Phylogeny of the subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea)

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Key words: phylogeny; Braconidae; subfamilies; morphology; ovipositor-shape; metasomal glands; biology.

A phylogenetic analysis of the subfamilies of the family Braconidae Nees, 1812 is presented. The analysis employing 96 phylogenetically informative characters was performed using the computerized parsimony programmes PAUP and Hennig86. The cladograms obtained show that the Braconidae can be divided into three major groups of subfamilies. These are a lineage comprising the mainly ectoparasitic cyclostomes and relatives, and two advanced endoparasitic groups, both apparently derived from somewhere near the endoparasitic cyclostome subfamily Rogadinae Foerster, 1862 sensu stricto. As a result of the phylogenetic analysis subfamily rank is given to the Exothecinae Foerster, 1862 (including the Hormiini Foerster, 1862), the Rhyssalinae Foerster, 1862 (including the Pambolini Marshall, 1885), the Charmontinae van Achterberg, 1979, and the Microtypinae Szépligeti, 1908. The tribes Meteorini Cresson, 1887 and Muesebeckiini Mason, 1969 are retained as tribes because this analysis did not provide conclusive arguments to separate these groups from the Euphorinae Foerster, 1862 sensu stricto and the Ichneutinae Foerster, 1862 sensu stricto, respectively. The limits of the subfamily Rogadinae Foerster, 1862 are narrowed to include only endoparasitic taxa.

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Contents

Introduction

The Braconidae is a very large family of parasitic wasps with more than 15,000 described species worldwide and possibly two or more times as many remaining to be described (van Achterberg, 1988b; Gauld & Bolton, 1988). These species are currently classified into about 40 subfamilies (van Achterberg, 1984a, 1988b, 1990b). The precise number accepted by braconid workers has not yet stabilized but application of cladistic methodology in recent years has led to the creation of a number of addi-

tional subfamilies to receive generally small numbers of difficult genera that had previously been dumped in dustbin subfamilies such as the Helconinae and Microgastrinae.

The relationships between the braconid subfamilies have been the subject of considerable discussion over the past couple of decades (Tobias, 1967; Čapek, 1969, 1970; Fischer, 1972; van Achterberg, 1976, 1984a; Maetô, 1987). Unfortunately, few firm conclusions have been reached, though it has been generally accepted that there are two major groupings of subfamilies, the old "cyclostomes" and relatives which are predominantly idiobiont ectoparasites and the remainder which are koinobiont endoparasites (van Achterberg, 1984a; Askew & Shaw, 1986; Gauld, 1988). The lack of a well-founded view partly results from the fact that of those studies with a phylogenetic background, many have concentrated on a particular character or small group of characters and, with the exception of van Achterberg (1976, 1984a, 1988b), none have dealt with a large data set. In the present study we have tried to assemble as many phylogenetically informative characters as possible, both from our own studies and from the literature, though whenever possible we have confirmed the latter. These characters include features of adult and larval external and internal morphology, and of biology. Unfortunately, it was not possible to code all characters for all taxa and for many of the small subfamilies, the biology, and internal anatomy of the adult and the morphology of the larvae are still unknown.

Table 1. Subfamily names treated here as junior synonyms, with notes and references as appropriate.

Subfamily name	Present treatment	References
Aneurobraconinae Fahringer, 1936	syn. of Agathidinae-Mesocoelina	van Achterberg, 1990c
Aphrastobraconinae Ashmead, 1900	tribe of Braconinae	
Brachistinae Foerster, 1862	tribe of Helconinae	
Calyptinae Marshall, 1887	syn. of Helconinae-Brachistini	
Capitoninae Viereck, 1910	syn. of Cenocoeliinae	
Centistinae Čapek, 1970	tribe of Euphorinae	
Cosmophorinae Muesebeck & Walkley, 1951	tribe of Euphorinae	
Dacnusinae Foerster, 1862	tribe of Alysiinae	
Diospilinae Foerster, 1862	tribe of Helconinae	
Gnathobraconinae Szépligeti, 1904	syn. of Braconinae	Shenefelt, 1979; Quicke & Huddleston, in press
Incubinae Essig, 1941	syn. of Aphidiinae	
Liophroninae Foerster, 1862	syn. of Euphorinae	
Mesocoeliinae Viereck, 1918	subtribe of Agathidinae-Agathidini	van Achterberg, 1990c
Meteorinae Cresson, 1887	tribe of Euphorinae	
Mimagathidinae Enderlein, 1905	tribe of Orgilinae	van Achterberg, 1987
Pambolinae Marshall, 1885	tribe of Rhyssalinae	
Praonopterinae Tobias, 1988	syn. of Mesostoiinae	Quicke & Huddleston, 1989
Pseudodicrogeniinae Fahringer, 1936	syn. of Braconinae	van Achterberg, 1976
Spathiinae Parfitt, 1881	tribe of Doryctinae	
Triaspinae Viereck, 1918	subtribe of Helconinae-Brachistini	
Vipiinae Gahan, 1917	subjective syn. of Braconinae	
Vipioninae Viereck, 1918	valid emendation of Vipiinae	van Achterberg, 1990c
Zelinae Ashmead, 1900 s. s.	syn. of Meteorini	van Achterberg, 1979c
Zelinae auct.	syn. of Homolobinae	van Achterberg, 1979c

For the purposes of the present study, some groups that have been previously treated as warranting separate subfamily status have been included within those subfamilies from which they are clearly derived (table 1; see also van Achterberg, 1976). The fossil subfamily Diospilitinae Tobias, 1987, recently formed for *Diospilites* Brues, 1933 (known from the Baltic Amber only) is excluded from the analysis because too little is known about its morphology. Though it has previously been suggested that it may warrant separate subfamily status (e.g. van Achterberg, 1988b), the genus *Mesocoelus* Schulz, 1911 is regarded here as being a highly derived agathidine in agreement with Sharkey (1986), Buckingham & Sharkey (1988), and van Achterberg (1990c). The genus *Dyscoletes* Haliday, 1840 included in the Helconinae by some previous workers, is here treated as belonging to the Blacinae in accordance with van Achterberg (1984a, 1988a).

In order to obtain as accurate a phylogeny as possible we have treated separately some groups that have, for the most part, been difficult to place or show somewhat intermediate combinations of characters. These are (1).— Rhyssalini which display a mixture of characters intermediate between those of the Doryctinae and the Rogadinae (especially in terms of biology and larval features) (Čapek, 1970), (2).— Exothecini, (3).— Hormiini which are are also frequently included in the Rogadinae but appear to be far less derived, (4).— Pselaphanini which have been associated with the Agathidinae but do not fit well there (see van Achterberg, 1985, 1990c), and is given subfamily-rank by van Achterberg, 1990c, (5).— Brulleiini which are currently placed in the Helconinae, but display characters suggesting relationships with other subfamilies (van Achterberg, 1979a, 1979b, 1983a) and (6).— Muesebeckiini which have been associated with both the Ichneutinae and with the Miracinae (Nixon, 1965; Mason, 1969; van Achterberg, 1984a; Tobias, 1986).

Terminology

Terminology follows that of van Achterberg (1979c, 1988a) for external adult morphology, Snodgrass (1941) for adult male genitalia and Čapek (1970) for larval cephalic structures. The Braconidae are protelian parasites, in this paper abbreviated to "parasites". Another fashionable term for this kind of parasite is "parasitoid".

Data matrix

Most of the data on adult external morphology are derived from the studies of one of us (CvA). Much of the data on adult labio-maxillary complex, adult head capsule, male genitalia, internal male reproductive system, male Hagen's glands, internal female reproductive system, venom apparatus, larval tracheal commissures, larval cephalic structures and emergence from cocoon have been extracted from the papers by, respectively, Tobias & Potapova (1987), Tobias & Potapova (1982), Tobias (1979), Maetô (1987), Buckingham & Sharkey (1988), Iwata (1959), Edson & Vinson (1979), De Leon (1934), Čapek (1969, 1970, 1973) and Čapek (1969, 1970). De Leon's data (op. cit.) on the location of the first thoracic spiracle and the presence of tracheal commissures in larval braconids have been checked both by our own examination of

larvae and by reference to more recent larval descriptions (e.g., Mashood Alam, 1952; Smith, 1952; Madel, 1963; Vinson, 1969; Quednau, 1970). Some re-interpretations have been found necessary, for example, in the Alysiinae the first thoracic spiracle is located in the prothoracic segment (see e.g., Smith, 1952; Obrtel, 1960; Guppy & Meloche, 1987). A few discrepancies have also been found between our own findings and those of Tobias & Potapova (1982), for example we have found that the neck strut of *Sigalphus* Latreille, 1802 (*S. irrorator* (Fabricius, 1775)) is well-developed both dorsally and ventrally (fig. 46), whereas that of *Histeromerus* Wesmael, 1838 (*H. mystacinus*

Table 2a. Original data matrix of the 96 characters. Unknown character states are indicated by a "-"; polymorphic or ambiguous characters by a "P".

ADELIINAE	1002000100	0000010011	0101100--0	0001111111	1100101000
	0102010000	-1000--000	0120111110	10111----1	1100--
AGATHIDINAE	00P2PP0-30	0P11P00011	P001101101	110011PP1P	P1P0PP1000
	0100100000	1110011000	0P20110101	10101P--11	010001
ALYSIINAE	0000020-30	0P01010011	P000P0020P	P000P111P1	111000P000
	0P0010001P	10011001PP	10PP000001	1100P00001	110011
AMICROCENTRINAE	00--021-00	0001000000	0000000100	0000010111	1100001000
	0100101000	1-0001-0-0	0---110101	10101----1	0101--
APHIDIINAE	0000000000	1000010011	1P01PP010P	1000010111	1110001P00
	0100100000	1100021P0P	012P11-1-2	1100100001	-11111
APOZYGINAE	01--000-30	0000010011	0000000200	0000011110	1110001100
	0000011002	01000-----	----------	----------	------
BETYLOBRACONINAE	0P00100000	0000000011	0000P00201	0000P11101	1110001000
	0000101001	0001000101	1010----11	----------	------
BLACINAE	0002000100	0P001P0011	0001100-0P	0000110111	1110000000
	0100100100	11100--000	0120110111	10001----1	0P0---
BRACONINAE	01PP020-31	10010P0P11	P000P00101	00000P1111	1110001000
	00101010P2	0001000101	01210PPP01	000000010P	0P0000
BRULLEIINI	00--000-30	0100100000	0001010100	0000000111	0100001-00
	0100-----	-----11---	----------	----------	-00---
CARDIOCHILINAE	0011P21-3P	1001P00011	010000P211	000P110011	P1P1101011
	1101000000	1110001000	0120111110	1111101111	010001
CENOCOELIINAE	0012100000	0100001021	0000020101	0000000111	11P0P01000
	0100101000	1110011000	0110110111	10101----1	00000-
CERCOBARCONINAE	00020P0010	0000100110	0010000100	0000010110	0100001100
	0100100000	--00011100	0020-----2	----------	------
CHELONINAE	10PPP00PP0	0000001011	000PP0021P	0P00P10111	11001P1000
	102010000	11P0001000	0110110110	1010111011	010001
DIRRHOPINAE	00--121---	0000000011	0101100201	0001110001	1110001000
	0-0------	----------	----------	10101----1	110---
DORYCTINAE	01000P0PP0	00000P00P1	0000P0020P	0000PP11P1	111000PP00
	0P00P0P0P2	0P0100011P	P02P0P0001	0000P001-0	000000
ECNOMIINAE	00--000000	0000000011	0000100-01	0000111111	1100001000
	0100-----	-----000-0	----------	----------	------
EUPHORINAE s.s.	00P2000PP0	0P00100011	P00PP1020P	P000110111	11P000P100
	0100100100	1110011000	01P0110P11	11P01110P1	0PPP1P
EXOTHECINAE s.s.	01000100P0	0P01000011	000000020P	0000011101	1110001000
	0000001011	000000011-	1120010011	0000000100	0P0000
GNAMPTODONTINAE	0P000P0-30	P001010011	P000000201	0000P111P1	1110001000
	0010101011	---11-0101	1020110001	00000----1	1100--
HELCONINAE s.s.	00P2000100	01001000PP	000PPP0101	0000PPP111	PP10001000

	01001000P0	11P0011000	0PP0110101	1010110-11	000001
HISTEROMERINAE	0100010100	0000000011	0000000200	0000P1P101	1110001000
	0100010100	--01000111	----000010	00000-----	0000--
HOMOLOBINAE	0002000100	0000100011	0001010201	0000010P11	1P00001000
	0100100100	1110011000	0000110111	10101----1	01000-
HORMIINI	0100000020	0P0P000011	000000020P	0000011101	111000P000
	0000101011	------01-0	-12-110011	00000--P0	01000-
ICHNEUTINAE s.s.	0002020-3P	P00P0P0011	0P0PP0P211	0PP001P111	11P0001000
	0100001000	11P0001101	0110111110	11001----1	1100--
KHOIKHOIINAE	00--021--1	100100P011	0100000111	000P110011	1111001011
	110101100-	----------	----------	----------	------
MACROCENTRINAE	0002010-30	0000000001	0001000201	0000010111	1100001000
	0100100000	1100011000	0110110101	1010110011	010101
MESOSTOINAE	01--1P0001	1001010011	0001000--0	0001011111	1110001000
	0100101010	-0010-----	----------	01001-----	------
METEORIDEINAE	0011000-00	0100100011	00001000P1	0000000110	1000000000
	01001--000	-1----10--	---0------	10000----1	11001-
METEORINI	0002000100	0100100011	0000010101	0000110111	1P00001100
	0100000100	1110011000	0PP0110111	1P10111111	000P11
MICROGASTRINAE	2012P21-30	P001000011	1100100-11	00000P1011	1101PP1011
	1101000000	11P0001000	0120111110	1PPPP11011	0101P1
MICROTYPINAE	0002P00100	0000100011	0001100201	0000010011	1100001000
	0100100100	11--0110--	----110101	10101----1	0100--
MIRACINAE	2002000-31	1001000011	0100100--1	0000111111	1110101010
	110201P000	----0-0000	0120111110	10101----1	1101--
MUESEBECKIINI	0002P20001	1001010011	0101100-11	0010111111	1110001000
	0100------	----------	----------	11101----1	110---
NEONEURINAE	2002120-3P	P001000010	1P0010010P	0000111111	1100101000
	0100001000	11000--000	0110----11	11101----1	011-1-
OPIINAE	0P000P00P0	0P01010011	000000020P	P0000111P1	111000P000
	0P00100010	10011001PP	P02P011001	11P0110101	110011
ORGILINAE	0002P10120	0100P00011	0001100-P1	0000010111	1110P11000
	0100101000	1100011000	-110110001	10101---11	01000-
PSELAPHANINAE	00--010100	0111010011	0000000101	1101010010	1110100000
	0100----0-	----------	----------	----------	------
RHYSSALINAE	0100000100	0000000011	0000000201	0000011101	110010000
	0100001010	00000--111	-01-000000	000000---0	-000--
ROGADINAE s.s.	0100PP0PP0	0P00000011	0000P0020P	0000P111P1	1110P0P000
	0000101010	0001000101	P0200P0001	0100P0---P	1P00P0
SIGALPHINAE	00P2000P00	0110100011	0000001PP1	0P00010110	1100P01100
	0100100000	1110011000	00--110101	10101----1	01000-
TELENGAIINAE	0100020-3-	1001000011	1000000-01	0000011101	1110001000
	0010101011	00010-----	----------	----------	------
TRACHYPETINAE	0012000100	0000100110	0010011100	0000010110	0100001100
	0100100000	1110011100	0020-----2	----------	------
VAEPELLINAE	01--120--1	1001000011	0000000201	0000011111	1110001000
	0000------	----------	----------	----------	------
XIPHOZELINAE	0002010--0	0000100001	0000010101	000001011P	1000001100
	0100100100	---0011000	0000----11	10101----1	1101--
YPSISTOCERINAE	00--020--1	1001010011	0000000200	0P0P1111P1	1110001000
	0100011012	-101-00111	1020----01	----------	------
UNORDERED	1 4 9 19 66				
OUTSTATES	00--000--0	0000000000	0000000-00	0000000000	0000000000
("ANCESTOR")	0000000000	0000000000	0000000000	000000--00	000-00

Wesmael, 1838), is strongly reduced both dorsally and ventrally (fig. 47). In these cases we have used our own findings. A considerable amount of new information, particularly on adult internal morphology, wing flexion lines and ovipositor structure (figs. 7-44) is presented.

Table 2b. Data matrix of the 96 characters used for the phylogenetic analysis. Both the unknown or ambiguous character states and the polymorphic characters are indicated by a "9".

ADELIINAE	1002000100	0000010011	0101100990	001111111	1100101000	0102010000
	9100099000	0120111110	1011199991	110099		
AGATHIDINAE	0092990930	0911900011	9001101101	1100119919	9190991000	0100100000
	1110011000	0920110101	1010199911	010001		
ALYSIINAE	0000020930	0901010011	9000900209	9000911191	1110009000	0900100019
	1001100199	1099000001	1100900001	110011		
AMICROCENTRINAE	0099021900	0001000000	0000000100	0000010111	1100001000	0100101000
	1900019090	0999110101	1010199991	010199		
APHIDIINAE	0000000000	1000010011	1901990109	1000010111	1110001900	0100100000
	1100021909	0129119192	1100100001	911111		
APOZYGINAE	0199000930	0000010011	0000000200	0000011110	1110001100	0000011002
	0100099999	9999999999	9999999999	999999		
BETYLOBRACONINAE	0900100000	0000000011	0000900201	0000911101	1110001000	0000101001
	0001000101	1010999911	9999999999	999999		
BLACINAE	0002000100	0900190011	0001100909	0000110111	1110000000	0100100100
	1110099000	0120110111	1000199991	090999		
BRACONINAE	0199020931	1001090911	9000900101	0000091111	1110001000	0010101092
	0001000101	0121099901	0000000109	090000		
BRULLEIINI	0099000930	0100100000	0001010100	0000000111	0100001900	0100999999
	9999911999	9999999999	9999999999	900999		
CARDIOCHILINAE	0011921939	1001900011	0100009211	0009110011	9191101011	1101000000
	1110001000	0120111110	1111101111	010001		
CENOCOELIINAE	0012100000	0100001021	0000020101	0000000111	1190901000	0100101000
	1110011000	0110110111	1010199991	000009		
CERCOBARCONINAE	0002090010	0000100110	0010000100	0000010110	0100001100	0100100000
	9900011100	0020999992	9999999999	999999		
CHELONINAE	1099900990	0000001011	0009900219	0900910111	1100191000	0102010000
	1190001000	0110110110	1010111011	010001		
DIRRHOPINAE	0099121999	0000000011	0101100201	0001110001	1110001000	0909999999
	9999999999	9999999999	1010199991	110999		
DORYCTINAE	0100090990	0000090091	0000900209	0000991191	1110009900	0900909092
	0901000119	9029090001	0000900190	000000		
ECNOMIINAE	0099000000	0000000011	0000100901	0000111111	1100001000	0100999999
	9999900090	9999999999	9999999999	999999		
EUPHORINAE s.s.	0092000990	0900100011	9009910209	9000110111	1190009100	0100100100
	1110011000	0190110911	1190111091	099919		
EXOTHECINAE s.s.	0100010090	0901000011	0000000209	0000011101	1110001000	0000001011
	0000000119	1120010011	0000000100	090000		
GNAMPTODONTINAE	0900090930	9001010011	9000000201	0000911191	1110001000	0010101011
	9991190101	1020110001	0000099991	110099		
HELCONINAE s.s.	0092000100	0100100099	0009990101	0000999111	9910001000	0100100090
	1190011000	0990110101	1010110911	000001		
HISTEROMERINAE	0100010100	0000000011	0000000200	0000919101	1110001000	0100010100
	9901000111	9999000010	0000099999	000099		

HOMOLOBINAE	0002000100	0000100011	0001010201	0000010911	1900001000	0100100100
	1110011000	0000110111	1010199991	010009		
HORMIINI	0100000020	0909000011	0000000209	0000011101	1110009000	0000101011
	9999990190	9129110011	0000099990	010009		
ICHNEUTINAE s.s.	0002020939	9009090011	0909909211	0990019111	1190001000	0100001000
	1190001101	0110111110	1100199991	110099		
KHOIKHOIINAE	0099021991	1001009011	0100000111	0009110011	1111001011	1101011009
	9999999999	9999999999	9999999999	999999		
MACROCENTRINAE	0002010930	0000000001	0001000201	0000010111	1100001000	0100100000
	1100011000	0110110101	1010110011	010101		
MESOSTOINAE	0199190001	1001010011	0001000990	0001011111	1110001000	0100101010
	9001099999	9999999999	0100199999	999999		
METEORIDEINAE	0011000900	0100100011	0000100091	0000000110	1000000000	0100199000
	9199991099	9990999999	1000099991	110019		
METEORINI	0002000100	0100100011	0000010101	0000110111	1900001100	0100000100
	1110011000	0990110111	1910111111	000911		
MICROGASTRINAE	2012921930	9001000011	1100100911	0000091011	1101991011	1101000000
	1190001000	0120111110	1999911011	010191		
MICROTYPINAE	0002900100	0000100011	0001100201	0000010011	1100001000	0100100100
	1199011099	9999110101	1010199991	010099		
MIRACINAE	2002000931	1001000011	0100100991	0000111111	1110101010	1102019000
	9999090000	0120111110	1010199991	110199		
MUESEBECKIINI	0002920001	1001010011	0101100911	0010111111	1110001000	0100999999
	9999999999	9999999999	1110199991	110999		
NEONEURINAE	2002120939	9001000010	1900100109	0000111111	1100101000	0100001000
	1100099000	0110999911	1110199991	011919		
OPIINAE	0900090090	0901010011	0000000209	9000011191	1110009000	0900100010
	1001100199	9029011001	1190110101	110011		
ORGILINAE	0002910120	0100900011	0001100991	0000010111	1110911000	0100101000
	1100011000	9110110001	1010199911	010009		
PSELAPHANINAE	0099010100	0111010011	0000000101	1101010010	1110100000	0100999909
	9999999999	9999999999	9999999999	999999		
RHYSSALINAE	0100000100	0000000011	0000000201	0000011101	110010000	0100001010
	0000099111	9019000000	0000009990	900099		
ROGADINAE s.s.	0100990990	0900000011	0000900209	0000911191	1110909000	0000101010
	0001000101	9020090001	0100909999	190090		
SIGALPHINAE	0092000900	0110100011	0000001991	0900010110	1100901100	0100100000
	1110011000	0099110101	1010199991	010009		
TELENGAIINAE	0100020939	1001000011	1000000901	0000011101	1110001000	0010101011
	0001099999	9999999999	9999999999	999999		
TRACHYPETINAE	0012000100	0000100110	0010011100	0000010110	0100001100	0100100000
	1110011100	0020999992	9999999999	999999		
VAEPELLINAE	0199120991	1001000011	0000000201	0000011111	1110001000	0000999999
	9999999999	9999999999	9999999999	999999		
XIPHOZELINAE	0002010990	0000100001	0000010101	0000010119	1000001100	0100100100
	9990011000	0000999911	1010199991	110199		
YPSISTOCERINAE	0099020991	1001010011	0000000200	0909111191	1110001000	0100011012
	9101900111	1020999901	9999999999	999999		
UNORDERED	1 4 9 19 66					
OUTSTATES	0099000990	0000000000	0000000900	0000000000	0000000000	0000000000
("ANCESTOR")	0000000000	0000000000	0000009900	000900		

Analysis of the character states

Autapomorph characters of taxa were excluded from the analyses; however, those known (or suspected) are mentioned in the discussion on each subfamily. Some other highly variable characters such as reductions in the numbers of labial or maxillary palpal segments, complete loss of forewing vein r-m and formation of a metasomal carapace (Tobias & Dudarenko, 1974; van Achterberg, 1988b), which previous studies have shown to have occurred on numerous independent occasions within the Braconidae, were also excluded from consideration. This left a total of 96 potentially phylogenetically informative characters. Undoubtedly more detailed biological investigations, such as on the occurrence of teratocytes and of calyx or venom gland-associated viruses (Stoltz & Vinson, 1979; Edson et al., 1982), of sperm ultrastructure (Quicke et al., in prep.), and studies on internal anatomy (see e.g., Buckingham & Sharkey, 1988; Whitfield et al., 1989) will yield many more useful characters, but unfortunately too little is known about these at present to allow their inclusion in our data matrix. Our polarity decisions for most characters agree with those previously published, which were generally based on outgroup comparisons using the Ichneumonidae or the Symphyta. Where the characters employed are new or our interpretations differ from previous ones we provide a more detailed discussion. For others, only references to previous works justifying polarity decisions are given. As with previous treatments, we have employed a hierarchical system of outgroups. Normally the Ichneumonidae have been treated as the primary outgroup and the Symphyta as the secondary outgroup; however, consideration of the extinct Praeichneumonidae (Rasnitsyn, 1983) and Eoichneumonidae (Rasnitsyn & Sharkey, 1988) has been helpful in interpreting some features, particularly with regard to wing venation.

Data were analysed using two computerized phylogenetic analysis programmes. (1) PAUP (version 2.4) of David Swofford, Illinois Natural History Survey, Urbana, Illinois; the most parsimonious trees were found using the options ADDSEQ= CLOSEST, SWAP= GLOBAL, MULPARS, HOLD= 5, MAXTREE= 100 (many other combinations of characters have been tested and analyses also performed using tree descriptions previously obtained with other parameter combinations as starting points). PAUP trees were constructed using only the 46 taxa listed in table 2; thus they were rooted using the ROOT= LUNDBERG option together with an OUTSTATES statement. (2) Hennig86 (version 1.5) of James Farris (Port Jefferson Station, New York) using the "ie" option. Hennig trees were constructed including an ANCESTOR taxon. The "outstates" were used for the "ancestor". First the unweighted data matrix was used with Lundberg rooting and Farris optimalisation. Later limited character weighting (tables 3, 4) was applied to get fully resolved trees. Characters for which we were uncertain about polarity (nos 3, 4, 8, 9, 28, 66, 87, 88, 94), were excluded from the rooting process in both cases.

In order to permit comparisons of the cladograms produced by Hennig86 and PAUP we used the latter's TOPOLOGY option. It allowed us to enter Hennig-generated trees as hand transcribed, nested sets. A 47th taxon ("Ancestor") comprising the same character states as used in the outstates statement was added to the PAUP data set to enable comparison of PAUP trees with Hennig output including an "Ancestor" taxon.

Both programmes found similar sets of trees; the most parsimonious trees found with both programmes are presented here (figs. 1-6). Characters that are known to be polymorphic within a taxon (table 2a: "P") were treated in the same way as unknowns, both being presented in the data matrix as "9" (table 2b). Two sets of simple character weights (tables 3, 4) were employed to get completely resolved trees. The weighting system is based on our judgement of the likelihoods of the various characters to show homeoplasy (parallelism or convergence), their consistencies within individual subfamilies, the accuracy with which they could be scored, and their completeness within our data set. Thus, in general, wing venation characters which involve losses or shifts of venation towards the wing base, and poorly-known features such as larval tracheal commissures were not weighted (i.e., weight= 1).

Table 3. Set 1 of simple weights.

WEIGHTS	2311111112	1331321111	1221112221	1111111122	1112121131	1111111311
	3222321111	1111321211	2123131122	111111		

Table 4. Set 2 of simple weights.

WEIGHTS	2211111111	1221221111	1221111111	1111111122	1111111121	1111111211
	2111221111	1111211211	2122121122	111111		

List of characters

Assumed plesiomorph character states are coded 0; justifications for polarity decisions or references are provided. Polystate characters were treated as either ordered or unordered as specified in each case.

1. Number of antennal segments: 0= variable; 1= fixed in many members of subfamily; 2= fixed in all members of subfamily. [Unordered.] The number of antennal segments in most ichneumonoids is variable and therefore we consider fixation to represent an apomorph condition (see also van Achterberg, 1988b).

2. Labrum: 0= flat and largely setose; 1= concave and largely glabrous. The labrum in ichneumonids is flat and setose and therefore we suppose that this is the plesiomorph condition in the Braconidae.

3. Glossa: 0= distally rounded (fig. 114); 1= bilobed, concave medially. Polarity uncertain.

4. Distal sclerites of maxilla: 0= more or less equally long, lacinia triangular (fig. 115); 1= lacinia shorter than galea, lacinia rectangular or triangular; 2= lacinia much shorter than galea, both rounded (fig. 117). [Unordered.] Polarity uncertain.

5. Epistomal suture: 0= complete; 1= partly reduced. The epistomal suture of most Ichneumonidae is well-developed except for some rather advanced groups (e.g., Campopleginae, Mesochorinae, Metopiinae) and therefore we consider its presence to be plesiomorphic for the Braconidae.

6. Occipital carina: 0= complete (fig. 140); 1= incomplete (fig, 130); 2= absent (figs. 136-139). [Ordered.] Reference: van Achterberg (1979a).

7. Hypostomal carina: 0= present; 1= absent. Reference: van Achterberg (1979b).

8. Hypostomal carina: 0= separate from neck strut (margin of foramen magnum);

1= linked with neck strut. Polarity uncertain.

9. Neck strut (margin of foramen magnum): 0= complete; 1= reduced dorsally; 2= reduced ventrally; 3= completely reduced. [Unordered.] Polarity uncertain.

10. Mid-longitudinal propleural carina: 0= present; 1= absent. A mid-longitudnal propleural carina is present in most Ichneumonidae and therefore we consider its presence to be plesiomorphic for the Braconidae.

11. Propleural flange: 0= present (figs. 131, 132); 1= absent (figs. 136-139). Reference: van Achterberg (1988b).

12. Pronope: 0= absent; 1= present. A pronope (van Achterberg, 1979c) is absent in the Ichneumonidae and therefore we consider its presence in Braconidae to be the apomorph state.

13. Subpronopes: 0= absent; 1= present (fig. 178). Subpronopes, as such, are not found in any Ichneumonidae as far as we are aware and therefore we consider their presence in some Braconidae to be apomorphic.

14. Prepectal carina: 0= present; 1= absent. Reference: van Achterberg (1979b).

15. Posterior depression of scutellum: 0= absent; 1= present (fig. 171). A posterior scutellar depression is absent in the Ichneumonidae and therefore we consider its presence in some Braconidae to be apomorphic. Reference: van Achterberg (1984a).

16. Anterior subalar depression: 0= carinate; 1= smooth. This region is typically carinate in the Ichneumonidae (Townes, 1969: 44) and therefore we consider loss of carination to be apomorphic.

17. Postpectal carina: 0= absent; 1= present. Reference: van Achterberg (1984a).

18. Propodeal spiracle: 0= circular or short-elliptical (less than 2.5 times longer than wide); 1= slit-shaped (more than 2.5 times longer than wide; figs. 174, 175). Propodeal spiracles in the Ichneumonidae are usually short and elliptical and therefore we consider very elongate spiracles in some Braconidae to be apomorphic.

19. Propodeal-metasomal junction: 0= just above hind coxae; 1= between hind coxae; 2= far above hind coxae. [Unordered.] References: van Achterberg (1979a, 1979b).

20. Forewing costal cell: 0= partly present; 1= completely absent. References: van Achterberg (1979a); Quicke & Holloway (in press).

21. Forewing marginal cell: 0= wide; 1= narrow. The forewing marginal cell is wide in the Ichneumonidae and most Eoichneumonidae and therefore we consider this to be the plesiomorph condition in the Braconidae.

22. Forewing marginal cell: 0= closed (vein SR1 completely or largely sclerotized); 1= open (more than 0.75 of vein SR1 unsclerotized). The marginal cell of most Ichneumonidae and of Eoichneumonidae is closed and therefore we take this to be the plesiomorph condition for the Braconidae.

23. Forewing parastigma: 0= normal; 1= elongate (more than half length of pterostigma). Ichneumonids generally have smaller and less clearly defined parastigmas than do braconids and therefore we consider the very large parastigmas of the Cercobarconinae and the Trachypetinae to be apomorphic.

24. Forewing vein 1-SR: 0= distinct; 1= absent (vein 1-SR+M arising from the parastigma). Vein 1-SR is distinct in the Eoichneumonidae (Rasnitsyn & Sharkey, 1988) and therefore we consider this to be the plesiomorph state for the Braconidae.

25. Forewing second submarginal cell (if complete): 0= large or medium-sized; 1=

small or absent. The second submarginal cell in the Eoichneumonidae is large and therefore we consider this to be the plesiomorph condition for the Braconidae.

26. Antero-medial forewing flexion line: 0= transverse, running through vein 2-SR+M and/or the immediately adjacent parts of veins 2-SR and 2-M; 1= oblique, through vein 2-SR and through distal part of 2-M; 2= longitudinal, through vein 2-SR but not through 2-M. [Ordered.] Examination of the best preserved fossils of Eoichneumonidae (Rasnitsyn & Sharkey, 1988) shows that vein 2-SR+M and the immediately contiguous parts of veins 2-SR and 2-M are comparatively weakly sclerotized thus strongly indicating that the principle flexion line in these insects ran antero-posteriorly from the first submarginal to the second subdiscal cell (i.e., state "0") and therefore we consider this to be the plesiomorph condition for the Braconidae. Because of the considerable differences between the venation of this part of the wing in the Braconidae and the Ichneumonidae and the associated uncertainties about vein homologies, ichneumonid wings were not considered in this polarity analysis.

27. Forewing vein m-cu (if largely sclerotized): 0= completely sclerotized, without bulla; 1= with a discrete, sub-anterior bulla and corresponding longitudinal flexion line. In ichneumonid wings, vein 1m-cu has no bulla and therefore we consider the presence of a bulla in Braconidae to be apomorphic.

28. Forewing vein r-m (when present): 0= completely sclerotized (tubular; fig. 175); 1= sclerotized with a discrete bulla posteriorly (fig. 166); 2= completely unsclerotized but still clearly indicated (fig. 131). [Ordered.] Polarity uncertain.

29. Angle between forewing veins 3-SR and base of SR1 (when both distinct): 0= greater than 135°; 1= less than 135°. In the Eoichneumonidae and in the Symphyta, veins 3-SR and SR1 form nearly a straight line (i.e., the angle between them is approximately 180°) and therefore we consider the marked reduction in this angle displayed by some braconids to be apomorphic.

30. Forewing vein 2-SR+M: 0= transverse (fig. 130); 1= longitudinal. References: van Achterberg (1979a); see also Rasnitsyn & Sharkey (1988).

31. Forewing vein M+CU1: 0= sclerotized; 1= largely unsclerotized. Vein M+CU1 is clearly sclerotized in the Eoichneumonidae and therefore we consider this to be the plesiomorph condition for the Braconidae.

32. Forewing veins 1-M and m-cu: 0= (sub)parallel or converging posteriorly; 1= diverging posteriorly. These veins are clearly converging posteriorly in the Eoichneumonidae and therefore we take this to be the plesiomorph condition for the Braconidae.

33. Forewing vein 1-M: 0= straight or evenly curved; 1= strongly curved anteriorly. An anteriorly straight vein 1-M is found in both the Ichneumonidae and the Eoichneumonidae and therefore we consider the curvature displayed by some braconids to be apomorphic.

34. Forewing vein m-cu: 0= more than 0.5 times length of vein 1-M; less than 1.5 times 1-M. A relatively long vein m-cu is found in the Eoichneumonidae and therefore we consider this to be the plesiomorph state for the Braconidae.

35. Forewing vein CU1b: 0= present; 1= absent. Vein Cu1b is present in both the Ichneumonidae and Eoichneumonidae and therefore we consider its absence in some Braconidae to be apomorphic.

