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# Sister-group relationships of the Platygastroidea and Chalcidoidea (Hymenoptera) — an alternate hypothesis to Rasnitsyn (1988)

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Accepted 15 February 1999

Gibson, G. A. P. (1999) Sister-group relationships of the Platygastroidea and Chalcidoidea (Hymenoptera) — an alternate hypothesis to Rasnitsyn (1988) — *Zoologica Scripta* 28, 125–138. Evidence for the hypothesis that Platygastroidea and (Chalcidoidea + Mymarommatoidea) are sister groups is reviewed and an alternate hypothesis of relationships is proposed for Platygastroidea. Platygastroidea is postulated to form a monophyletic group with Pelecinidae, Proctotrupeoidea and Vanhorniidae based on common possession of an annular pronotum and a mesopleural-mesotrochanteral muscle. Hypotheses of character-state transformation are illustrated diagrammatically to explain distribution of the mesotrochanteral depressor muscle and relative structure of the pronotum, mesothoracic spiracle, prepectus, and pronotal-mesepisternal attachment throughout the nonaculeate Apocrita. The states of 16 characters are defined in one table and another table summarises the distribution of the states in Orussidae and Apocrita. Retention of an independent prepectus and a mesotergal-mesotrochanteral depressor muscle indicates that Chalcidoidea + Mymarommatoidea are a relatively early clade of Apocrita but does not indicate exact relationships. Chalcidoidea + Mymarommatoidea are indicated as possibly being more closely related to Diapriidae or Ceraphronoidea based on other characters. It is postulated that structure of the mesocoxal articulation of taxa assigned to the Evaniomorpha may represent a retained symplesiomorphy rather than a synapomorphy. Mesocoxal articulatory structure is illustrated by scanning electron photomicrographs.

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## Introduction

Rasnitsyn (1980, 1988) are arguably two of the most influential works on the phylogenetics of Hymenoptera. Königsmann (1977; 1978a, b) attempted the first comprehensive, rigorous phylogenetic analysis of familial level relationships of Hymenoptera and presented the first truly testable hypothesis of apocritan relationships (Königsmann 1978a; fig. 7 a,b). However, the data used by Königsmann were based largely on the literature and were insufficient to resolve almost all apocritan relationships (Whitfield 1992; fig. 1). Rasnitsyn (1980; fig. 38) proposed an almost fully resolved hypothesis of higher-level relationships that included fossil taxa and substantial data from comparative morphology (Rasnitsyn 1969, 1980). Because the works of Königsmann and Rasnitsyn were in German and Russian, respectively, details of the studies were largely unavailable to much of the English speaking systematics community. Despite this, the presence of alternative hypotheses stimulated other

studies (e.g. Naumann & Masner 1985; Gibson 1985, 1986a; Carpenter 1986; Johnson 1988), the results of which Rasnitsyn (1988) embodied in a revised, English summary of his prior hypotheses.

The Platygastroidea *sensu* Masner (1993) is comprised of Platygastriidae and Scelionidae. Masner (1956) first proposed excluding these two families from the Proctotrupeoidea and classifying them in their own superfamily, which he then called the Scelionoidea. Rasnitsyn (1980) included Platygastriidae and Scelionidae in his new superfamily Diaprioidea, as well as Austroniidae, Diapriidae, Monomachidae, Serphitidae, and Mymaridae. Some putatively primitive features of Platygastriidae (structure of pronotum, enlarged second metasomal tergum, and parasitism of Diptera larvae) were said to show a link with Diapriidae. Platygastriidae were also said to share with Scelionidae some primitive features (first metasomal segment composed of tergum and sternum) as well as some derived features (annular pronotum, male genitalia

similarly reduced), and the family was illustrated as having uncertain relationships between Scelionidae and Diapriidae (Rasnitsyn 1980; fig. 38).

Rasnitsyn (1980) concluded that the evidence for phylogenetic relationships of Chalcidoidea was contradictory because some features indicated a relationship with the extinct family Mesoserphidae and other features with Diapriidae. He illustrated the Chalcidoidea as being derived either from Mesoserphidae or questionably from the ancestor of Diapriidae + Cynipoidea (Rasnitsyn 1980; fig. 38). Rasnitsyn (1980) further proposed that the family Mymaridae was derived from Scelionidae. The type genus of Mymaridae was originally described in Proctotrupidae and the family was often classified in Proctotrupeoidea until Ashmead (1899). Since Ashmead (1904) most classifications have included Mymaridae in Chalcidoidea. Rasnitsyn (1980) considered that mymarids were derived from scelionids primarily because their members share a similar distinctive type of first instar larvae, termed 'mymariform' by Clausen (1940), and because he considered that mymarids share a multitude of parallelisms with mymaromatids. Rasnitsyn (1980) classified mymaromatids as a subfamily of the extinct Cretaceous family Serphitidae, following Kozlov & Rasnitsyn (1979), and considered that serphitids were also derived from scelionids, but independently and at a different time than mymarids. Kozlov & Rasnitsyn (1979) proposed that mymaromatids were related to serphitids partly because they lack certain features characteristic of mymarids and chalcidoids, but also because mymaromatids and serphitids share an otherwise unique feature for the parasitic Hymenoptera, a two-segmented petiole (Gibson 1986a; fig. 36). Duisburg (1868) described the first mymaromatid as a species of *Proctotrupes* Latreille (Proctotrupeoidea), but otherwise mymaromatids have generally been classified in Chalcidoidea or, more recently, as their own superfamily (Noyes & Valentine 1989; Gibson 1993).

Gibson (1986a) proposed that Chalcidoidea, including Mymaridae but excluding Mymaromatidae, was monophyletic based on three autapomorphies: prepectus externally visible, at least dorsally adjacent to the mesoscutum (Gibson 1986a; figs 18–20, 24–27), mesothoracic spiracle positioned at the exposed lateral margin of the mesoscutum (Gibson 1986a; figs 18–29), and uniquely structured multiporous plate sensilla present on the antennal flagellum (Gibson 1986a; fig. 4). Gibson (1986a) also postulated that Mymaromatidae are the sister group of Chalcidoidea based on three apomorphies: unique loss of two of the three plesiomorphic sites of origin of the mesotrochanteral depressor muscle ( $fu_2$ - $tr_2$  and mesoscutal portion of  $t_2$ - $tr_2$ ), unique origin of a horizontal

phragma that extends anteriorly under the mesoscutum from each axilla (Gibson 1986a; fig. 35) as site of origin for all or part of the remaining mesotrochanteral depressor — the mesotergal-mesotrochanteral muscle (Gibson 1986a; fig. 34), and loss of an annular basal ring from the male genital capsule. Because all of the features that indicate a Mymaromatidae + Chalcidoidea sister-group relationship are internal, they could not be examined for Serphitidae, which are only preserved as amber inclusions. Consequently, Gibson (1986a) could not disprove a Mymaromatidae + Serphitidae sister-group relationship, but he did give reasons why these two families could not have been derived from Scelionidae as proposed by Rasnitsyn (1980).

Rasnitsyn (1988) subsequently classified Mymaridae in Chalcidoidea and recognized Mymaromatidae as a family separate from Serphitidae. He also postulated that Serphitidae are the sister group of Scelionidae + Platygastridae and that these taxa form a monophyletic group together with Chalcidoidea, Mymaromatidae, and the extinct Jurassic family Jurapriidae. Mymaromatidae were considered as having uncertain relationships relative to Chalcidoidea and Serphitidae (Rasnitsyn 1988; fig. 3).

Since Rasnitsyn (1988), several authors have included a Platygastroidea + Chalcidoidea sister-group relationship in their own studies, either republishing Rasnitsyn's (1988) cladogram or a variant of that cladogram, or for interpreting distribution of character states within Hymenoptera, or as rationale for selecting study taxa or for polarizing characters (Whitfield 1992, 1998; Downton & Austin 1994; Heraty *et al.* 1994; Austin & Field 1997; Downton *et al.* 1997; Quicke 1997). The purpose of this paper is to propose an alternate hypothesis of relationships for Platygastroidea based on analysis of character-state transformation for two of the characters that indicate Chalcidoidea is monophyletic and the sister group of Mymarommatoidea. The two character systems are the structure of the mesotrochanteral depressor muscle and the relative structure and position of the pronotum, prepectus, and mesothoracic spiracle, which were first described and illustrated throughout Hymenoptera by Gibson (1985). Neither character supports a Platygastroidea + Chalcidoidea sister group relationship. Rather, both characters indicate that Platygastroidea is most closely related to Peleciniidae + Proctotrupidae + Vanhorniidae. This alternate hypothesis is proposed so that relevant taxa are included in future phylogenetic analyses of Platygastroidea and Chalcidoidea. It is hoped that publication of an explicit character state matrix (Table 1) and the presence of alternative hypotheses will stimulate additional comparative morphology and phylo-

**Table 1** Plesiomorphic and apomorphic states postulated for 16 characters of the mesotrochanteral-depressor muscle and prothoracic complex in Orussidae and Apocrita. State 0 is hypothesized as plesiomorphic for Apocrita for all characters except 13, which is unordered.

