig. 33: 154).

Daly (1964) appropriately cautions that sulci are lines of support or strength and should be used only cautiously as boundaries for hypothetical sclerites. However, the groove delineating the slender episternal region may represent a relictual suture rather than a sulcus because there is no apparent functional reason why a strengthening apodeme should be developed secondarily in this position. The apodeme does not strengthen the cuticle against the antagonistic pull of two large muscles, as for example do the pseudosternal sulci. There is no obvious functional explanation why muscle 154 simply should not be continued along the ventrolateral margin of the episternum from the pseudosternal apodeme (Fig. 33) unless the intervening apodeme is a relictual suture.

If the sinuate groove does represent a suture, it could be a remnant of either the paracoxal suture or the trochantinal suture. In *Raphidia*, the trochantin is a partly detached elongate-slender sclerite that basally is widened and fused with the katepisternum (Figs. 17, 19). Two muscles, muscle 130 (tergal-trochantinal) (Fig. 22: 130) and muscle 132 (basalar-trochantinal) (Fig. 23: 132) are attached to it. Xyelids lack such a semidetached sclerite but the sinuate groove delineates a similarly shaped region in the same approximate position (cf. Figs. 19, 21). No muscles originate from this region in xyelids and they lack any muscles that can be homologized with muscles 130 and 132 of raphidiids. Because of the coincidence of position the narrow region could be interpreted as the trochantin, and the groove as the trochantinal suture, if the trochantin was fused with the episternum and the trochantinal muscles were lost from the groundplan of the Hymenoptera. Alternatively, the groove could be a relictual paracoxal suture. The paracoxal suture delineates an anterodorsal preepisternum from a posteroventral katepisternum in raphidiids (Figs. 5, 17). No muscles originate from the katepisternum in *Raphidia* but muscles 128, 129, and 154 (Figs. 22, 23) originate from the preepisternum at, and dorsal to, the paracoxal apodeme. There is no definitive katepisternum in *Xyela* because muscle 128/129 originates from the episternum immediately anterior to the mesocoxa (Fig. 24). The xyelid structure could have evolved from a raphidiid-like structure by two transformation series. The paracoxal suture simply could have been lost so the lower episternum is a composite of preepisternum + katepisternum, with muscles 128/129 and 154 secondarily extended ventrally over the "katepisternum." Alternatively, the katepisternum could have been reduced progressively as the preepisternum was increased in size because of secondary enlargement of muscles 128/129 and 154 in the ancestors of Hymenoptera. Enlargement of the muscles, resulting in expansion of the preepisternum and progression of the paracoxal suture toward the ventral margin of the episternum could result in a structure like that exhibited by xyelids, in which the paracoxal suture is separated only very narrowly from the posterior margin of the episternum ventromesally (Figs. 18, 20, 21) but laterally curves dorsally to remain partly extended to the pleural ridge pit (Figs. 20, 21). As corollaries of this second hypothesis, the ventral process is segregated more distinctly in xyelids than in raphidiids

(cf. Figs. 17, 18) and the katepisternum is restricted to the linear ventral edge and narrow ventrolateral angle of the episternum (Figs. 20, 21).

Shcherbakov (1980) combined both of what I term the "trochantinal suture" and "paracoxal suture" hypotheses in his interpretation of xyelid structure. He interpreted the groove along the posteroventral margin of the episternum, from the discrimen to the lateral end of the pseudosternal sulcus, as the paracoxal suture, and the apically curved portion of the groove as the trochantinal suture (Fig. 3). He interpreted also the very narrow region posterior to the paracoxal suture as the postepisternum sensu Rasnitsyn (1969),² the region posterior to the trochantinal suture as the trochantin, and the posterolateral angle of the episternum dorsal to the trochantin as the katepisternum (Fig. 3). I differ from Shcherbakov (1980) in postulating that the trochantin was not present in the groundplan of the hymenopteran pleuron and that the katepisternum was reduced through expansion of the preepisternum as described above. I interpret the posteroventral episternal groove as a relictual paracoxal suture that segregates a remnant of the katepisternum from the secondarily enlarged preepisternum (Figs. 2, 4). Shcherbakov's (1980) hypothesis of a postepisternum separate from the katepisternum in xyelids is incorrect because he misinterpreted the anapleural cleft (Fig. 3), but his hypothesis of both a trochantin and a paracoxal suture cannot be refuted at present. Discovery of intermediate states in fossils of ancestors of Hymenoptera or studies of the morphogenesis of the skeletomusculature of xyelids might help to resolve this question.

Epimeron. As stated above, the mesepimeron of xyelids is similar to that of raphidiids except that it is angled obliquely and relatively smaller. A tiny pleural ridge pit near the midlength of the pleural suture (Figs. 6, 8-10) is the point of attachment for muscle 153 (Fig. 28: 153). The mesepimeron is not divided into an anepimeron and katepimeron because the paracoxal suture does not extend through the epimeron. However, many xyelids have an upper and lower epimeral region slightly differentiated by a difference in convexity (Figs. 9, 10), or even by a darker-colored line in light-colored specimens. The upper and lower epimeral regions are not distinguished by any apodeme internally and any external line merely reflects the internal broad line of confluence between muscles 161 and 151 (Fig. 28).