36. Forewing vein a: 0= present; 1= absent. Forewing veins a and 2A, and hind-

wing veins r and m-cu are all absent in the Ichneumonidael; however, their presence is plesiomorphic with regard to the Hymenoptera as a whole. Further, vein a is distinct in the Eoichneumonidae which may be the sister group of the Braconidae (Rasnitsyn & Sharkey, 1988) and therefore we consider the presence of these veins in various Braconidae to be plesiomorphic for present purposes. We are aware, however, that in reality these veins may represent re-expressions of previously "hidden" genetic information and thus might on future analysis be better regarded as apomorphies.

37. Forewing vein 2A: 0= present; 1= absent. Reference: van Achterberg (1979b); see also notes on character 36.

38. Hindwing vein r: 0= present; 1= absent. Reference: van Achterberg (1979b); see also notes on character 36.

39. Hindwing vein m-cu: 0= present (in at least most members of taxon); 1= absent (in all members of taxon or rarely variably present). See notes on character 36 above.

40. Hindwing vein 2-CU: 0= present; 1= absent. Hindwing vein 2-CU is present in the Ichneumonidae though it is unclear if it is present in the Eoichneumonidae; taking the Ichneumonidae as the outgroup we consider the presence of vein 2-CU to be plesiomorphic for the Braconidae.

41. Hamuli on hindwing vein R1: 0= 7 or more; 1= fewer than 7. The usual number of proper hamuli in the Ichneumonidae is 10 (Townes, 1969), and therefore we consider that a reduced number is apomorphic; 7 was chosen as a cut-off arbitrarily.

42. Hindwing vein 2A: 0= distinct; 1= absent. Reference: van Achterberg (1979b); see also notes on character 36 above.

43. Hindwing plical cell: 0= large or medium-sized; 1= small. The plical cell of Symphyta is usually well-developed though that of the Ichneumonidae is generally smaller. Taking the Symphyta as the outgroup we consider reductions in the size of the plical cell to be apomorphic.

44. Fore tibial spur: 0= short; 1= long (almost as long as the basitarsus). Reference: van Achterberg (1984a).

45. Hind coxae: 0= medium-sized; 1= large, often considerably longer than the first metasomal tergite. Reference: van Achterberg (1984a).

46. Hind tibial pegs: 0= absent; 1= present. A transverse apical row of pegs on the hind tibia does not occur in the Ichneumonidae as far as we are aware and therefore we consider their presence in some Braconidae to be apomorphic.

47. Dorsope of first metasomal tergite: 0= absent; 1= present. Reference: van Achterberg (1984a).

48. First metasomal segment: 0= not tubular basally (tergum and sternum separate); 1= tubular basally (tergum and sternum fused). The first metasomal segment of the Eoichneumonidae does not appear to be tubular basally and therefore we consider that the tubular conditions found in some Braconidae and in many Ichneumonidae are independent apomorph developments.

49. Spiracles of first metasomal tergite: 0= in notum (fig. 62); 1= in epipleuron (figs. 64, 65). Reference: van Achterberg (1976); Mason (1983).

50. First metasomal sternite: 0= divided into distinct anterior and posterior parts; 1= not divided. Reference: Mason (1983).

51. Lateral membrane of first metasomal tergite: 0= smooth; 1= finely, longitudi-

nally striate (fig. 65). The striate condition appears to be unique to certain Braconidae and therefore we consider it to be a derived state; see also Mason (1983).

52. Spiracle of second metasomal tergite: 0= in notum; 1= in epipleuron. Reference: Mason (1983).

53. Third metasomal tergite with posteriorly-diverging antero-lateral grooves: 0= absent; 1= present (fig. 135). Posteriorly-diverging antero-lateral grooves are absent in most of the Ichneumonidae (but present in many less derived Pimplinae) and we therefore consider their presence in some Braconidae to be apomorphic. Without doubt these grooves have been secondarily lost in some Braconinae (Quicke, 1987b) and they are not present in all Gnamptodontinae.

54. Number of metasomal segments with spiracles: 0= 7; 1= 6; 2= 5 or fewer. [Ordered.] The Symphyta and the majority of Apocrita have eight abdominal (and hence seven metasomal) spiracles (Gauld & Bolton, 1988), reductions therefore are believed to be apomorphic (van Achterberg, 1988b).

55. Eighth metasomal sternite of male: 0= produced medio-anteriorly; 1= simple, more or less straight. In the Ichneumonidae the ninth sternite of males is strongly produced medio-anteriorly (Peck, 1937; Pratt, 1939) and therefore we consider this to be the plesiomorph condition in the Braconidae.

56. Eighth metasomal sternite of male: 0= more or less straight posteriorly; 1= emarginate medio-posteriorly. In the Ichneumonidae the posterior margin of the eighth sternite is not medially cleft (Peck, 1937; Pratt, 1939) and therefore we consider the presence of an emargination to be apomorphic.

57. Cuspidal processes (lateral) of male genitalia: 0= present as a lobe-like or articulated process; 1= absent or very reduced. References: Telenga (1952); Tobias (1967); van Achterberg (1988b).

58. Cuspidal processes (lateral) of male genitalia: 0= continuous with volsella (except some Agathidinae q.v.; if absent also scored as "0"); 1= articulated with volsella (slender with apical teeth; figs. 73, 85, 86). References: Tobias (1967); van Achterberg (1988b).

59. Parameres of male genitalia: 0= well-developed; 1= very short, not reaching beyond middle of digitus. The parameres of the Ichneumonidae are well-developed (Peck, 1937; Pratt, 1939) and therefore we consider reduction as shown by some Braconidae to be apomorphic.

60. Basal ring (gonobase) of male genitalia: 0= short (fig. 73); 1= moderately thickened (figs. 74, 75); 2= strongly elongate (figs. 77, 78). [Ordered.] In the Ichneumonidae the basal ring is generally short medio-ventrally (Peck, 1937; Pratt, 1939) and we therefore consider this to be the plesiomorph condition for the Braconidae.

61. Testes (scrotum): 0= fused medially (dorsal to gut; fig. 98); 1= separate or (rarely) fused ventral to the gut (figs. 99, 101). The testes are fused medially dorsal to the gut in the Ichneumonidae studied by Maetô (1987) though they are often separate in the Symphyta (Togashi, 1970). Taking the Ichneumonidae as the primary outgroup, we have treated testes that are fused above the gut as showing the plesiomorph condition in the Braconidae.

62. Vas deferens insertion on to accessory gland: 0= posterior or medial (fig. 55); 1= anterior (terminal or nearly so; figs. 98-101). In the Ichneumonidae studied by

Maetô (1987) and in the Symphyta studied by Togashi (1970) the vas deferens arises more or less posteriorly and therefore we consider this to be the plesiomorph condition for the Braconidae.

63. Vas deferens: 0= clearly differentiated (usually long; figs. 53, 98); 1= absent or nearly so (figs. 99-101). Most Ichneumonidae have a long, clearly defined vas deferens (Maetô, 1987) and therefore we consider this to be the plesiomorph condition for the Braconidae.

64. Accessory glands (male): 0= ovoid or sub-oval; 1= elongate, tubular (fig. 55). In the Ichneumonidae studied by Maetô (1987) the accessory glands are ovoid and therefore we consider this to be the plesiomorph condition for the Braconidae.

65. Hagen's glands (male): 0= absent or if similar glands present then these do not open on to the sclerotized part of metasomal tergum 8; 1= opening on sclerotized part of metasomal tergum 8. Reference: Buckingham & Sharkey (1988).

66. Ovarioles: 0= more than 2 pairs (4-30, typically more than 8 pairs); 1= 2 pairs (fig. 56); 2= 1 pair only. [Ordered.] Most Ichneumonidae and Symphyta have more than 2 pairs of ovarioles; however, ichneumonids typically have fewer than symphytans (Iwata, 1958, 1960), and the ichneumonids generally accepted as being less derived (e.g., Cryptinae (= Phygadeuontinae), ectoparasitic Pimplinae and Tryphoninae) have smaller numbers, typically 3-6 pairs. Taking the Ichneumonidae as the primary outgroup we consider that fewer than 3 pairs of ovarioles should be considered as apomorphic for the Braconidae. More than 2 pairs of ovarioles may, however, be a secondary development in the Braconidae and therefore this character was not used in rooting the cladograms.

67. Number of mature eggs: 0= generally fewer than 100; 1= generally more than 100. A small number of eggs is generally associated with these being larger, having sequential maturation (synovigeny) and the wasps having an idiobiont life-history strategy. Since idiobionts are believed to be primitive with respect to koinobionts (Gauld & Bolton, 1988) we consider the same to be true of a small number of mature eggs. Further, in the more primitive ichneumonids (e.g., Cryptinae (= Phygadeuontinae), ectoparasitic Pimplinae and Tryphoninae) the number of mature eggs is also small (Iwata, 1960) and therefore we have treated possession of fewer than 100 mature eggs to be plesiomorphic for the Braconidae.

68. Venom gland reservoir: 0= thin-walled with little muscle, uninnervated (type II; fig. 124); 1= thick-walled, highly muscular, innervated (type I; fig. 119). References: Togashi (1963); Robertson (1968); Edson & Vinson (1979); Edson et al., (1982); Maetô (1987). See remark under "Results".

69. Venom gland reservoir: 0= undivided (figs. 123, 124); 1= divided into two or more parts in most members of taxon (fig. 122). The venom gland reservoir is not divided in any of the Ichneumonidae studied to date (Togashi, 1963) and therefore we consider an undivided reservoir to represent the plesiomorph condition for the Braconidae.

70. Cuticular lining of venom gland reservoir: 0= smooth (figs. 119, 124); 1= spirally ridged (figs. 120, 123). There appears to be no evidence of obviously spirally ridged linings of the venom gland reservoirs in the Ichneumonidae (Togashi, 1963) and therefore we consider spiral ridging in some Braconidae to be apomorphic. See Beard (1971) for a functional interpretation.

71. Venom glands: 0= tubular and broadly joined to reservoir or primary duct (fig. 120); 1= globular or sub-globular (i.e., with distinct, narrow, non-glandular branched ducts leading to reservoir or primary duct; fig. 119)). Venom glands in the Ichneumonidae and homologous glands in the Symphyta are tubular and broadly attached to the reservoir (Togashi, 1963; Robertson, 1968) and therefore we consider this to be the plesiomorph condition for the Braconidae.

72. Venom glands: 0= branched (fig. 57); 1= unbranched. The venom glands of nearly all ichneumonids studied to date are branched (Togashi, 1963) as are the homologous glands of the Symphyta (Robertson, 1968) and therefore we consider this to be the plesiomorph condition for the Braconidae.

73. Insertion of venom gland(s): 0= apical (anterior; fig. 120); 1= medial (fig. 119); 2= basal (posterior) or on primary duct (figs. 122-124). [Ordered.] The venom glands of nearly all ichneumonids studied to date insert apically or sub-apically on the reservoir (but basally in the tryphonine genus *Netelia* Gray) (Togashi, 1963) and we therefore consider basal insertion as being a more derived state than a medial or sub-apical one in agreement with Robertson (1968).

74. Insertion of venom gland(s) (or venom gland duct(s)) on to reservoir: 0= single; 1= multiple. In the ichneumonids studied by Togashi (1963) the venom gland filaments arise more or less at a single point on the reservoir; however, in the Symphyta, which generally have more gland filaments, the insertions form a more or less confluent patch. We therefore consider that a single insertion should be considered as plesiomorphic for the Braconidae.

75. Dorsal ovipositor valve: 0= with a mid-longitudinal septum (figs. 7-9, 11-19); 1= without a mid-longitudinal division (figs. 10, 20-44). The upper valves are separate in less derived Symphyta (e.g., Tenthredinidae) and, although fused, are mid-longitudinally divided (except at the extreme apex) in the Stephanidae and many Ichneumonidae. We therefore consider the absence of a mid-longitudinal septum as apomorphic. The fused dorsal cavities in *Hormius* and in *Gnamptodon* (figs. 10, 20) may be independently acquired autapomorphies. However, it should be noted that the ovipositor of *Gnamptodon* is extremely short (and to a lesser degree also that of *Hormius*) and therefore, there is a possibility that the sections obtained here missed any remaining and much shortened septem (Quicke et al., in prep.).

76. Dorsal ovipositor valve: 0= less deep medially than submedially; 1= deeper medially than submedially. In most ichneumonids, and in particular in the less derived subfamilies Cryptinae (= Phygadeuontinae), Pimplinae, and most Tryphoninae, the dorsal ovipositor valves are largely divided medially and therefore we take that to be the plesiomorph condition for the Braconidae.

77. Dorsal ovipositor valve: 0= straight or weakly concave ventrally; 1= distinctly concave ventrally (figs. 18, 21, 22, 24-28). Upper valve of ovipositor is usually weakly concave (though often medially cleft) in the Ichneumonidae (e.g., Pimplinae) and therefore we consider a distinctly concave valve the apomorph condition.

78. Egg-tube: 0= closed medio-dorsally by ventral ovipositor valves (figs. 7-12, 16, 17); 1= medio-dorsally bordered by dorsal ovipositor valve (figs. 13, 15, 21-36). In most ichneumonids and in particular in the less derived subfamilies Cryptinae (= Phygadeuontinae), Ichneumoninae, Pimplinae, and most Tryphoninae, the egg-tube is closed dorsally by the lower ovipositor valves and therefore we take this to be the

plesiomorph condition for the Braconidae.

79. Valvilli (if present): 0= located near to apex of ovipositor (figs. 89, 91, 97); 1= located more or less medially or basally (figs. 90, 93, 95, 96). The one or more valvilli in less derived subfamilies of Ichneumonidae (e.g., Pimplinae, Cryptinae (= Phygadeuontinae), and Tryphoninae) are located close to the apex of the ovipositor and therefore we take this to be the plesiomorph condition for the Braconidae.

80. Number of valvilli on each ventral ovipositor valve: 0= 2 (or rarely 3 or 4) valvilli (figs. 89, 90, 93, 95; Quicke et al., in prep.: Cheloninae may have up to 4 valvilli); 1= 1 valvillus (figs. 91, 94, 96, 97); 2= none (fig. 83). [Unordered.] Many less derived Ichneumonidae (e.g., Cryptinae (= Phygadeuontinae), Pimplinae, and Tryphoninae) have two valvilli (Quicke et al., in prep.), though there are exceptions with reduced numbers in all cases. The only other Hymenoptera with valvilli are certain members of the Aculeata, which have two closely opposed valvilli. Therefore, we consider the possession of two valvilli plesiomorphic for the Braconidae; both the possession of a single valvillus and the complete absence of valvilli should be treated as apomorph conditions. The function(s) of the valvilli is as yet unclear, and therefore, we treat this character as unordered.

81. Larval antennae: 0= papilliform (fig. 59); 1= disc-shaped or absent (fig. 60). Reference: Čapek (1970).

82. Larval mandibles: 0= toothed (fig. 59); 1= smooth. Reference: Čapek (1970).

83. Larval mandible blade length: 0= approximately equal to basal width of mandible (fig. 59); 1= considerably longer than basal width of mandible (fig. 60). Both Capek (1970) and van Achterberg (1988b) considered long mandibular blades to be plesiomorphic for the Braconidae. However, larvae of virtually all Ichneumonidae studied have a short mandible blade (Beirne, 1941), and therefore taking the Ichneumonidae as the primary outgroup we are treating short blades as plesiomorphic.

84. Larval mandibles: 0= simple (figs. 59, 60); 1= apically bifid. Ichneumonid larvae generally have simple mandibles (Beirne, 1941; Gerig, 1960; Short, 1978) and therefore we consider this to be plesiomorphic for the Braconidae.

85. Larval epistome: 0= complete (fig. 59); 1= incomplete or absent. Reference: Capek (1970).

86. Larval first thoracic spiracle: 0= in first segment (posterior part; fig. 126); 1= in second segment (anterior part). The thoracic spiracle in the ichneumonid larvae studied by Gerig (1960) is sited in the posterior part of the first thoracic segment and therefore we consider this to be the plesiomorph state for the Braconidae.

87. Larval post-ventral tracheal commissure: 0= present; 1= absent. Polarity uncertain.

88. Larval ventral abdominal tracheal commissures: 0= present; 1= absent. Polarity uncertain.

89. Larval (first instar) caudal vesicle: 0= absent (fig. 126); 1= present. Most ichneumonid larvae have an elongate tail but do not have a caudal vesicle as found in some braconids (Thorpe, 1932); *Banchus* Fabricius may be an exception. Therefore we consider the presence of a caudal vesicle to be apomorphic in the Braconidae.

90. Biology: 0= ectoparasitic; 1= endoparasitic. References: Askew & Shaw (1986); Gauld (1988); van Achterberg (1988b). See also character 95.

91. Pupation site: 0= outside of host; 1= inside of host. Reference: van Achterberg (1988b). See also character 95.

92. Host: 0= larval Coleoptera; 1= others. References: van Achterberg (1984a); Gauld (1988).

93. Host: 0= immature insects; 1= adult insects. References: van Achterberg (1984a, 1988b); Gauld (1988).

94. Emergence hole from cocoon: 0= irregular (ragged-edged; fig. 129); 1= regular (straight-edged, with or without a cap; figs. 127, 128). Polarity uncertain, but most ichneumonids have ragged-edged ones and likely to be the plesiomorphic state.

95. Final ectoparasitic feeding phase: 0= entirely ectoparasitic or endoparasitic with a final ectoparasitic feeding phase; 1= endoparasitic with no final externalized feeding phase. Reference: van Achterberg (1984a). Together with characters 90 and 91 these characters may have to be re-defined, with particular emphasis to the behaviour of the final instar larvae. Feeding may be absent in the final larval instar of endoparasites, as in the Euphorinae (including Meteorini) and many Microgastrinae, but the larvae emerge from the host allowing for formation of specialized cocoons (M.R. Shaw, personal communication).

96. Number of larval instars: 0= 5; 1= fewer than 5 (usually 3 but 4 in some Alysiinae, Opiinae, Macrocentrinae, Euphorinae and Microgastrinae). The number of larval instars in the Ichneumonidae is typically 5 (see for example, Gerig, 1960; Gauld & Bolton, 1988) and therefore we consider this to be the plesiomorph number for the Braconidae.

Results

The best of the cladograms obtained from both the Hennig86 and PAUP analyses (in terms of parsimony and resolution) are presented in figs. 1-6. For the Hennig generated trees we have illustrated a consensus tree based on 15 trees obtained without weighting, that was fully resolved up to the asterisk (fig. 1). In order to resolve beyond that point the lengths of the 15 trees were recalculated using the weights of set 2 (table 4). This resulted in five maximally parsimonious trees, which again differed from the consensus tree only in the part beyond the asterisk (fig. 2). Arbitrarily fig. 2A has been chosen because it minimizes the number of required losses of hindwing vein 2-CU (character 40). Fig. 2E is also of interest because of the position of the Meteorideinae near the Euphorinae-lineage (both have dorsope in common, absent in the other lineage). However, the position of the Sigalphinae closer to the Homolobinae (figs. 2B-D) seems unlikely because of the general features of the venation and because of the presence of subpronopes.

Figs. 3-6 show trees generated using PAUP, fig. 3 shows the best tree obtained without weighting; the tree given in fig. 4 is slightly longer but nevertheless shows an interesting solution. Figs. 5 and 6 show the most parsimonious trees obtained using weight sets 1 and 2, respectively. We have not presented any consensus-tree of the parsimonious trees generated with the PAUP programme because these displayed many unresolved parts and therefore are comparatively uninformative.

As the PAUP generated trees were rooted using an "outstates" statement and their lengths do not include an "ancestor" they appear at first sight to be shorter than the Hennig86 trees, whose lengths are calculated to include an ancestor. In order to

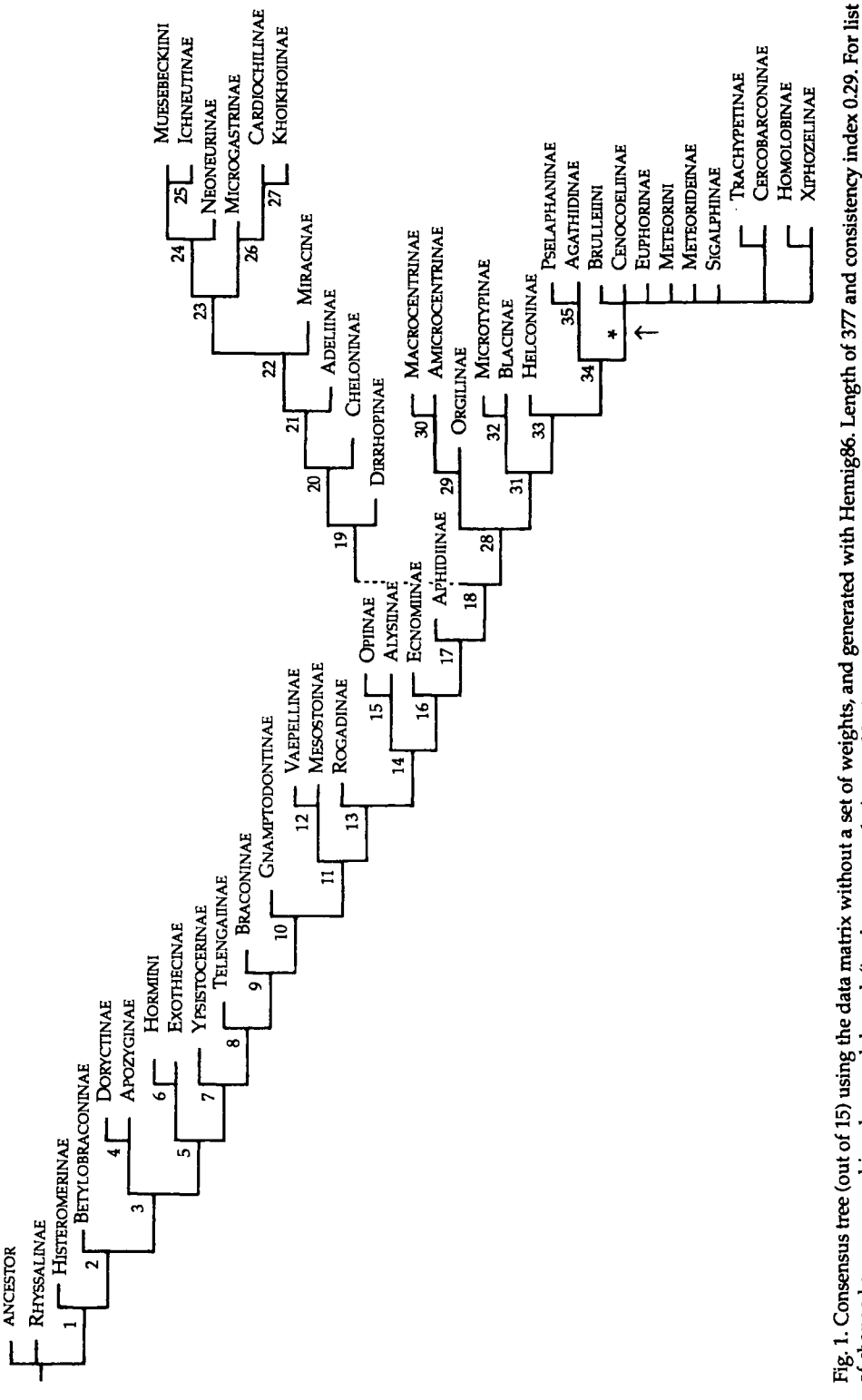

Fig. 1. Consensus tree (out of 15) using the data matrix without a set of weights, and generated with Hennig86. Length of 377 and consistency index 0.29. For list of changed synapomorphies along each branch (i.e., between nodes), see table 6.

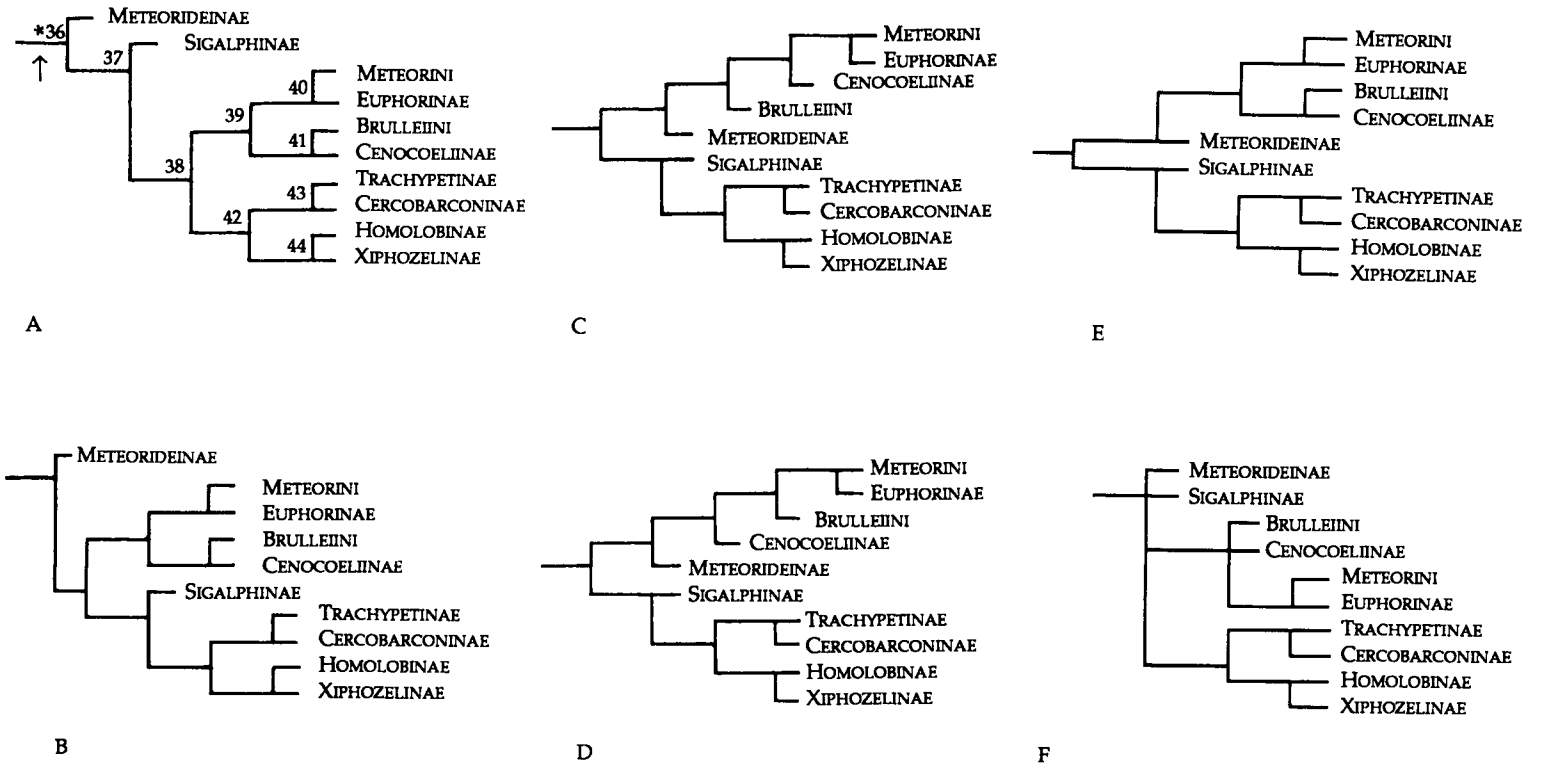

Fig. 2. A-E are parts of the consensus tree fig. 1 behind asterisk resolved with Hennig86 and using the second set of weights (table 4). Total length of the resulting five parsimonious trees (including the resolved part of fig. 1) is 491. Weighting did not affect resolved part of tree of fig. 1. F is consensus tree of A-E.

Table 6. Apomorphy list of fig. 1+2A. The acquired synapomorphies at each node are listed; r= reversal; (r)= partial reversal; T1= first metasomal tergite, etc.; S1= first metasomal sternite, etc.

Node	characters changed to apomorphous state
1	47 (dorsope present); 64 (accessory gland elongate); 79 (valvilli located more or less medially or basally)
2	60 (basal ring of male genitalia moderately thickened); 76 (dorsal ovipositor valve deeper medially than submedially); 80 (one valvillus); 8r (hypostomal carina linked with neck strut); 52r (spiracle of T2 in epipleuron)
3	9 (margin of foramen magnum completely reduced); 73 (venom gland insertion basal or on primary duct); 79r (valvilli located near apex of ovipositor)
4	16 (anterior subalar depression smooth); 39 (hindwing m-cu absent); 48 (T1 tubular basally); 60 (basal ring of male genitalia strongly elongate); 63 (vas deferens absent or nearly so)
5	6 (occipital carina incomplete); 14 (prepectal carina absent); 59 (parameres very short); 92 (non-coleopterous host)
6	72 (venom glands unbranched); 79 (valvilli located more or less medially or basally); 9(r) (margin of foramen magnum reduced ventrally); 64r (accessory glands ovoid or sub-oval); 70r (cuticular lining of venom gland reservoir smooth)
7	6 (occipital carina absent); 10 (mid-propleural carina absent); 11 (propleural flange absent); 90 (endoparasitism occurs)
8	30 (forewing 2-SR+M longitudinal); 53 (T3 with antero-lateral grooves); 55 (S8 of male simple); 69r (venom gland reservoir undivided)
9	39 (hindwing m-cu absent)
10	91 (pupation inside host or host cocoon); 95 (external feeding phase after endoparsitism); 10r (mid-propleural carina present); 88r (larval ventral abdominal tracheal commissures present)
11	82 (larval mandible smooth); 85 (larval epistome incomplete or absent; 9r (margin of foramen magnum complete); 53r (T3 without antero-lateral grooves); 60r (basal ring of male genitalia short)
12	5 (epistomal suture partly reduced); 10 (mid-propleural carina absent)
13	81 (larval antenna disc-shaped or absent); 11r (propleural flange present)
14	52 (T2 spiracle in epipleuron); 61 (testes separate or fused ventral to gut); 96 (larval instars fewer than 5); 2r (labrum flat and largely setose); 57r (cuspidal process absent or very reduced); 70r (venom gland reservoir with smooth cuticular lining)
15	9 (margin of foramen magnum completely reduced); 16 (anterior subalar depression smooth); 65 (Hagen's glands with opening on sclerotized part of metasomal tergum 8)
16	25 (forewing second submarginal cell small or absent); 62 (vas deferens anterior inserted on to accessory gland); 72 (venom glands unbranched); 75 (dorsal ovipositor valve without a mid-longitudinal septum); 78 (egg-tube medio-dorsally bordered by dorsal ovipositor valve); 6r (occipital carina present); 14r (prepectal carina present); 59r (parameres well-developed); 64r (accessory gland ovoid or sub-oval); 68r (venom gland thin-walled with little muscle and not innervated); 71r (venom glands tubular and broadly joined to reservoir or primary duct)
17	24 (forewing 1-SR absent); 67 (number of mature eggs more than 100); 37r (forewing 2A present)
18	4 (lacinia much shorter than than galea); 8 (hypostomal carina linked with margin of foramen magnum); 83 (larval mandible blade considerably longer than basal width of mandible); 86 (larval first thoracic spiracle in second segment); 89 (larval caudal vesicle present); 84r (larval mandible simple); 95r (external feeding phase present)
19	22 (forewing marginal cell open); 35 (forewing CU1b absent); 54 (number of metasomal spiracles 5 or fewer); 56 (S8 emarginate medio-posteriorly); 87 (larval post-ventral tracheal commissure absent); 55r (S8 produced medio-anteriorly); 80r (two valvilli present)
20	1 (number of antennal segments frequently fixed); 29 (forewing 3-SR and base of SR1 with angle less than 135°); 45 (hind coxa large); 43r (hindwing plical cell large to medium-sized); 79 (valvilli located more or less medially or basally)
21	37 (forewing 2A absent); 77 (dorsal valve distinctly concave ventrally)

22 1 (number of antennal segments always fixed); 9 (margin of foramen magnum completely reduced); 10 (mid-propleural carina absent); 11 (propleural flange absent); 14 (prepectal carina absent); 43 (hindwing plical cell small); 49 (first metasomal spiracle in epipleuron); 51 (membrane of T1 finally striate); 8r (hypostomal carina separate from foramen carina); 24r (fore wing 1-SR distinct)

23 6 (occipital carina absent); 84 (larval mandible apically bifid); 54(r) (number of metasomal spiracles 6); 56r (S8 more or less straight posteriorly); 91r (pupation outside of host or host cocoon)

24 57 (cuspidal process absent or very reduced); 95 (external feeding phase absent); 49r (first metasomal spiracle in notum); 51r (membrane of T1 smooth); 54r (number of metasomal spiracles 7); 73(r) (venom gland insertion medially)

25 16 (anterior subalar depression smooth); 24 (forewing 1-SR absent); 33 (forewing 1-M curved anteriorly); 68 (venom gland reservoir thick-walled, muscular and innervated); 70 (venom gland reservoir with spirally ridged lining); 91 (pupation inside host or host cocoon); 1r (number of antennal segments variable); 45r (hind coxae medium-sized)

26 3 (glossa bilobed and concave medially); 7 (hypostomal carina absent); 44 (fore tibial spur long); 50 (S1 not divided)); 63 (vas deferens absent or nearly so); 38r (hindwing r present); 84(r) (larval mandible simple)

27 88 (larval first thoracic spiracle in second segment); 1r (number of antennal segments variable); 4(r) (lacinia shorter than galea); 25r (fore wing second submarginal cell large to medium-sized); 37r (forewing 2A present); 46r (hind tibial pegs absent); 86r (larval thoracic spiracle in first segment)

28 8 (hypostomal carina linked with margin of foramen magnum); 66 (two pairs of ovarioles); 91r (pupation outside of host or host cocoon)

29 6 (occipital carina incomplete); 57 (cuspidal process absent or very reduced); 46 (hind tibial pegs present); 73(r) (venom gland insertion medially)

30 94 (emergence hole from cocoon regular); 19r (metasomal junction just above hind coxae); 25r (fore wing second submarginal cell large to medium-sized); 43r (hindwing plical cell large to medium-sized); 46r (hind tibial pegs absent)

31 15 (scutellar depression present posteriorly); 63 (vas deferens absent or nearly so)

32 58 (cuspidal process articulated with volsella)

33 12 (pronope present); 28 (forewing r-m with bulla); 24r (forewing 1-SR reduced); 72r (venom glands branched)

34 87 (larval post-ventral tracheal commissure absent); 40r (hindwing 2-CU present)

35 6 (occipital carina absent); 13 (subpronopes present); 14 (prepectal carina absent); 31 (forewing M+CU1 unsclerotized); 32 (forewing 1-M and m-cu diverging posteriorly); 45 (hind coxae large); 15r (scutellar depression absent posteriorly); 38r (hindwing r present)

36 79 (valvilli located more or less medially or basally; 43r (hindwing plical cell large to medium-sized); 73(r) (venom gland insertion medially)

37 48 (T1 tubular basally); 25r (forewing second submarginal cell large to medium-sized)

38 26 (flexion line oblique, through 2-SR and 2-M); 40 (hindwing 2-CU absent)

39 72 (venom glands unbranched); 92r (coleopterous hosts)

40 35 (forewing CU1b absent); 58 (cuspidal process articulated); 82 (larval mandible smooth); 95 (external feeding phase present)

41 3 (glossa bilobed and concave medially); 19 (metasomal juction rather far above hind coxae); 57 (cuspidal process absent or very reduced); 8r (hypostomal carina separate from margin of foramen magnum); 36r (forewing vein a present); 48r (T1 not tubular basally)

42 68 (venom gland reservoir thick-walled, highly muscular and innervated); 12r (pronope absent)

43 18 (propodeal spiracle slit-shaped); 23 (forewing parastigma elongate); 73 (venom gland insertion basal or on primary duct); 80 (valvilli absent); 20r (forewing costal cell partly present); 30r (forewing 2-SR+M longitudinal); 40r (hindwing 2-CU present); 41r (seven or more hamuli)

44 58 (cuspidal process articulated); 37r (hindwing 2A present); 73r (venom gland insertion apical)

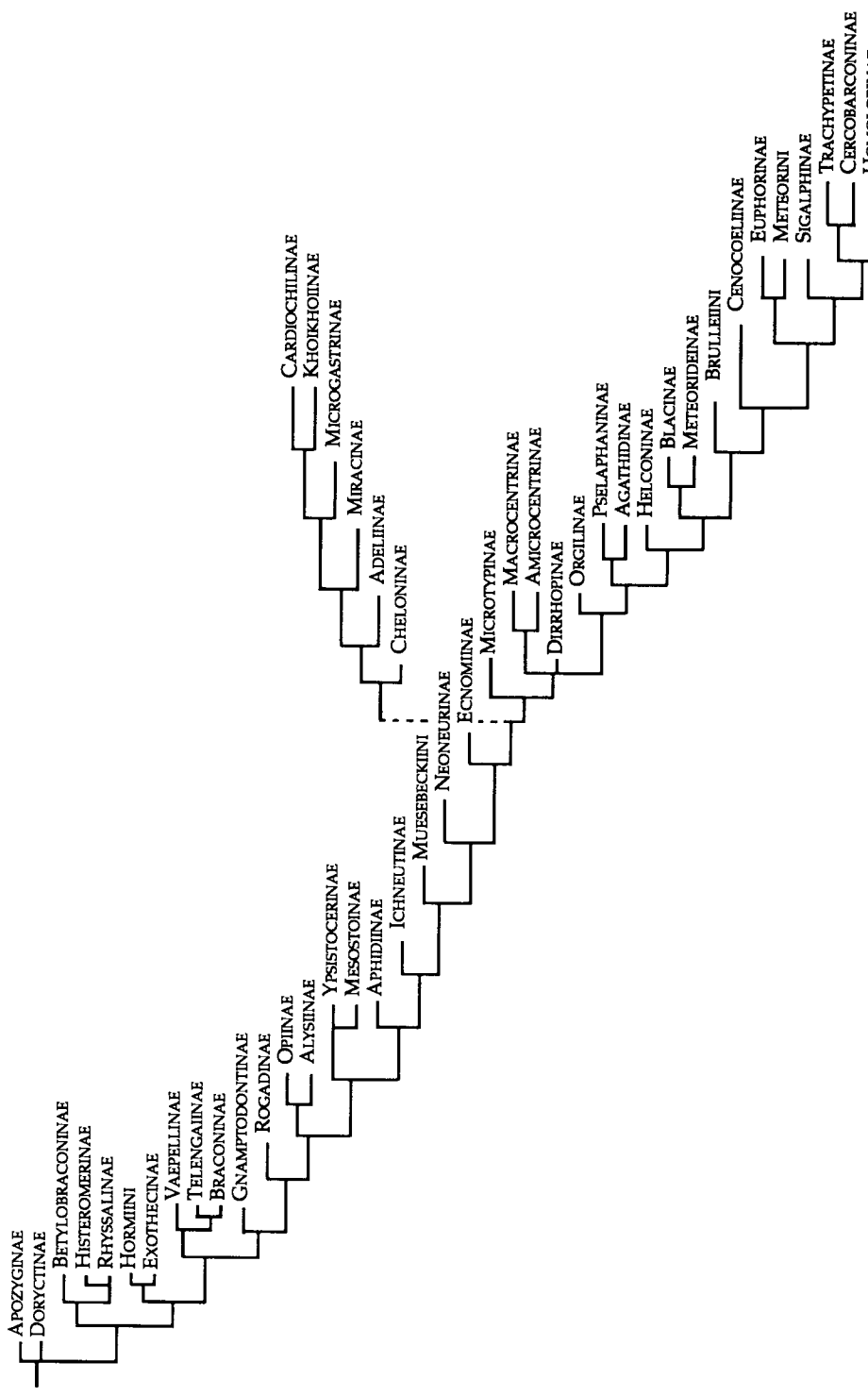

Fig. 3. Shortest tree generated with PAUP using the data matrix without a set of weights. Length of tree 351 and consistency index 0.311.