1.	$t_2$ - $tr_2$ with portion anterior to transscutal articulation: 0 = yes; 1 = no
2.	origin of anterior portion of $t_2$ - $tr_2$ : 0 = mesoscutum; 1 = axillar phragma
3.	$fu_2$ - $tr_2$ with portion posterior to transscutal articulation: 0 = no; 1 = yes
4.	$fu_2$ - $tr_2$ : 0 = present; 1 = absent
5.	$fu_2$ - $tr_2$ site of origin: 0 = from mesofurcal plate medial to $tr_2$ - $tr_2$ ; 1 = from mesofurcal lateral arm posterior to $t_2$ - $tr_2$
6.	$pl_2$ - $tr_2$ : 0 = absent; 1 = present
7.	axillar phragmata: 0 = absent; 1 = present
8.	basalare: 0 = large; 1 = small
9.	position of spiracle relative to mesoscutum: 0 = below exposed lateral margin; 1 = at or above exposed lateral margin
10.	prepectus as independent sclerite: 0 = yes; 1 = no
11.	position of free prepectus relative to pronotum: 0 = concealed under posterolateral margin dorsally; 1 = exposed between pronotum and mesepisternum, at least dorsally
12.	size of free prepectus relative to pronotum: 0 = small, within ventral half; 1 = extending almost entire height of pronotum; 2 = small, within dorsal half
13.	spiracle relative to pronotal cuticle in taxa without a free prepectus: 0 = with pronotal lobe below spiracle; 1 = surrounded by pronotal cuticle; 2 = between pronotum and mesepisternum, without pronotal cuticle below or surrounding spiracle
14.	pronotum with posterolaterally differentiated area: 0 = no; 1 = elongate area along most of height of pronotum behind spiracle; 2 = area below spiracle; 3 = small area surrounding spiracle
15.	relationship of pronotum and mesepisternum: 0 = moveable; 1 = rigidly associated without interlocking mechanism; 2 = rigidly associated by tongue-and-groove interlocking mechanism over most of height
16.	pronotal cuticle continuous posteroventrally (pronotum annular): 0 = no; 1 = yes

genetic analyses in order to test putative relationships of Chalcidoidea, Mymarommatoidea, Platygastroidea and Proctotrupoidea.

### Material and methods

Hypotheses of character-state distribution and transformation of the mesotrochanteral depressor muscle and prothoracic structure are based primarily on examination of the taxa listed in Gibson (1985; Appendix 3) and in 'Materials' in Gibson (1986a, b). The scanning electron photomicrographs in Gibson (1985, 1986a) that illustrate structure of the different taxa are not republished here in order to reduce duplication. Scanning electron photomicrographs are used to illustrate the hypothesis that the coxal structure characteristic of Ichneumonomorpha *sensu* Rasnitsyn (1988) was derived secondarily from the coxal structure characteristic of Evaniomorpha *sensu* Rasnitsyn (1988). Discussion of states for this paper is limited primarily to those possessed by nonaculeate Apocrita and those that influence hypotheses of ground-plan states for Apocrita. Gibson (1985) should be referred to for comprehensive descriptions of the mesotrochanteral depressor muscle and prothoracic structures in Symphyta and Aculeata. The states of 16 structural features discussed in this paper are defined in Table 1 and their distribution throughout extant, nonaculeate Hymenoptera is summarised in Table 2. The characters and their states are defined independent of the hypotheses of transformation postulated in the text. Aculeata is included in the character matrix as a single group and Orussidae is included as the hypothesized sister group of

Apocrita. State 0 is hypothesized as the plesiomorphic state for all characters within Apocrita except for character 13, which is unordered.

### Abbreviations used in figures

<i>ax</i>	axilla
<i>bc</i>	basicoxite
<i>cf</i>	mesocoxal foramen
<i>cg</i>	coxal groove
<i>dc</i>	disticoxite
<i>fu<sub>2</sub></i>	mesofurca
<i>fu<sub>2</sub>-tr<sub>2</sub></i>	mesofurcal-mesotrochanteral depressor muscle
<i>ma</i>	mesal articulation
<i>ml</i>	mesal lobe
<i>mp</i>	mesotrochantinal plate
<i>ms</i>	mesoscutum
<i>ph</i>	phragma
<i>pl<sub>2</sub></i>	mesopleuron
<i>pl<sub>2</sub>-tr<sub>2</sub></i>	mesopleural-mesotrochanteral depressor muscle
<i>t<sub>2</sub>-tr<sub>2</sub></i>	mesotergal-mesotrochanteral depressor muscle

### Evidence for monophyly of Platygastroidea + Pelecinidae + Proctotrupidae + Vanhorniidae

*Structure of the mesotrochanteral depressor muscle ( $t_2$ - $tr_2$ ).* The mesotrochanteral depressor is a mesothoracic muscle that inserts into the dorsomedian margin of the mesotrochanter via a tendon that passes through the mesocoxa. Upon contraction the muscle retracts the base of the trochanter into the apex of the coxa, thereby rotating the trochanter and femur ventrally toward the midline of the body and lifting the body (Gibson 1986b). Although the site of inser-

**Table 2** Matrix of characters and states described for the mesotrochanteral-depressor muscle and prothoracic complex in Orussidae and Apocrita (na = not applicable). State 0 hypothesized as plesiomorphic for Apocrita for all characters except 13, which is unordered.

Taxon	Character States															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Orussidae	0	0	0	0	0	0	0	0	0	0	0	0	na	0	0	0
Chalcidoidea	0	1	1	1	na	0	1	1	1	0,1	0,1	1,2	na,1	0,1	0,1	0
Mymaromatidae	0	1	0	1	na	0	1	1	0	0?	0?	2?	na?	0	1?	0
Scelionidae	1	na	0	1	na	1	0	1	0	1	na	na	1	0,2 <sup>4</sup> ,3	2	1
Platygastridae	1	na	0	?	?	?	0	1	0	1	na	na	1	0	2	1
Aulacidae	1	na	0	0	1	0	0	1	0	1	na	na	2	0	1	0
Austroniidae	?	?	?	?	?	?	?	1	0	0	0	2	na	0	1	0
Ceraphronoidea	0	0	1	1	na	0	0	1	0	1	na	na	1	1	1	0
Cynipoidea	1	na	0	0	1	0	0	1	0	1	na	na	1	0	2	0
Diapriidae	1	na	1,0 <sup>2</sup>	0	1,0 <sup>2</sup>	0	0	1	0	1	na	na	1	0	2	0
Evaniiidae	1	na	0	0	1	1	0	1	0	1	na	na	1	0	2	0
Gasteruptionidae	1	na	0	0	1	0	0	1	0	1	na	na	2	0	1	0
Heloridae	1	na	0	0	1	0	0	1	0	1	na	na	1	0	2	0
Ichneumonoidea	1	na	0	0	1	0	0	1	0	1	na	na	0	0	1	0
Megalyridae	0	0	1	0	1	0	0	1	0	1	na	na	1	0,1	1	0
Monomachidae	1	na	0	0	1	0	0	1	0	0	0	1	na	0	0	0
Peleciniidae	1	na	0	0	1	1	0	1	0	1	na	na	1	3	2	1
Peradeniidae	?	?	?	?	?	?	?	1	0	1?	na?	na?	1?	0	2?	0
Proctotrupidae	1	na	0	0	1	1	0	1	0	1	na	na	1	0,3	2	1
Roproniidae	1	na	0	0	1	0	0	1	0	0	0	2	na	0	1	0
Stephanidae	1	na	1	0	0	0	0	0	0	0	0	0	na	0	0	0
Trigonalyidae	1	na	0	0	1	0	0	1	0	1	na	na	1	0	1	0
Vanhorniidae	1	na	0	0	1	1	0	1	0	1	na	na	1	3	2	1
Aculeata	1,0 <sup>1</sup>	na, 0 <sup>1</sup>	0	0	1	0, 1 <sup>3</sup>	0	1	0	0, 1	0	1	na, 1, 2	0	0, 1, 2	0

1. Some Formicidae.
2. Ismarinae.
3. Survey insufficient to determine exact distribution.
4. If with a differentiated region below the spiracle (the netrion), then this region never extended dorsally behind the spiracle.

tion is consistent throughout Hymenoptera, the number of constituent parts and sites of origin of the mesotrochanteral depressor are variable.