Though the epimeron is not subdivided by a paracoxal suture, based on sites of muscle origins the upper and lower epimera are approximations of the anepimeron and katepimeron. Matsuda (1970) showed that the pleural ridge pit approximates the position of the dorsal arc of the paracoxal suture through the pleuron in pterygotes (Fig. 1). Matsuda (1970) also stated that the apodeme of the pleural ridge pit is connected to the tergum by muscle 153 (Matsuda 1970, fig. 23B: t-p12) and to the furca by muscle 151 (fig. 23B: p-s1), and that muscle 161 (fig. 23B: t-p16) and muscle 164 (fig. 23B: t-p14) originate from the anepimeron dorsal to the apodeme of the pleural ridge pit. There are four epimeral muscles in *Xyela* excluding muscle 163, which secondarily originates from the pleural wing process (Figs. 28, 31) (see above). Muscle 153 originates from the pleural ridge at the line of confluence between muscle 151, below, and muscle 161, above, and muscle 164 originates dorsal to the line of confluence between muscles 161 and 151 (Fig. 28). These muscle positions indicate that the region dorsal to the line of confluence between muscles 151 and 161 approximates the anepimeron, and the region ventral to the line of confluence approximates the katepimeron. They are, however, only approximations.

Discussion

This study apparently resolves most questions regarding the groundplan structure and homologies of the mesopleurosternum of Hymenoptera. Homology of the paracoxal suture is tentative but probably cannot be resolved definitively without morphogenetic studies of

²Rasnitsyn (1969) considered that the katepisternum was subdivided by the anapleural cleft in some Hymenoptera, and named the ventrally delineated part of the katepisternum as the postepisternum.

the skeletomusculature. There is no evidence that the sternum is exposed anterior to the mesocoxae in Hymenoptera, except for the prepectus, which, following Matsuda (1970), is hypothesized as an isolated part of the presternum. Because this hypothesis is based on coincidence of position rather than evolutionary continuity of structure it has to be tested by more comprehensive studies of the intersegmentalia of Neuroptera and other Pterygota. Likewise, more extensive studies are required to determine whether the basalar cleft is symplesiomorphic for Hymenoptera, or is a secondarily derived synapomorphic feature of the order.

Regions postulated as the sternum in Encyrtidae or Eupelmidae (Apocrita: Chalcidoidea) by Richards (1956, fig. 2), Compere (1962, fig. 2), and Matsuda (1960*b*, fig. 6; 1970, fig. 160), were shown by Gibson (1986*b*) to be secondary skeletal features correlated with enlarged tergal-pleural muscles (Gibson 1986*b*, table 1, 5:pl₂-t_{2c}) in a thorax highly modified for a unique method of jumping. The regions previously proposed as sternal in many Symphyta are also secondary subdivisions of the episternum resulting from origin of a strengthening apodeme between each dorsoventral indirect flight muscle and preepisternal-basalar muscle. These two muscles are relatively much larger in xyelids than in raphidiids and this may be partly correlated with, and compensate for, secondary loss of analogous muscles associated with the trochantin (130:tergal-trochantinal and 132:basalar-trochantinal) in raphidiids. However, enlargement of the muscles most likely is correlated primarily with predominance of the mesothorax for powering flight in Hymenoptera. This functional difference between Neuroptera and Hymenoptera explains not only differences in relative size of the two dorsoventral muscles but also differences in structure of the ventral episternum. Correlated with the two enlarged preepisternal muscles of Hymenoptera are a strongly reduced katepisternum because of the secondarily enlarged preepisternum, and pseudosternal sulci to strengthen the enlarged preepisternum against the antagonistic pull of the two muscles.

Study of the skeletomusculature of xyelids indicates the potential value of musculature for systematics as well as for comparative morphology of Hymenoptera. Sites of muscle insertion often are useful as evidence of homology because they remain unless function of the muscle is modified through fusion or loss of the structure into which the muscle is inserted. Daly (1963) stated that in the Hymenoptera studied by him, muscle 145 (anepisternal-preepisternal) was inserted into the basalare as muscle pl₂-ba_{2a}. Although this is not true for *Xyela*, it must be true for those Hymenoptera that have lost secondarily the postspiracular sclerite (see Gibson 1985). Sites of muscle origin tend to be more variable because they change with skeletal modifications to retain functional efficiency. Because they tend to be more variable, sites of muscle origin are less reliable indicators of homology than are sites of insertion [see Matsuda (1965, p. 290) for discussion of the limitations of musculature in determining homologies], but the differences between taxa can be interpreted as transformation series in phylogenetic analyses.

Musculature can provide a wealth of phylogenetic data because of the large number of muscles in the insect body that can be used for character analysis, and because differences in muscle origin and insertion can occur independently of obvious external differences between taxa. The potential value of musculature largely remains unrealized because very little is known of character state distribution of muscles in insects. Within Hymenoptera, a few studies (Shcherbakov 1981; Gibson 1985, 1986*b*; Johnson 1988) employed selected thoracic muscles for comparative morphology or phylogenetics, following the pioneering comparative work of Daly (1963), but detailed tabulation of musculature has been made for very few Hymenoptera (see Matsuda 1970), including only two taxa of Parasitica, *Stenobracon deesae* Cameron (Ichneumonoidea: Braconidae) (Alam 1951) and Eupelmidae (Chalcidoidea) (Gibson 1986*b*).