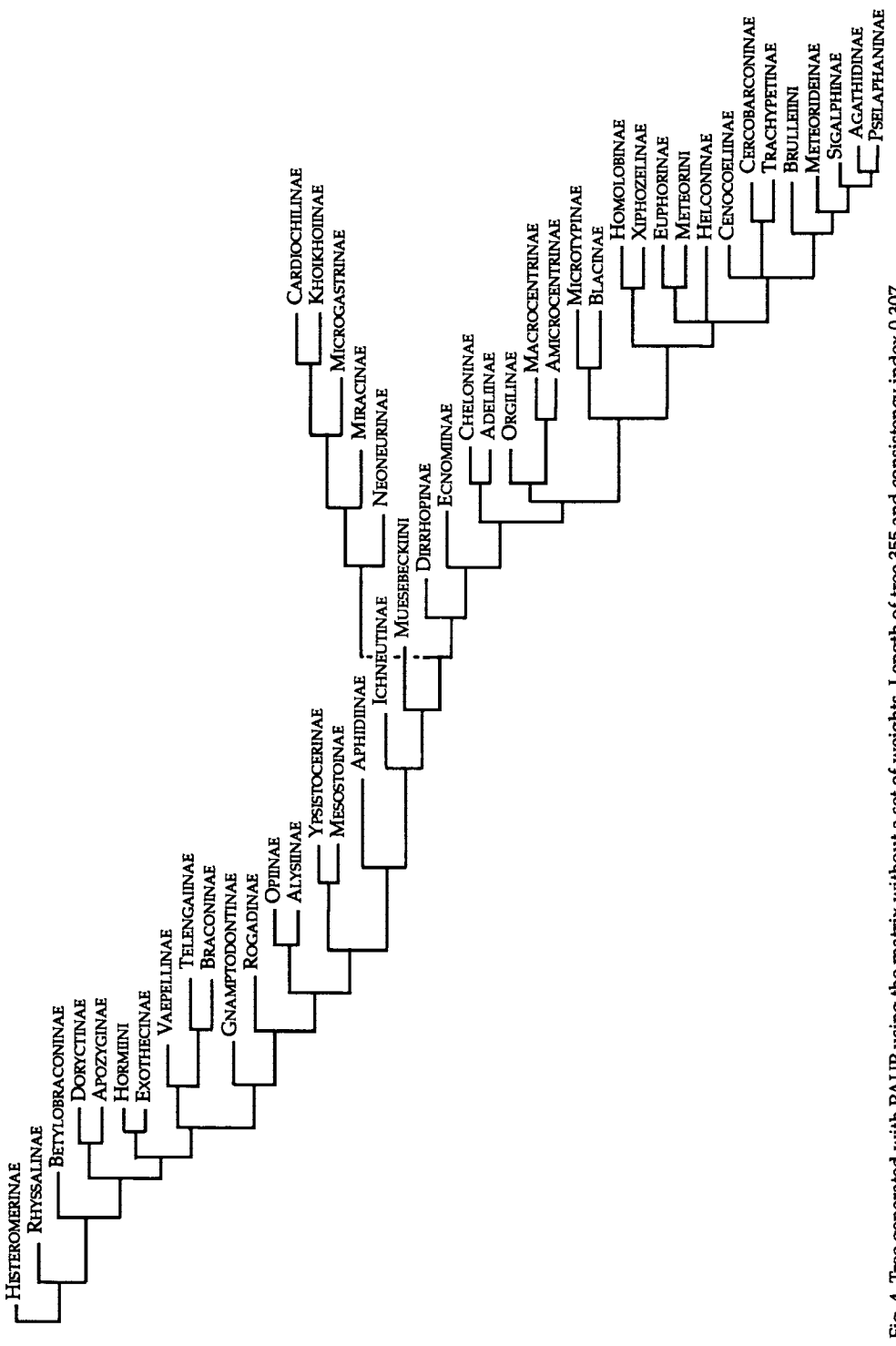

Fig. 4. Tree generated with PAUP using the matrix without a set of weights. Length of tree 355 and consistency index 0.307.

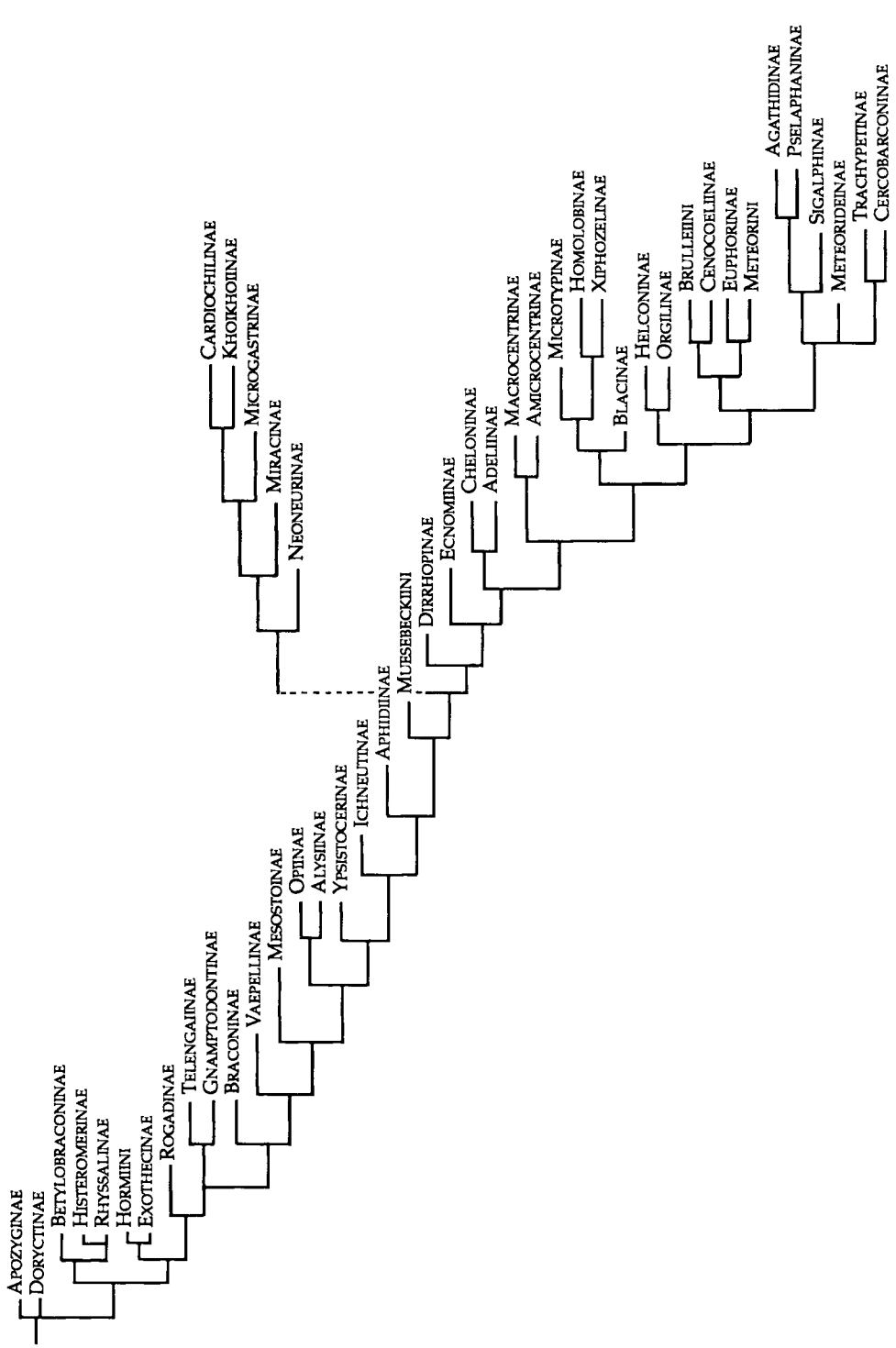

Fig. 5. Tree generated with PAUP using the data matrix with the first set of weights (table 3). Length of tree 466 and consistency index 0.335.

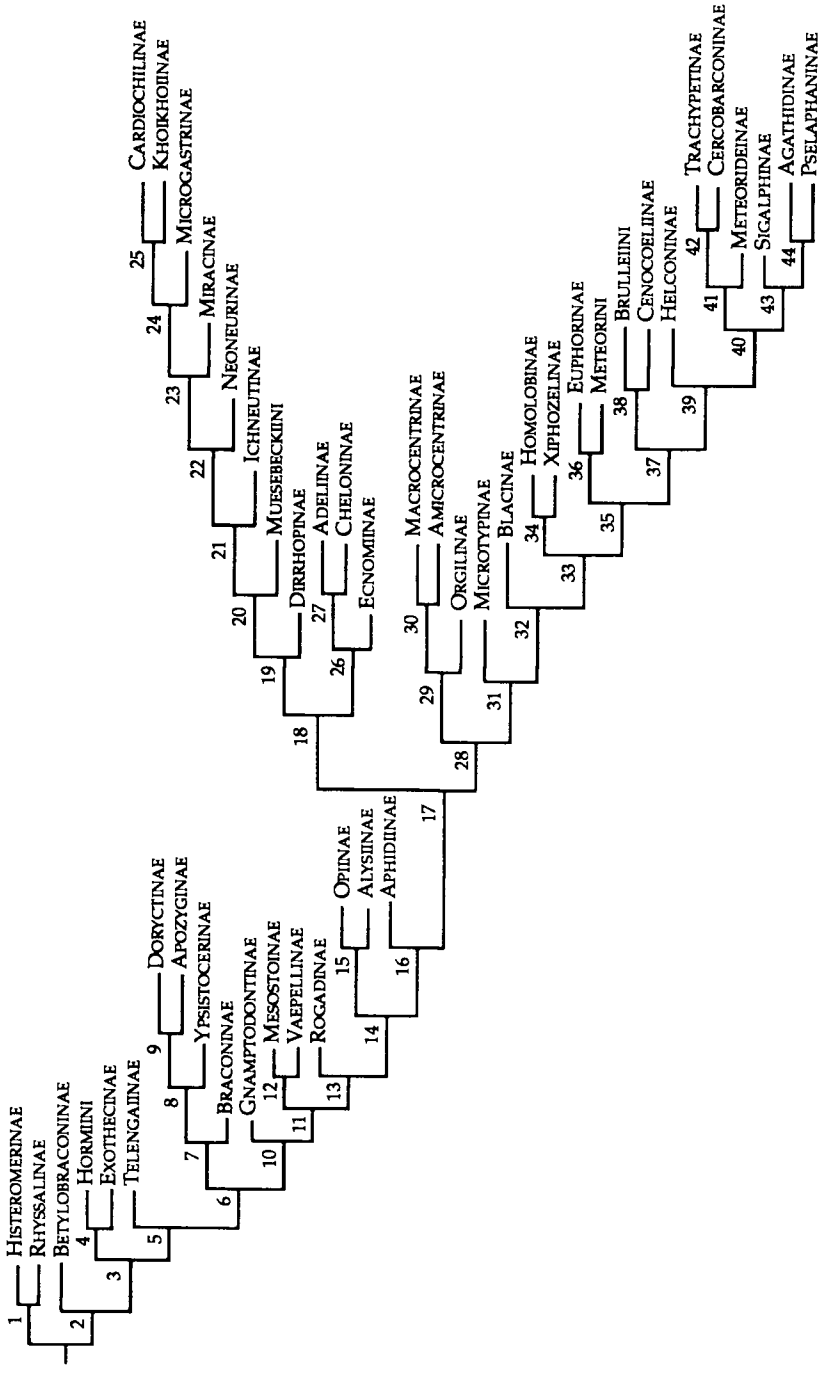

Fig. 6. Tree generated with PAUP using data matrix with the second set of weights (table 4). Length of tree 402 and consistency index 0.333. For list of changed synapomorphies along each branch (i.e., between nodes), see table 7.

Table 7. Apomorphy list of fig. 6. The acquired synapomorphies at each node are listed; r = reversal; (r)= partial reversal; T1= first metasomal tergite, etc.; S1= first metasomal sternite, etc.

Node	characters changed to apomorphous state
1	no synapomorphies known
2	55 (S8 simple); 60 (basal ring of male genitalia moderately thickened; 80 (one valvillus); 8r (margin of foramen magnum and hypostomal carina linked); 52r (second metasomal spiracle in notum)
3	9 (margin of foramen magnum reduced ventrally); 14 (prepectal carina absent); 59 (parameres very short); 73 (venom gland insertion basal or on primary duct); 76 (dorsal ovipositor valve deeper medially than submedially)
4	72 (venom glands unbranched); 92 (non-coleopterous hosts); 64r (accessory gland ovoid or sub-oval); 70r (venom gland lining smooth)
5	6 (occipital carina completely absent); 9 (margin of foramen magnum completely reduced); 11 (propleural flange absent); 53 (T3 with antero-lateral grooves)
6	16 (anterior subalar depression smooth); 39 (hindwing m-cu absent); 79r (valvilli located near apex of ovipositor)
7	10 (mid-propleural carina absent); 60 (base ring of male genitalia strongly elongate)
8	56 (S8 emarginate medio-posteriorly); 62 (vas deferens insertion anterior); 30r (forewing 2-SR+M transverse); 53r (antero-lateral grooves of T3 absent); 55r (S8 produced medio-anteriorly)
9	48 (T1 tube-shaped basally); 6r (occipital carina complete); 10r (mid-propleural carina present); 11r (propleural flange present); 59r (parameres well-developed)
10	90 (endoparasitic); 91 (pupation inside host or host cocoon); 92 (non-coleopterous hosts); 69r (venom gland reservoir undivided)
11	82 (larval mandibles smooth); 85 (larval epistome incomplete or absent); 53r (antero-lateral grooves of T3 absent); 60r (base ring of male genitalia short)
12	5 (epistomal suture partly reduced); 10 (mid-propleural carina absent); 9r (margin of foramen magnum complete)
13	81 (larval antenna disc-shaped or absent); 11r (propleural flange present)
14	61 (testes separate or fused ventral to gut); 95 (external feeding phase absent); 96 (larval instars fewer than 5); 2r (labrum flat and largely setose); 57r (cuspidal process present)
15	9 (margin of foramen magnum completely reduced); 16 (anterior subalar depression smooth); 65 (Hagen's glands opens on sclerotized part of metasomal T8)
16	24 (forewing 1-SR absent); 52 (second metasomal spiracle in eplipleuron); 62 (vas deferens insertion anterior); 67 (number of mature eggs more than 100); 72 (venom glands unbranched); 75 (dorsal ovipositor valve without septum); 78 (medio-dorsally egg-tube bordered by dorsal valve); 6(r) (occipital carina partly reduced); 9r (margin of foramen magnum complete); 14r (prepectal carina present); 37r (forewing 2A present); 59r (parameres well-developed); 64r (accessory glands ovoid or sub-oval); 71r (venom gland tubular and broadly joined to reservoir or primary duct); 88r (larval ventral abdominal tracheal commissures present)
17	4 (lacinia much shorter than galea); 25 (forewing second submarginal cell small or absent); 83 (larval mandible blade longer than basal width of mandible); 86 (larval first thoracic spiracle in second segment); 89 (larval caudal vesicle present); 16r (anterior subalar depression crenulate); 68r (venom gland reservoir thin-walled, with little muscle and not innervated); 70r (venom gland reservoir lining smooth); 73(r) (venom gland insertion medial); 82r (larval mandible smooth); 95r (external feeding phase present)
18	35 (forewing CU1b absent); 87 (larval post-ventral tracheal commissure absent); 55r (S8 produced medio-anteriorly); 80r (two or more valvilli)
19	6 (occipital carina absent); 10 (mid-propleural carina absent); 22 (forewing marginal cell open); 57 (cuspidal process absent or very reduced); 77 (dorsal ovipositor valve distinctly concave ventrally); 79 (valvilli located more or less medially or basally)
20	11 (propleural flange absent); 14 (prepectal carina absent); 29 (forewing angle between 3-SR and SR1 less than 135°); 37 (forewing 2A absent); 82 (larval mandibles smooth)

21 9 (margin of foramen magnum completely reduced); 24r (forewing 1-SR distinct)

22 1 (number of antennal segments always fixed); 45 (hind coxae large); 94 (emergence hole regular); 28(r) (forewing r-m with bulla); 91r (pupation outside host or host cocoon)

23 49 (first metasomal spiracle in epipleuron); 51 (membrane of T1 striate); 54 (number of metasomal spiracles 6); 63 (vas deferens absent or nearly so); 73 (venom gland insertion basal or on primary duct); 57r (cuspidal process present)

24 3 (glossa bilobed and concave medially); 7 (hypostomal carina absent); 44 (fore tibial spur long); 50 (S1 not divided); 84 (larval mandibles bifid apically); 38r (hindwing r present)

25 88 (larval ventral abdominal tracheal commissures absent); 1r (number of antennal segments variable); 4(r) (lacinia shorter than galea); 25r (forewing second submarginal cell large to medium-sized); 37r (fore wing 2A present); 46r (hind tibial pegs absent); 86r (larval first thoracic spiracle in first segment); 94r (emergence hole irregular)

26 6r (occipital carina complete); 43r (hindwing plical cell large to medium-sized)

27 1 (number of antennal segments fixed in many members); 29 (forewing angle between 3-SR and base of SR1 less than 135°); 45 (hind coxa large); 54 (humber of metasomal spiracles 5 or fewer); 56 (S9 emarginate medio-posteriorly)

28 8 (hypostomal carina linked with margin of foramen magnum); 66 (two pairs of ovarioles); 91r (pupation outside of host or host cocoon)

29 6 (occipital carina reduced); 46 (hind tibial pegs present); 57 (cuspidal process absent or very reduced)

30 94 (emergence hole regular); 19r (metasomal junction just above hind coxae); 25r (forewing second submarginal cell large to medium-sized); 43r (hindwing plical cell large to medium-sized); 46r (hind tibial pegs absent)

31 15 (scutellar depression present); 58 (cuspidal process articulated); 63 (vas deferens absent or nearly so)

32 79 (valvilli located more or less medially or basally); 28(r) (forewing r-m with one bulla)

33 26 (flexion line oblique, through 2-SR and 2-M); 24r (forewing 1-SR present); 25r (forewing second submarginal cell large to medium-sized); 43r (hindwing plical cell large to medium-sized)

34 42r (hindwing 2A present); 68 (venom gland reservoir thick-walled, highly muscular and innervated); 72r (venom glands branched); 73r (venom gland insertion apical)

35 12 (pronope present); 92r (coleopterous hosts)

36 35 (forewing CU1b absent); 48 (T1 tubular basally); 82 (larval mandibles smooth); 87 (larval post-ventral tracheal commissures absent); 95 (external feeding phase absent)

37 3 (glossa bilobed and concave medially); 58r (articulation of cuspidal processes absent)

38 19 (metasomal junction (rather) far above hind coxae, but intermediate in Brulleiini); 57 (cuspidal process absent or very reduced); 8r (hypostomal carina separate from margin of foramen magnum); 36r (forewing vein a present)

39 73 (venom gland insertion basally or on primary duct; 26r (flexion line tranverse); 72r (venom glands branched); 79r (valvilli located near apex of ovipositor)

40 92 (non-coleopterous hosts); 40r (hindwing 2-CU present)

41 80 (valvilli absent; unknown for Meteorideinae); 91 (pupation inside host or host cocoon); 95 (external feeding phase absent); 83r (larval mandible blade about equal to basal width of mandible); 85r (larval epistome complete)

42 18 (propodeal spiracle slit-shaped); 23 (forewing parastigma elongate); 48 (T1 tubular basally); 68 (venom gland reservoir thick-walled, highly muscular and innervated); 12r (pronope absent); 20r (forewing costal cell present); 30r (forewing 2-SR+M transverse); 41r (seven or more hindwing hamuli)

43 13 (subpronope present); 27 (forewing m-cu with bulla); 32 (forewing 1-M and m-cu diverging posteriorly); 45 (hind coxa large)

44 6 (occipital carina reduced); 14 (prepectal carina absent); 31 (forewing M+CU1 unsclerotized); 43 (hindwing plical cell small); 15r (scutellar depression absent); 38r (hindwing r present)

permit direct comparison of lengths we entered the topology of the Hennig86 generated trees into PAUP using a topology statement and an "ancestor" was included. The lengths of all trees presented here, as calculated by PAUP, are given in table 5. For each tree, the lengths were calculated with and without an "ancestor" and for both of these, with no differential weights (i.e. WEIGHTS UNITY), with weights set 1 and with set 2 (tables 3, 4).

Table 5. Lengths of cladograms depicted in figs. 1+2A, 3-6 measured with PAUP. The shortest tree per series is indicated by an asterisk. In brackets the consistency index is given.

A. With "ancestor" included			
Cladogram	no weigths	with weights set 1	with weights set 2
Fig. 1+2A	366 * (0.298)	491 (0.318)	429 (0.312)
Fig. 3	371 (0.294)	493 (0.316)	431 (0.311)
Fig. 4	373 (0.292)	492 (0.317)	430 (0.312)
Fig. 5	378 (0.288)	491 (0.318)	431 (0.311)
Fig. 6	369 (0.295)	483 * (0.323)	423 * (0.317)
B. With "ancestor" excluded			
Fig. 1+2A	349 * (0.312)	471 (0.331)	410 (0.327)
Fig. 3	351 (0.311)	470 (0.332)	410 (0.327)
Fig. 4	355 (0.307)	471 (0.331)	410 (0.327)
Fig. 5	357 (0.305)	466 (0.335)	408 (0.328)
Fig. 6	350 (0.311)	460 * (0.339)	402 * (0.333)

Interestingly, the Hennig86 tree (fig. 1+2A) was shorter than that found with PAUP working on the same unweighted data; though, ofcourse the construction of the PAUP trees, unlike the Hennig ones, did not involve an ancestor. Further, the trees found by PAUP both using no weights (fig. 3) and using weights set 1 (fig. 5) were longer than those obtained by running the data with weights set 2 (fig. 6), and then measuring than either the resulting cladograms without weights or with weights set 1, respectively (table 5). These findings highlight the problems of finding the maximally parsimonious trees for large data sets and show that it can be very profitable to try a number of different approaches, programmes, starting points, or weighting systems. Of the two cladograms that ought to be preferred on the grounds of parsimony (figs. 1+2a and 6), the one shown in fig. 6 fits better in several respects with present ideas of the junior author. Among those features that seem to make good sense are the placement of the Sigalphinae with the Agathidinae and the Pselaphaninae, the Ecnomiinae near the Cheloninae, the Braconinae close to the Doryctinae, and the more basal placement of the Homolobinae and the Xiphozelinae (as compared with their positions in fig. 1).

Significantly, large parts of the two preferred cladograms (figs. 1+2A, 6) are similar, and many of the differences involve the positions of a number of small and aberrant groups such as Telengaiinae, Ypsistocerinae, Ecnomiinae, and Ichneutinae (including Muesebeckiini) for which large parts of the data matrix are unknown. Major differences concern the positions of the Braconinae, the Agathidinae + Pselaphaninae, and the Homolobinae + Xiphozelinae. Obviously, additional characters are necessary for a more secure placement of these groups. The other cladograms are included to show some interesting solutions; e.g., fig. 3 with the Microtypinae as the

most basal group of the Helconoid lineage and close to the Macrocentrinae. In fig. 4 the Orgilinae are the most basal group of the Helconoid lineage and the Telengaiinae are the sister group of the Braconinae, as in figs. 3 and 5. In fig. 5 the Orgilinae are the sister group of the Helconinae.

A basal placement of the Doryctinae + Apozyginae (figs. 3, 5) is probably incorrect; both are morphologically more derived than the Rhyssalinae or the Betylobraconinae, and are probably close to the Braconinae (fig. 6). The position of the Blacinae is remarkably variable; in fig. 6 it is the sister group of the main part of the Helconoid lineage, in fig. 5 it is the sister group of the Microtypinae + Homolobinae + Xiphozelinae, in figs. 1 and 4 it is the sister group of the Microtypinae and in fig. 3 the sister group of the Meteorideinae (as suggested in van Achterberg, 1988a). Judging from the position of the valvilli in the ovipositor the Blacinae are not closely related to the Microtypinae as showed in figs. 3 and 6. Important is the placement of the Agathidinae + Pselaphaninae. In two cladograms (figs. 5, 6), and to a lesser degree in a third (fig. 4), it is placed with the rest of the Braconidae with vein 2-CU of hindwing present (Sigalphinae to Trachypetinae). The development of vein 2-CU of hindwing is obviously a reversal (thus a synapomorphy for this group); in this group there is a strong tendency to develop a subpronope and all are (as far as is known) koinobiont endoparasites of larvae of Lepidoptera. The clustering as in fig. 2 is less parsimonious for the characters mentioned above.

The computer-generated cladograms agree in several aspects with the handmade cladogram published in 1984 (van Achterberg, 1984a). The main difference is the placement of the Helconoid and Microgastroid lineages at the end of the "cyclostome" lineage (thus not as a (nearly) basal trifurcation as suggested in the 1984-cladogram). However, our analyses may have given undue emphasis to endoparasitism (characters 90 and 95), because most probably ectoparastism partly evolved towards complete endoparasitism (separately in the Rogadinae and Opiinae + Alysiinae, and partly towards endoparasitism with a final ectoparasitic phase in the Helconoid + Microgastroid lineages (van Achterberg, 1988b; M.R. Shaw, personal communication). Feeding may be absent in the final larval instar of the latter groups, as in the Euphorinae and many Microgastrinae (M.R. Shaw, personal communication). Many additional biological data are given by Shaw & Huddleston (in press). The placement of the Ichneutinae s.l., Adeliinae and Miracinae in the Microgasteroid lineage (figs. 1, 6) fits better in with several discovered characters reported in this paper, e.g., the internal morphology of the ovipositor.

Judging from all the cladograms generated it is obvious that the polarity of character 68 as generally accepted in the literature is incorrect for the Braconidae. The thick walled muscular reservoir of the venom gland (type II of Edson & Vinson, 1979) is plesiomorphic; further it seems to be related primarily to ectoparasitism within the Braconidae. Endoparasitism is generally considered to have evolved from ectoparasitism, and the latter being the plesiomorph state. The thin walled reservoir with little muscle (type I) is the apomorph state in the Braconidae and is probably a result of adaptations involved in becoming koinobiont endoparasites.

Notes on the subfamilies and selected tribes of the family Braconidae

Adeliinae Viereck, 1918

(figs. 24, 95, 152)

A small subfamily characterized by fixation of the number of antennal segments at 20 and by the extreme reduction of forewing vein r. In all of our analyses the Adeliinae appear close to or are the sister group of the Cheloninae in accordance with the generally accepted views. Adeliinae are endoparasites of concealed microlepidopterous larvae (Nepticulidae). Records from Gracillariidae and Eucosmidae are erroneous (M.R. Shaw, personal communication).

Agathidinae Nees, 1814

(figs. 44, 54, 81, 82, 110, 178, 179)

Most agathidines can be recognized by their extremely narrow forewing marginal cell though the condition in *Mesocoelus* Schulz, 1911 is hardly recognizable (Sharkey, 1986; van Achterberg, 1990c). The morphology of the tergal glands on abdominal terga 7 and 8 in males with their medial brush of setae (fig. 110) appears to be diagnostic (Buckingham & Sharkey, 1988). The group is also characterized by the presence of a distinct, pre-apical bulla in the forewing vein m-cu (fig. 179). Several species have a distinct trace of a ramellus from forewing vein r-m and some have a trace of hindwing vein 2r-m though the latter is also to be found in many Microgastrinae and faintly in some Meteorini (e.g., *Zele* Curtis, 1832) and Cardiochilinae (e.g., *Wesmaelella* Spinola, 1853). Some Agathidinae have an articulated cuspidal process on the male genitalia (Tobias, 1967) but this is not true of all genera (e.g., *Coccygidium* Saussure, 1892 and *Braunsia* Kriechbaumer, 1894; fig. 82). In those species with an articulated process it is not slender and does not bear apical teeth. Therefore it seems most likely that the articulated processes found in some agathidines have been acquired independently from those of the Euphorinae group and those found in the Histeromerinae. Agathidinae are solitary endoparasites of larval Lepidoptera; reports of gregarious parasitism may be erroneous (M.R. Shaw, personal communication).

Alysiinae Stephens, 1829

(figs. 19, 70, 80, 111, 148)

The 3-7 toothed mandibles of the adults make the Alysiinae one of the most easily recognisable subfamilies of Braconidae. No other members of the Braconidae with exodont mandibles are known; the monotypic tribe Exodontiellini Wharton, 1977, which has been treated as belonging to the Opiinae (Wharton, 1977, 1988) is considered by the junior author to be a derived member of the Alysiini. Alysiinae are endoparasites of cyclorraphous dipterous larvae.

Amicrocentrinae van Achterberg, 1979

(figs. 31, 49, 50, 162)

Large Afrotropical braconids displaying an ophionoid facies (Gauld & Huddleston, 1976). They display several apomorph characters notable among which are the medio-basal pit on the first metasomal tergite, the large, perpendicularly-setose (reticulately-setose) plical cell of hindwing, the long hind tibia (more than 1.9 times

hind femur length), the distally expanded marginal cell of hindwing, the much reduced labial and maxillary palps, and the lack of any normal trachea separating the larval spiracular atrium and the closing apparatus. Nevertheless, from the analyses presented here they clearly form a sister group to the Macrocentrinae though their ovipositors lack the modifications of the latter. Amicrocentrinae are solitary endoparasites of boring lepidopterous larvae (van Achterberg, 1979a).

Aphidiinae Haliday, 1833
(figs. 21, 22, 113-115, 149)

Although in the past this group has been treated as a separate family there is now virtually universal agreement among braconid workers that they are in fact a specialized group of Braconidae (van Achterberg, 1984a & 1988b). Monophyly of the group is indicated by their biology (endoparasitism of nymphal and adult aphids), the presence of only one pair of ovarioles (Iwata, 1959) and the simple larval spiracles (when present) which are not divided into a distinct atrium and closing apparatus (Capek, 1973). Nevertheless, it should be noted that there are considerable differences in wing venation and ovipositor structure (figs. 21, 22) within the subfamily showing that there has been considerable specialization within the group.

Apozygiinae Mason, 1978
(figs. 98, 104, 106, 107, 141)

Originally the presence of forewing vein 2m-cu in members of the Chilean genus *Apozyx* Mason, 1978 led Mason (1978) to name a new family, the Apozygidae, for its reception. This view was followed by Rasnitsyn & Sharkey (1988). However, the formation of the head (particularly the presence of a hypoclypeal depression and a concave and largely glabrous labrum) and of the metasoma (fusion of tergites 2 and 3) clearly show *Apozyx* to be a cyclostome braconid (M.J. Sharkey, personal communication). The presence of vein 2m-cu in this genus must therefore be considered as a re-expression or even a new development otherwise this vein must almost certainly have been lost independently in two separate braconid lineages. *Apozyx* is unique among the Braconidae in having metasomal sternites 2 and 3 evenly sclerotized and fused (fig. 104). In all of our parsimony analyses the Apozyginae appear as the sister group of the Doryctinae. Nothing is known about the biology of *Apozyx*.