Figure 1 illustrates diagrammatically the known states of the mesotrochanteral depressor for Hymenoptera based on Gibson (1985), plus a hypothetical ground plan structure for Apocrita (Fig. 1C). Based on the observed structures in Symphyta and Apocrita, the apocritan ground plan structure is hypothesized to have consisted of an anterior tergal portion arising from the mesoscutum ( $t_2$ - $tr_{2a}$ ), a posterior tergal portion arising from each axilla ( $t_2$ - $tr_{2b}$ ), and a furcal portion ( $fu_2$ - $tr_2$ ) arising from the vertical plate of the mesofurca medial to  $t_2$ - $tr_2$  (Fig. 1C). No extant apocritan is known to possess these states, though *Megalyra* Westwood (Megalyridae) differs only in the position of  $fu_2$ - $tr_2$  (Fig. 1G). All Symphyta except Tenthredinoidea have two parts to the mesotrochanteral depressor (Fig. 1A). A tubular portion of the muscle, the mesotergal-mesotrochanteral muscle ( $t_2$ - $tr_2$ ), originates posterolaterally on the mesoscutum anterior to the scutellum and in Xiphydriidae and Orussidae anterior to the transscutal articulation (Gibson 1985; figs 39, 40). A second, much

smaller, fan-like portion of the muscle originates from near the dorsal edge of the vertical plate of the mesofurca where this bifurcates to form the lateral arms. This portion is called the mesofurcal-mesotrochanteral muscle ( $fu_2$ - $tr_2$ ). Both muscle portions insert into a golf tee-like pedicel (Gibson 1985; fig. 37) within the mesothorax above the coxa.

Structure of the mesotrochanteral depressor is much more varied in Apocrita. Individuals of Stephanidae, and Diapriidae except Ismarinae, are similar to most sawflies because they have a tubular  $t_2$ - $tr_2$  as well as a smaller  $fu_2$ - $tr_2$  that originates from the same relative position as  $fu_2$ - $tr_2$  in sawflies. However, in stephanids and nonisarine diapriids the tergal portion originates from within each axilla posterior to the transscutal articulation (Fig. 1D; Gibson 1985; figs 41, 42). Megalyridae also have  $t_2$ - $tr_2$  and  $fu_2$ - $tr_2$ , but  $t_2$ - $tr_2$  is composed of subequally large portions originating from the mesoscutum ( $t_2$ - $tr_{2a}$ ) and from within each axilla ( $t_2$ - $tr_{2b}$ ), and  $fu_2$ - $tr_2$  originates from each mesofurcal lateral arm posterior to  $t_2$ - $tr_2$  rather than medially between  $t_2$ - $tr_2$  and the mesofurcal plate (Fig. 1G; Gibson 1985; fig. 44). Ceraphronoidea also have  $t_2$ - $tr_{2a}$  and  $t_2$ - $tr_{2b}$ ,

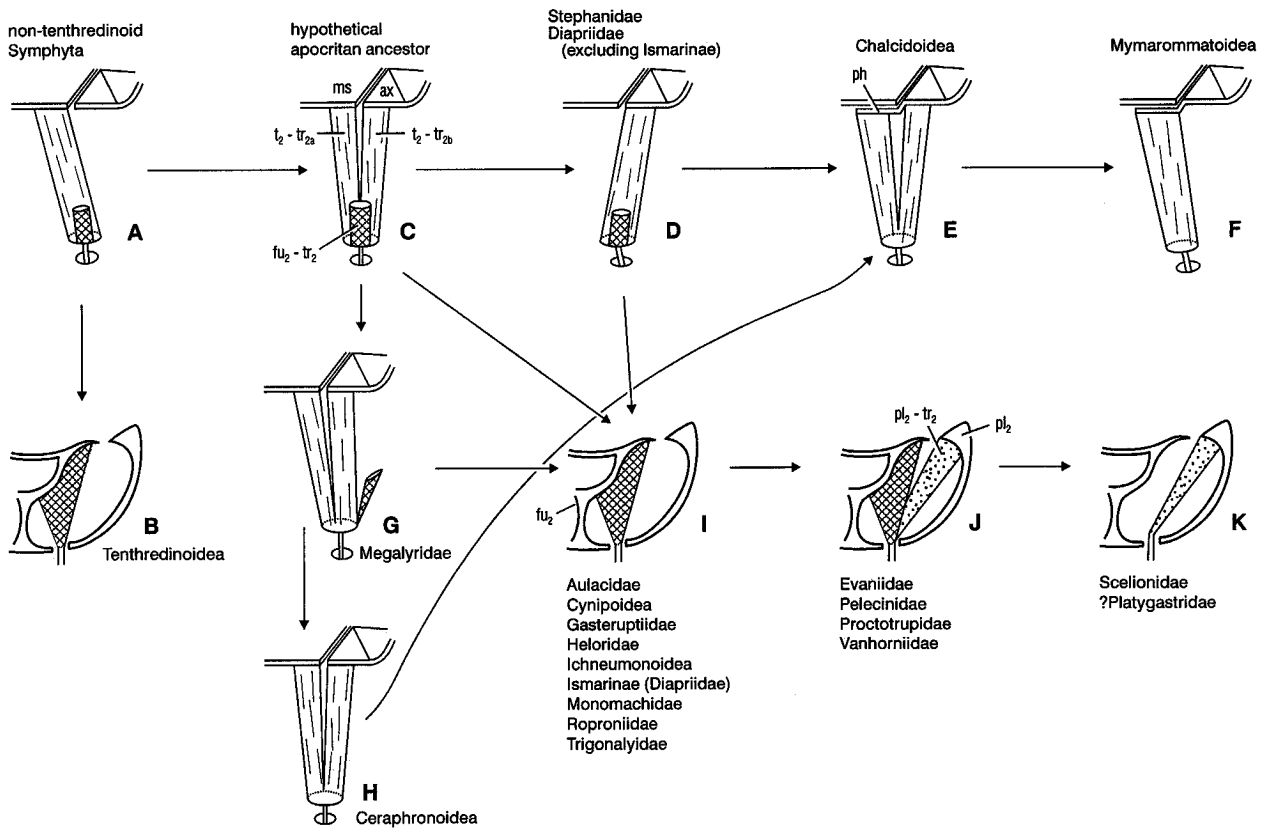


Fig. 1 Structure and hypothesized transformation of the mesotrochanteral depressor muscle in Hymenoptera.

but lack  $fu_2-tr_2$  (Fig. 1H; Gibson 1985; fig. 43). Chalcidoidea lack  $fu_2-tr_2$  and most have  $t_2-tr_2$  composed of an anterior and posterior portion (Gibson 1985; fig. 45) (for exceptions see Gibson 1986b, 1989). However, in Chalcidoidea the anterior portion of  $t_2-tr_2$  does not originate from the mesoscutum but from a phragma that projects under the mesoscutum from the anterior margin of each axilla (ph, Fig. 1E; Gibson 1985; figs 38, 45). Mymarommatidae also lack  $fu_2-tr_2$  and have axillar phragmata, but  $t_2-tr_2$  originates entirely from the phragma (Fig. 1F). Possibly correlated with the absence of the posterior portion of  $t_2-tr_2$  is the absence of a differentiated dorsal axillar surface in mymarommatids (Gibson 1986a; fig. 11). All other nonaculeate Apocrita lack  $t_2-tr_2$ . Individuals of Aulacidae, Cynipoidea, Gasteruptiidae, Heloridae, Ichneumonoidea, Ismarinae (Diapriidae), Monomachidae, Roproniidae and Trigonalyidae have  $fu_2-tr_2$  originating as a conical or fan-shaped muscle from each mesofurcal lateral arm ( $fu_2$ , Fig. 1I; Gibson 1985; figs 47,48,49), whereas individuals of Evaniidae, Peleciniidae, Proctotrupidae and Vanhorniidae have muscle fibers originating from both the mesofurcal lateral arm ( $fu_2-tr_2$ ) and from an invagination of the mesopleuron adjacent to the lateral arm ( $pl_2$ ,

Fig. 1J; Gibson 1985; fig. 50). The portion originating from the pleuron is called the mesopleural-mesotrochanteral ( $pl_2-tr_2$ , Fig. 1J) muscle and it is the only part of the mesotrochanteral depressor possessed by Scelionidae (Fig. 1K; Gibson 1985; fig. 51). Gibson (1985) confirmed that Platygastriidae lack  $t_2-tr_2$ , and Rasnitsyn (1988) stated that  $pl_2-tr_2$  is absent from Platygastriidae based on observation of a species of *Isoctibus* Förster. Individuals of Platygastriidae must have some sort of mesotrochanteral depressor in order to lift the body. Because of the small body size of platygastriids it has yet to be substantiated whether their mesotrochanteral depressor is thoracic in origin and, if so, furcal and/or pleural, or whether the thoracic depressor muscles have been lost entirely and an intrinsic coxal muscle serves as the depressor of the mesocoxa.