Comparison of the mesothoracic muscles tabulated for Eupelmidae by Gibson (1986*b*) with those studied for *Xyela* illustrate the potential of the study of skeletomusculature in

phylogenetic analysis. Similar upper and lower mesepimeral regions are delineated in Xyelidae (Figs. 9, 10) and in many Chalcidoidea (Gibson 1986b, fig. 2). However, in *Xyela* the upper mesepimeron is the site of origin for muscles 161 and 164, and the lower mesepimeron is the site of origin for muscle 151 (Fig. 28), whereas in Eupelmidae muscle 151 originates from the upper mesepimeron (Gibson 1986b, figs. 7, 8:12), and muscle 161 originates from the lower mesepimeron (figs. 7, 8:16), along with a muscle (pl_2-3ax_3a) secondarily transferred from the metapleuron (figs. 7, 8:19). Muscle 164 apparently is divided into two parts and originates from the region designated as mesepisternum (Gibson 1986b, cf. fig. 8 with fig. 7:8, 9). Eleven of the 18 selected mesothoracic muscles studied for *Xyela* are shared with eupelmids (110=6, 128/129=3, 142=5, 151=12, 153=4, 154=10, 157=13, 161=16, 163=7, 164=8+9, and 165=17). Seven muscles apparently are lost secondarily from eupelmids (137, 141, 144, 145, 156, 158, and 160). Each of the muscles represents a character that potentially could help resolve the phylogeny of Hymenoptera, if the musculature of a sufficient diversity of Hymenoptera were known for comprehensive analysis of transformation series. For example, though muscle 165 is shared between xyelids and chalcidoids it is absent from most Apocrita, including Aculeata (Gibson 1985), and though muscle 164 is reported as single in Symphyta and in Aulacidae (Apocrita: Parasitica) (Shcherbakov 1981) it has two elements in Chalcidoidea (Gibson 1986b), Braconidae (Alam 1951), and Peleciniidae (Shcherbakov 1981) (Parasitica), as well as in Scoliidae, Vespidae, and Mellinidae (Aculeata) (Shcherbakov 1981). More comprehensive knowledge of states of these and other muscles throughout Hymenoptera could help to resolve relationships within the order, including whether Parasitica is paraphyletic relative to Aculeata.

Conclusions

Morphology and systematics are inextricably interrelated. Ideally, the two should function together in a positive, cyclical feedback system in which discoveries in one field stimulate discoveries and advances in the other field. Recent research in Hymenoptera illustrates this synergistic relationship. Explicit hypotheses of infraordinal relationships by Königsmann (1977) and Rasnitsyn (1980) stimulated basic comparative morphology in Hymenoptera (Gibson 1985, 1986a; Naumann and Masner 1985; Johnson 1988; Whitfield et al. 1989), which in turn provided new information for resolving questions of monophyly and relationships. This new information was then used by Rasnitsyn (1988) to modify and improve his previous (Rasnitsyn 1980) concepts and reconstructed phylogeny of Hymenoptera.

Resolution of the homologies of the mesopleurosternum of members of Xyelidae in this study further demonstrates the positive interrelationship between morphology and systematics. The phylogenetic hypothesis that Xyelidae represent the basal lineage of Hymenoptera provides the rationale for my interpretation of the groundplan structure of the mesopleurosternum in Hymenoptera, and invalidates most previous hypotheses of structure that were based on more derived Symphyta and Apocrita. In turn, the discovery that the upper episternal region of xyelids is homologous with the anepisternum provides new support for the hypothesis that Xyelidae are the basal lineage of Hymenoptera. I interpret the attached anepisternum of Xyelidae as a uniquely retained symplesiomorphy because other Symphyta have the region detached as a separate sclerite, the postspiracular sclerite. Separation of the anepisternum from the preepisternum through intersection of the basalar and anapleural clefts is hypothesized as a synapomorphy for Hymenoptera other than Xyelidae. This latter transformation of structure does not support Rasnitsyn's (1980, 1988) hypothesis that non-xyelid Hymenoptera have a biphyletic origin from Xyelidae. Rasnitsyn's biphyletic hypothesis requires that the anepisternum was separated as a postspiracular sclerite independently in Tenthredinoidea and in other non-xyelid Symphyta, i.e. is homoplastic.

Modern cladistic analyses require interpretation of homology rather than similarity, but past morphology has been based largely on coincidence of position. Results of this study indicate that all hypotheses of structural homology previously postulated in Hymenoptera should be verified prior to credible cladistic analyses [see, for example, Shcherbakov's (1981) reanalysis of the mesepimeron in Apocrita]. At present, perceived homoplasy is as likely due to errors of observation or interpretation as it is the result of independent evolution. Relatively recent explicit hypotheses of Xyelidae as the basal lineage of Hymenoptera, and the Orussidae as the extant sister group of Apocrita, provide a minimal framework for reinterpreting transformation of structure based on the evolutionary history of the order. In turn, substantial progress in phylogenetics of Hymenoptera requires a renaissance in comparative morphology, not just new and improved computer algorithms for analyzing presumed transformation series or myopic faith that new techniques, such as molecular systematics, will resolve all problems.