Betylobraconinae Tobias, 1979
(figs. 74, 119, 132)

This subfamily was originally described (Tobias, 1979) on the basis of a highly specialized female of an Australian genus, *Betylobracon* Tobias, 1979. Although *Betylobracon* does not have a distinct hypoclypeal depresson, some more recently discovered genera and species, and males in particular, are clearly cyclostome thus confirming Tobias' original interpretation of its relationships (van Achterberg, in prep.). This has now been verified further through examination of the internal anatomy of *Betylobracon* and the less highly modified genus *Mesocentrus* Szépligeti, 1900, which have "type I" venom gland reservoirs with a spiral cuticular lining (fig. 119). The large fore telotarsus may be convergent with that found in the Ypsistocerinae and may possibly indicate a hypogeic lifestyle. Nothing is known about the biology of

Indo-Australian members of the subfamily; but a provisionally included Nearctic species has been reared from a lepidopterous host (van Achterberg, in prep.).

Blacinae Foerster, 1862

(figs. 34, 164)

As far as we are aware, the Blacinae are not characterized by any autapomorph character state. The biology of Blacinae is poorly known, but the majority are endoparasites of coleopterous larvae. Records of dipterous hosts may be erroneous, but the aberrant Dyscoletini van Achterberg, 1984 are endoparasites of larval Mecoptera (van Achterberg, 1988a).

Braconinae Nees, 1812

(figs. 13-15, 48, 53, 55, 56, 59, 66, 77, 105, 108, 116, 129, 136-138)

A very large, highly diverse and cosmopolitan subfamily. The vast majority of species possess antero-lateral metasomal scent glands which can be evaginated to release a characteristic odour when the wasps are disturbed. Other important apomorphies include the long and proximally expanded vein 1-M of hindwing (though this is not expanded in the Adeshini van Achterberg, 1983), the absence of a lateral propleural carina, and the fused and tubular accessory glands of the males (fig. 55; however, also fused in some Aphidiinae and probably in the Trachypetinae but in these the glands are ovoid). Braconines are principally solitary or gregarious ectoparasites of concealed coleopterous and lepidopterous larvae. However, some genera and species, notably of the Braconini, attack concealed dipterous, symphytan and possibly also gall-forming homopterous larvae (Chadwick & Nikitin, 1976). Many of these hosts are associated with discrete structures such as flowerheads, seedpods and galls. Members of one subtribe of Braconini, the Aspidobraconina van Achterberg, 1984, are endoparasites of exposed butterfly pupae (van Achterberg, 1984a; Quicke, 1987c; Gauld, 1988) though it is not known into what host stage oviposition takes place. The report of ovo-larval parasitism (from label-data of *Aspidobracon* van Achterberg, 1984; van Achterberg, 1984b) is unlikely (unless poly-embryony occurs) because several of the reared species are gregarious. Without doubt though, endoparasitism in this group of Braconinae has evolved independently from that of the other endoparasitic braconids.

Brulleiini van Achterberg, 1983

(fig. 169)

The Brulleiini includes two subtribes, the Brulleiina from the East Palaearctic and Indo-Australian regions and the Pseudohelconina van Achterberg, 1990 from the Afrotropical region (van Achterberg, 1983a & 1990a). They have traditionally been included within the Helconinae; however, the vein m-cu of the forewing is postfurcal (but not or hardly so in the Pseudohelconina), the hind trochanter is (rather) slender, and the fore tarsus is 1.3-2.5 times longer than the fore tibia (but up to 1.5 times in the Helconinae). The position of the Brulleiini is rather uncertain, but since more and more intermediates to the Helconinae s. s. become known (especially in the subtribe Pseudohelconina) it becomes more likely that it cannot be separated by apomorph character states from the Helconinae and thus should remain in that subfamily (van

Achterberg, 1990a). In our analyses the Brulleiini generally appears closer to the Cenocoellinae than to the Helconinae s.s., but the synapomorphies giving rise to this are not particularly strong (tables 6, 7).

Cardiochilinae Ashmead, 1900
(figs. 28, 64, 68, 158)

A rather uniform subfamily dominated by the genus *Cardiochiles* Nees, 1818. In most species the latero-tergites of the first metasomal tergite are not clearly differentiated from the tergum posteriorly (fig. 64; Mason, 1983) (a feature also found in the tribe Proteropinae van Achterberg, 1976 of the Ichneutinae), and vein SR1 of forewing is more or less strongly curved basally. The Cardiochilinae are very closely related to the Khoikhoiinae which Mason (1983) differentiated largely on the basis of the mid-longitudinally grooved first metasomal tergite. However, several species of *Cardiochiles* have an almost equally developed groove (as indeed do many Microgastrinae). Possibly apomorph character states, such as the smooth tubercles in the anterior subalar depression and the secondary edge of the inner side of the scapus, may be sufficient to retain the Khoikhoiinae as a separate subfamily. Cardiochilinae are solitary endoparasites of larval Lepidoptera. In common with the Microgastrinae and Cheloninae the calyx gland secretions of the females wasps contain numerous virus-like particles which are injected into the host larva at the time of oviposition and these particles play an important part in modifying the host's physiology such that the parasite is not overcome by the host's immune system (Stoltz & Vinson, 1979). The Cardiochilinae often have three valvilli per lower ovipositor valve and thus resembling the Cheloninae and Miracinae.

Cenocoeliinae Szépligeti, 1901
(figs. 40, 101, 170)

A very distinctive group that is rather abundant in the Neotropical region but is also widely distributed elsewhere. Characterized by a combination of having the metasoma inserted very high on the propodeum (also shown by members of the tribe Evaniodini Fischer, 1981 of the Doryctinae) and the presence of a complete postpectal carina (elsewhere found only in the Cheloninae, some Euphorinae and Cercobarconinae). Cenocoeliinae are endoparasites of concealed coleopterous larvae.

Cercobarconinae Tobias, 1979
(figs. 57, 86, 174)

A small subfamily of large Australian braconid wasps displaying a typical ophionoid facies (Gauld & Huddleston, 1976). They are characterized by having an extremely elongate propodeal spiracle (even more elongate than in the Trachypetinae). Like the Trachypetinae they have a short, strongly curved, sometimes almost "u"-shaped, ovipositor, have the first three metasomal tergites enlarged, almost concealing the more posterior ones, and have muscularized venom glands reservoirs. Muscularized venom reservoirs occur within the Helconoid lineage futher only in the Homolobinae and Xiphozelinae; together these four subfamilies formed a separate group in the 1984-cladogram (group III; van Achterberg, 1984a). Both subfamilies also appear, on the basis of dissections of rehydrated material, to have peculiar ovaries each formed from two bundles of ovarioles (fig. 125); re-examination of this

feature in fresh specimens would be well worth while. It is doubtful whether the Cercobarconinae and Trachypetinae should be kept distinct at subfamily level and they may be better considered as tribes within a single subfamily. The hosts of the Cercobarconinae are as yet unknown but the short ovipositor and massive, muscular, venom gland reservoir (fig. 57) strongly suggest that they attack an exposed host that needs to be rapidly subdued by envenomation.

Charmontinae van Achterberg, 1979 **stat. nov.**
(fig. 30)

Up to the present the tribe Charmontini van Achterberg, 1979 have been included in the Homolobinae (van Achterberg, 1979c). However, the Charmontini van Achterberg, 1979 (*Charmon* Haliday, 1833) do not fit well with the Homolobinae in that their valvillus is located close to the apex of the lower ovipositor valve, whereas, in the Homolobinae s.s. it is far more removed from the apex (fig. 94). In addition, both *Charmon* and *Charmontia* van Achterberg, 1979 have a longitudinally ridged ovipositor, which is virtually identical to the condition shown by *Macrocentrus* Curtis, 1833 (figs. 29, 30). Together, these features indicate that *Charmon* should be removed from the Homolobinae and placed closer to the Macrocentrinae. However, there are several significant differences between the Charmontini and the Macrocentrinae and thus the former is here raised to subfamily rank. Important differences in this respect are that the Charmontinae have vein 2A of hindwing present, no comb of teeth-like pegs on the trochantelli, vein r-m of forewing absent, occipital carina present, and a lower metasomal junction. Interestingly, Čapek (1970) had already indicated the larval similarities between the genera *Charmon* (as *Eubadizon*) and *Macrocentrus* before the ovipositor features shown in figs. 29 and 30 were discovered here. The Charmontinae are endoparasites of concealed lepidopterous larvae and have thin-walled venom reservoirs with little muscle.

Cheloninae Nees, 1816
(figs. 23, 69, 92, 151)

A large but rather homogeneous subfamily characterized by the combination of having the first three metasomal tergites fused to form a carapace and having a complete postpectal carina (elsewhere only found in the Cenocoeliinae, some Euphorinae and Cercobarconinae). The Chelonines often have as many as four valvilli per valve and in this respect resemble the Miracinae and Cardiochilinae. Cheloninae are solitary, koinobiont endoparasites of lepidopterous larvae. The egg is laid into the host's egg, but development is not completed until the host has nearly completed its own development and often spun its cocoon.

Dirrhopinae van Achterberg, 1984
(fig. 153)

The Dirrhopinae is a small subfamily proposed by van Achterberg (1984a) for the rare, and mainly Holarctic genus *Dirrhope* Foerster, 1851. *Dirrhope* species are endoparasites of larval Nepticulidae (Lepidoptera).

Doryctinae Foerster, 1862
(figs. 11, 12, 67, 78, 140)

The Doryctinae is a very large and heterogeneous subfamily. Most members can be recognized by the presence of a longitudinal row of peg-like setae (chaetobothria; fig. 140) on the fore tibia (also found in Histeromerinae and some Braconinae) in conjunction with a relatively long vein M+CU of hindwing compared with vein 1-M (vein 1-M is always at least twice longer than M+CU in the Braconinae). Similar rows of peg-like setae are also found in several groups of non-braconid Hymenoptera, and it is difficult to know therefore, whether their presence in the Doryctinae (and some Braconinae) should be considered as apomorphic or plesiomorphic and whether they may indicate a close relationship between these two subfamilies, as suggested in fig. 6. The possibility of a close relationship between them is further indicated by the male genitalia of both groups which have particularly elongate basal rings, and by the presence of a highly modified, ventrally elongate, scapus in the Australian doryctine genus *Syngaster* Brullé, 1846 which closely resembles that of many Braconinae. Most Doryctinae are ectoparasites of concealed (wood- or bark-boring) coleopterous larvae. A few genera attack other concealed hosts, notably lepidopterous and dipterous larvae. *Sericobracon* Shaw & Edgerly, 1985 is a parasite of Embioptera (Shaw & Edgerly, 1985). One species of *Heterospilus* Haliday, 1836 is parasitic in sphecid nests and another attacks stem-boring sawfly larvae (Marsh, 1982). There is also evidence that one species at least of the genus *Allorhogas* Gahan, 1912 may be completely phytophagous (de Macedo & Monteiro, 1989).

Ecnomiinae van Achterberg, 1985
(figs. 61, 150)

A monotypic subfamily separated by van Achterberg (1985) to receive the Indo-Australian genus *Ecnomius* Mason, 1979. The group may be recognized by the antero-ventrally protruding pronotal sides and by the very large hindwing plical lobe. The presence of just two pairs of ovarioles with a few large, mature eggs suggests a relationship with the cyclostome group of subfamilies and their relatives such as the Ichneutinae. Knowledge of the larvae and more detailed information on the internal anatomy of both sexes would undoubtedly help considerably with interpretation of the relationships of this group. The biology of *Ecnomius* is unknown but the large eggs strongly suggest that it may be ectoparasitic.

Euphorinae Foerster, 1862 s.s.
(figs. 37, 39, 42, 168)

A large and very heterogeneous subfamily notable for parasitizing adult holometabolous and adults and nymphs of paurometabolous insects (Shaw, 1985, 1988). This subfamily has in the past usually been treated as including the Meteorini Cresson, 1887 q.v. (e.g., van Achterberg, 1979c, 1988b). Shaw (1985) excluded the genus *Zele* Curtis, 1832 from the latter group, leaving only the genus *Meteorus* Haliday, 1835, and considered, not surprisingly, that the Meteorinae is holophyletic and almost certainly the sister group of the Euphorinae s.s. However, Maetô (1990) considered *Zele* and three species groups of *Meteorus* to from a monophyletic group. In our paper both genera are included in the Meteorini and in all trees the Meteorini proved to be the sister group of the Euphorinae s.s. For an extended discussion on this matter see "Meteorini". Euphorinae attack a wide range of host orders (more than any other subfamily of Braconidae) and Shaw (1988) attributes this diversifica-

tion in host utilization to the use, by some species, of larval Chrysomelidae as hosts. Shaw proposes that ancestral euphorines then shifted to using adult chrysomelids living in the same sites as their larvae, and this opened the way to the utilization of adults of other insect orders and finally to nymphs of paurometabolous groups.

Exothecinae Foerster, 1862
(figs. 75, 126, 133)

For remarks on this subfamily, see "Rogadinae".

Gnamptodontinae Fischer, 1970
(figs. 20, 109, 112, 123, 142)

In the past the Gnamptodontinae have been included within both the Opiinae and the Rogadinae (sensu lato). That they should be treated as a separate subfamily was recognized by van Achterberg (1983b). They are immediately identifiable by the presence of a medially straight or curved, peribasal groove on the second metasomal tergite (fig. 142; a similar though medially pointed groove may be present in some Betylobraconinae) though in a few species this has been secondarily lost. The occurrence, in some species, of posteriorly-diverging, antero-lateral grooves on the third metasomal tergite (character 53) suggests an affinity with the Braconinae or Telengaiinae and the presence of a large, bilobed inter-tergal gland between the sixth and seventh metasomal tergites (fig. 109) reinforce the idea of a relationship with the Braconinae. However, the absence of the prepectal carina (character 14) and the basic structure of the Hagen's glands (character 65; fig. 112) may indicate that they belong to the Opiinae/Alysiinae group. Gnamptodontinae are parasites of Nepticulidae larvae; from their hosts' remains they appear to be endoparasites (M. R. Shaw, personal communication) but this has yet to be verified.

Helconinae Foerster, 1862
(figs. 41, 171, 172)

A large and heterogeneous assemblage with a cosmopolitan distribution. The relatively complex wing venation of many species together with the utilization of concealed coleopterous larvae as hosts has led them to be considered as having an origin close to the base of the non-cyclostome lineage. We have been unable to discern any autapomorphy for the Helconinae and it is possible therefore that the group may be paraphyletic. Because of this and because the Brulleiini in particular appear to show affinities with some other groups (van Achterberg, 1979a, 1979b; especially with the Cenocoeliinae, figs. 1-3, 5, 6)) we have treated that group separately in our analysis. As far as is known all Helconinae are endoparasitic koinobionts, and with a few exceptions such as *Calohelcon* Turner, 1918 which may be a parasite of larval Cossidae (Quicke & Holloway, in press), all attack coleopterous larvae.

Histeromerinae Fahringer, 1930
(figs. 7, 47, 52, 58, 62, 73, 90, 102, 103, 121, 130)

This small, highly specialized group, comprising two described Holarctic species and an undescribed one from Papua New Guinea, has previously been associated with both the Doryctinae and the Braconinae (van Achterberg, 1984a). *Histeromerus* Wesmael, 1838 does not display any of the autapomorphies listed above for the

Braconinae and has a dense cluster of thickened setae on the fore tibia rather than a longitudinal row as found in the Doryctinae. Further, the male genitalia have a medially very short basal ring (fig. 73) unlike that of any of the Braconinae or Doryctinae and the venom gland apparatus is completely different (figs. 58, 121). The Histeromerinae are characterized by several autapomorphies notable among which are the highly elongate hind basitarsus and the presence of only two rectal pads (fig. 102; other Braconidae have 4 (fig. 105) except for the braconine genus *Euurobracon* Ashmead, 1900 in which there are usually 12 or more (Quicke, 1989)). Among the cyclostome subfamilies the Histeromerinae are unique in having an articulated cuspidal process on the male genitalia (fig. 73). However, the fine detail of this process differs from that seen, for example, in the Euphorinae, Homolobinae, Meteorinae and Xiphozelinae, and therefore this is almost certainly an example of parallelism (see also van Achterberg, 1988b). Also unique in the Braconidae is the largely separated dorsal valves of ovipositor (fig. 7). Histeromerinae are parasites (probably ectoparasites) of concealed coleopterous larvae including Anobiidae, Cerambycidae, Cisidae, Elateridae, Lucanidae, and Lyctidae.

Homolobinae van Achterberg, 1979
(figs. 35, 45, 94, 99, 165)

The Homolobinae (= Zelinae auct.; van Achterberg, 1979c) are a group that is difficult to characterize with a cosmopolitan distribution. Most species are medium-sized and display an ophionoid facies (Gauld & Huddleston, 1976). The most significant character states appear to be the anterior location of the insertion of the venom glands on to the venom gland reservoir, the thick-walled and rather heavily muscularized venom gland reservoirs, and the presence of an articulated cuspidal process. On the basis of outgroup comparisons we have interpreted the anterior insertion of the venom glands as plesiomorphic, but as no other braconids display this arrangement (and specifically none of the ectoparasitic groups which we believe to be ancestral) this may in fact be a synapomorphy for the Homolobinae + Xiphozelinae. Edson & Vinson (1079) classified the venom gland reservoir as "type 2" (= thin-walled with little muscle and no innervation) under "*Zele*"; "*Zele mellea*" is *Homolobus truncator* (Say) (van Achterberg, 1979c). Repeated examinations of reservoirs of Homolobinae and Xiphozelinae show them to be distinctly more heavily muscularized than those of other members of the non-cyclostome lineage with the marked exception of the Cercobarconinae and Trachypetinae, and we have accordingly classified them as "type 1". It should be noted however, that the latter two subfamilies display a far more extremely muscularized condition than do the Homolobinae and Xiphozelinae. More work on the histology of these systems would no doubt be rewarding. An articulated cuspidal process also links these two subfamilies, and in addition implies links with the Blacinae, Euphorinae, Meteorinae and Microtypinae (also van Achterberg, 1984a). Homolobinae are koinobiont endoparasites of exposed lepidopterous larvae. The formerly included tribe Charmontini van Achterberg, 1979 is given subfamily rank.

Hormiini Foerster, 1862
(figs. 10, 134)

For remarks on this tribe, see "Rogadinae". Included in the subfamily Exothecinae Foerster, 1862.

Ichneutinae Foerster, 1862 s.s.
(figs. 25, 180)

Although a rather small group, the Ichneutinae are particularly interesting because they display a set of characters that appear to be intermediate between those of the principally ectoparasitic cyclostome group of subfamilies and the remaining endoparasitic ones. The most distinctive feature of the subfamily is the strongly curved forewing vein 1-M though this feature is absent in the tribe Proteropini van Achterberg, 1976 and a similarly curved vein is present in the Muesebeckiini Mason, 1969, a group which in the past has been associated with both the Ichneutinae (van Achterberg, 1976, 1984a) and with the Miracinae (previously included in the Microgastrinae). Because of differences in both biology and morphology of the Muesebeckiini from that of the Ichneutinae we have treated that group separately here. Ichneutinae (excluding the Muesebeckiini q.v.) are endoparasites of hymenopterous (symphytan) larvae. The scarcity of Symphyta in the tropics may explain the principally north temperate distribution of the subfamily.

Khoikhoiinae Mason, 1983
(fig. 159)

This is a poorly characterized subfamily, closely related to the Cardiochilinae, q.v. To date the Khoikhoiinae are only known from South Africa. Their biology is unknown.

Macrocentrinae Foerster, 1862
(figs. 29, 161)

This is an easily recognized subfamily because all species have a cluster of toothlike pegs on the trochantellus. Most species are medium-sized to large and many display an ophionoid facies (Gauld & Huddleston, 1976). The group has a cosmopolitan distribution. Macrocentrinae are solitary or gregarious endoparasites of lepidopterous larvae. Some species are polyembryonic.

Mesostoinae van Achterberg, 1975
(fig. 143)

This endemic and highly specialized Australian subfamily is thus far known from only three species (van Achterberg, 1975; Quicke & Huddleston, 1989). They are characterized by the flagellum which is strongly flattened for its whole length and the rather strongly anteriorly protruding mesoscutum. The males of the species known to date are brachypterous. The actual host is unknown but they have been reared from a gall on *Banksia*-shrubs. The highly reduced larval cephalic structures and toothless mandibles strongly suggest that they are endoparasites.

Meteorideinae Čapek, 1970
(fig. 173)

A small, poorly-known subfamily based on the genus *Meteoridea* Ashmead, 1900 and a new genus which will be described soon (van Achterberg, in press). Most

species have a characteristic facies (fig. 173), and have the ovipositor concealed. Usually they are characterized by having the third metasomal sternite very enlarged (Shenefelt, 1957; van Achterberg, 1984a). Members of this subfamily are gregarious endoparasites of Lepidoptera ovipositing into the larva, but emerging as adults from the pupa.

Meteorini Cresson, 1887
(figs. 36, 38, 96, 127, 167)

Shaw (1985) incorrectly excluded the genus *Zele* Curtis, 1832 from his Meteorinae, and included this genus in the Homolobinae. As shown in figs. 94 and 96 both *Homolobus* Foerster, 1862 and *Zele* have a single valvillus situated submedially or subbasally, respectively. In *Meteorus* Haliday, 1835. (not illustrated) the valvillus is also subbasally located and thus resembles *Zele* more than *Homolobus* in this respect. Shaw (1985) claimed the apical thread of the cocoon to be an autapomorphy of the genus *Meteorus*, but it is absent in many *Meteorus* species (e.g., *M. ictericus* (Nees, 1812)). According to Shaw (1985), including *Zele* in the Meteorini leads to a paraphyletic group; whether this is true or not, in our opinion it has to be included and it may indicate the superfluous nature of recognizing a tribe "Meteorini". The characters given by Shaw (1985) to separate the Meteorini as a subfamily from the Euphorinae are firstly the 6-segmented maxillary palp (a plesiomorph character state, which occurs also in several genera of the Euphorinae s.s., as listed in Shaw (1985)). Secondly, regarding the setosity of the metasoma (which is sparse in the Euphorinae s.s.): it is variable as well in the genus *Meteorus* (normally sparse, but males of some species have the tergites extensively setose and in one species from India, this is also so in the females) and *Zele* has the metasoma largely setose. The genus *Eadya* Huddleston & Short, 1978 (included by Shaw in the Euphorinae s.s.) has tergite 3 extensively setose laterally. In general, setosity is a variable character at a higher level (above the level of genera) in nearly all large subfamilies and is a less suitable character to define monophyly of a group. The apical thread of the cocoon (as mentioned above) is also a more variable character, and not suited to characterize the genus *Meteorus*. The Meteorini and Euphorinae s.s. have relatively fewer pairs of ovarioles (only 4-6 pairs) than other related subfamilies (Iwata, 1959). Finally the biology of the Euphorinae s.s. (parasites of adult insects (as far as holometabolous insects concerned), and both nymphs and adults of Heteroptera, Psocoptera and Saltatoria) is less exclusive as suggested by Shaw (1985). E.g., *Eadya* is a parasite of larval Chrysomelidae (Huddleston & Short, 1978), as at least one *Meteorus* species (Shaw, 1988). According to the phylogenetic analysis presented in this paper the Meteorini (including *Zele*) is the sister group of the Euphorinae s.s., and it seems justified to insert this group in the Euphorinae s.s. The possible paraphyletic nature of the Meteorini needs further investigation (Maetô, 1990). The Meteorini are solitary or gregarious, koinobiont endoparasites of lepidopterous and coleopterous larvae.

Microgastrinae Nees, 1814
(figs. 27, 63, 93, 157)

A very large, cosmopolitan group of rather small wasps which includes many economically important species. Members of this subfamily always have 18 antennal segments. Many species also have a trace of hindwing vein 2r-m but this is not

unique to the subfamily. Many characters indicate that the Microgastrinae are the sister group of the Cardiochilinae + Khoikhoiinae. Microgastrinae are solitary or gregarious, koinobiont endoparasites of lepidopterous larvae.

Microtypinae Szépligeti, 1908 **stat. nov.**
(figs. 33, 163)

The genus *Microtypus* Ratzeburg, 1848 has often been placed in the Orgilinae but it was removed from there and included in the Homolobinae by van Achterberg (1984a, 1988b). As a result of the phylogenetic analysis presented here, this group is given subfamily rank; see under "Results" for further remarks.

Miracinae Viereck, 1918
(figs. 26, 65, 124, 156)

A small subfamily comprising the genera *Mirax* Haliday, 1833 and *Centistidea* Rohwer, 1914. Previously *Mirax* was included in the Microgastrinae because the first metasomal spiracle is located in the membranous epipleural area (fig. 65). Members of the Miracinae are distinguishable from the Microgastrinae because they have only 14 antennal segments and they have a distinct postero-ventral area on the pronotum. As in the Cheloninae at least some species have three pairs of valvilli per lower valve. *Mirax* is a parasite of Nepticulidae and Lyonetiidae larvae.

Muesebeckiini Mason, 1969
(fig. 154)

The placement of the Muesebeckiini has yet to be satisfactorily settled. The shape of forewing vein 1-M suggests an affinity with the Ichneutini (Ichneutinae), where they were placed by Mason (1969) and van Achterberg (1976, 1984a), but they differ in that they have lepidopterous rather than hymenopteran hosts and also in several important features of adult and larval morphology. They have been placed with *Mirax* by Nixon (1965) and Tobias (1986). Muesebeckiini are most probably endoparasites of Nepticulidae. The Muesebeckiini are retained in the Ichneutinae because of ambiguous results of the phylogenetic analysis; it may be considered to be the sister group of the Ichneutinae (fig. 1) or at least to be closely related to it (figs. 3-6).

Neoneurinae Bengttson, 1918
(figs. 72, 84, 155)

A small but distinctive group of braconids possessing many autapomorph features. The paraglossa is much enlarged and longer than the glossa (Tobias & Potapova, 1987), the anterior subalar depression has a tubercle, the hind trochantellus is usually not or hardly differentiated from the femur, the forewing often has an additional vein, and the stipital sclerite of the final instar larva is very long and slender (Čapek, 1970). Neoneurinae are endoparasitic within the metasomas of worker ants, a feature which has led some workers to propose a relationship with the Euphorinae (e.g., Tobias, 1967); however, as van Achterberg (1984a) argues, parasitism of adult insects has certainly evolved independently more than once in the Braconidae and many morphological features of the Neoneurinae suggest a relationship with the Microgastroid lineage.

Opiinae Foerster, 1862
(figs. 18, 147)

The Opiinae are a large group, but difficult to characterize. Opiinae appear to be closely related to the cyclostome set of subfamilies, and indeed many species of Opiinae have a distinct hypoclypeal depression though this is somewhat different in form to that found in the Braconinae (Wharton, 1988). No known opiines spin a cocoon in the host puparium. Members of the Opiinae are endoparasites of cyclorraphous dipterous larvae, principally (but not exclusively) of leafminers and those living in fruits.

Orgilinae Foerster, 1862
(figs. 32, 97, 160)

The Orgilinae are quite a small subfamily with apparently no unique defining characters. In the past they have frequently been united with the Agathidinae but van Achterberg (1984a) expressed doubt about this relationship. As treated here the Orgilinae comprise three tribes. There are good grounds for uniting the Orgilini and the Mimagathidini, but the position of the third tribe (Antestrigini van Achterberg, 1987) is less certain (van Achterberg, 1987). The Mesocoeliini which were included provisionally within the Orgilinae by van Achterberg (1984a) were transferred to the Agathidinae (Sharkey, 1986; Buckingham & Sharkey, 1988; van Achterberg, 1990c).

Pselaphaninae van Achterberg, 1985
(fig. 177)

Small Neotropical subfamily, containing only the monotypic genus *Pselaphanus* Szépligeti, 1902. Included in the Agathidinae by van Achterberg, 1985, and given subfamily rank later (van Achterberg, 1990c). It is nevertheless a sister group of the former according to all our analyses. The biology is unknown.

Rhyssalinae Foerster, 1862 **stat. nov.**
(figs. 8, 9, 89, 131)

For remarks on this subfamily, see "Rogadinae".

Rogadinae Foerster, 1862 s.s.
(figs. 16, 17, 91, 145, 146)

The Rogadinae s.l. has usually been interpreted as including a number of cyclostome tribes that differ widely in biology and share few synapomorphies with one-another (van Achterberg, 1984a; Shaw, 1983). The most highly specialized tribes (Rogadini and Spinariini van Achterberg, 1988) are koinobiont endoparasites of lepidopterous larvae and have associated larval adaptations including toothless mandibles and disc-shaped antennae. Other groups of Rogadinae s. l. are idiobiont ectoparasites (e.g., Exothecini Foerster, 1862, Hormiini Foerster, 1862, and Rhyssalini Foerster, 1862). The differences between these groups are such that some tribes have been swapped between the Rogadinae and the Doryctinae. Without doubt, the Rogadinae s. l. do not form a natural group and this is shown clearly by the fact that the Exothecini, Hormiini and Rhyssalini which we treated separately in our analysis, do not appear near to the Rogadinae s.s. As a result of this phylogenetic analysis the Rhyssalinae and Exothecinae (including the Hormiini) are recognized as separate

subfamilies. Obviously more work will be required to sort out the detailed relationships between these various groups.

Sigalphinae Blanchard, 1845
(figs. 43, 46, 83, 175)

In the past this little-known subfamily was placed, mistakenly, in the Cheloninae because of the carapace-like metasomas. However, this is without doubt an example of parallelism (Tobias & Dudarenko, 1974; van Achterberg, 1988b). Despite all members having a somewhat similar appearance, notably in the form of the metasoma and the presence of hindwing vein 2-CU, we are not aware of any autapomorphy. Limited observations on sigalphines indicate that they may oviposit in recently emerged, first instar, lepidopterous larvae; statements that they are ovo-larval parasites appear to be without foundation, resulting only from their past inclusion in the Cheloninae (M. R. Shaw, personal communication).

Telengaiinae Tobias, 1962
(figs. 71, 76, 135)

Known only from the E. Palaearctic genus *Telengaia* Tobias, 1962. It can be recognized by the combination of having the first three metasomal tergites fused and having a wide, elliptically depressed, precoxal sulcus. It lacks any clear synapomorphies with other cyclostome subfamilies except for reductions such as the loss of the occipital and prepectal carinae and the presence of weak antero-lateral, posteriorly-diverging grooves on the third metasomal tergite. The latter suggest an affinity with either the Gnamptodontinae or the Braconinae. Nothing is known about the biology of this subfamily.

Trachypetinae Schulz, 1911
(figs. 51, 88, 100, 125, 175)

This monotypic Australian subfamily is readily characterized by having vein SR1 of forewing abruptly and strongly bent anteriorly near to its middle (fig. 175; Tobias, 1979). It is clearly closely related to the Cercobarconinae q.v., also from Australia, and in all of our analyses these two subfamilies appear together as sister groups. Synapomorphies linking these two include an elongate parastigma and a very elongate propodeal spiracle. The biology is unknown.

Vaepellinae Quicke, 1987
(fig. 144)

This monotypic subfamily from tropical West Africa is characterized by the following combination of characters: the body is covered by a velvet-like setosity, the scapus is long and club-shaped, the ocelli are strongly reduced and the presence of an extensive array of sensillae on the posterior part of the malar space (Quicke, 1987a). The setosity of the body, robust legs and reduced ocelli are probably convergent adaptations to those found in the termitophilous Ypsistocerinae. Tobias (1988) suggests that *Vaepellis* Quicke, 1987 should be regarded as an aberrant braconine, but unlike the Braconinae, it does not have vein 1-M of hindwing much longer than vein M+CU. Nothing is known about the biology of this group.

Xiphozelinae van Achterberg, 1979
(figs. 60, 85, 117, 118, 120, 128, 166)

The Xiphozelinae are characterized by having a deep and round laterope situated far from the base of the first metasomal tergite (van Achterberg, 1979b). They are rather large braconids displaying an ophionoid facies (Gauld & Huddleston, 1976). Xiphozelinae are endoparasites of exposed noctuid larvae.

Ypsistocerinae Cushman, 1923
(figs. 79, 122, 139)

This small, highly specialized group of Neotropical braconids is associated with termite nests though it is not yet known whether or not they actually parasitize the termites or instead attack other inquilines. The relationships of the Ypsistocerinae are difficult to identify because of their numerous autapomorph character states. However, the form of the venom apparatus (fig. 122) suggests that they may be closely related to the Doryctinae.

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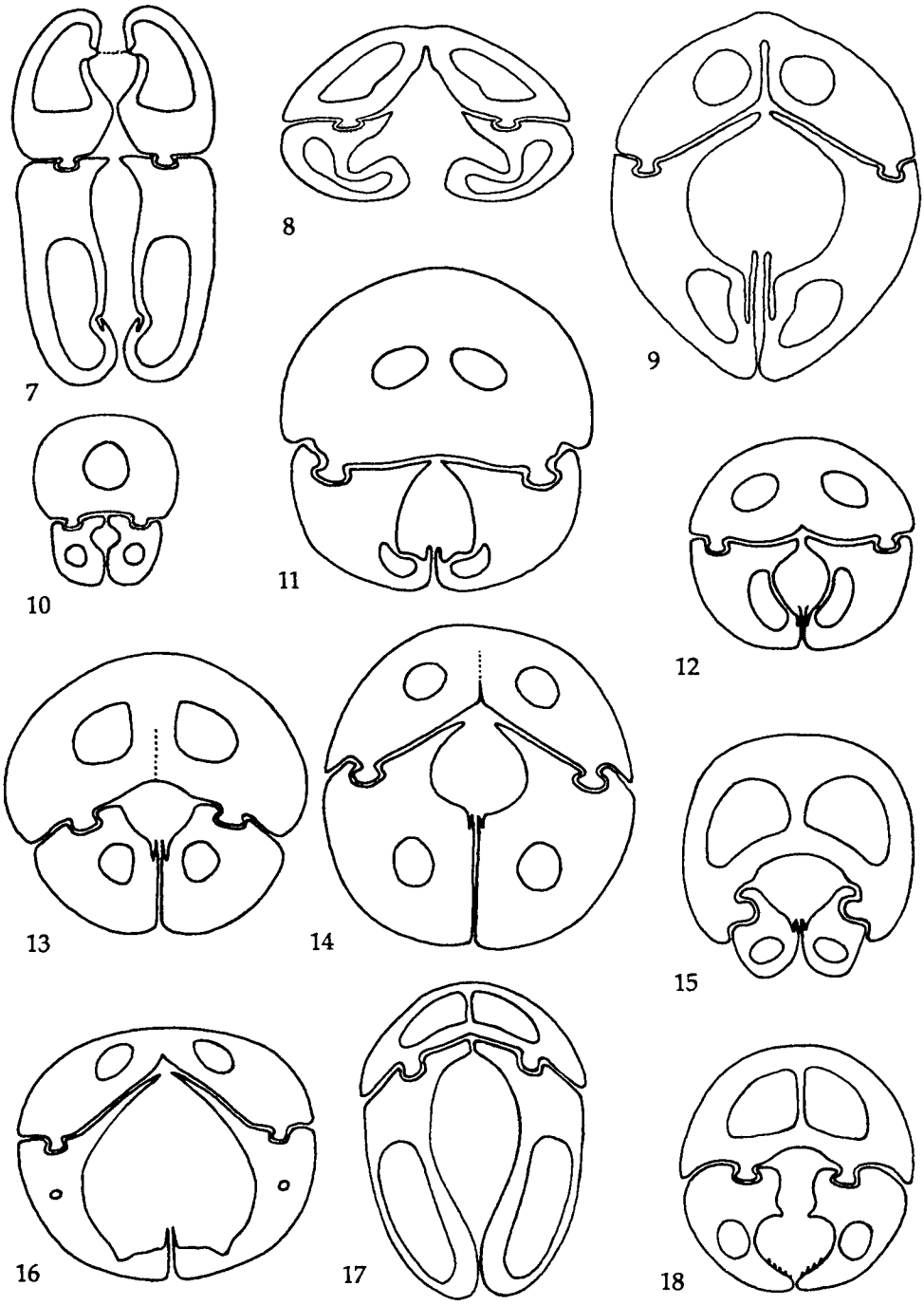


Fig. 7, Histeromerinae (*Histeromerus*); 8, 9, Rhyssalinae (*Rhyssalus* and *Rhysipolis*, respectively); 10, Hormiini (*Hormius*); 11, 12, Doryctinae (*Zombrus* and *Spathius*, respectively); 13-15, Braconinae (*Pycnobracon*, *Mesobracon*, and *Iphiaulax*, respectively); 16, 17, Rogadinae (*Spinaria* and *Aleiodes*, respectively); 18, Opiinae (*Opius*). 7-18, transverse sections of ovipositors of Braconidae.