*Discussion.* Rasnitsyn (1988) hypothesized that the mesotergal-mesotrochanteral depressor was lost from the ancestor of Mesoserphidae (node 49) and was secondarily regained in nonismarine Diapriidae and Chalcidoidea (node 66). Secondarily regaining a tergal portion of the mesotrochanteral depressor likely explains the unusual fan-shaped  $t_2-tr_2$  of some Formicidae (Gibson 1985; fig. 46), the only Aculeata known to have a tergal component to

the depressor. In many instances the muscle fibers originating from the tergum are obviously a continuation of fibers originating from the pleuron (Gibson 1985). It therefore seems likely that the tergal component of the mesotrochanteral muscle in Formicidae was derived secondarily through expansion of  $pl_2-tr_2$  onto the tergum and is not homologous with  $t_2-tr_{2a}$ . The mesotergal-mesotrochanteral muscle of chalcidoids and mymarommatids is tubular and inserts into a golf tee-like apodeme as for other nonaculeate apocritans that have this muscle. Unlike Formicidae, there is no structural evidence for  $t_2-tr_2$  being secondarily regained in Chalcidoidea + Mymarommatidae.

In order to explain the known character-state distribution, Rasnitsyn (1988) further hypothesized that the mesofurcal-mesotrochanteral depressor was modified into a mesopleural-mesotrochanteral depressor in the ancestor of Scelionidae + Platygastridae (node 67), that this muscle also evolved independently in the ancestor of Pelecinidae + (Proctotrupidae + Vanhorniidae) (node 50), and that the 'mesopleural'-mesotrochanteral muscle was lost from Chalcidoidea (node 66). This latter statement is a lapsus for mesofurcal-mesotrochanteral muscle because the mesopleural-mesotrochanteral depressor was not hypothesized to have evolved until the following node. The hypotheses of Rasnitsyn (1980) require two losses, two reversal gains, and two independent gains of muscles. A simpler hypothesis is that the structure of the mesotrochanteral depressor in Scelionidae represents the terminal state in a transformation series consisting of the states illustrated in Fig. 1 (C or D or G → I → J → (K)), that Ismarinae independently lost  $t_2-tr_{2a}$  within Diapriidae (D → I), and that structures of the mesotrochanteral depressor in Chalcidoidea and Mymarommatidae represent a third transformation series (C → D → E → F or C → G → H → E → F). This hypothesis requires only three losses and one muscle gain, and indicates Scelionidae is more closely related to one or more of Evaniidae, Pelecinidae, Proctotrupidae, and Vanhorniidae than to Chalcidoidea + Mymarommatidae. Presence of  $pl_2-tr_2$  in at least some Aculeata (Formicidae) indicates that  $fu_2-tr_2$  has been expanded onto the pleuron more than once in Hymenoptera and further study is necessary to confirm that the taxa listed as having only  $fu_2-tr_2$  (Table 2) do not have some members with both  $fu_2-tr_2$  and  $pl_2-tr_2$ .

The axillar phragmata of chalcidoids and mymarommatids might have evolved in one of two ways relative to the mesotrochanteral depressor. A phragma might have been extended anteriorly from each axilla between the mesoscutum and an existing  $t_2-tr_{2a}$  to separate this muscle from the mesoscutum and provide a new site of origin. Alternatively, the ancestor of Chalcidoidea + Mymarommatidae might have lacked  $t_2-tr_{2a}$  because of previous loss and an axillar

phragma evolved subsequently in order to secondarily increase the surface area for  $t_2-tr_{2b}$ . The larger surface area for this muscle, the more power generated for greater jumping ability (Gibson 1986b). Although the second alternative is less parsimonious because of the extra evolutionary events required, I postulate it for evolution of axillar phragmata because I can think of no functional rationale for the first hypothesis. I therefore do not interpret the anterior, phragmal portion of  $t_2-tr_2$  in chalcidoids and mymarommatids as homologous with  $t_2-tr_{2a}$  of Ceraphronoidea and Megalyridae and consider that the following transformation series is most likely: C → D → E → F (Fig. 1). Structure of the mesotergal-mesotrochanteral muscle therefore indicates that Chalcidoidea + Mymarommatidae are more likely the sister group to some combination of the taxa having states I + (J + K) (Fig. 1) if they and Platygastroidea constitute a monophyletic lineage.

#### *Pronotal structure and position of the mesothoracic spiracle.*

Structure of the pronotum, presence and structure of the basalare and prepectus, and position of the mesothoracic spiracle vary throughout Hymenoptera. The relative structures for nonaculeate Apocrita are illustrated diagrammatically in Fig. 2. Gibson (1985) showed that Orussidae and Stephanidae have very similar structures. The mesothoracic spiracle lies between the pronotum and mesepisternum, below the lateral margin of the mesoscutum near the ventral margin of an elongate basalare and the anterodorsal margin of an independent (free) prepectus (Fig. 2A; Gibson 1985; figs 15, 16). The prepectus extends ventrally to the ventral edge of the pronotum beside the procoxa (Gibson 1986a; fig. 15). These structural relationships are not externally visible in orussids and stephanids because the spiracle and sclerites are overlain by the posterior margin of the pronotum, partly by a distinct pronotal lobe (Gibson 1985; fig. 36; 1986a; fig. 15). The pronotum and mesepisternum are connected by membrane so that they are moveable relative to one another. Gibson (1985) hypothesized these as the groundplan structures for Apocrita because of common possession by Orussidae and Stephanidae. Apocrita other than Stephanidae have a much smaller basalare and different structures or positions of the pronotum, prepectus and spiracle relative to one other.

Ichneumonoidea have a unique pronotal structure. The pronotum may or may not have a distinct pronotal lobe above the mesothoracic spiracle but there is a small lobe below the spiracle that lies between the pronotum and mesepisternum. The pronotum and mesepisternum are rigidly associated but there is no distinct tongue-and-groove interlocking mechanism (Gibson 1985; fig. 27). This structure is hypothesized to be similar to the postulated apocritan groundplan except for having a reduced

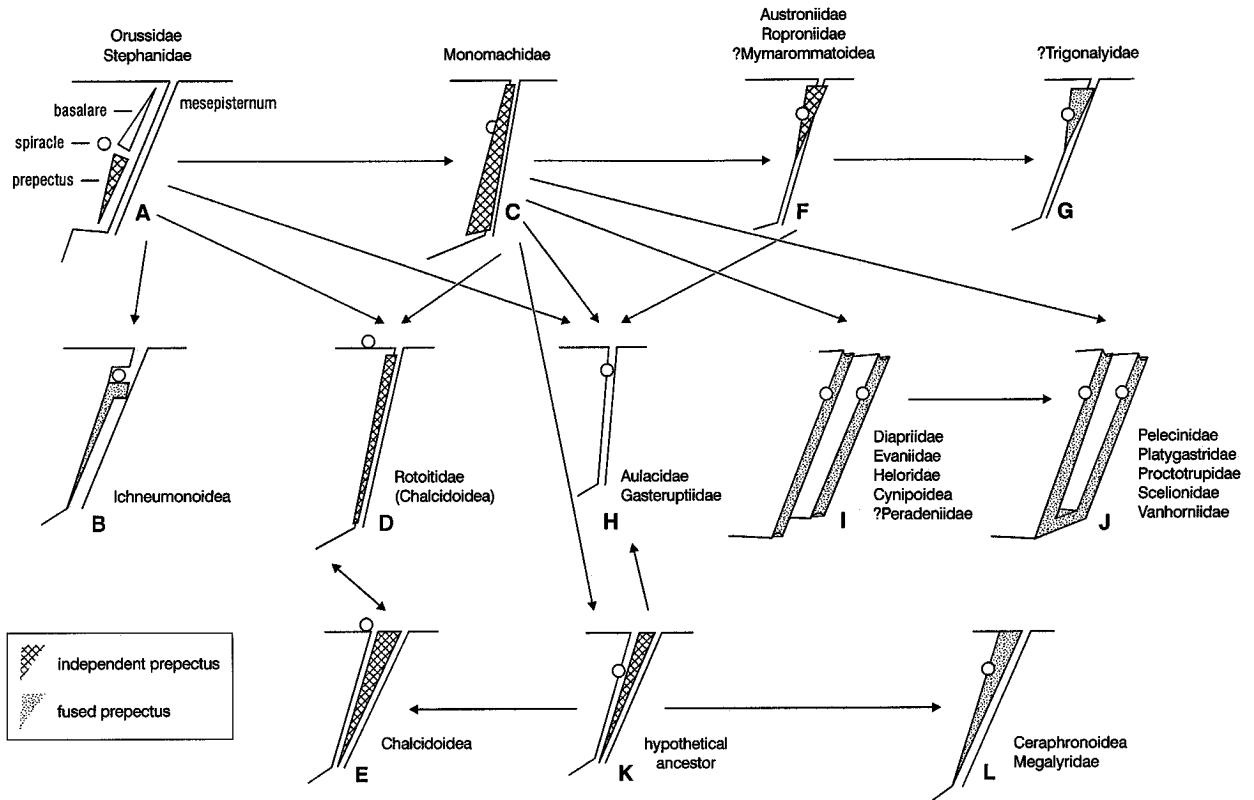


Fig. 2 Structure and hypothesized transformation of the prepectus relative to the pronotum and mesothoracic spiracle in Apocrita.

basalare and the prepectus fused along the posterolateral margin of the pronotum (Fig. 2B). An internal ridge along the posterolateral margin of the pronotum (Gibson 1985; fig. 28) is interpreted as a remnant of the fused prepectus, and the lobe of the pronotum below the spiracle is interpreted as the dorsal margin of the prepectus. Evidence for fusion of the prepectus with the pronotum is based partly on the presence and position of an apodeme for the occlusor muscle of the mesothoracic spiracle (Gibson 1985; fig. 28b). The spiracular occlusor muscle originates from the prepectus in Hymenoptera with an independent prepectus, often from an apodeme that is indicated externally by a pit on the prepectus (Gibson 1985; fig. 16). The presence and position of the pit and apodeme, when present, are hypothesized to indicate the fate of the prepectus (Gibson 1985).