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APPENDIX. List of abbreviations used for structures

aepm:	anepimeron	plr:	pleural ridge
aeps:	anepisternum	plrp:	pleural ridge pit
ancl:	anapleural cleft	pls:	pleural suture
anps:	anapleural suture	plwp:	pleural wing process
ba:	basalare	pre:	prepectus
bacl:	basalar cleft	prep:	preepisternum
dsc:	discrimen	pss:	postspiracular sclerite
epm:	epimeron	pst:	pseudosternum
fup₂:	mesofurcal pit	psta:	pseudosternal apodeme
inpl:	interpleurite	psts:	pseudosternal sulcus
kepm:	katepimeron	sp:	spiracle
keps:	katepisternum	tchn:	trochantin
lepm:	lower epimeron	tepl:	transepimeral line
no₁:	pronotum	tg:	tegula
pcxa:	paracoxal apodeme	uepm:	upper epimeron
pcxs:	paracoxal suture	vtpl:	ventropleurite (ventral process)
pl₂:	mesopleuron		
pl₃:	metapleuron		

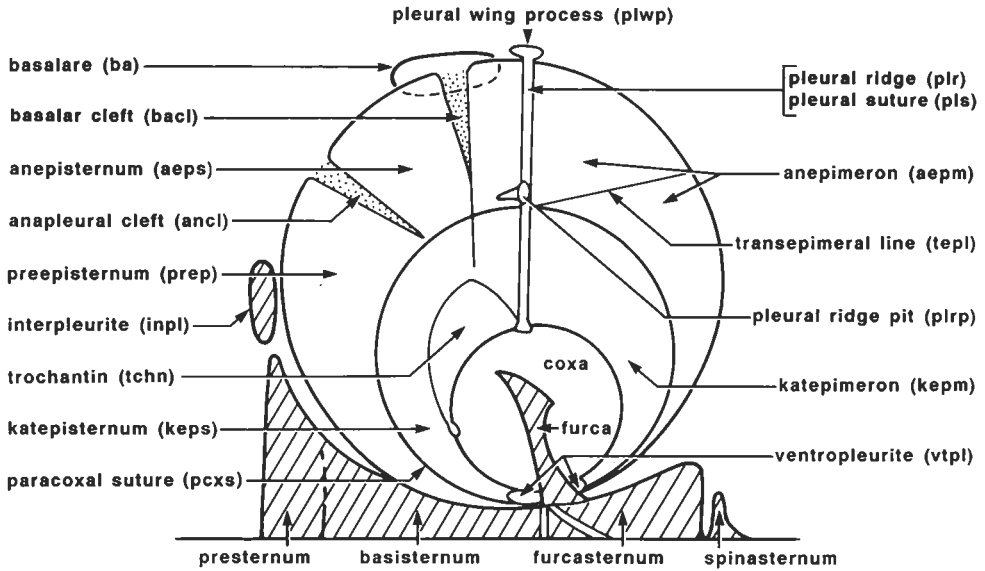


FIG. 1. Schematic representation of primitive pterothoracic pleurosternum based on subcoxal theory of pleuron origin (after Matsuda 1970) (sternal elements crosshatched).