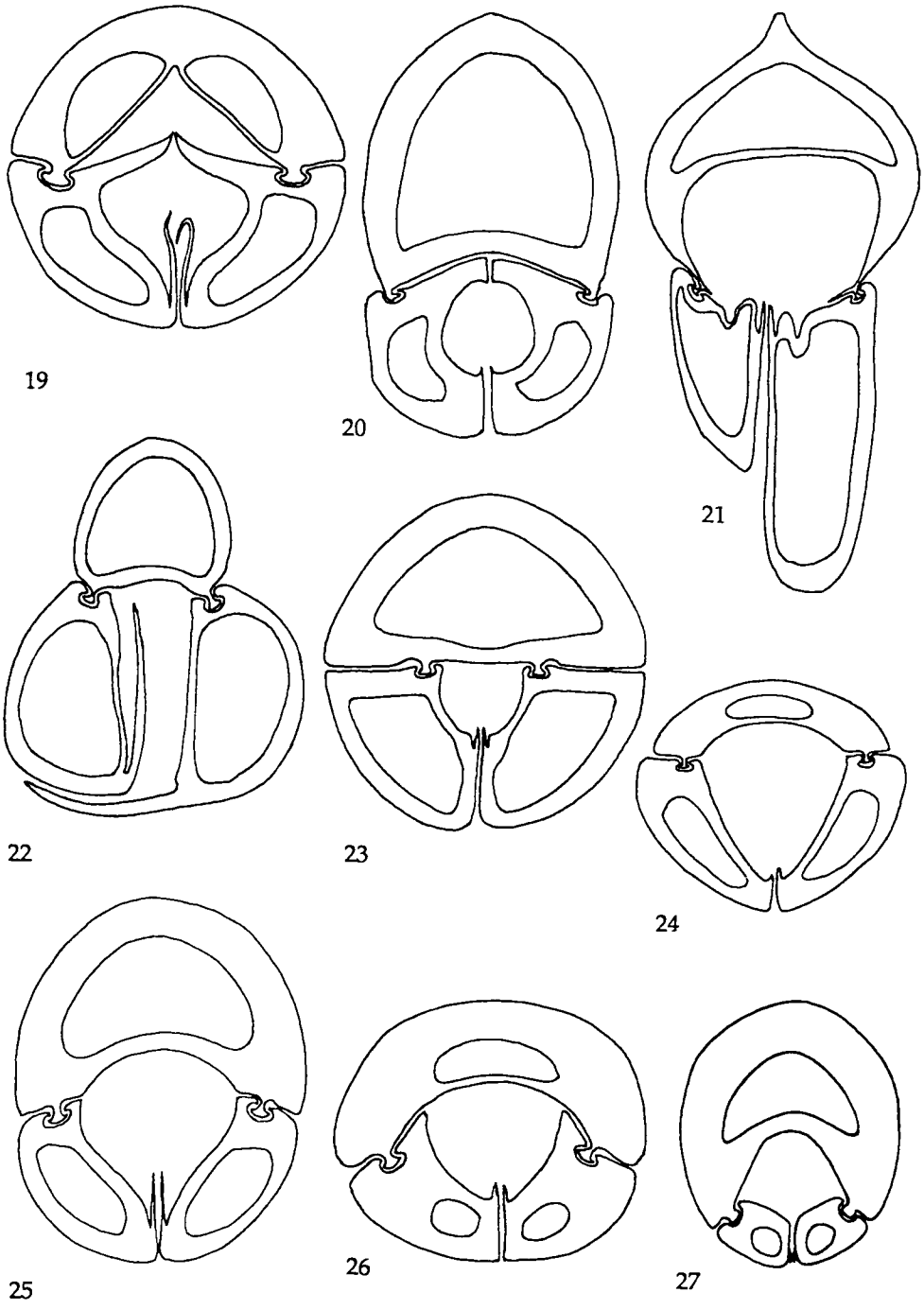


Fig. 19, Alysiinae (*Phaenocarpa*); 20, Gnamptodontinae (*Gnamptodon*); 21, 22, Aphidiinae (*Aphidius* and *Ephedrus*, respectively; left lower valve of *Aphidius* retracted, resulting in lower height); 23, Cheloninae (*Chelonus*); 24, Adeliinae (*Adelius*); 25, Ichneutinae (*Ichneutes*); 26, Miracinae (*Mirax*); 27, Microgastrinae (*Apanteles*). 19-27, transverse sections of ovipositors of Braconidae.

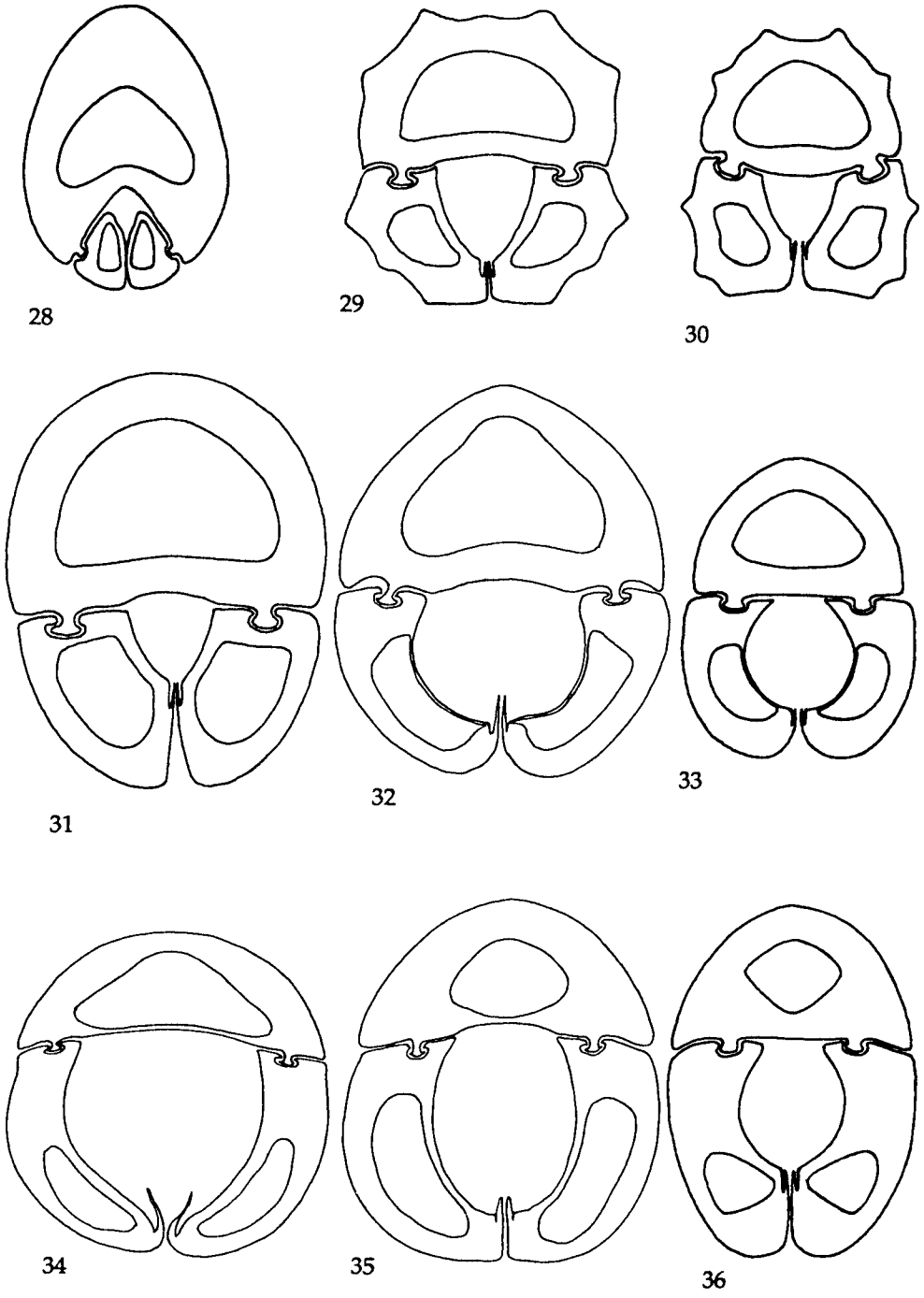
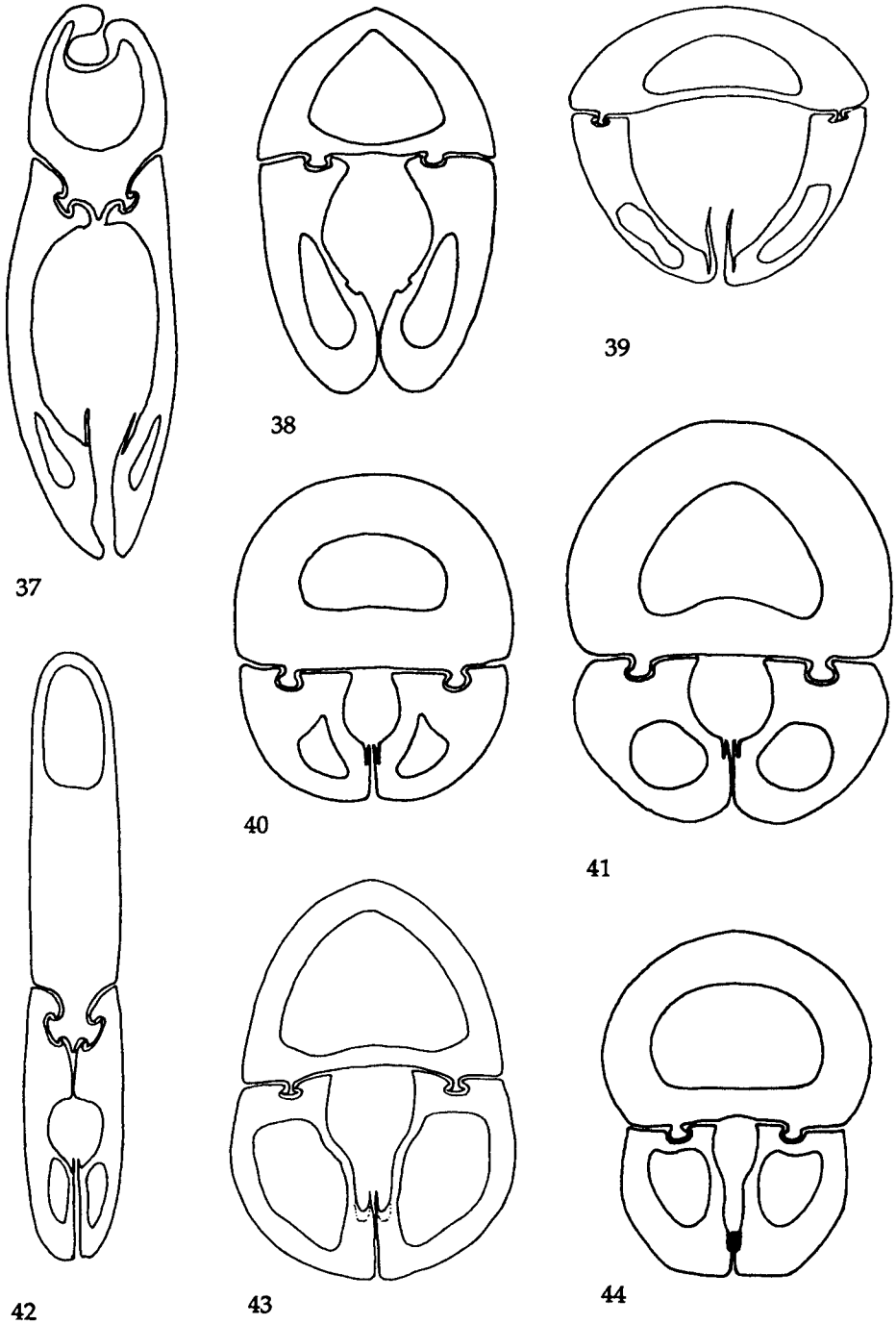


Fig. 28, Cardiochilinae (*Cardiochiles*); 29, Macrocentrinae (*Macrocentrus*); 30, Charmontinae (*Charmon*); 31, Amicrocentrinae (*Amicrocentrum*); 32, Orgilinae (*Orgilus*); 33, Microtypinae (*Microtypus*); 34, Blacinae (*Blacus*); 35, Homolobinae (*Homolobus*); 36, Meteorini (*Meteorus*). 28-36, transverse sections of ovipositors of Braconidae.



Figs. 37, 39, 42, Euphorinae s.s. (*Centistes*, *Peristenus*, and *Pygostolus*, respectively); 38, Meteorini (*Zele*); 40, Cenocoeliinae (*Cenocoelius*); 41, Helconinae (*Helcon*); 43, Sigalphinae (*Minanga*); 44, Agathidinae (*Braunsia*). 37-44, transverse sections of ovipositors of Braconidae. N.B. The section depicted in fig. 37 is rather basal and shows part of the "laminated bridge" medio-dorsally.

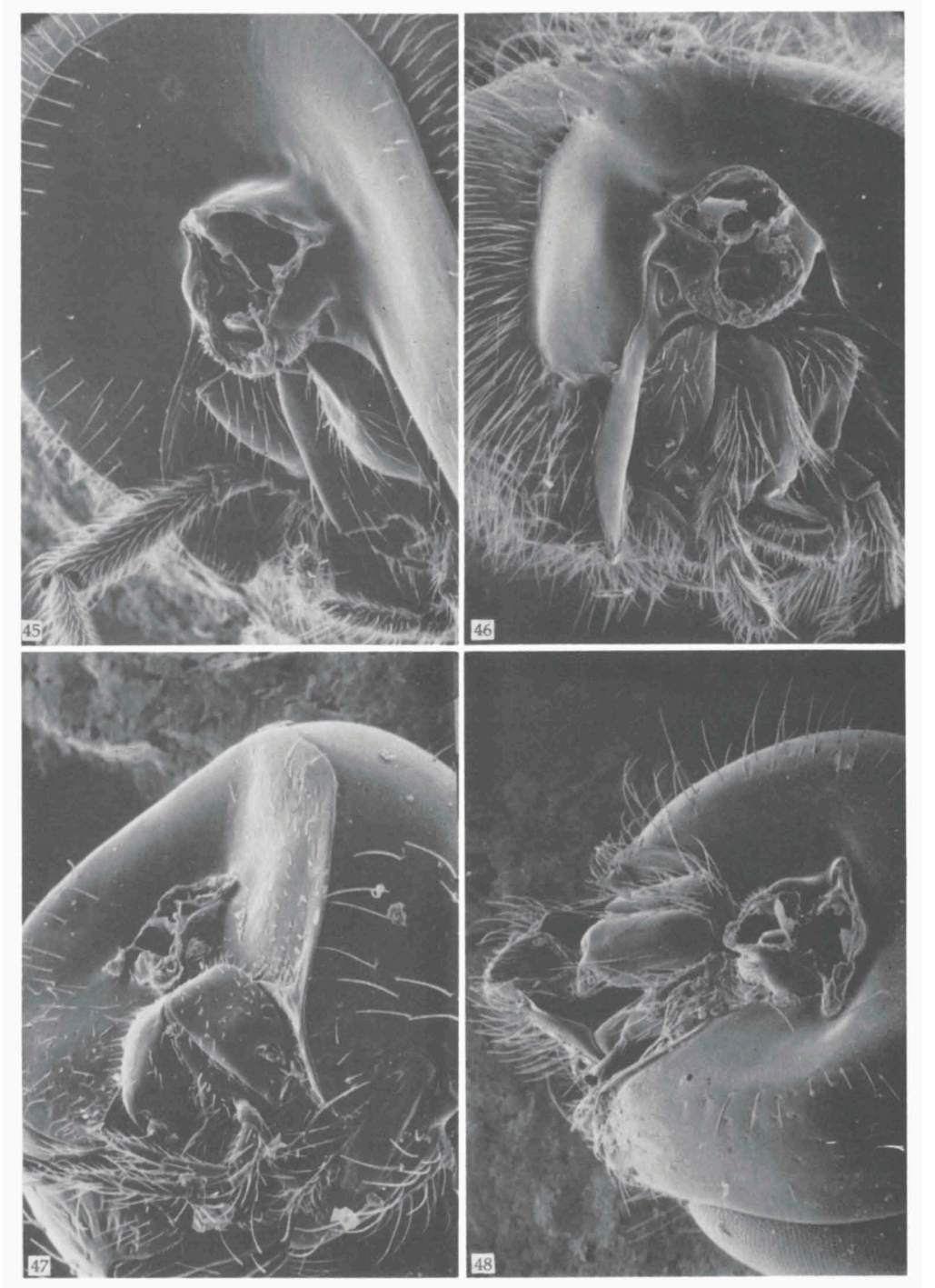
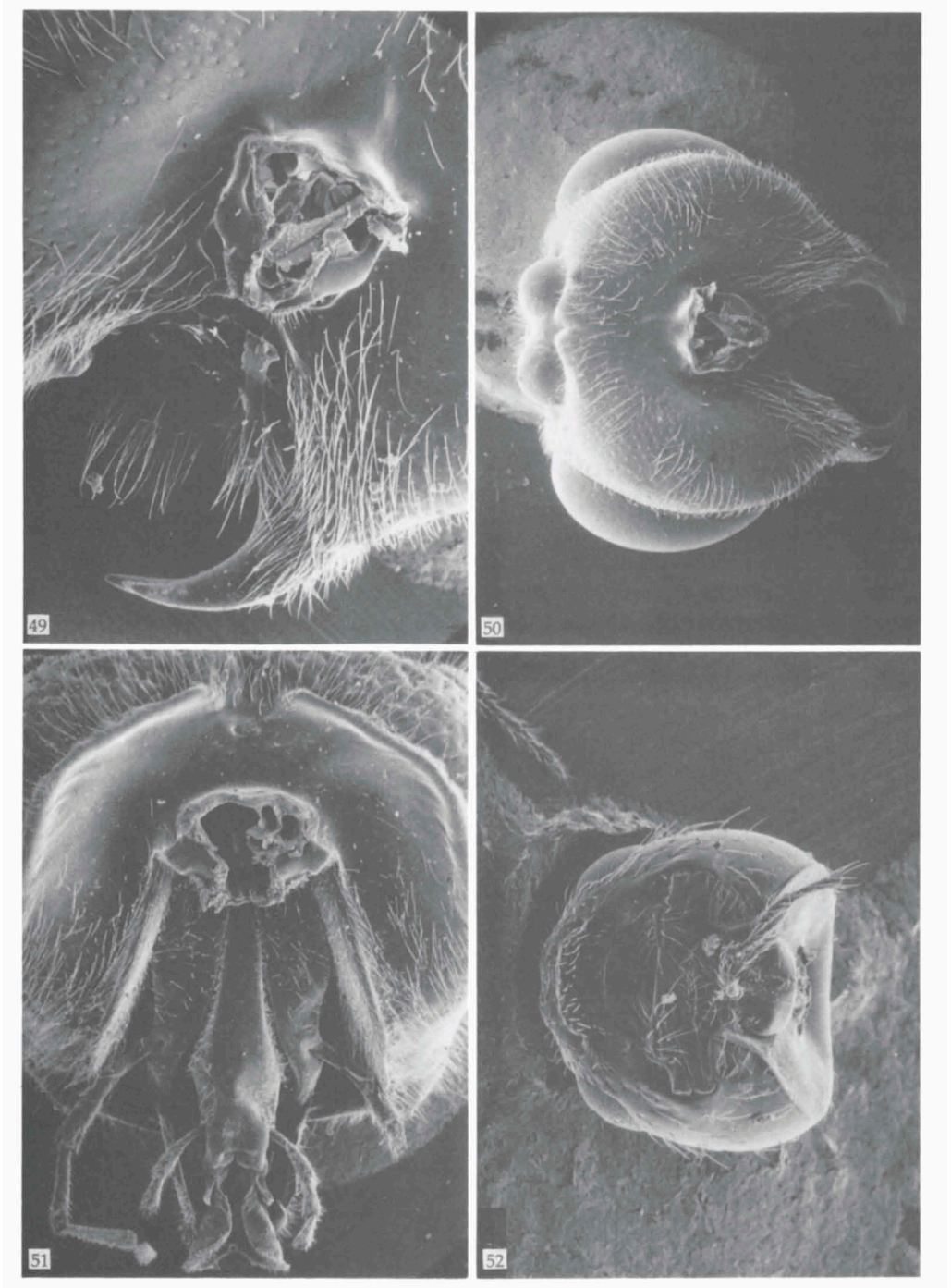
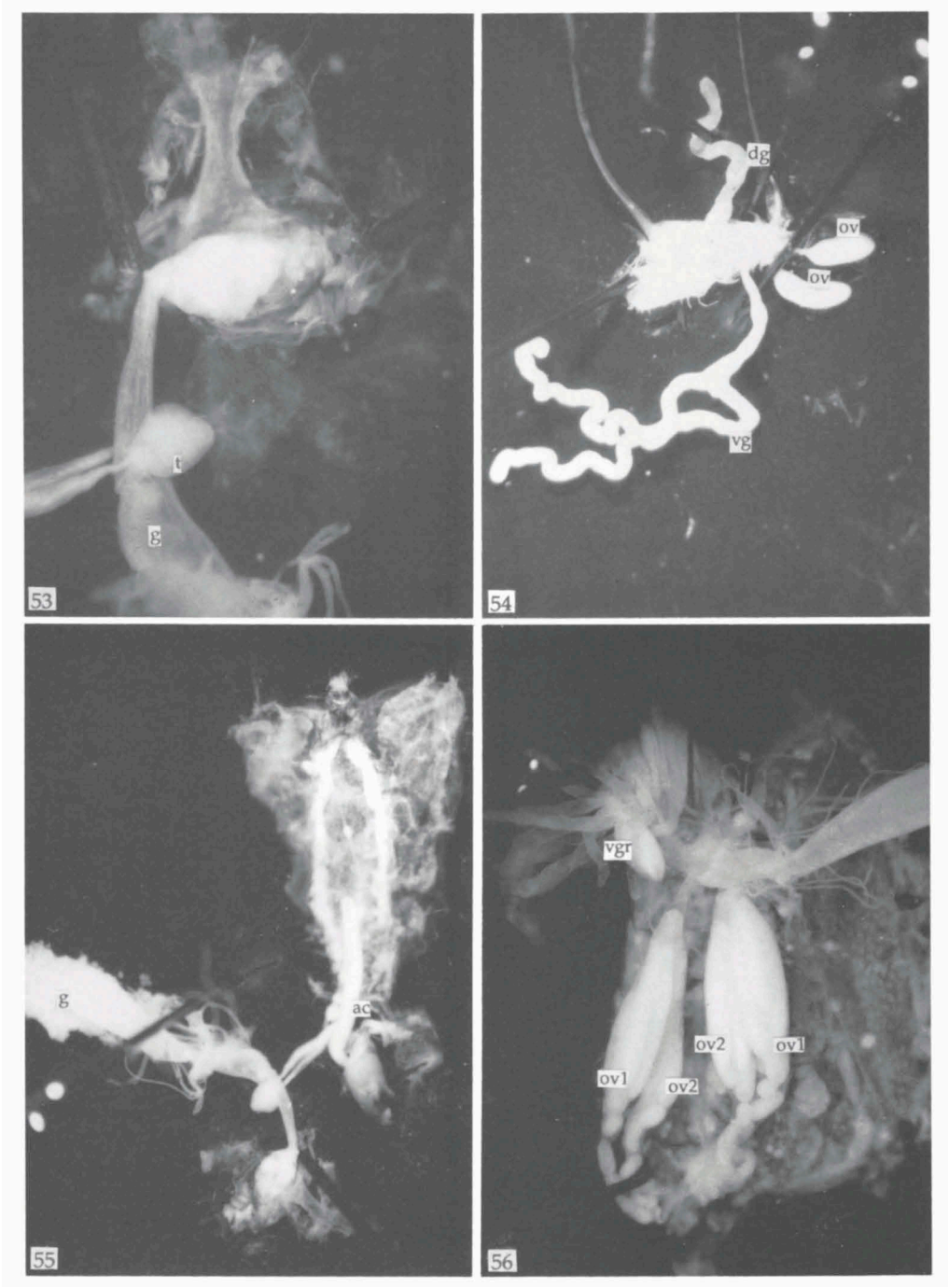


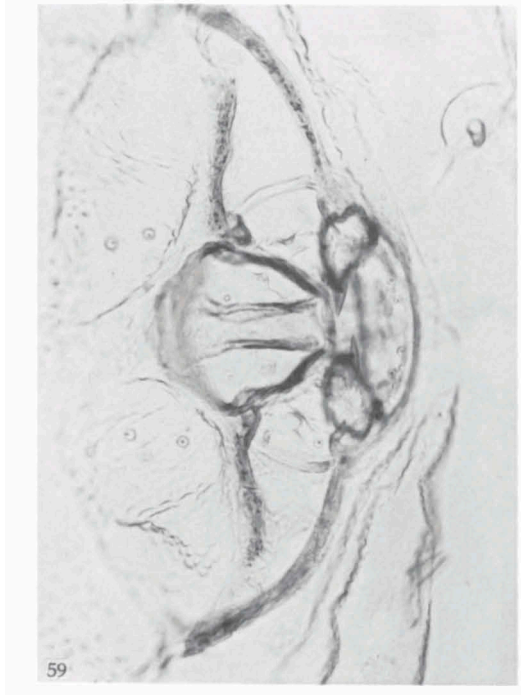
Fig. 45, Homolobinae (*Homolobus*); fig. 46, Sigalphinae (*Sigalphus*); fig. 47, Histeromerinae (*Histeromerus*); fig. 48, Braconinae (*Archibracon*). 45-48, head, posterior aspect.



Figs. 49, 50, Amicrocentrinae (*Amicrocentrum*); fig. 51, Trachypetinae (*Trachypetus*); fig. 52, Histeromerinae (*Histeromerus*). 49-52, head; 49-51, posterior aspect; 52, ventral aspect.



Figs. 53, 55, 56, Braconinae (*Atanycolus* (53, 55) and *Digonogastra* (56)); fig. 54, Agathidinae (*Alabagrus*). 53-56, internal male genitalia (53 shows fusion of testes above gut; 55 shows elongate accessory gland); 54, 56, internal female genitalia (54 shows small ovaries and venom apparatus; 56 shows two pairs of ovaria and muscularized venom gland reservoir. t= testis; g= gut; ac= accessory gland; vgr= venom gland reservoir; ov1, ov2= ovaria; vg= venom gland; dg= Dufour's gland.



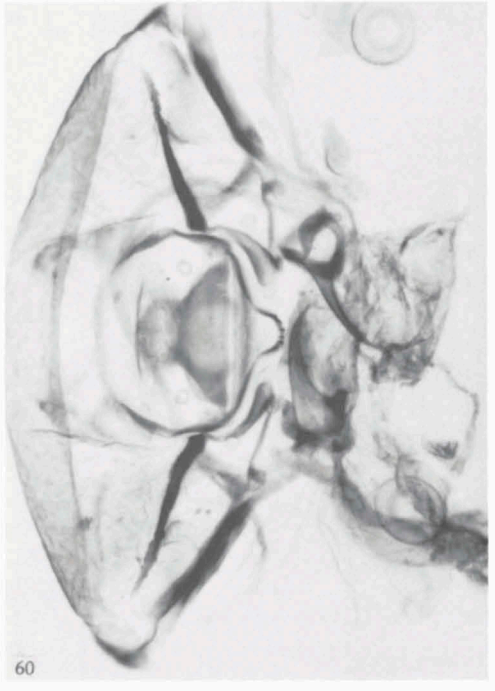


Fig. 57, Cercobarconinae (*Megalohelcon*); fig. 58, Histeromerinae (*Histeromerus*); fig. 59, Braconinae (*Digonogastra*); fig. 60, Xiphozelinae (*Xiphozele*). 57, 58, venom gland and reservoir; 59, 60, head skeleton of third larval instar. vg= venom gland; vgf= venom gland filaments; vgr= venom gland reservoir; tr= tubular reservoir with spiral thickening.

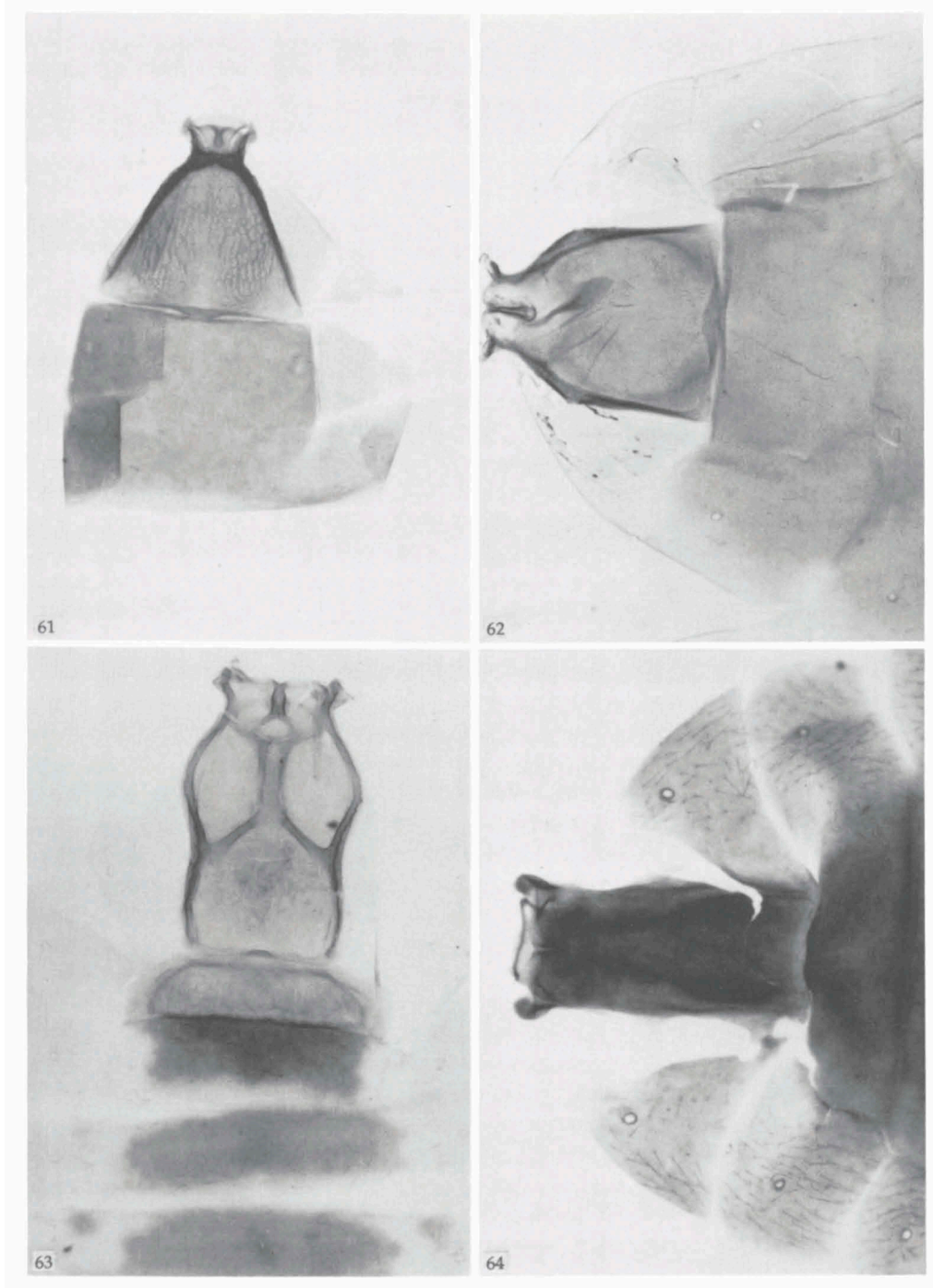


Fig. 61, Ecnomiinae (*Ecnomios*); fig. 62, Histeromerinae (*Histeromerus*); fig. 63, Microgastrinae (? *Xanthomicrogaster*); fig. 64, Cardiochilinae (*Cardiochiles*). 61-64, first metasomal tergite, dorsal aspect.

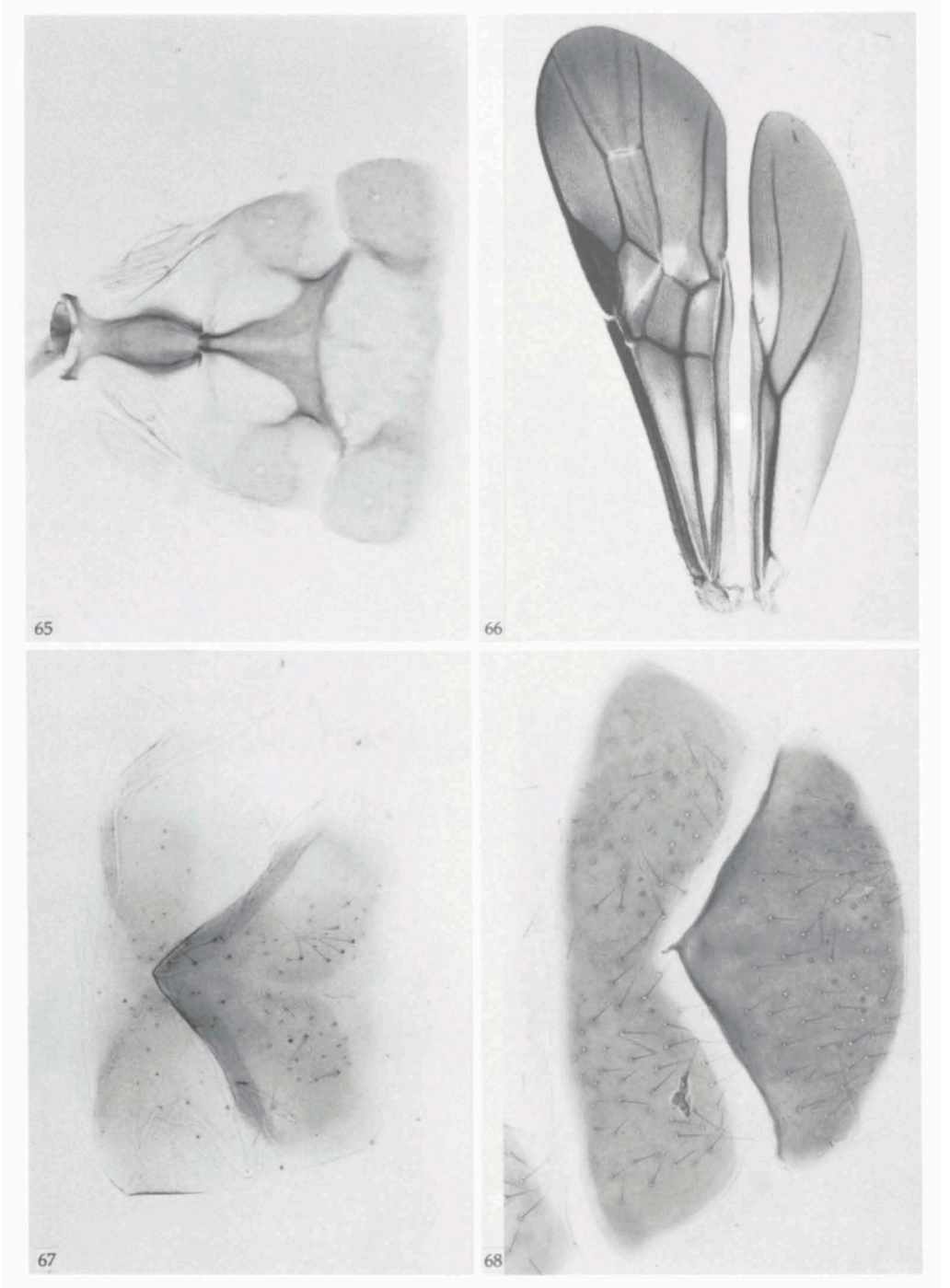


Fig. 65, Miracinae (*Mirax*); fig. 66, Braconinae (*Soter*); fig. 67, Doryctinae (*Doryctes*); fig. 68, Cardiochilinae (*Cardiochiles*). 65, three basal metasomal tergites, dorsal aspect; 66, wings, to show flexion line through vein 2-SR+M of forewing; 67, 68, seventh and eighth metasomal sternites of male.