In Chalcidoidea the mesothoracic spiracle lies between the pronotum and the lateral margin of the mesoscutum, at or anterior to the anterodorsal margin of the prepectus. Also, most chalcidoids have an independent prepectus that extends to the lateral margin of the mesoscutum and that is exposed between the pronotum and mesepisternum at least dorsally (Fig. 2E) (Gibson 1986a). The prepectus is fused to the pronotum in Eucharitini (Eucharitidae)

(Heraty 1994) and in all Perilampidae (Perilampinae) except *Steffanolampus* Peck. In such instances the mesothoracic spiracle lies between the dorsal margin of the composite structure and the mesoscutum in the same relative position as in other chalcidoids with an independent prepectus. The spiracle actually originates from the extreme dorsal edge of the composite structure because it is enclosed dorsally by cuticle (Heraty 1988). Perilampids and eucharitines also have the composite pronotal-prepectal structure rigidly associated with the mesepisternum. The posterolateral margin of the composite structure is inflected into a strong ridge against which the anterior margin of the mesepisternum abuts, but there is no distinct tongue-and-groove interlocking mechanism. Most chalcidoids with an independent prepectus have the prepecti appearing as separate sclerites on either side of the mesosoma. However, they often form a single continuous sclerite ventrally along the anterior margin of the mesepisternum (Gibson 1986a; fig. 18). Domenichini (1978) hypothesized that this single sclerite evolved through fusion of the two prepecti with the prothoracic spinisternum. The structure is not normally visible because the ventral region is covered by the procoxae and sometimes is very slender (Gibson 1986b; figs 10, 11). Subse-

quent to Gibson's (1986a) hypothesis that an exposed prepectus was a synapomorphy for Chalcidoidea, Boucek & Noyes (1987) described the family Rotoitidae based on *Rotoita basalis* from New Zealand. The mesothoracic spiracle in *R. basalis* is in the same position as in other chalcidoids, but the species was described as apparently lacking a prepectus. Gibson (1993) illustrated a second, yet undescribed rotoitid genus from Chile. Some specimens have the pronotum abutting the mesepisternum as in *R. basalis* (Boucek & Noyes 1987; fig. 1) but other, critical-point dried, specimens have the pronotum separated slightly from the mesepisternum. These specimens have a very slender prepectus that extends almost the entire height of the pronotum in the membrane between the pronotum and mesepisternum. Slide-mounted specimens show that the prepecti extend only to the ventral margins of the pronotum and are not continuous across the venter (Fig. 2D). Subsequent examination of the slide that Boucek & Noyes (1987) used to illustrate *R. basalis* also revealed a slender prepectus along each anterolateral margin of the mesepisternum, which apparently are concealed under the pronotum in air-dried specimens similarly to specimens of the undescribed rotoitid genus. Some Mymaridae are also known to have an almost linear prepectus between the pronotum and mesepisternum (Gibson 1986a; fig. 27).

Mymarommatidae apparently have the mesothoracic spiracle, or at least a remnant of the spiracle, concealed under the posterolateral edge of the pronotum. Although not visible externally (Gibson 1986a; fig. 10), in slide-mounted specimens what appears to be the circular opening of a spiracle is visible distinctly below the lateral margin of the mesoscutum (Gibson 1986a; fig. 12). Gibson (1985; fig. 12) showed a spindle-shaped structure that occupies about the dorsal half of the pronotum near its posterolateral margin. The spindle-shaped structure covers the region occupied by the presumed mesothoracic spiracle. Because of the small size of mymarommatids it has not been possible to demonstrate whether the spindle-shaped structure is the prepectus and, if so, whether it is free or fused to the inner surface of the pronotum. The states of several characters are postulated tentatively for Mymarommatidae in Table 2 based on the spindle-shaped structure being the prepectus.

Individuals of Aulacidae and Gasteruptiidae have the mesothoracic spiracle externally visible between the posterolateral margin of the pronotum and the anterior margin of the mesepisternum. The pronotum and mesepisternum are rigidly associated but there is no evidence of an interlocking mechanism or of a prepectus (Gibson 1985) (Fig. 2H). All other nonaculeate Apocrita either have an independent prepectus or one that appears to be fused

with the pronotum. Furthermore, all other apocritans except some Aculeata apparently have the prepectus extending dorsally behind the mesothoracic spiracle to the lateral margin of the mesoscutum (Gibson 1985). Individuals of Austroniidae, Monomachidae and Roproniidae have an independent prepectus. Monomachidae have a large prepectus that extends from the mesoscutum almost to the midline of the thoracic venter (Fig. 2C; Gibson 1985; fig. 15), whereas Austroniidae and Roproniidae have a much smaller prepectus within the dorsal half of the pronotum (Fig. 2F; Gibson 1985; fig. 19). Ceraphronoidea (Gibson 1985; figs 29–31) and Megalyridae (Gibson 1985; fig. 32) have the mesothoracic spiracle originating near the posterolateral margin of the pronotum below the lateral margin of the mesoscutum (Fig. 2L). A variedly distinct region is differentiated posterior to the spiracle along the height of the pronotum in ceraphronoids (Gibson 1985; figs 29a, 30a) and some megalyrids (e.g. *Dinapsis* Waterston and *Ettchellsia* Cameron). The differentiated region is interpreted as the remnants of a prepectus that was fused to the posterior margin of the pronotum (Fig. 2L) after it was exposed secondarily between the pronotum and mesepisternum (Fig. 2K). This hypothesis is supported by the presence an apodeme for the spiracular occlusor muscle near the posteroventral angle of the pronotum in Ceraphronoidea (Gibson 1985; cf. figs 29–31). The putative pronotal-prepectal complex is rigidly associated but is not interlocked with the anterior margin of the mesepisternum. Individuals of Cynipoidea, Diapriidae, Evaniidae, Heloridae, Peleciniidae, Platygastroidea, Proctotrupidae, and Vanhorniidae also have the pronotum and mesepisternum rigidly associated. The mesothoracic spiracle lies below the lateral margin of the mesoscutum, either apparently between the pronotum and mesepisternum or on the pronotum. It is often stated that the spiracle arises from the pronotum in Peleciniidae, Proctotrupidae (Gibson 1985; fig. 22), and Vanhorniidae (e.g. Rasnitsyn 1980), but the spiracle is enclosed internally by inflected cuticle in all the taxa, including cynipoids, diapriids, evaniids, helorids, and platygastroids. The spiracle sometimes appears to originate from a small differentiated region of the pronotum adjacent to the posterolateral margin in Scelionidae, though the narrow pronotal region posterior to the spiracle is on a slightly lower plane. The inflected cuticle that in part surrounds the spiracle was called the posterior pronotal inflection by Gibson (1985), and a relatively deep groove is formed between it and the outer margin of the pronotum along most of the height of pronotum (Gibson 1985; figs 20, 22, 24–26). The anterior margin of the mesepisternum fits into the groove in a tongue-and-groove interlocking mechanism. The presence of a spiracular occlusor muscle apodeme (Gibson 1985; figs 20b, 22, 24,

25b) indicates that the posterior pronotal inflection likely is the remnant of a prepectus that was fused along the inner posterolateral margin of the pronotum after the prepectus had been extended dorsally to the mesoscutum behind the spiracle. Individuals of *Peradenia clavipes* Naumann & Masner (1985) have a deep pit within a crenulate furrow along the posterolateral margin of the pronotum, about one-third the height from the ventral margin of the pronotum. I suspect that this pit is an invagination that forms an occlusor muscle apodeme and therefore I tentatively postulate that the prepectus is fused to the pronotum and forms a posterior pronotal inflection in Peradeniidae (Table 2). This has to be confirmed by dissections. Individuals of Cynipoidea, Diapriidae, Evaniidae, and Heloridae have the pronotum  $\sqcap$ -like in cross section because the pronotal cuticle is not continuous ventrally (Fig. 2I), whereas Pelecinidae, Proctotrupidae, Vanhorniidae, and Platygastroidea have an annular pronotum because the pronotal cuticle is continuous posterovertrally beneath the procoxae (Fig. 2J; Gibson 1985; figs 22, 24). Although Gibson (1985) stated that Trigonalyidae also possess a posterior pronotal inflection interlocking mechanism, this is partly inaccurate. Most of the groove is formed between a pronotal lobe and what is interpreted as the remnants of a prepectus that is fused to the posterior margin of the pronotum (Gibson 1985; Fig. 26). The region posterior to the spiracle is visible externally and is on a slightly lower plane, but there is no distinct groove or tongue-and-groove interlocking mechanism formed along the posterolateral edge of the pronotum below the spiracle. This structure might have evolved through fusion of a relatively small prepectus to the inner margin of the pronotum (Fig. 2G).