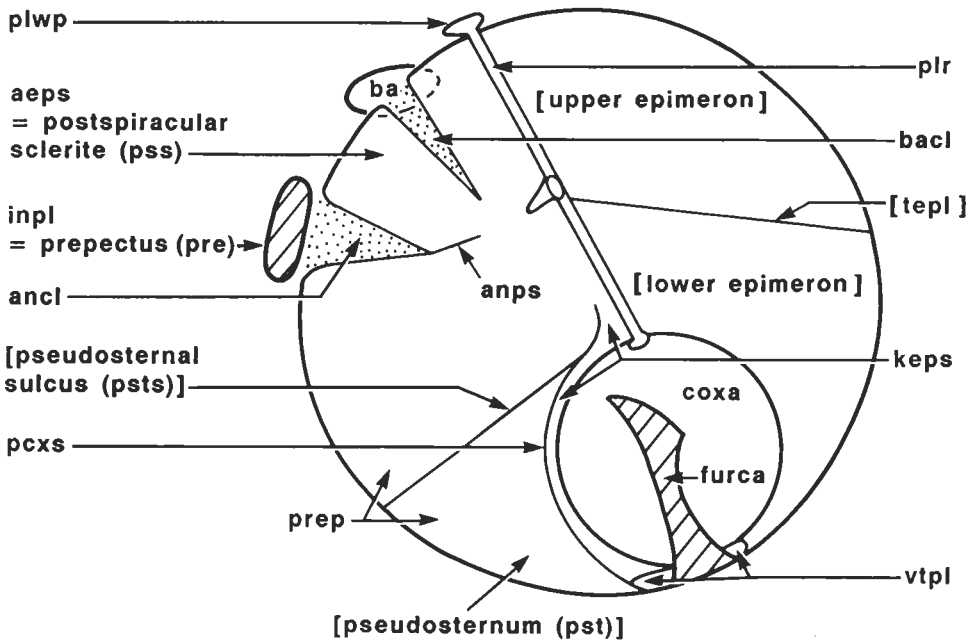
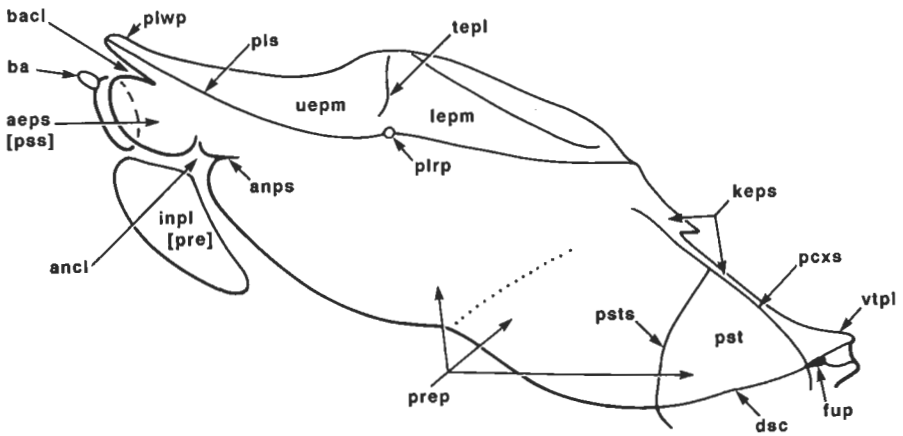
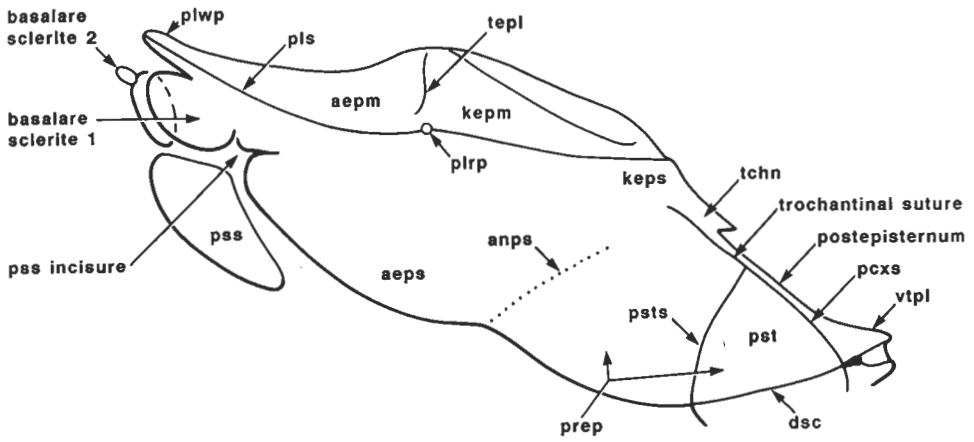
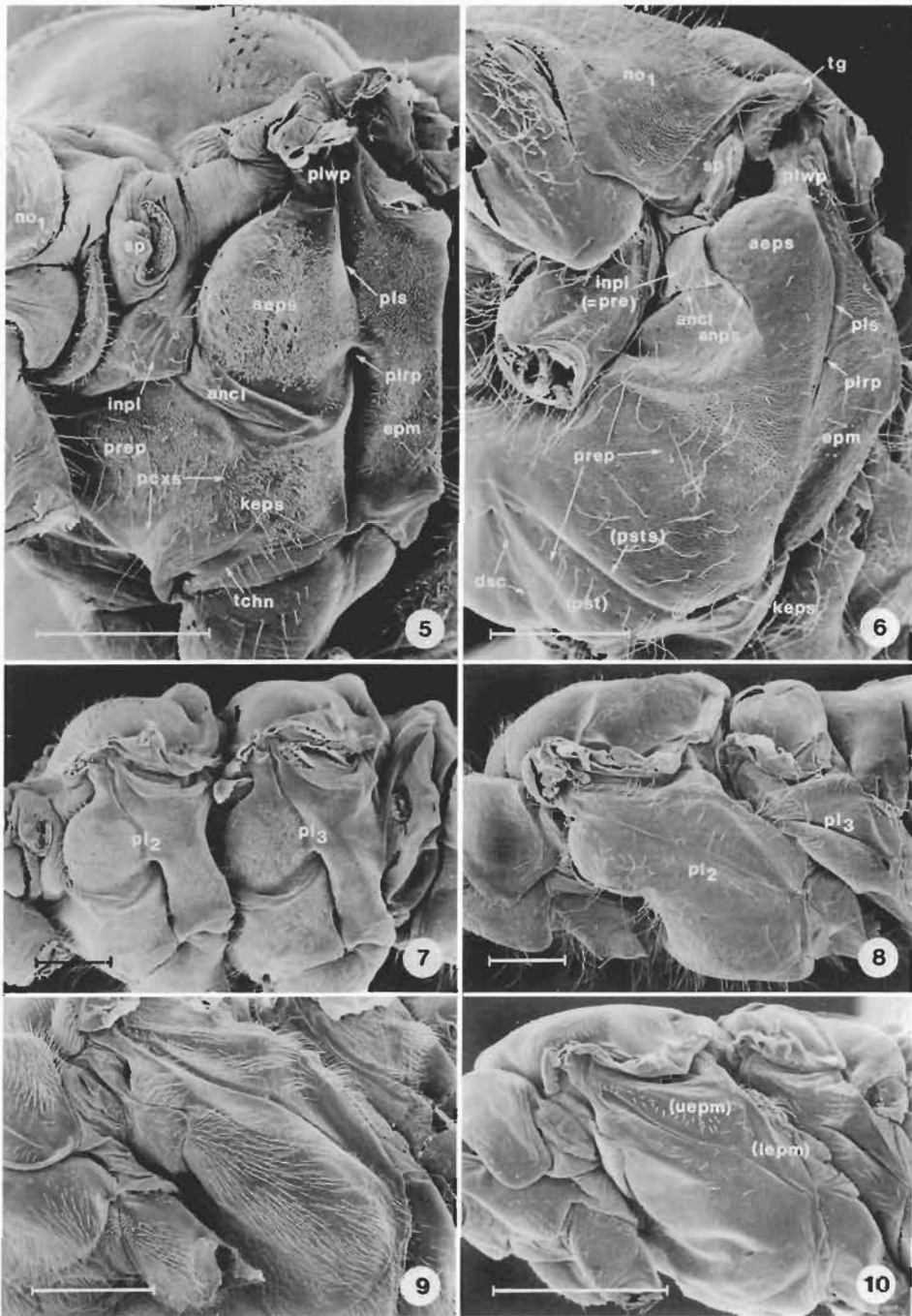