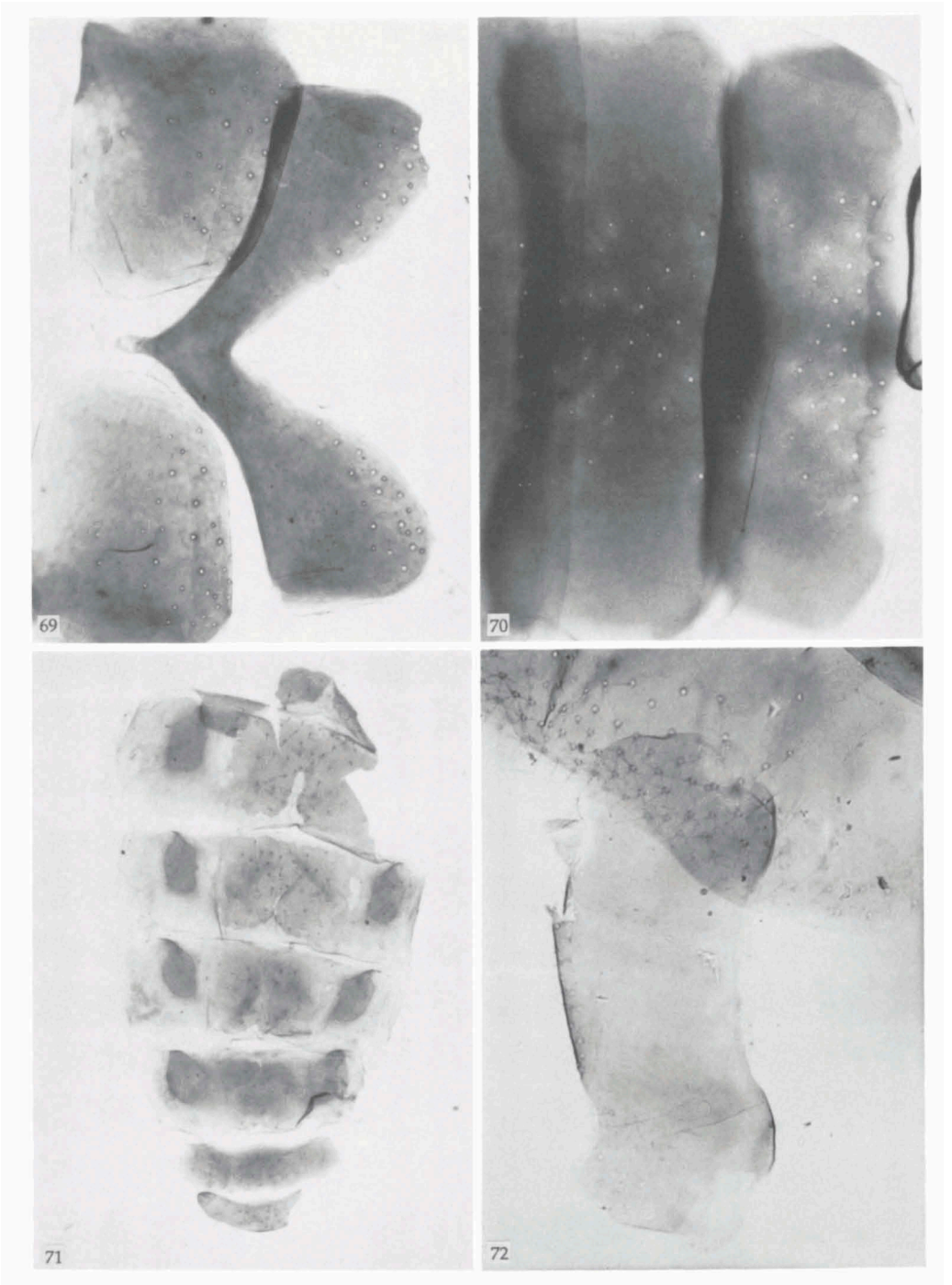


Fig. 69, Cheloninae (*Chelonus*); fig. 70, Alysiinae (*Alysia*); fig. 71, Telengaiinae (*Telengaia*); fig. 72, Neoneurinae (*Neoneurus*). 69, 70, seventh and eighth metasomal sternites of male; 71, third-eighth metasomal sternites of male; 72, ninth metasomal tergite of male, lacking Hagen's glands.

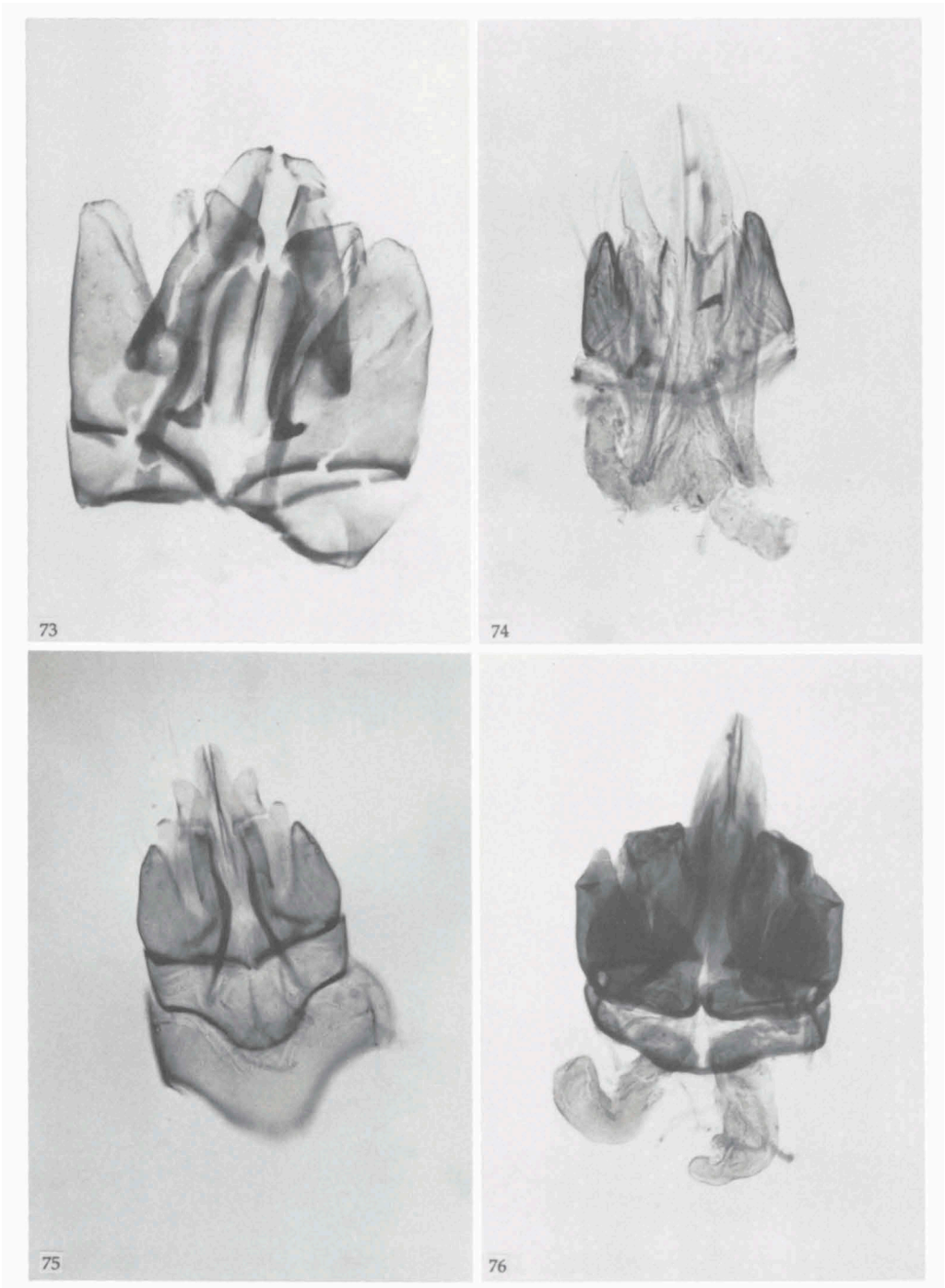


Fig. 73, Histeromerinae (*Histeromerus*); fig. 74, Betylobraconinae (*Mesocentrus*); fig. 75, Exothecinae (*Colastes*); fig. 76, Telengaiinae (*Telengaia*). 73-76, external male genitalia and in 74 and 76 with (re-hydrated) accessory glands.

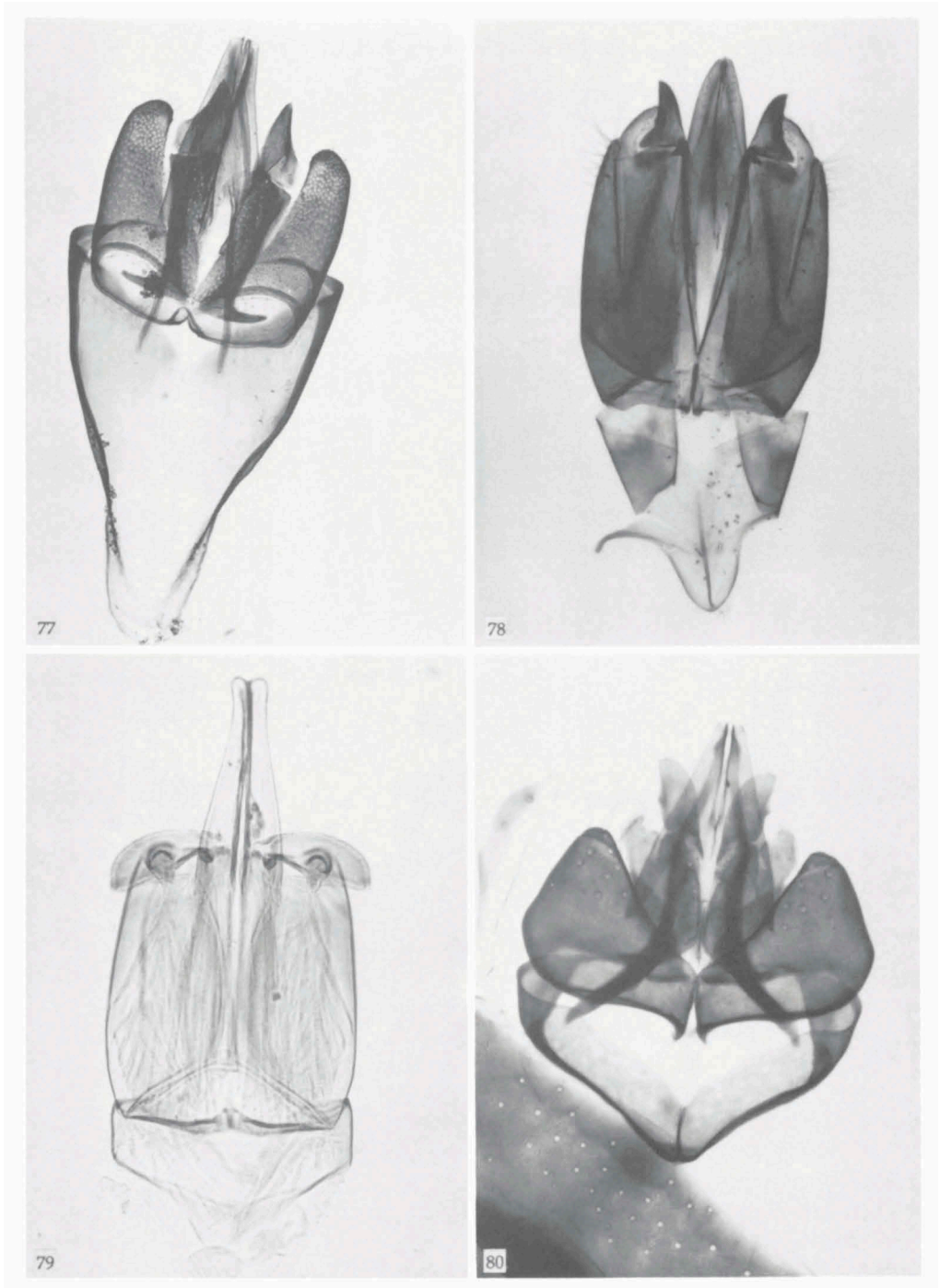
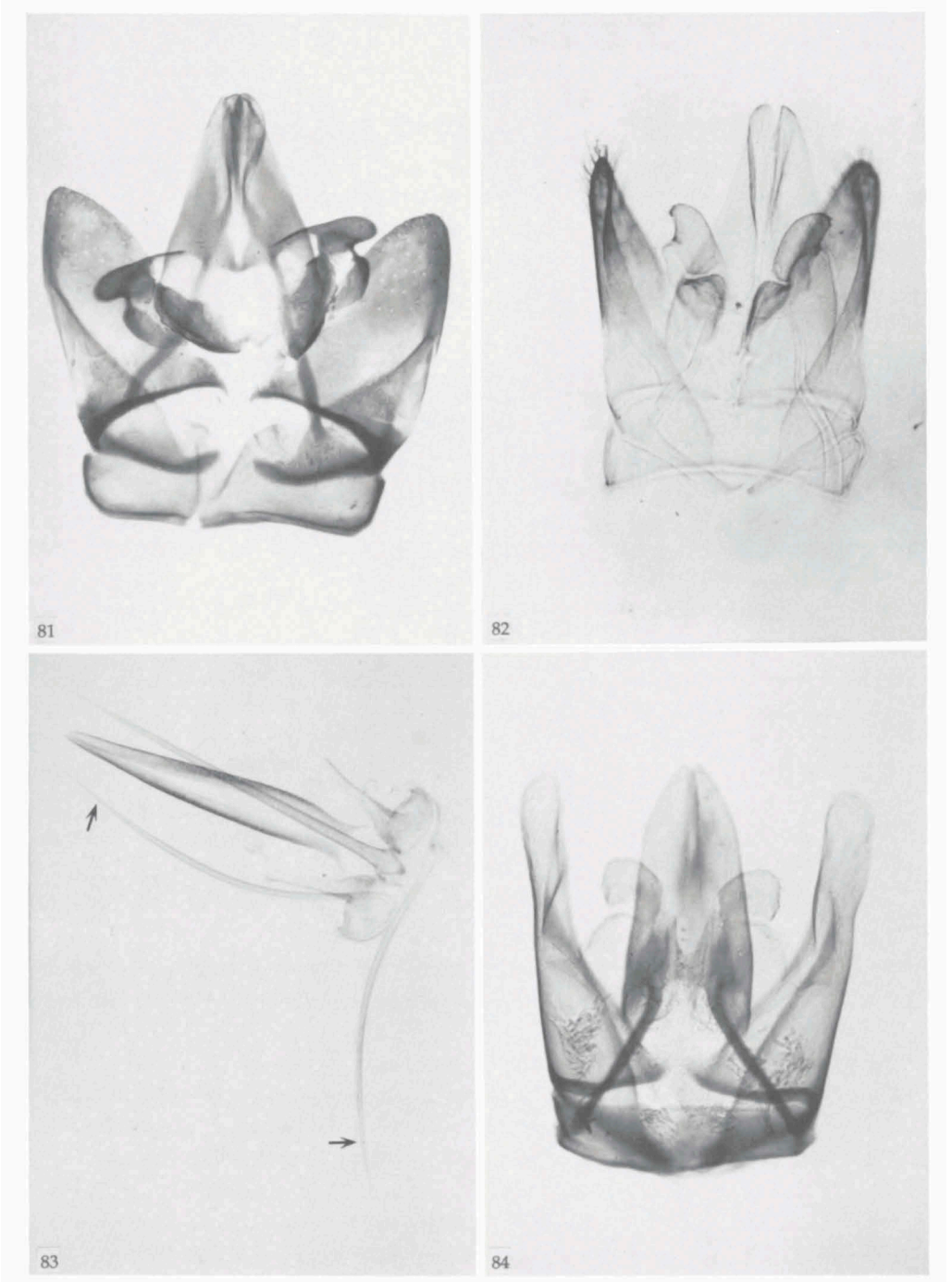
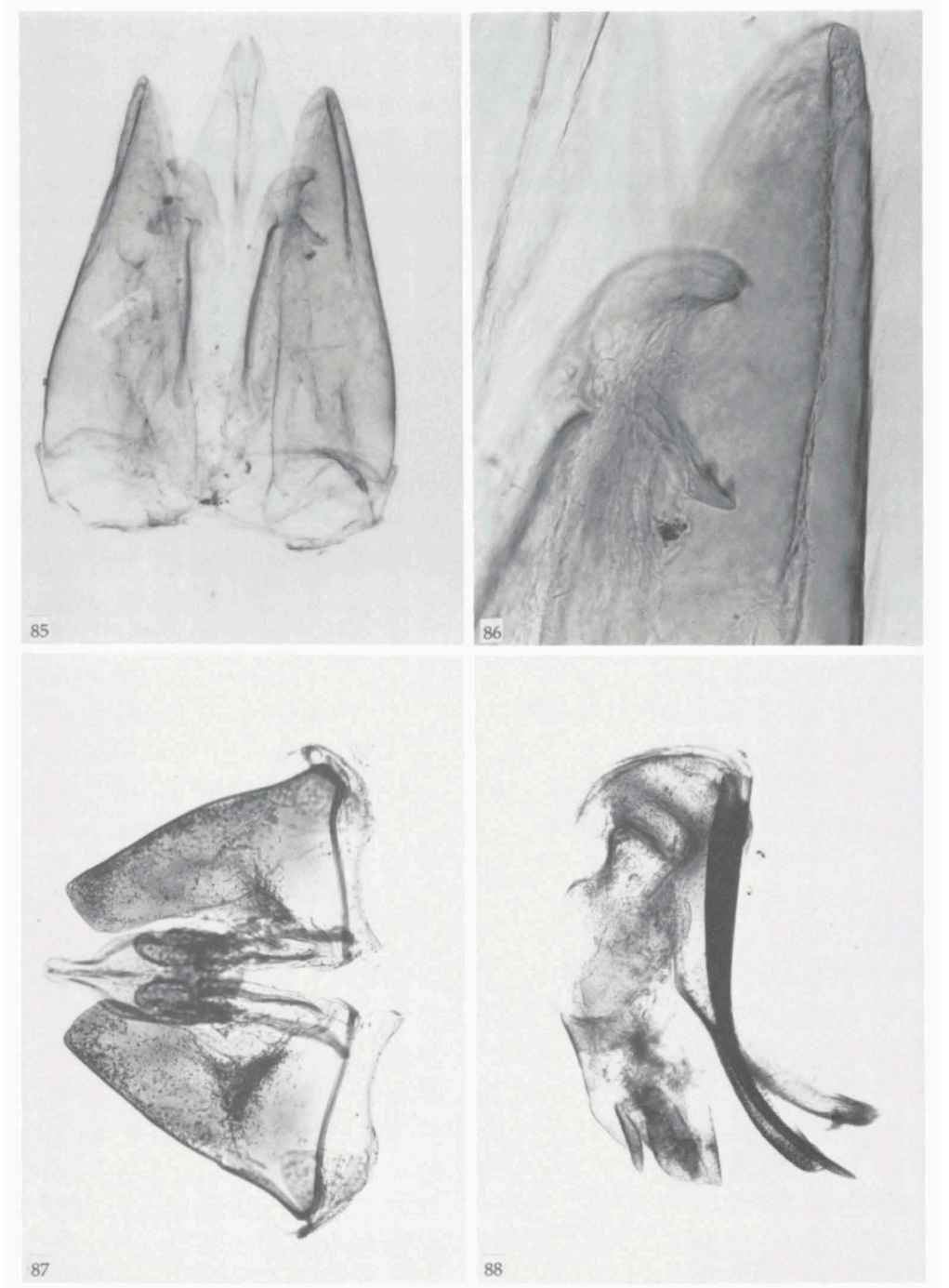


Fig. 77, Braconinae (*Iphiaulax*); fig. 78, Doryctinae (*Acrophasmus*); fig. 79, Ypsistocerinae (*Termitobracon*); fig. 80, Alysiinae (*Alysia*). 77-80, external male genitalia.



Figs. 81, 82, Agathidinae (*Agathis* and *Braunsia*, respectively); fig. 83, Sigalphinae (new genus from W. Africa of the Acampsini); fig. 84, Neoneurinae (*Neoneurus*). 81, 82, 84, external male genitalia; 83, external female genitalia, lower ovipositor valves dissociated showing location of valvillus.



Figs. 85, 86, Xiphozelinae (*Xiphozele*); fig. 87, Cercobarconinae (*Megalohelcon*); fig. 88, Trachypetinae (*Trachypetus*)). 85-87, external male genitalia, 86, detail of digitus; 88, external female genitalia.

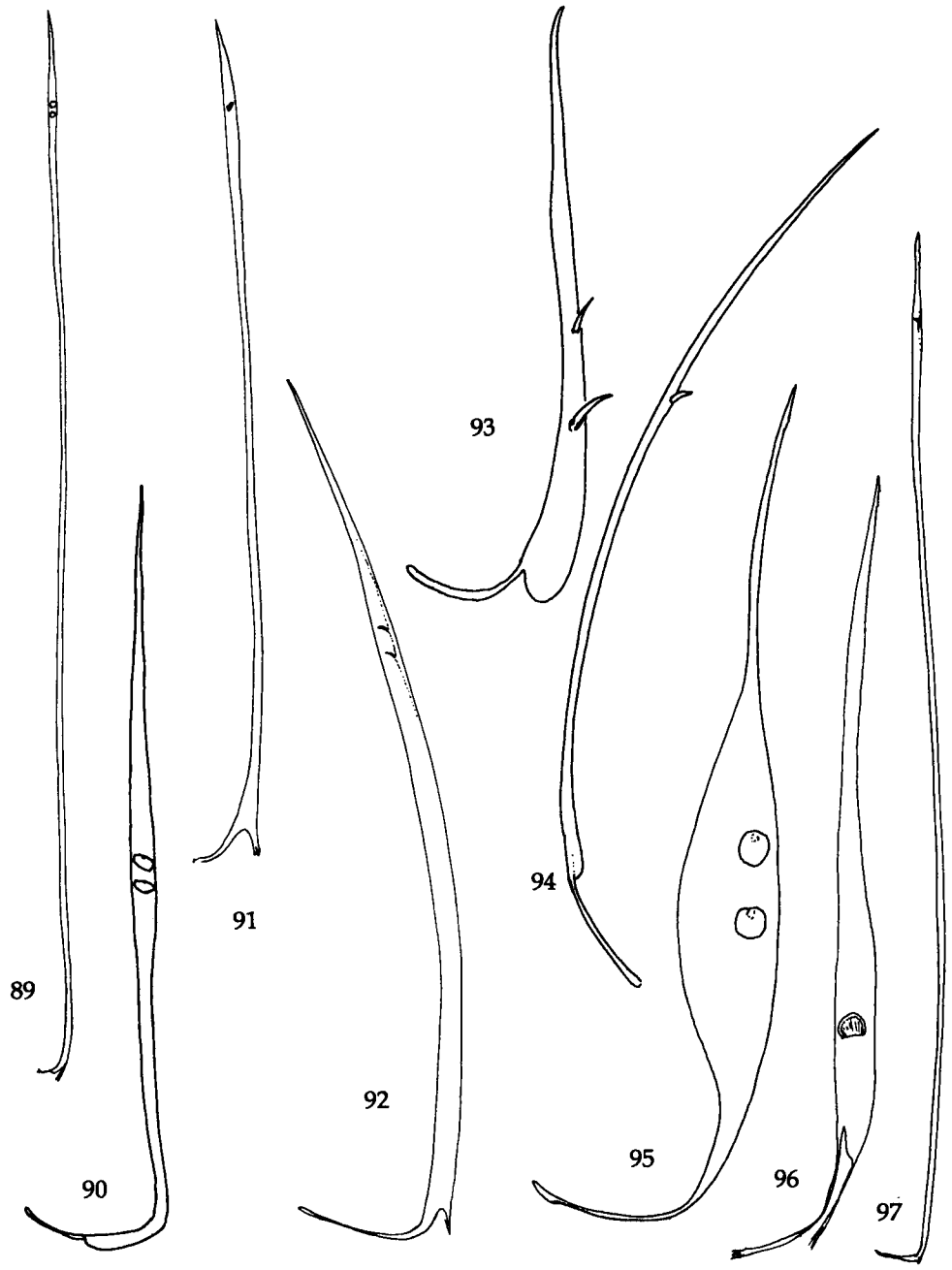
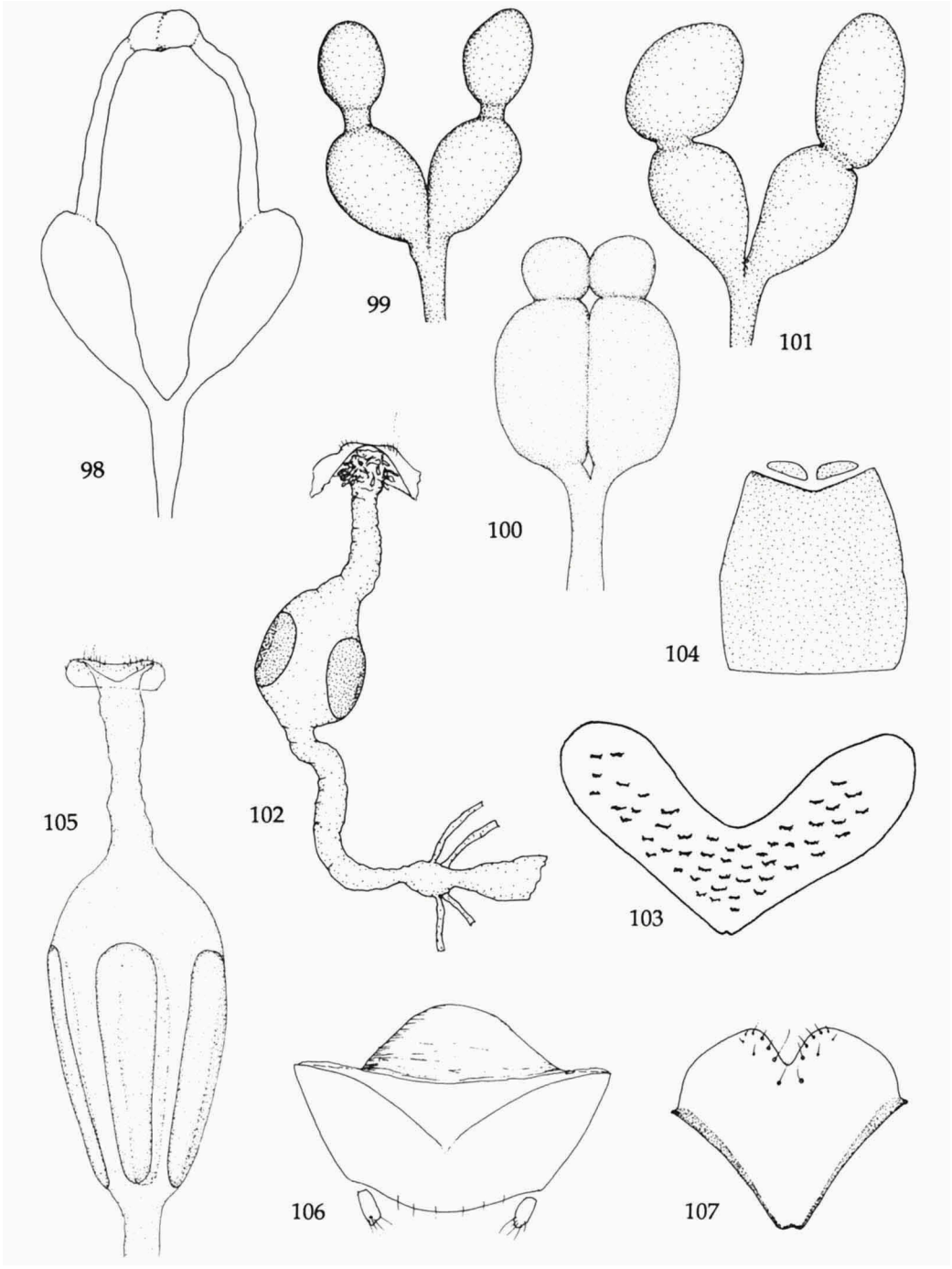


Fig. 89, Rhyssalinae (*Rhyssalus*); fig. 90, Histeromerinae (*Histeromerus*); fig. 91, Rogadinae (*Spinaria*); fig. 92, Cheloninae (*Phanerotoma*); fig. 93, Microgastrinae (*Protomicroplitis*); fig. 94, Homolobinae (*Homolobus*); fig. 95, Adeliinae (*Adelius*); fig. 96, Meteorini (*Zele*); fig. 97, Orgilinae (*Orgilus*). 89-97, lower ovipositor valve with valvilli indicated.



Figs. 98, 104, 106, 107, Apozyginae (*Apozyx*); fig. 99, Homolobinae (*Homolobus*); fig. 100, Trachypetinae (*Trachypetus*); fig. 101, Cenocoeliinae (*Cenocoelius*); figs. 102, 103, Histeromerinae (*Histeromerus*); fig. 105, Braconinae (*Iphiaulax*). 98-101, testes and vas deferens (as far as present); 102, 105, rectum, dorsal aspect, stained with chlorazol black after aqueous KOH treatment; 103, 107, eighth metasomal sternite; 104, first (posterior part)-third metasomal sternites; 106, eighth and ninth metasomal tergites, with inter-tergal reservoir. All of males.

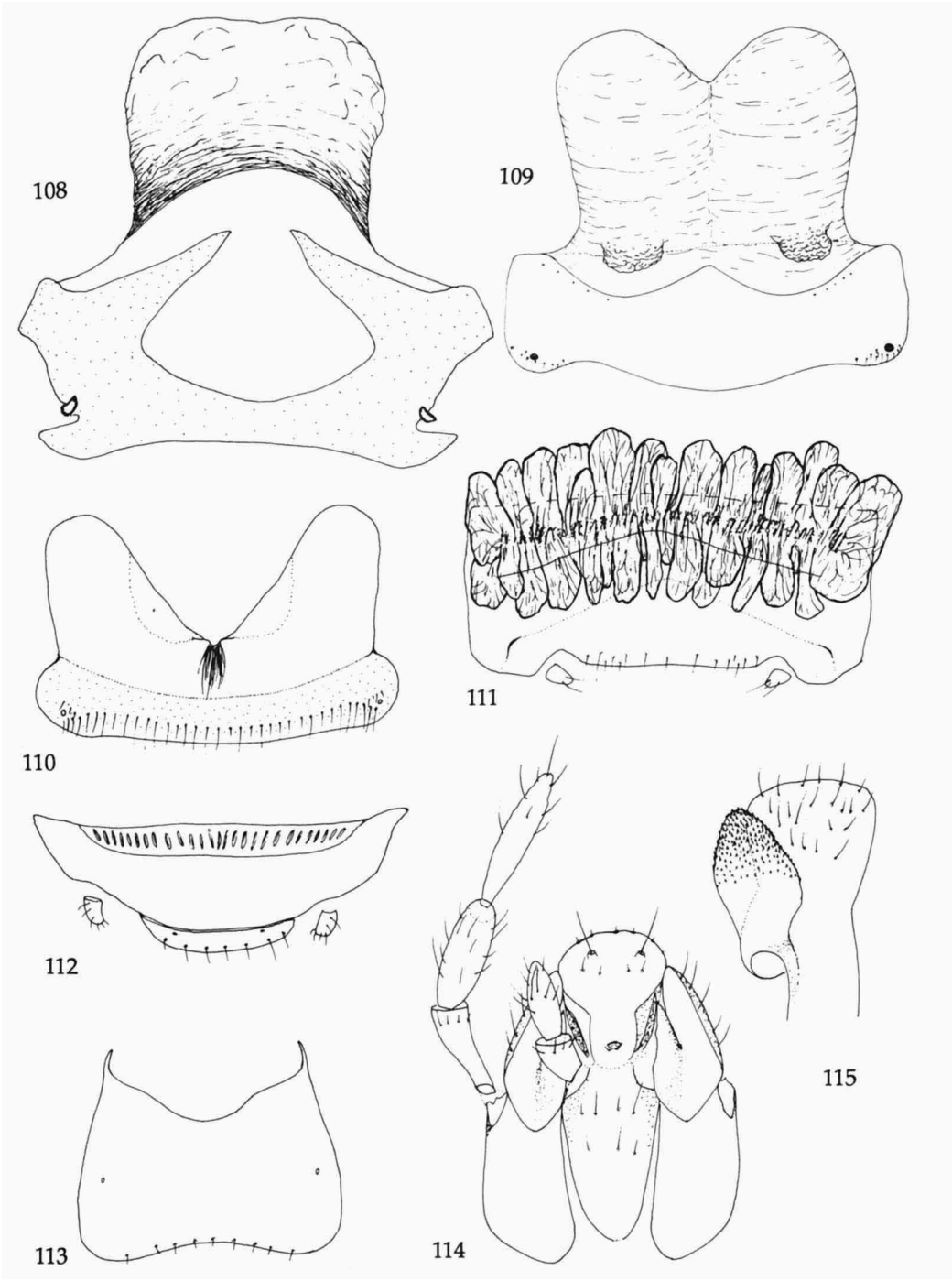


Fig. 108, Braconinae (*Atanycolus*); figs. 109, 112, Gnamptodontinae (*Gnamptodon*); fig. 110, Agathidinae (*Braunsia*); fig. 111, Alysiinae (*Alysia*); figs. 113-115, Aphidiinae (*Monoctonus*). 108-110, 113, seventh metasomal tergites showing Hagen's glands, treated with KOH, dorsal aspect; 111, 112, eighth and ninth metasomal tergites; 114, glossa and palpi; 115, galea and lacinia.