**Discussion** Figure 2 illustrates diagrammatically the structures and relative positions of the prepectus, mesothoracic spiracle and pronotum for nonaculeate Hymenoptera. The individual figures include hypotheses about the fate of the prepectus and possible transformation series that resulted in the different structures. Differences in external and internal appearance of the pronotum and different means by which the posterolateral margin of the pronotum and anterolateral margin of the mesepisternum are connected suggest that the prepectus was lost independently at least five times in nonaculeate Hymenoptera: at least once through loss (Fig. 2H) and at least four times through fusion with the pronotum (Figs 2B, 2G, 2I, 2L). A tongue-and-groove interlocking mechanism resulting from a deep posterolateral pronotal inflection along the height of the pronotum could indicate a single fusion and monophyly of the taxa illustrated by Fig. 2I + 2J. This transformation series would indicate that an annular pronotum (Fig. 2J) was derived secondarily for some functional

reason. Pelecinidae, Vanhorniidae, and most Proctotrupidae are endoparasitoids of beetle larvae concealed in the ground or wood. A ring-like structure enhances strength of the pronotum and prothorax by resisting compression, and may have evolved in response to physical forces acting on the adult during emergence from the ground or wood. If so, the ventral pronotal cuticle likely is of secondary origin and is not homologous with ventrally fused prepecti as proposed by Rasnitsyn (1980). Alternatively, the different nonannular (Fig. 2I) and annular (Fig. 2J) structures might indicate at least two independent fusions, in which case the annular structure might have evolved through ventral fusion of the prepecti. In either case, common possession of an annular pronotum indicates Platygastroidea + Pelecinidae + Proctotrupidae + Vanhorniidae are monophyletic and that Chalcidoidea is at most the sister group of this assemblage. If an annular pronotum in Platygastroidea results from an historical event, common ancestry, it may no longer serve a functional or at least the same functional purpose as in the other three families. Masner (1993) hypothesized that pumping movements of the head and propleura into the mesosoma against the circular pronotum increased turgor pressure to extrude the concealed ovipositor of platygastroids.

The position of the mesothoracic spiracle at the lateral margin of the mesoscutum is autapomorphic for Chalcidoidea, whereas position of the spiracle at or above the dorsal margin of the prepectus and an independent prepectus are both symplesiomorphic for Chalcidoidea. Consequently, none of the states help establish chalcidoid sister-group relationships. Mymarommatidae apparently have the plesiomorphic position for the mesothoracic spiracle relative to the mesoscutum, plus possibly the prepectus extending above the spiracle to the lateral edge of the mesoscutum (Fig. 2F). If these interpretations are accurate they suggest the prepectus was initially extended dorsally to the lateral edge of the mesoscutum in the common ancestor of Mymarommatidae + Chalcidoidea, and that the spiracle moved dorsally to the lateral edge of the mesoscutum in the common ancestor of Chalcidoidea to regain a superficially plesiomorphic position relative to the prepectus. Thus, the chalcidoid structure would not be indicated to have evolved from a stephanid-like condition (Fig. 2A 2D → 2E), but from a monomachid-like structure (Fig. 2A → 2C → 2D → 2E) or from some ancestor that had the prepectus secondarily exposed between the pronotum and mesepisternum (Fig. 2A → 2C → 2K → 2E → 2D). It is necessary to establish relationships of Rotoitidae within Chalcidoidea in order to determine whether their prepectal structure is the ground-plan state for Chalcidoidea rather than an exposed prepectus. An exposed prepectus currently is hypothesized

as a synapomorphy for the superfamily (see Gibson, Heraty & Woolley, in press).

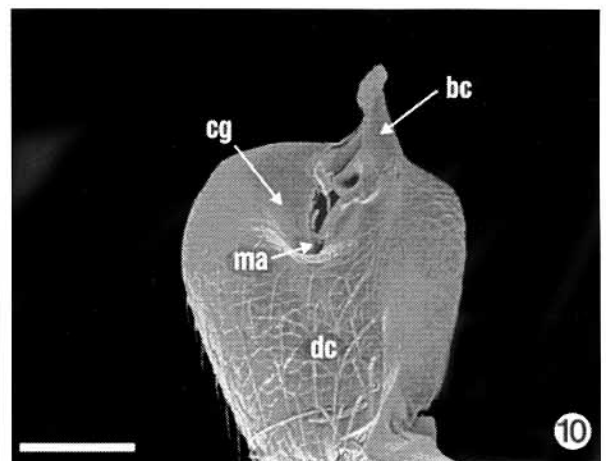
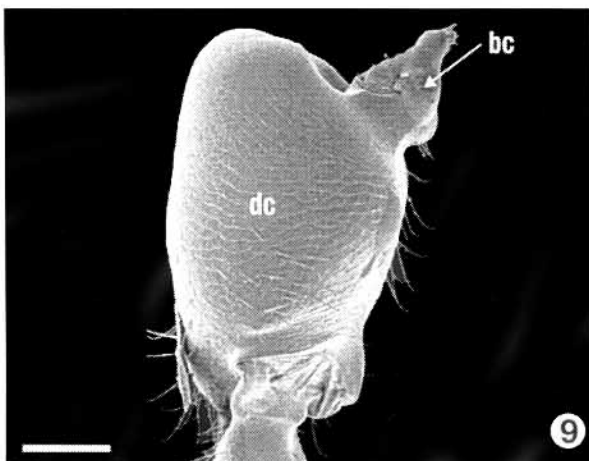
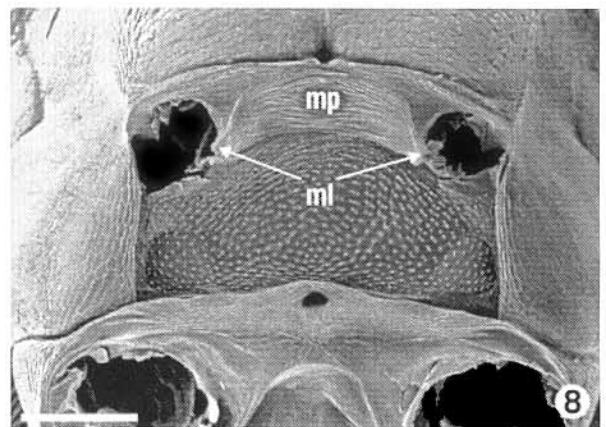
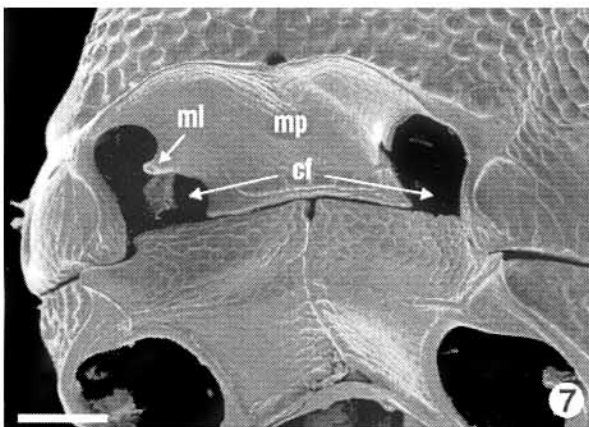
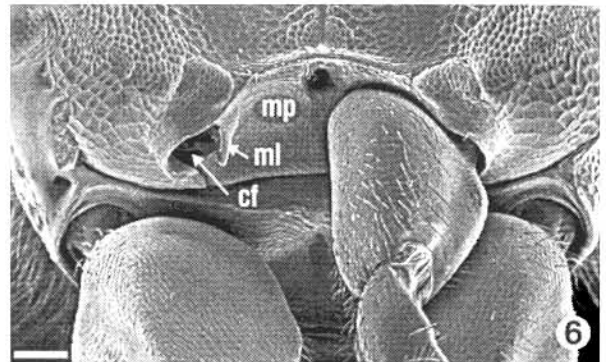
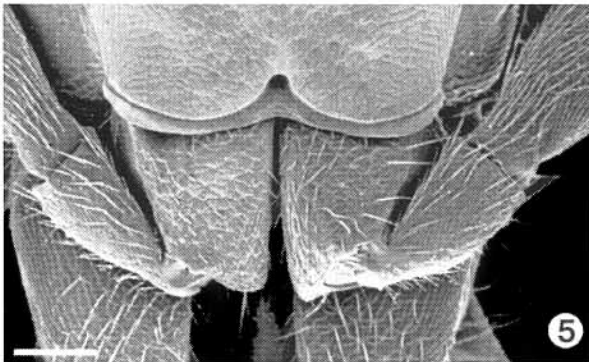
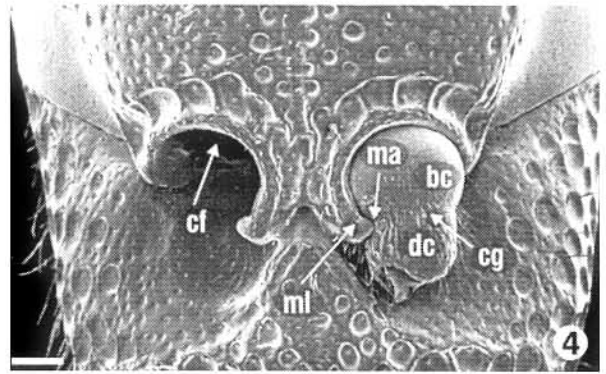
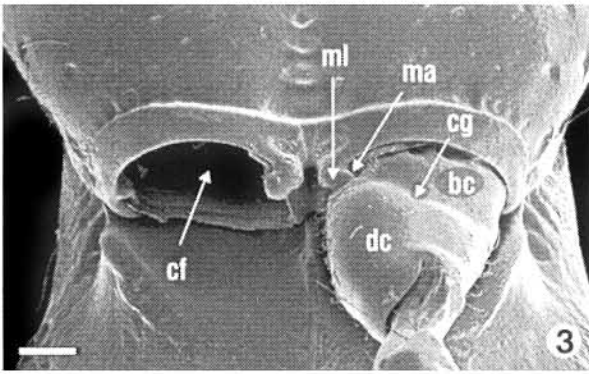
## Discussion