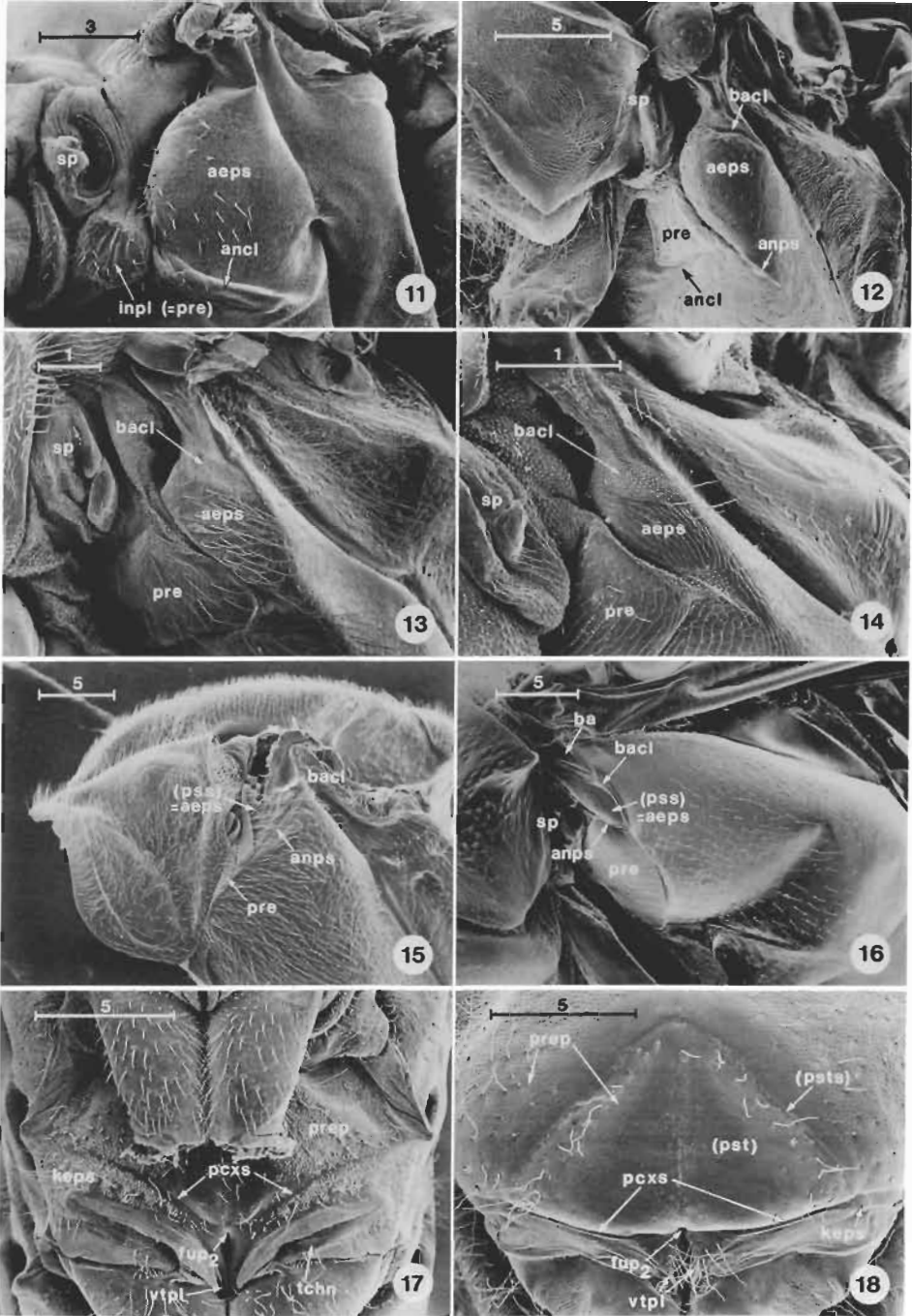
FIG. 2. Schematic representation of hypothetical groundplan structure of mesopleurosternum of Hymenoptera (sternal elements crosshatched; "=" denotes equivalent terms used in Hymenoptera; secondary features of Hymenoptera in parentheses). For abbreviations see Appendix.