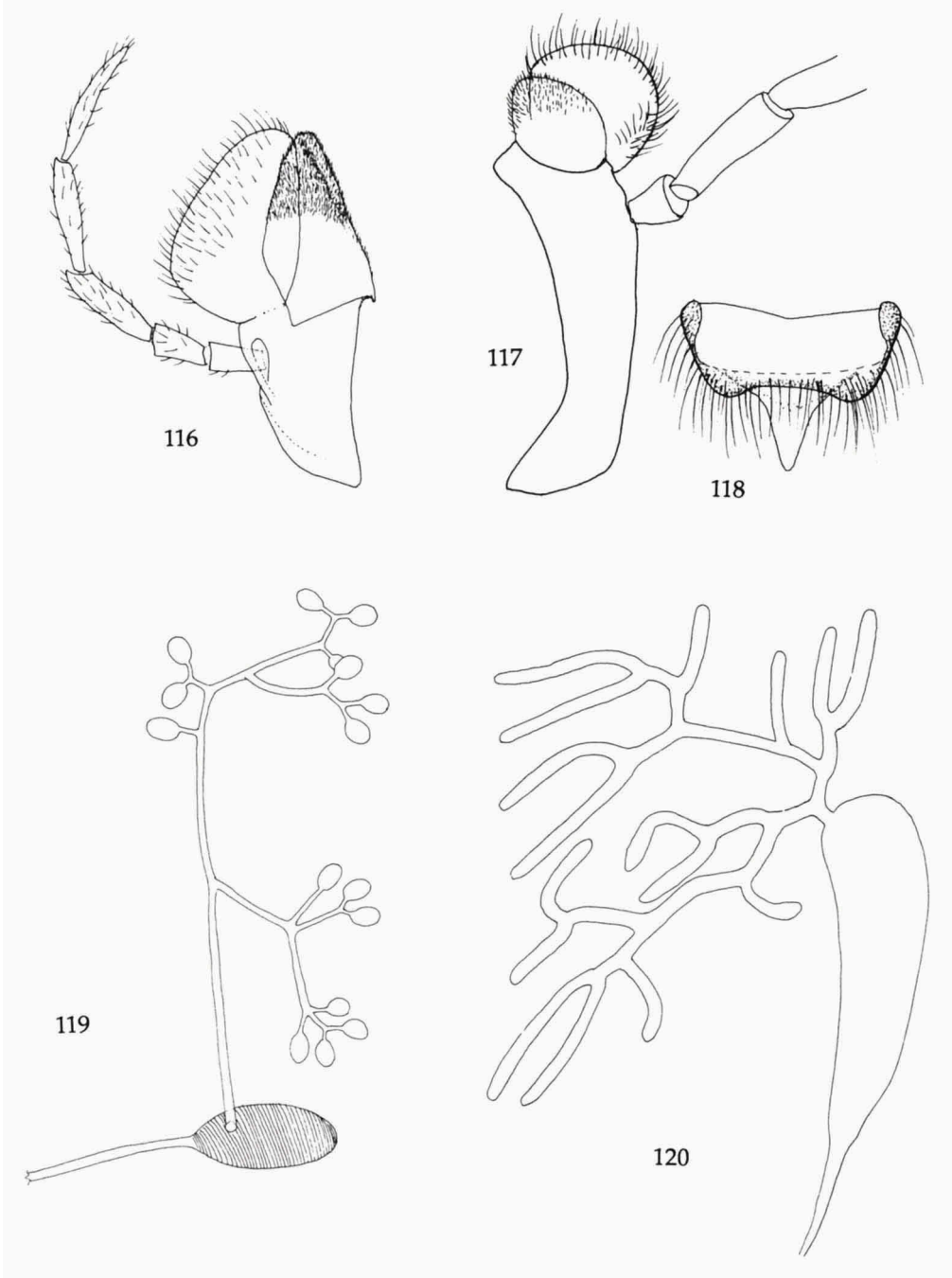


Fig. 116, Braconinae (*Iphiaulax*), ♀; fig. 117, 118, 120, Xiphozelinae (*Xiphozele*), ♀; fig. 119, Betylobraconinae (*Betylobracon*), ♀. 116, 117, galea and lacinia; 118, labrum, dorsal aspect; 119, 120, venom gland and reservoir.

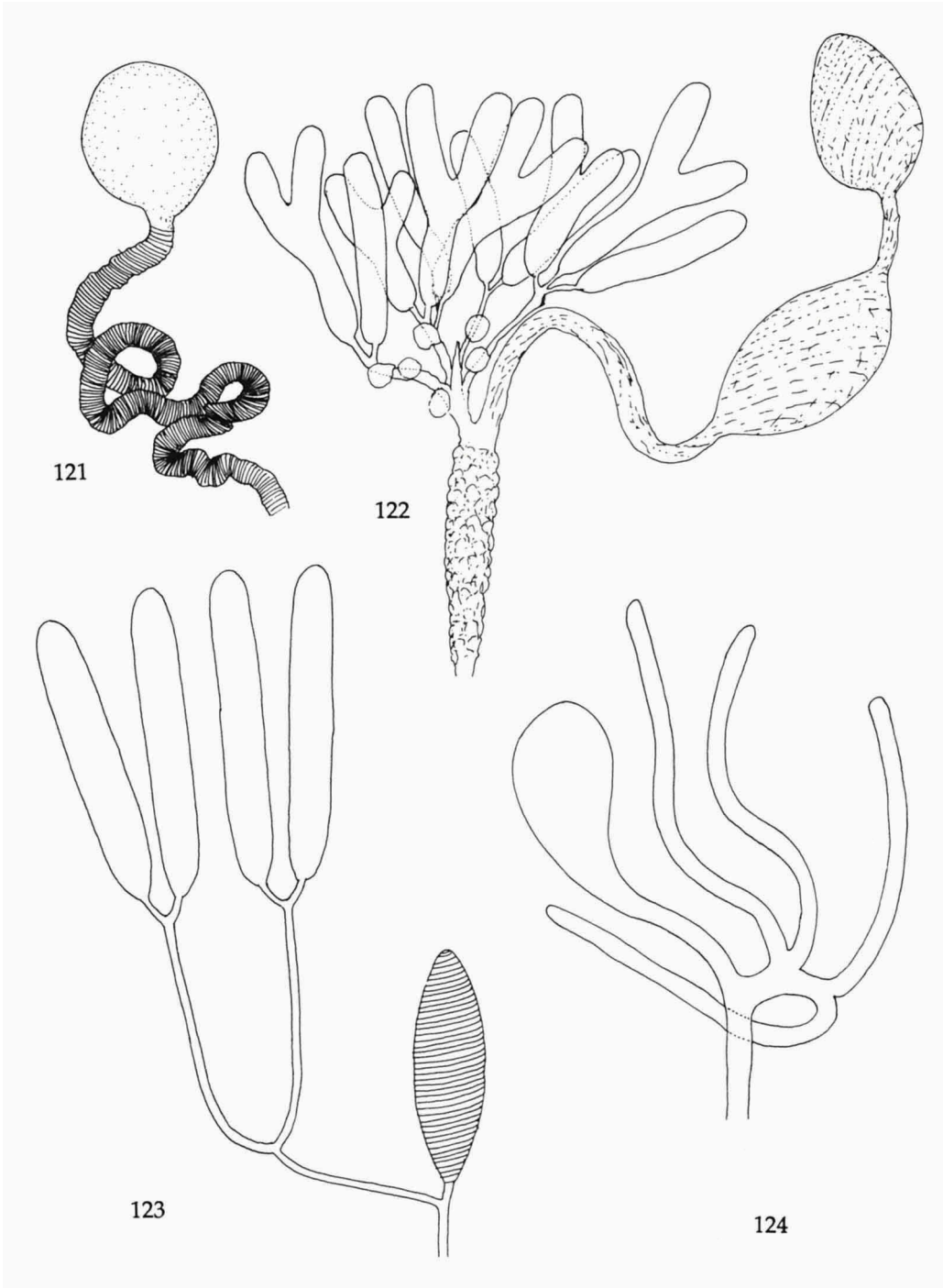


Fig. 121, Histeromerinae (*Histeromerus*), ♀; fig. 122, Ypsistocerinae (*Termitobracon*), ♀; fig. 123, Gnamptodontinae (*Gnamptodon*), ♀; fig. 124, Miracinae (*Mirax*), ♀. 121, putative gland and its tubular venom reservoir with spiral thickening; 122-124, venom gland and reservoir.

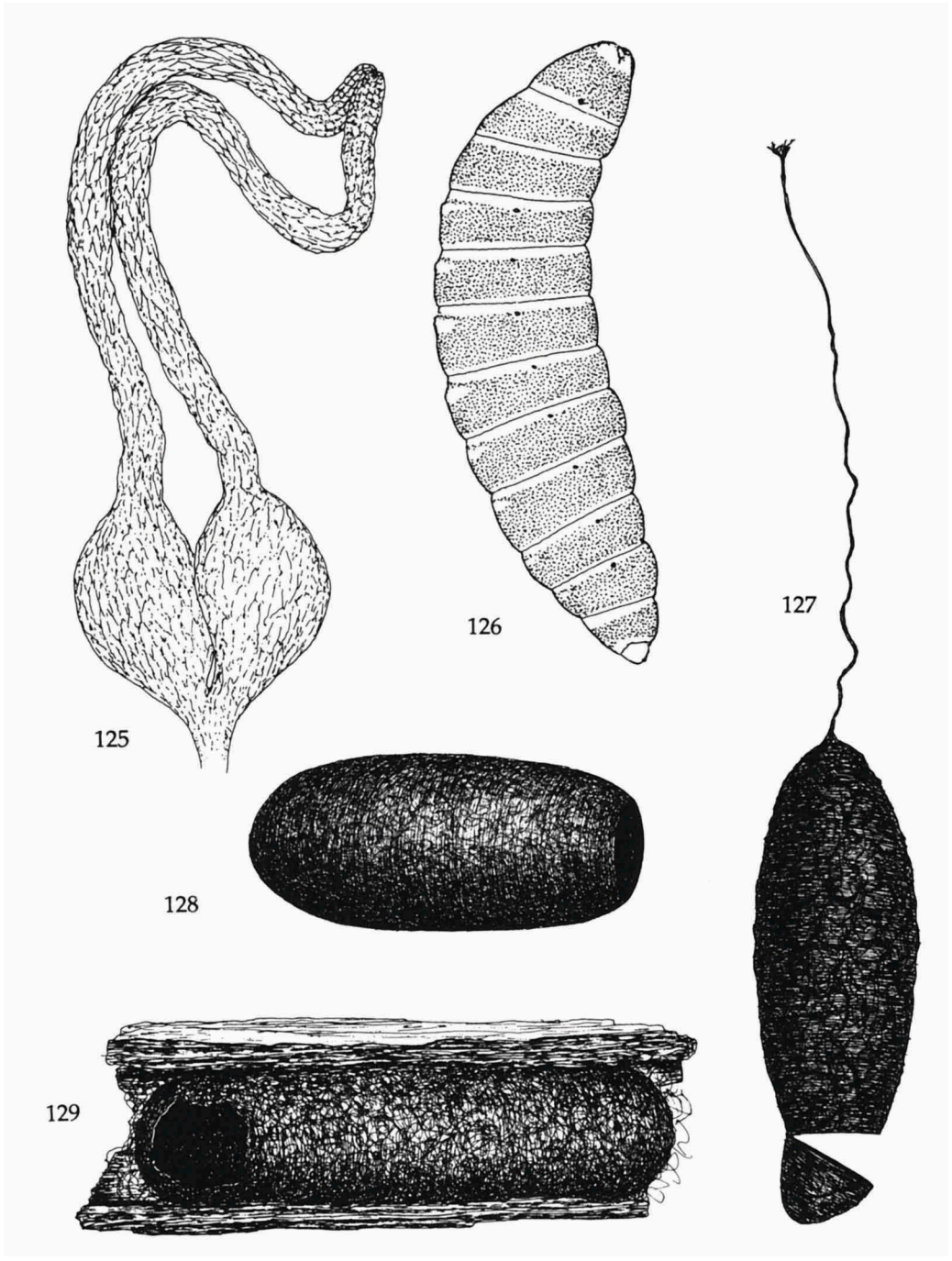


Fig. 125, Trachypetinae (*Trachypetus*), ♀; fig. 126, Exothecinae s.s. (*Colastes*); fig. 127, Meteorini (*Meteorus*); fig. 128, Xiphozelinae (*Xiphozele*); fig. 129, Braconinae (*Bracon*). 125, ovary (rehydrated); 126, final instar larva; 127, hanging cocoon; 128, cocoon; 129, cocoon, partly exposed by removing surrounding *Plantago*-stem; 127-129 showing shape of emergence hole.

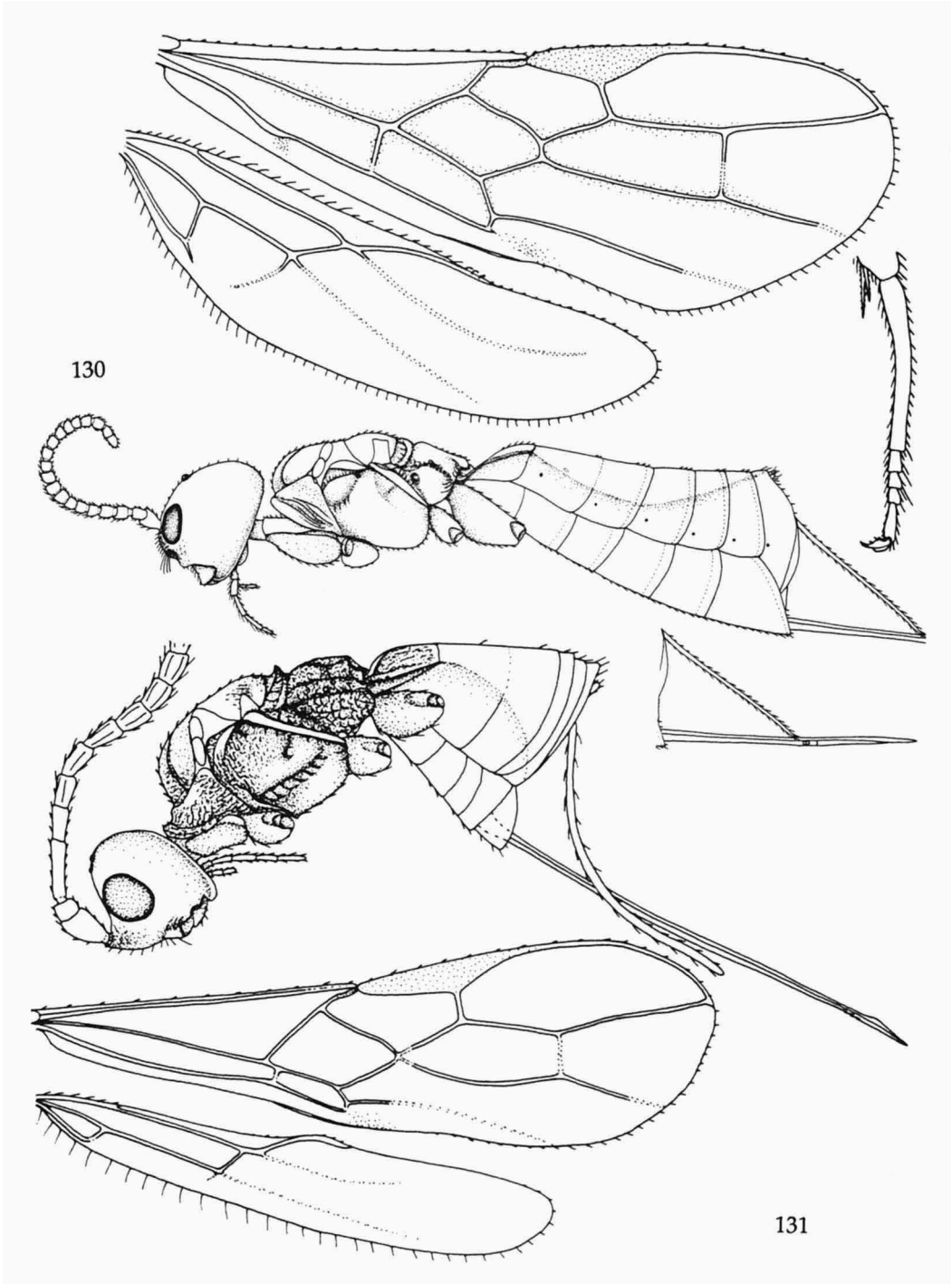


Fig. 130, Histeromerinae (*Histeromerus*), ♀; fig. 131, Rhyssalinae (*Rhyssalus*), ♀. 130 (including hind tarsus), 131, habitus and wings.

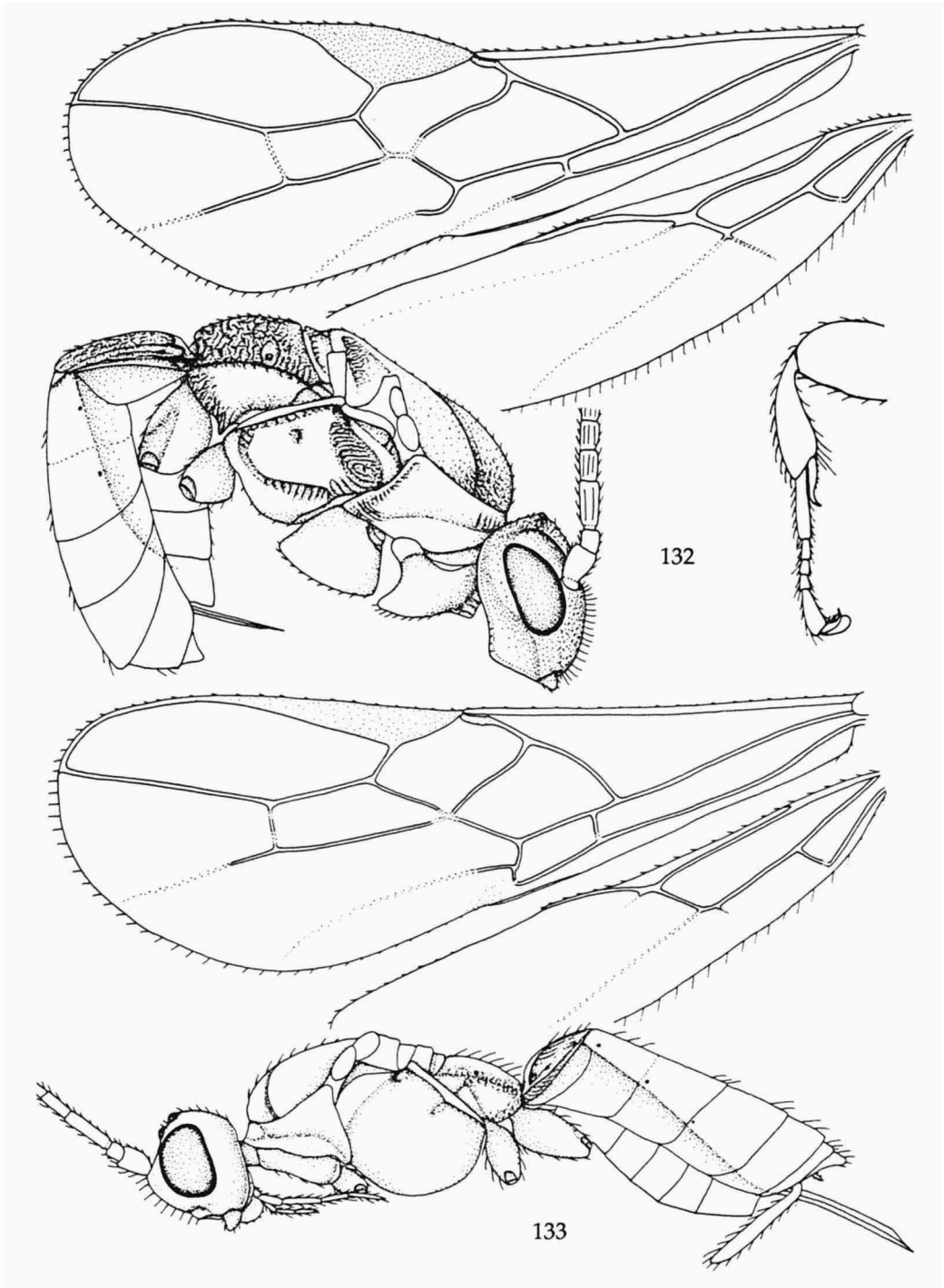


Fig. 132, Betylobraconinae (*Betylobracon*), ♀; fig. 133, Exothecinae s.s. (*Shawiana*), ♀. 132 (including part of fore leg), 133, habitus and wings.

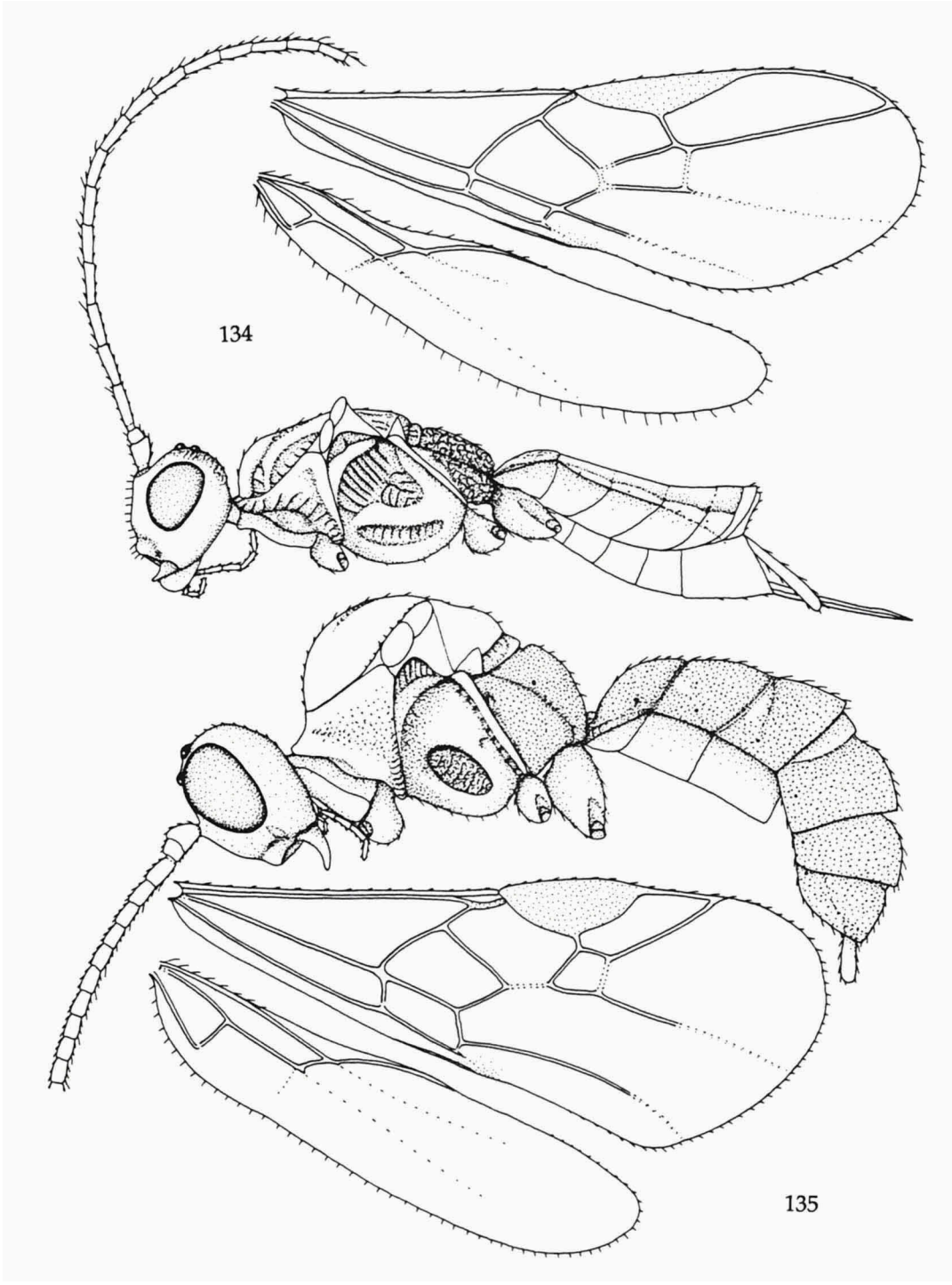
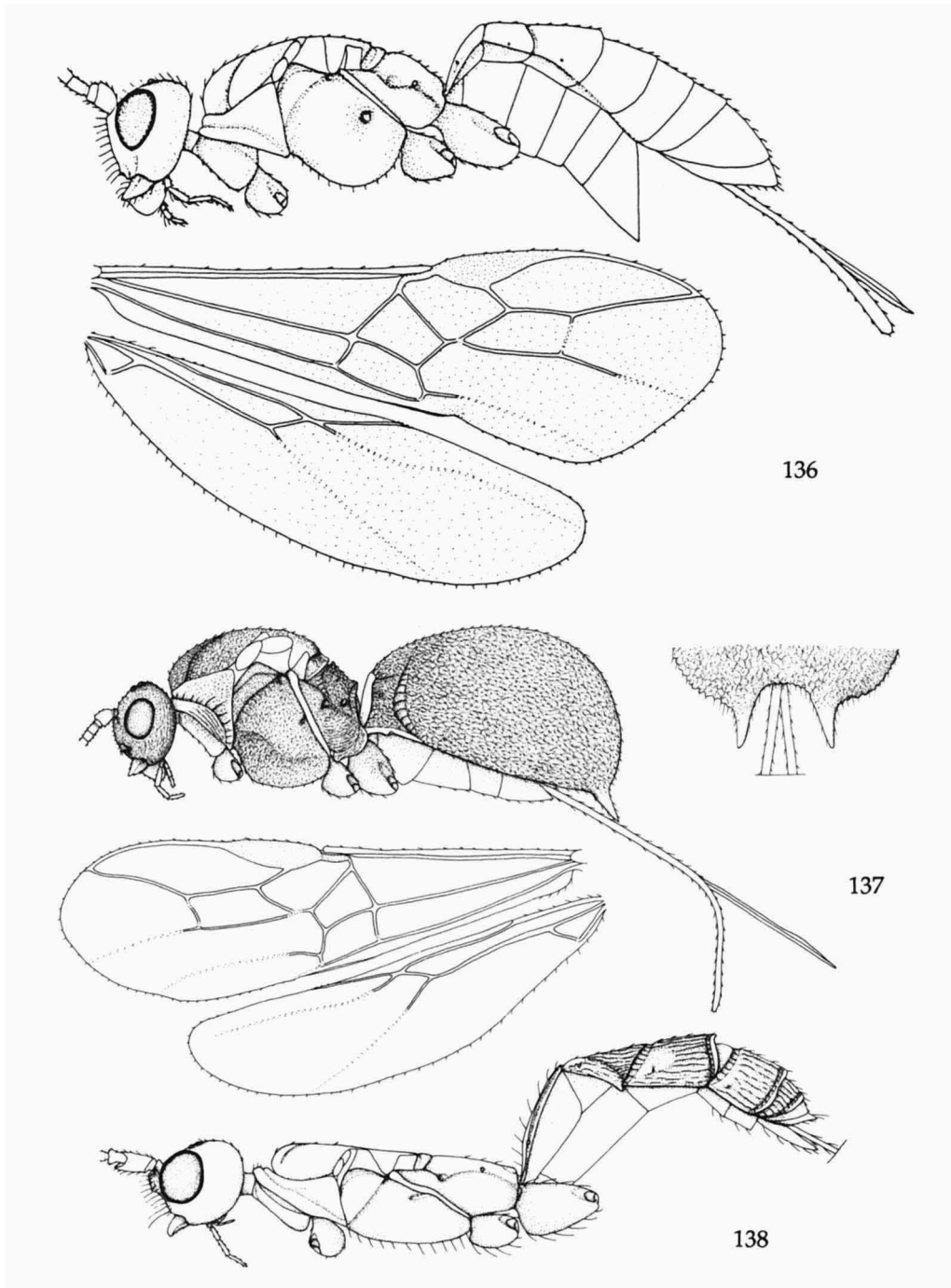


Fig. 134, Hormiini (*Pseudohormius*), ♀; fig. 135, Telengaiinae (*Telengaia*), ♀. 134, 135, habitus and wings.



Figs. 136-138, Braconinae (*Bracon*, *Physaraia*, and *Odontoscapus*, respectively), ♀♀. 136, 137 (latter including apex of metasoma), habitus and wings; 138, habitus.

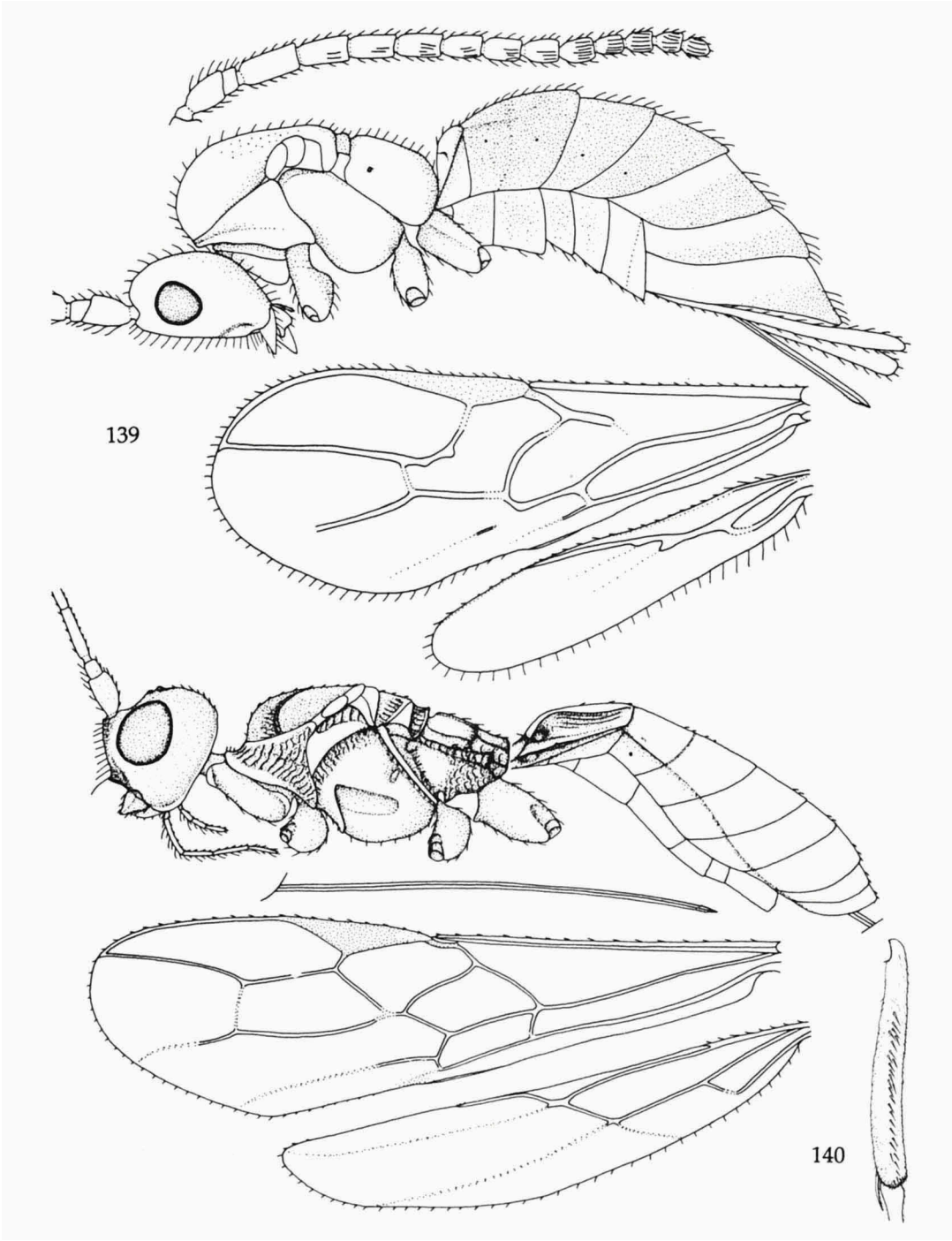


Fig. 139, Ypsistocerinae (*Ypsistocerus*), ♀; fig. 140, Doryctinae (*Ontsira*), ♀. 139, 140 (including fore tibia), habitus and wings.

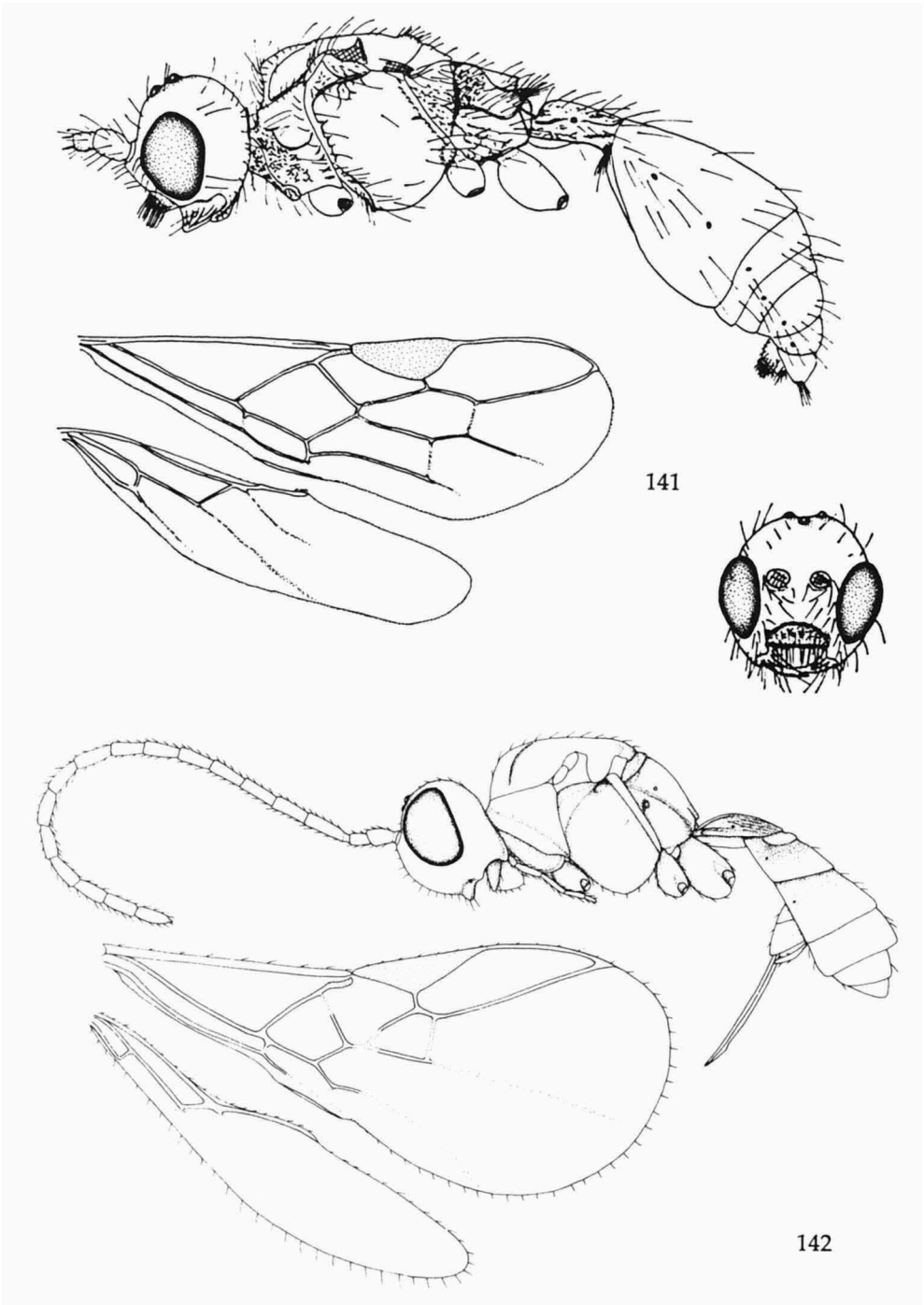


Fig. 141, Apozyginae (*Apozyx*), ♂; fig. 142, Gnamptodontinae (*Gnamptodon*), ♀. 141 (including frontal aspect of head), 142, habitus and wings; 141 after Mason, 1978.