Rasnitsyn (1988; pp. 126, 127) hypothesized eight synapomorphies for Pelecinidae + (Proctotrupidae + Vanhorniidae). None of the putative synapomorphies are convincing evidence for monophyly of these taxa or exclude a sister-group relationship with Platygastroidea. Stated structure of the pronotum, 'annular, short dorsomedially, rigidly connected with mesopleuron' and presence of a mesopleural-mesotrochanteral muscle are both shared with Platygastroidea, and 'prepectus fused with pronotum forming internal pronotal inflection' (Rasnitsyn 1988) is shared with a more inclusive group that includes Platygastroidea. The described structure of the metasoma ('metasoma closed at rest apically, with apical tergum and sternum weakly movable, and with ovipositor internal') and 'male genitalia with cuspides lost' (Rasnitsyn 1988) are not only shared with Platygastroidea but also by other parasitic Hymenoptera. Rasnitsyn (1988) hypothesized the same metasomal structures as synapomorphic for Heloridae (node 53) and absence of male cuspides as synapomorphies for nodes 53 (54–55) and 65. Absence of the trochantellus from the middle and hind legs is shared with Scelionidae and Peradeniidae (Naumann & Masner 1985; character 18), the forewing venational character of 'RS<sub>2</sub>-like 2r-m present' (Rasnitsyn 1988) can not be evaluated because of loss of the veins from Platygastroidea, and parasitism of ground-dwelling beetle larva does not preclude a platygastroid sister-group relationship. Likewise, none of the features hypothesized as synapomorphies for Jurapriidae + Chalcidoidea + Mymarommatidae + Serphitidae + Scelionidae + Platygastridae (node 65) are uniquely possessed by these taxa. Both Serphitidae and Jurapriidae have extensive forewing venation, including a stigma, and Rasnitsyn (1985) initially used venational features of Jurapriidae to support a relationship of this family with Diaprioidea. Chalcidoidea, Mymarommatidae and Platygastroidea do share a strongly reduced forewing venation that consists, at most, of a single vein complex without any enclosed cells. The venation of Scelionidae and most Chalcidoidea is very similar, consisting of what is usually called the submarginal, marginal, stigmal and postmarginal veins. However, loss of venation is reductional. An annular pronotum and presence of pl<sub>2</sub>-tr<sub>2</sub> are both nonreductional derived features that are shared by Platygastroidea + Pelecinidae +

Proctotrupidae + Vanhorniidae. The former state is autapomorphic for the group whereas the latter state is possessed also by Evaniidae and some Aculeata.

Austin & Field (1997) polarised features of the platygastroid ovipositor system based on the ovipositor structures of several chalcidoid families because they said a platygastroid + chalcidoid relationship was suggested by the molecular study undertaken by Dowton *et al.* (1997). However, the relationships indicated in Dowton *et al.* (1997) differed depending on the method of analysis. Dowton & Austin (1994) used comparative sequence information from the mitochondrial 16S rRNA gene to infer relationships among 15 families of apocritan wasps and Dowton *et al.* (1997) enlarged the study to 23 families. The initial study used two species of Aphelinidae and one species of Pteromalidae to represent Chalcidoidea, two species of Scelionidae to represent Platygastroidea, one species of Ibaliidae to represent Cynipoidea, and one species each of Roproniidae and Vanhorniidae to represent Proctotrupoidea. The second study added eight additional families of parasitic wasps, including a second family of Cynipoidea (Figitidae), five additional families of Proctotrupoidea, and the family Megalyridae. Strict consensus of the six most parsimonious trees discovered by Dowton & Austin (1994) supported the monophyly of Chalcidoidea, indicated Chalcidoidea + Scelionidae as sister groups, and these as forming an unresolved trichotomy with Ibaliidae and (Roproniidae + Vanhorniidae) (Dowton & Austin 1994; fig. 2). Topology-dependent permutation tail probability (T-PTP) testing resolved the polychotomy and indicated Chalcidoidea + Scelionidae as the sister group of Ibaliidae + (Roproniidae + Vanhorniidae) (Dowton & Austin 1994; fig. 3). After the eight additional families were included by Dowton *et al.* (1997), strict consensus of the three most parsimonious trees discovered indicated Diapriidae as the sister group of Chalcidoidea and placed these two groups as part of an unresolved trichotomy along with Heloridae and an undescribed family from New Zealand. Scelionidae was indicated as the sister group of Pelecinidae and this clade was left as part of an unresolved polychotomy (Dowton *et al.* 1997; fig. 1). Reanalysing the results to find the most parsimonious tree for the most parsimonious of the three most parsimonious alignments found by PAUP resulted in a fully resolved tree but one with quite a different topology. The most parsimonious tree of the most parsimonious alignment indicated Chalcidoidea as the sister group of Scelionidae and that these formed the terminal clade in a

**Figs 3–10** 3–6. Ventral view of mesothorax showing mesocoxae: —3. *Megischus* sp. (Stephanidae), ♀, right coxa removed; —4. *Hyptia* sp. (Evaniidae), ♀, right coxa removed; —5. *Brasema* sp. (Eupelmidae), ♀; —6. *Pteromalus* sp. (Pteromalidae), ♀, right coxa removed. —7 and 8. Ventral view of mesothorax showing mesocoxal and metacoxal foramina: —7. *Epistenia* sp. (Pteromalidae), ♀ —8. *Brasema* sp., or —9 and 10. Mesocoxa of *Pteromalus* sp., ♀ —9. lateral view; —10. basolateral view. (Scalebar = 100 microns.)



successively nested series of relationships involving seven families of Proctotrupoidea (Dowton *et al.* 1997; fig. 2).