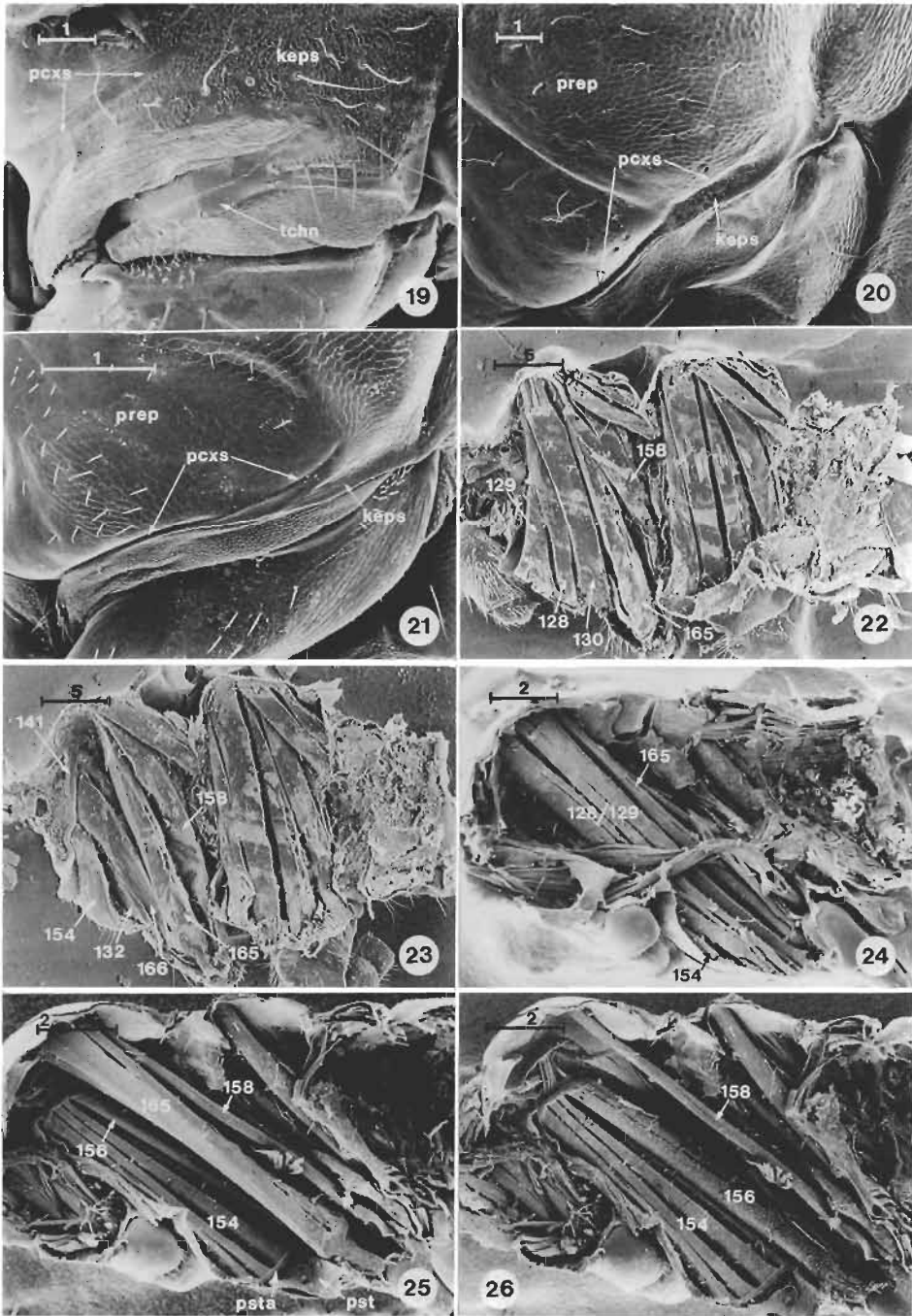
FIGS. 3, 4. Mesopleurosternal structure of *Xyela* (Xyelidae): 3 (top), after Shcherbakov (1980); 4 (bottom), based on proposed hypotheses of homology. For abbreviations see Appendix.



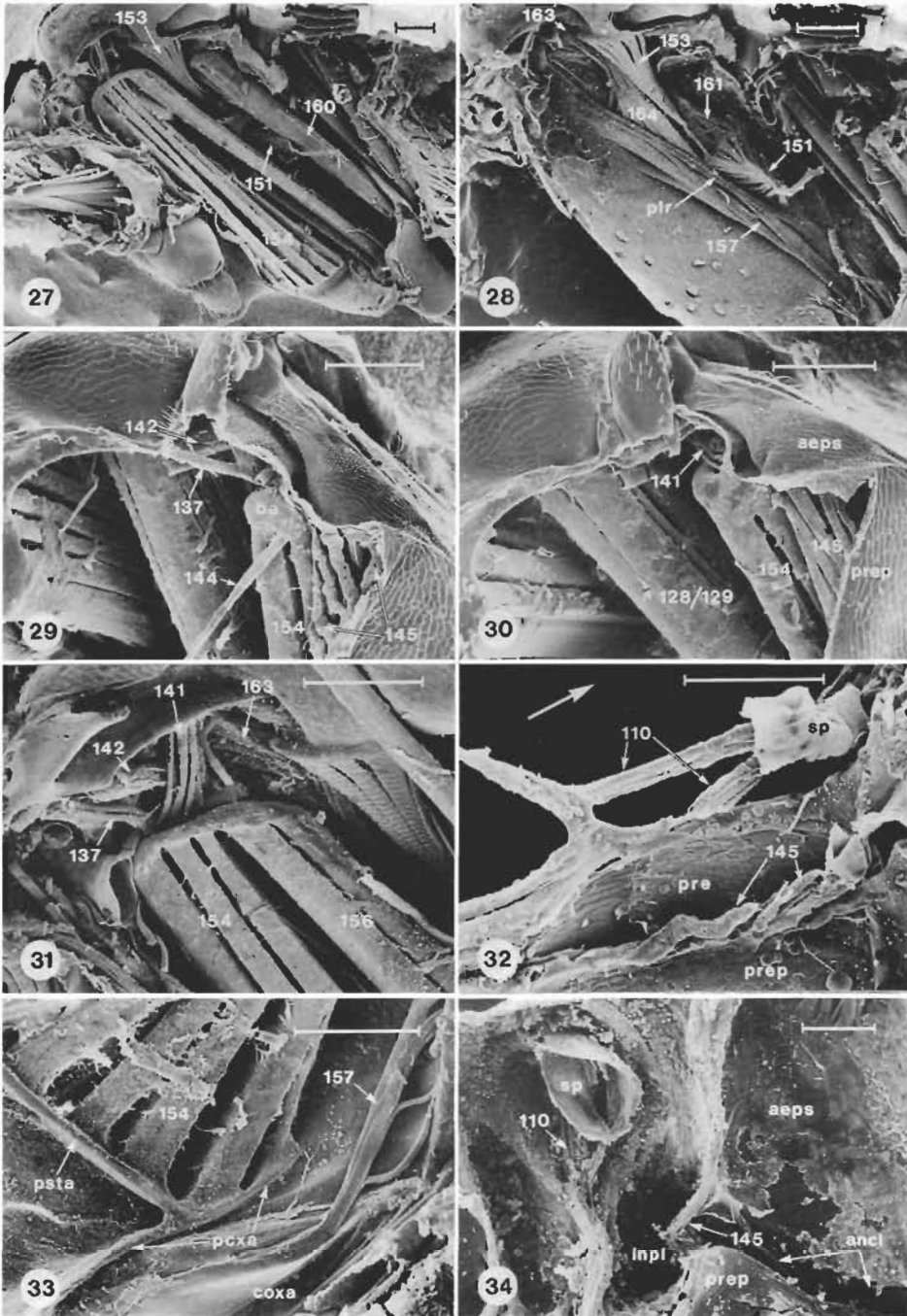
FIGS. 5–10. (scale bar = 500 μ m). 5 and 6, lateral mesothorax: 5, *Raphidia (Agulla)* sp.; 6, *Macroxyela ferruginea* (Say), pronotum faced dorsally. 7–10, lateral thoraces: 7, *R. (A.)* sp.; 8, *M. ferruginea*; 9, *Pleroneura brunneicornis* Rohwer; 10, *Xyela minor* Norton. For abbreviations see Appendix.



FIGS. 11–18. (scale bar = 100 μm). 11–16, lateral view of upper mesepisternum and mesepimeron: 11, *Raphidia* (*Agulla*) sp.; 12, *Macroxyela ferruginea* (Say); 13, *Pteroneura brunneicornis* Rohwer; 14, *Xyela minor* Norton; 15, *Tenthredo* sp. (Tenthredinoidea: Tenthredinidae); 16, *Syntexis libocedrii* Rohwer (Siricoidea: Anaxyelidae). 17 and 18, ventral view of lower mesepisternum: 17, *Raphidia* (*Agulla*) sp.; 18, *Macroxyela ferruginea* (Say).
For abbreviations see Appendix.



FIGS. 19–26 (scale bar = 100 μ m). 19–21, lateral view of lower mesepisternum: 19, *Raphidia (Agulla)* sp.; 20, *Macroxyela ferruginea* (Say); 21, *Pleroneura brunneicornis* Rohwer. 22 and 23, *R. (A.)* sp. thoracic muscles, sagittal section: 22, first section; 23, muscles 128, 129, and 130 removed. 24–26, *X. minor* thoracic muscles, sagittal section: 24, first section; 25, muscle 128/129 removed; 26, muscles 128/129 and 165 removed. For abbreviations see Appendix; for numbered muscles see Table 1.



FIGS. 27-34 (scale bar = 100 μ m). 27-33, thoracic muscles of *Xyela minor* Norton: 27, sagittal section with muscles 128/129, 165, and 158 removed; 28, outer muscles adjacent to pleural wall; 29 and 30, outer views of upper mesepisternum with pronotum, prepectus, and different muscles removed; 31, inner view of muscles of upper mesepisternum; 32, inner view of detached upper mesepisternum (arrow denotes direction of dorsum); 33, inner view of lower mesepisternum and mesocoxa. 34, inner view of detached upper mesepisternum of *Raphidia (Agulla)* sp. For abbreviations see Appendix; for numbered muscles see Table 1.