Austin & Field (1997), Whitfield (1998), and Basibuyuk & Quicke (in press) based their inferences of chalcidoid and platygastroid relationships on the most parsimonious tree of the most parsimonious alignment rather than on results indicated by strict consensus of the three most parsimonious trees. Acceptance of the former methodology over the latter was likely because it resulted in fully resolved relationships and, possibly, because it supported the platygastroid-chalcidoid sister-group relationship proposed by Rasnitsyn (1988). However, the former analysis also indicated Cynipoidea as the basal-most clade of Apocrita, a highly contentious relationship supported by no other study. The nested series of relationships involving Chalcidoidea, Platygastridea, and Proctotrupoidea postulated by Dowton *et al.* (1997; fig. 2) includes only nine taxa, but requires independent evolution of a tongue-and-groove pronotal-mesepisternal interlocking mechanism five times, independent evolution of an annular pronotum three times, independent evolution of a mesopleural-mesotrochanteral muscle three times, and independent loss of a mesotergal-mesotrochanteral muscle five times. Results of the strict consensus tree from Dowton *et al.* (1997; fig. 1) indicate Scelionidae as the sister group of Peleciniidae, which is consistent with the alternate hypothesis presented here, and that Diapriidae is the sister group of Chalcidoidea. Diapriidae share symplesiomorphic states of the mesotrochanteral-depressor with Chalcidoidea and have a structure of the pronotal complex that indicates Chalcidoidea can at most be the sister group of a clade including several nonaculeate apocritan families in addition to Diapriidae.

A Chalcidoidea + Scelionidae sister-group relationship could be supported by structure of their mesofurca. Heraty *et al.* (1994) found that the structure of the mesofurcal bridge in Scelionidae and most Chalcidoidea was similar (bowed with the median process virtually absent). The mesofurcal bridge is absent from Mymarommatidae, Platygastridae, some Chalcidoidea and some other Apocrita (Heraty *et al.* 1994).

Quicke *et al.* (1994) showed that Chalcidoidea share a specialized structure of the lower valvulae of the ovipositor (overlapping rather than abutting) with Mymarommatidae, Platygastridea, Diapriidae, Monomachidae, Proctotrupoidea, Vanhorniidae & Ceraphronoidea. Basibuyuk & Quicke (1997; fig. 8 BD) also showed that Chalcidoidea share a row of modified erect setae that oppose the distal hamuli on the hind wing with Diapriidae, Ceraphronoidea and a new family from New Zealand (the hind wing of Mymarommatoidea is reduced to an apically bifurcate, haltere-like structure, Gibson 1986a; fig. 33). Conse-

quently, Diapriidae share both of the specialized structures and a potentially ancestral state of the mesotrochanteral depressor muscle with Chalcidoidea, and Ceraphronoidea share both structures plus states of the mesotergal-mesotrochanteral muscle and prepectus that could either be ancestral to those of Chalcidoidea or derived from a common ancestor. A Ceraphronoidea + (Mymarommatoidea + Chalcidoidea) sister-group relationship would indicate that the portion of the mesotergal-mesotrochanteral muscle arising from each axillar phragma in Chalcidoidea and Mymarommatoidea is homologous with  $t_2$ - $tr_{2a}$  of Ceraphronoidea (Fig. 1, C → G → H → E → F). It would also indicate that the differentiated region of the pronotum posterior to the spiracle in Ceraphronoidea likely evolved through fusion of the prepectus with the pronotum after the prepectus had become secondarily exposed in a common ancestor of Ceraphronoidea + Chalcidoidea (Fig. 2, A → C → K → E → D). Current interpretation of the prepectal-pronotal structure of Mymarommatoidea does not support this second interpretation. An ancestral or sister-group relationship of Ceraphronoidea with (Mymarommatoidea + Chalcidoidea) would also not seem to be supported by the structure of the mesocoxal articulation. Rasnitsyn (1980, 1988) and Johnson (1988) supported inclusion of Ceraphronoidea in Evaniomorpha (Ceraphronoidea, Megalynidae, Evaniidae, Aulacidae, Gasteruptionidae and Trigonalyidae *sensu* Johnson) based on the degree of elongation of the mesal lobes of the mesothorax that articulate with the mesocoxae. An ancestral or sister-group relationship between Ceraphronoidea and Chalcidoidea is likely only if the mesocoxal articulatory structure of Evaniomorpha represents an intermediate stage in a transformation series from the structure of Orussidae (Johnson 1988; figs 11, 12) or Stephanidae (Fig. 3; Johnson 1988; fig. 13) to the structure characteristic of Ichneumonomorpha (Chalcidoidea, Platygastridea, Proctotrupoidea, Cynipoidea), that is, a retained symplesiomorphy rather than a synapomorphy that supports monophyly of Evaniomorpha. In Stephanidae (Fig. 3) and Evaniomorpha (Fig. 4) both the mesal lobes of the mesopleuron and the mesal articulation of each mesocoxa are external, and the mesocoxal foramina are large and closely approximated (Johnson 1988). In Stephanidae the mesal lobe articulates very near the basal rim of the mesocoxa, whereas in Evaniomorpha the lobes are comparatively long and each articulates on the surface of the coxa far from the basal rim (Johnson 1988). In both cases the mesal lobe articulates within a coxal groove that divides the mesocoxa into a basal basicoxite and an apical disticoxite (Figs 3, 4; Johnson 1988). In Ichneumonomorpha the mesal lobes are not visible externally (Fig. 5), the 'coxal groove' is very deeply impressed, and the basicoxite is highly reduced and some-

times completely invaginated within the mesocoxa' (Johnson 1988; p. 873), and the 'coxal cavities are strongly constricted and displaced laterally' (Johnson 1988; p. 874). Johnson (1988; p. 879) did not consider that there was 'any evidence that this state (evaniomorph structure) is part of a transformation series leading to that found in the Ichneumonomorpha', and he considered that the ichneumonomorpha structure evolved 'as a single transformation series leading from no coxal groove through a shallow, broad groove with a wide basicoxite to the deeply impressed groove with reduced basicoxite' (Johnson 1988; p. 873). A different postulated transformation series that would support an intermediate mesocoxal structure for taxa assigned to Evaniomorpha includes: (1) an initial external elongation of the mesothoracic mesal lobes from a stephanid-like condition (Fig. 3) to form a plate-like structure between the mesocoxae (Fig. 4; Johnson 1988; fig. 18), and (2) subsequent inflection of the cuticular plate bearing the mesal lobes dorsad between the mesocoxae toward the metasternum and metacoxal foramina (Figs 6,7,8). Such a cuticular inflection would result in lateral displacement of the mesal lobes and articulation (Figs 6,7,8), reduction in size and lateral displacement of the mesocoxal foramina (Figs 6,7,8), and constriction and internalization of the basicoxite to form the internal coxal lobe characteristic of Ichneumonomorpha (Figs 9, 10; Gibson 1986b; fig. 14; Johnson 1988; figs 28-33). If this hypothesized transformation series is correct, the externally elongated portion of the mesothorax that includes the mesal articulatory lobes in Evaniomorpha (Fig. 4) is homologous with what is called the mesotrochantinal plate in Chalcidoidea (Figs 6,7,8; Gibson 1989; figs 109, 110, 119; Gibson 1986b; fig. 13) and the externally visible portion of the mesocoxa in the Ichneumonomorpha is homologous with the disticoxite in the Evaniomorpha. It would also indicate that the mesocoxal articulatory structure characteristic of Ichneumonomorpha is synapomorphic, whereas the articulatory structure characteristic of Evaniomorpha is a retained symplesiomorphy rather than a synapomorphy.

## Conclusions

Sister-group relationships of (Mymarommatoidea + Chalcidoidea) and Platygastroidea remain controversial. Retention of plesiomorphic states of the prepectal-pronotal structural complex and of the mesotrochanteral depressor muscle indicates Chalcidoidea is a relatively basal clade within Apocrita rather than an apical clade as proposed by Dowton *et al.* (1997; fig. 2). Common or similar states shared with Diapriidae and Ceraphronoidea might also support a relatively basal position for Chalcidoidea within Apocrita. Certainly there is at least as strong morphological evidence that Platygastroidea forms a monophyletic

lineage with Pelecinidae, Proctotrupidae and Vanhorniidae, as with Chalcidoidea. Apocritan relationships hypothesized on the basis of the 16S rRNA gene using different numbers of families and analytical methods are too variable to strongly support or refute alternate hypotheses of relationships based on comparative morphology. Future studies of ovipositor structure (Austin & Field 1997), evolution of parasitism (Dowton *et al.* 1997; Whitfield 1998), grooming behaviour (Basibuyuk & Quicke 1999), or any other analyses should examine the possibility and implications of monophyly of Platygastroidea + Pelecinidae + Proctotrupidae + Vanhorniidae. Monophyly of Evaniomorpha *sensu* Rasnitsyn (1980, 1988) and relationships with (Mymarommatoidea + Chalcidoidea) and other Apocrita also require further study.

## Acknowledgements

Jennifer Read (ECORC) is gratefully acknowledged for preparing the figures and table, and for organizing and checking the references. Drs L. Masner (ECORC, retired), J. Huber (Canadian Forest Service, Ottawa), and one anonymous reviewer offered valuable suggestions for improvement of the manuscript. I also thank Dr J. Noyes (The Natural History Museum, London) for the loan of type material of *R. basalis*, and Dr A.P. Rasnitsyn (Palaeontological Institute, Moscow) for providing a translation of the original description of Jurapriidae plus additional comments.

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