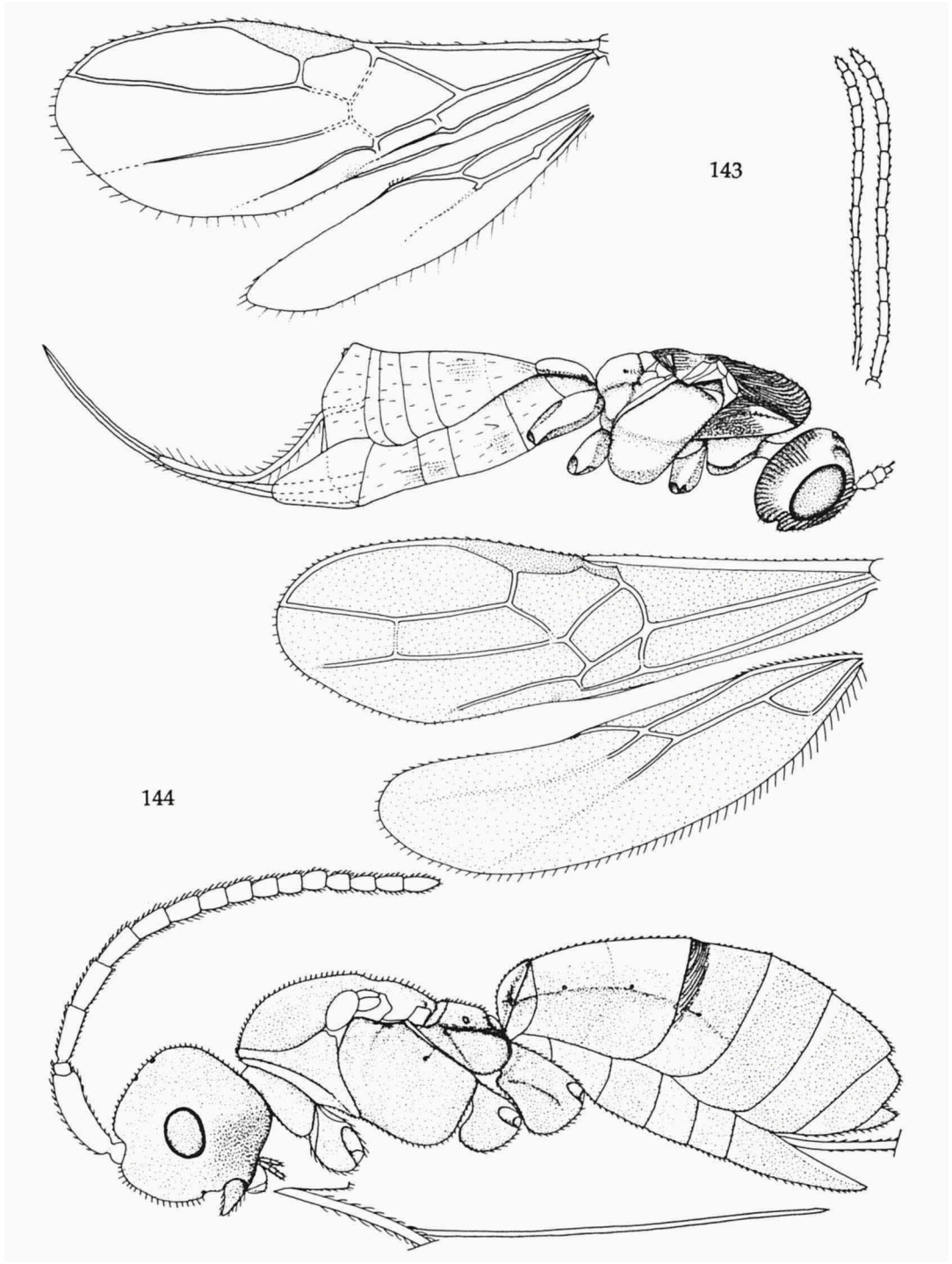
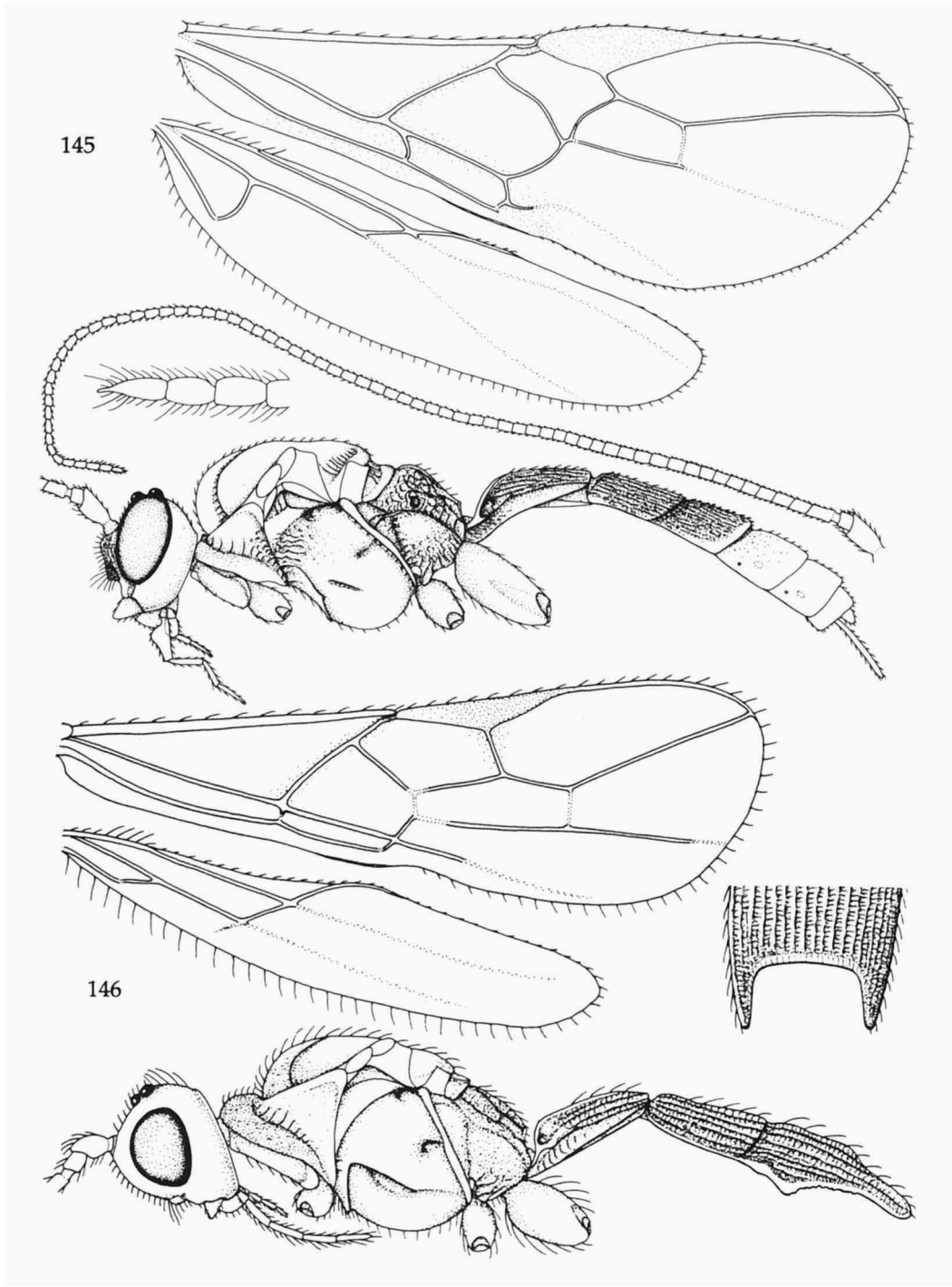


Fig. 143, Mesostoinae (*Mesostoa*), ♀; fig. 144, Vaepellinae (*Vaepellis*), ♀. 143 (including lateral and frontal aspects of flagellum), 144, habitus and wings.



Figs. 145, 146, Rogadinae s.s. (*Rogas*, ♀ and *Acanthormius*, ♂, respectively). 145, 146 (including apex of metasoma), habitus and wings.

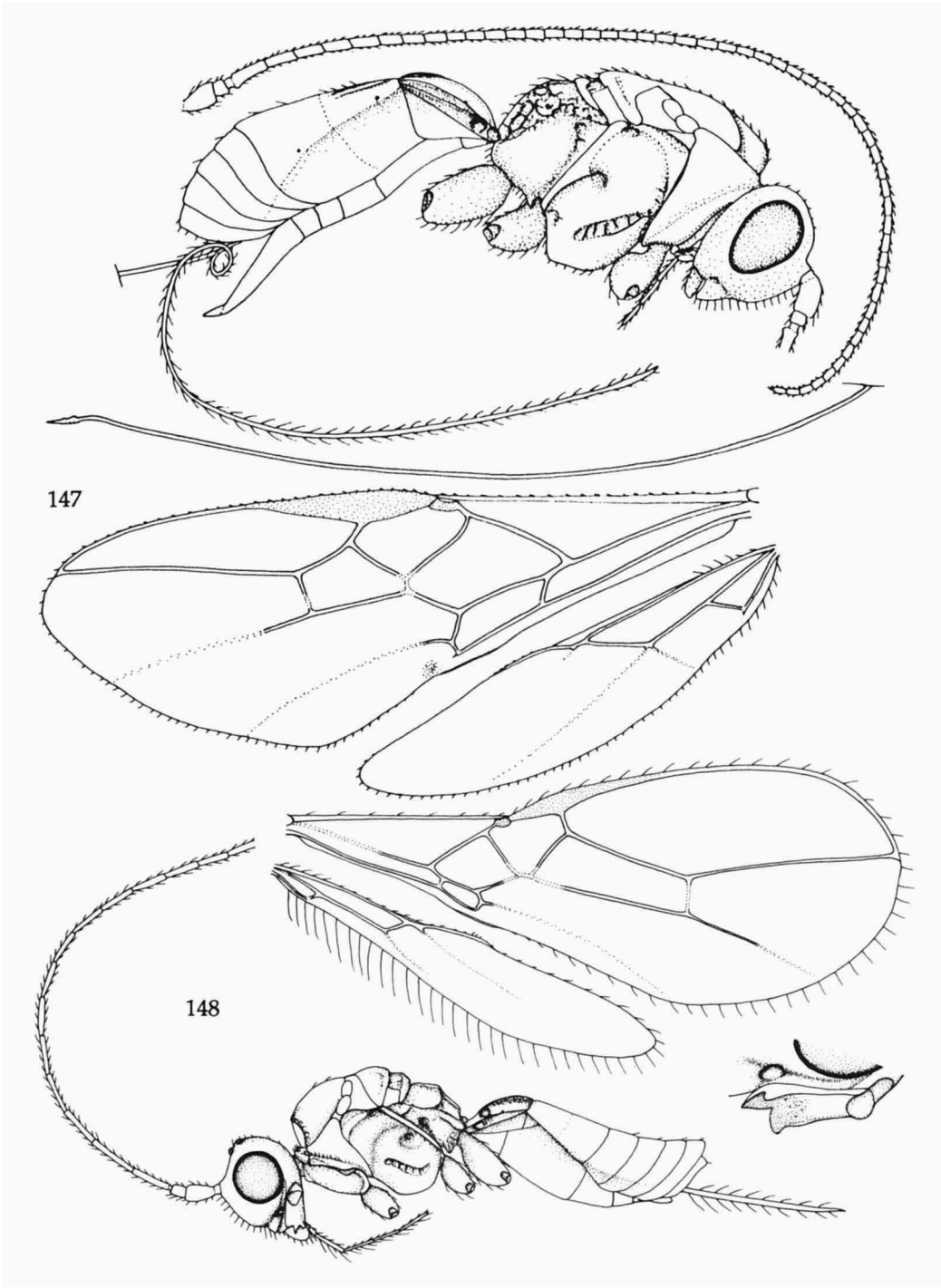


Fig. 147, Opiinae (*Diachasmimorpha*), ♀; fig. 148, Alysiinae (*Phaenocarpa*), ♀. 147, 148 (including detail of left mandible), habitus and wings.

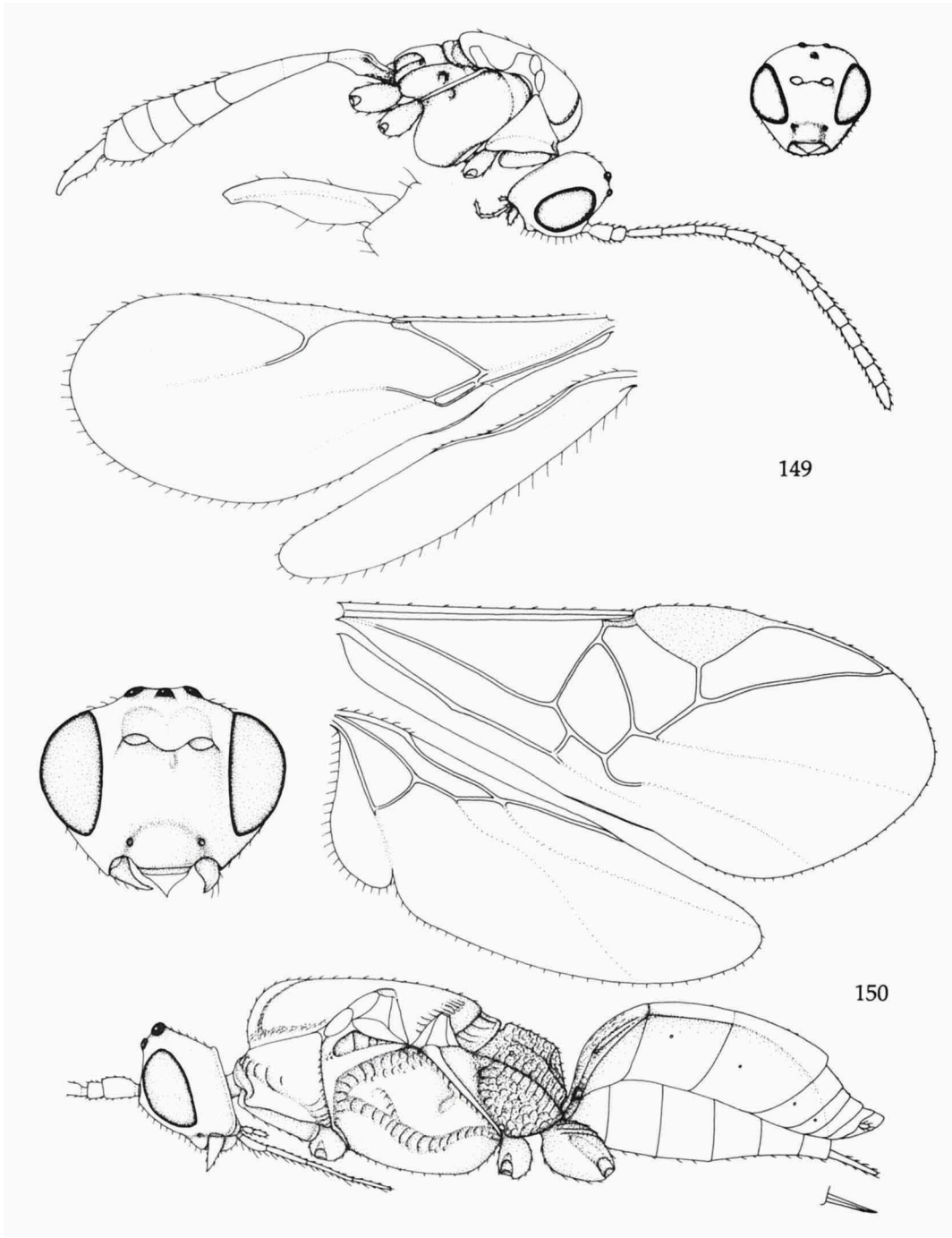


Fig. 149, Aphidiinae (*Monoctonus*), ♀; fig. 150, Ecnomiinae (*Ecnomios*), ♀. 149, 150, habitus, wings and frontal aspect of head.

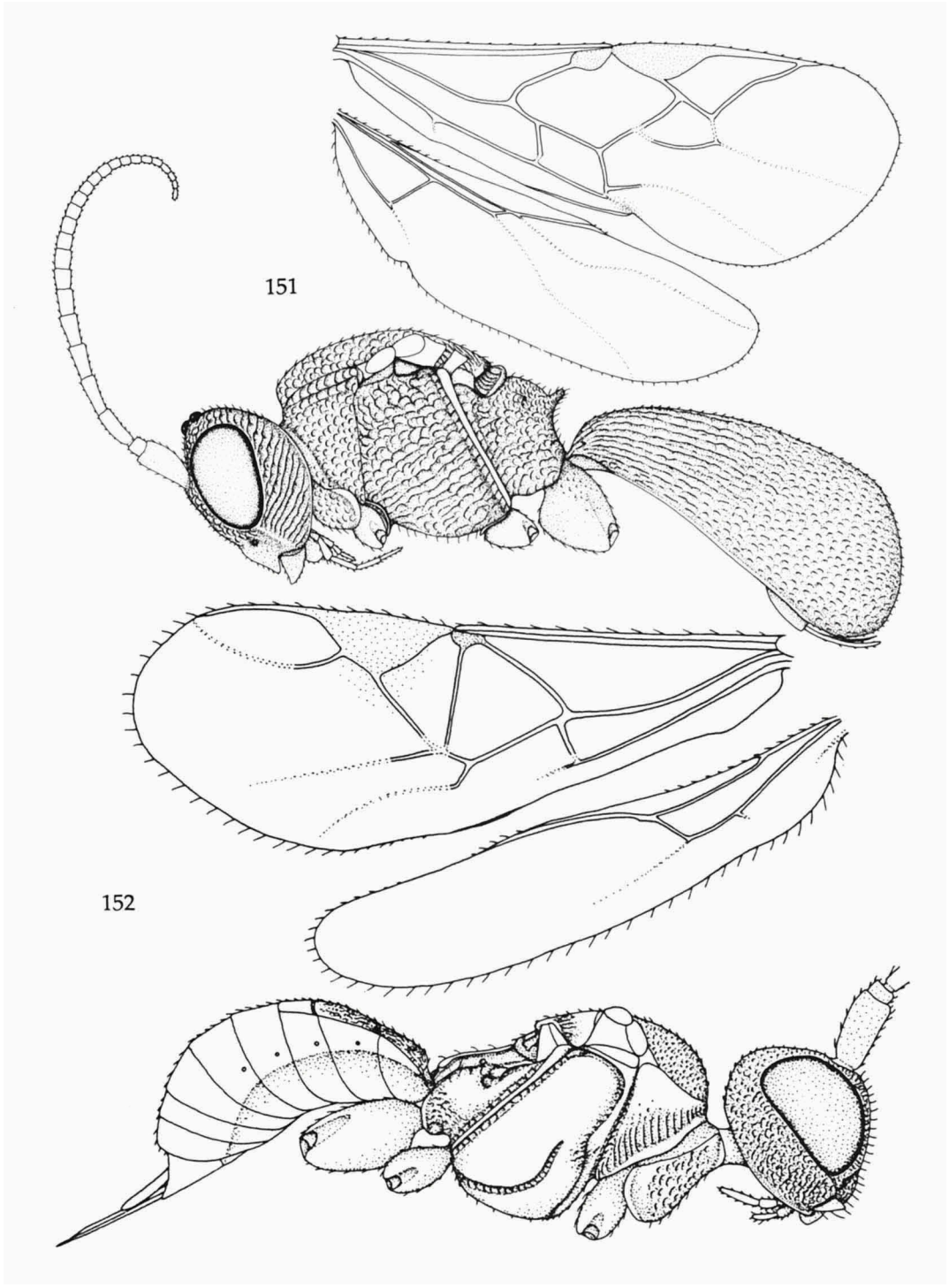


Fig. 151, Cheloninae (*Chelonus*), ♀; fig. 152, Adeliinae (*Paradelius*), ♀. 151, 152, habitus and wings.

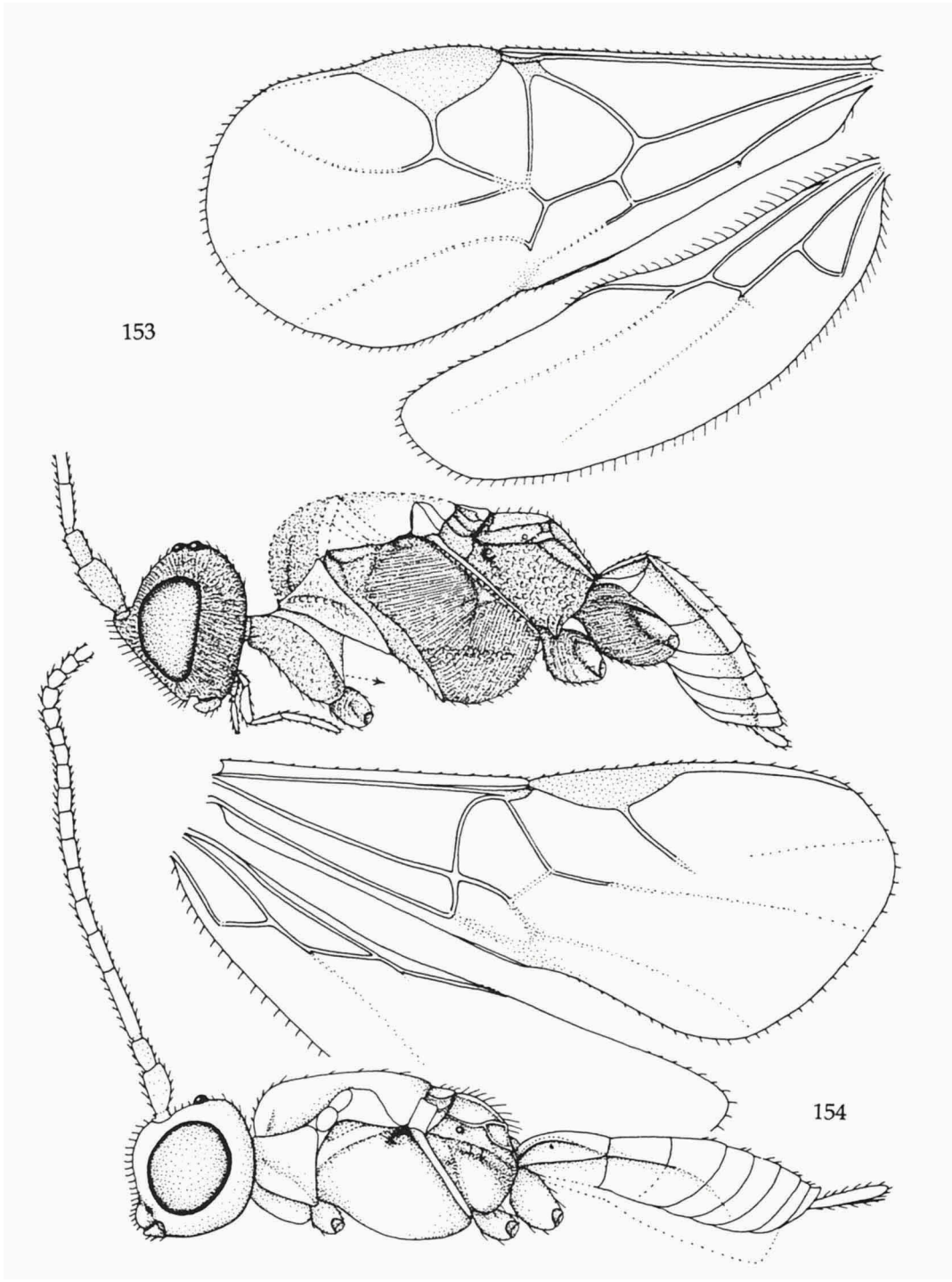


Fig. 153, Dirrhopiinae (*Dirrhope*), ♀; fig. 154, Muesebeckiini (*Oligoneurus*), ♀. 153, 154, habitus and wings.

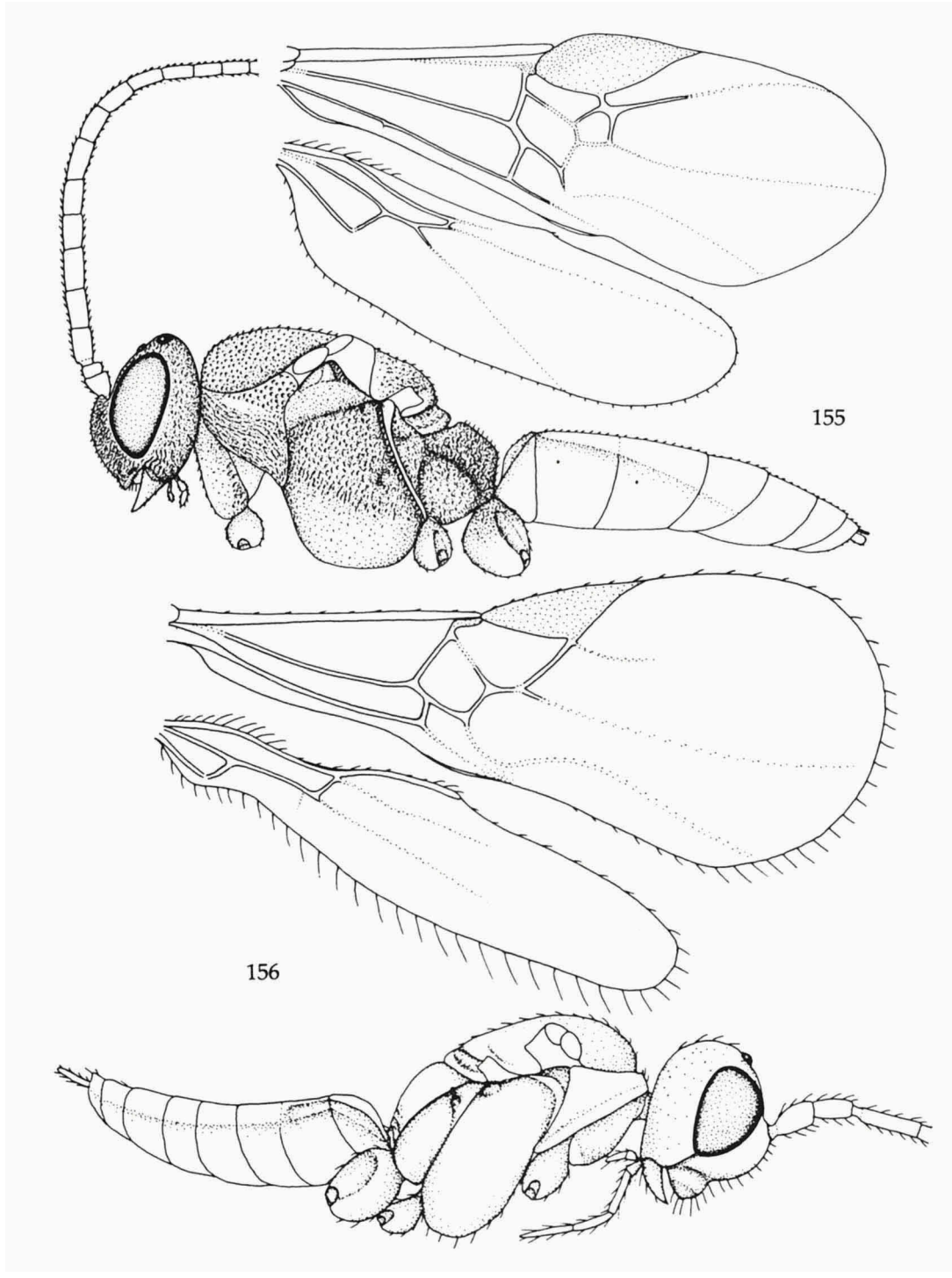


Fig. 155, Neoneurinae (*Euneoneurus*), ♂; fig. 156, Miracinae (*Mirax*), ♀. 155, 156, habitus and wings.

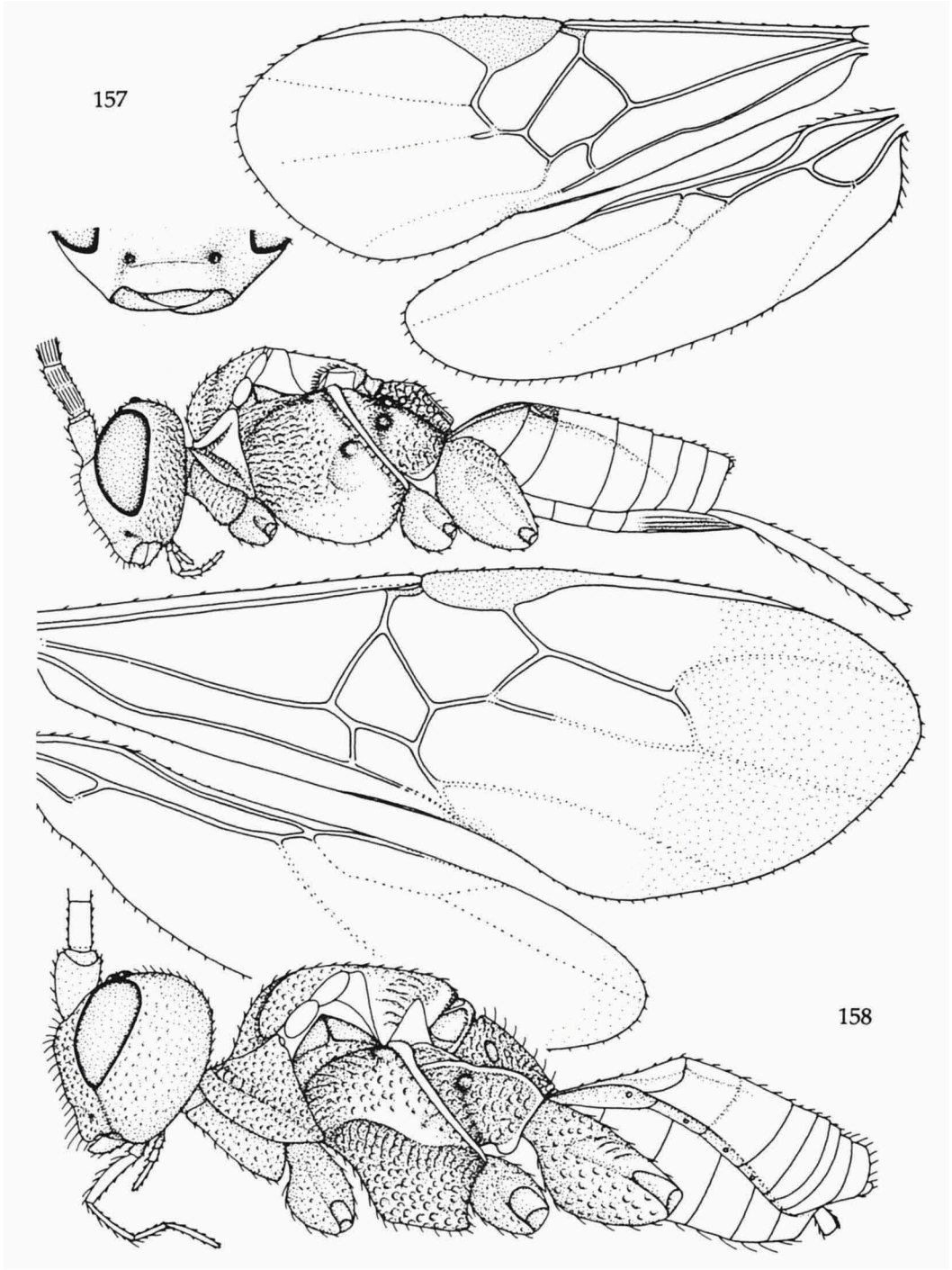


Fig. 157, Microgastrinae (*Apanteles*), ♀; fig. 158, Cardiochilinae (*Hartemita*), ♀. 157 (including detail of clypeus), 158, habitus and wings.

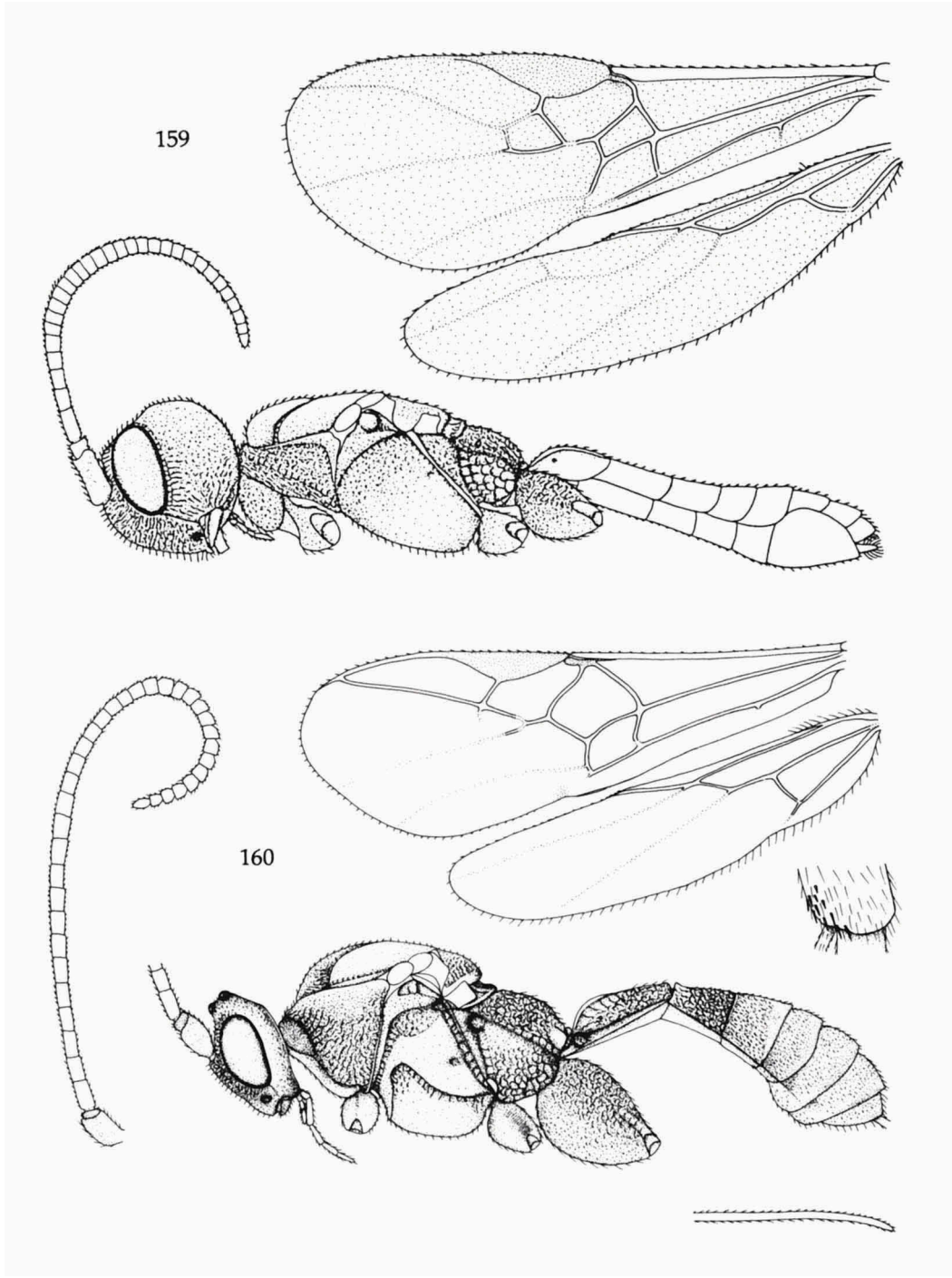


Fig. 159, Khoikhoiinae (*Khoikhoia*), ♀; fig. 160, Orgilinae (*Orgilus*), ♀. 159 (including apex of hind tibia), 160, habitus and wings.

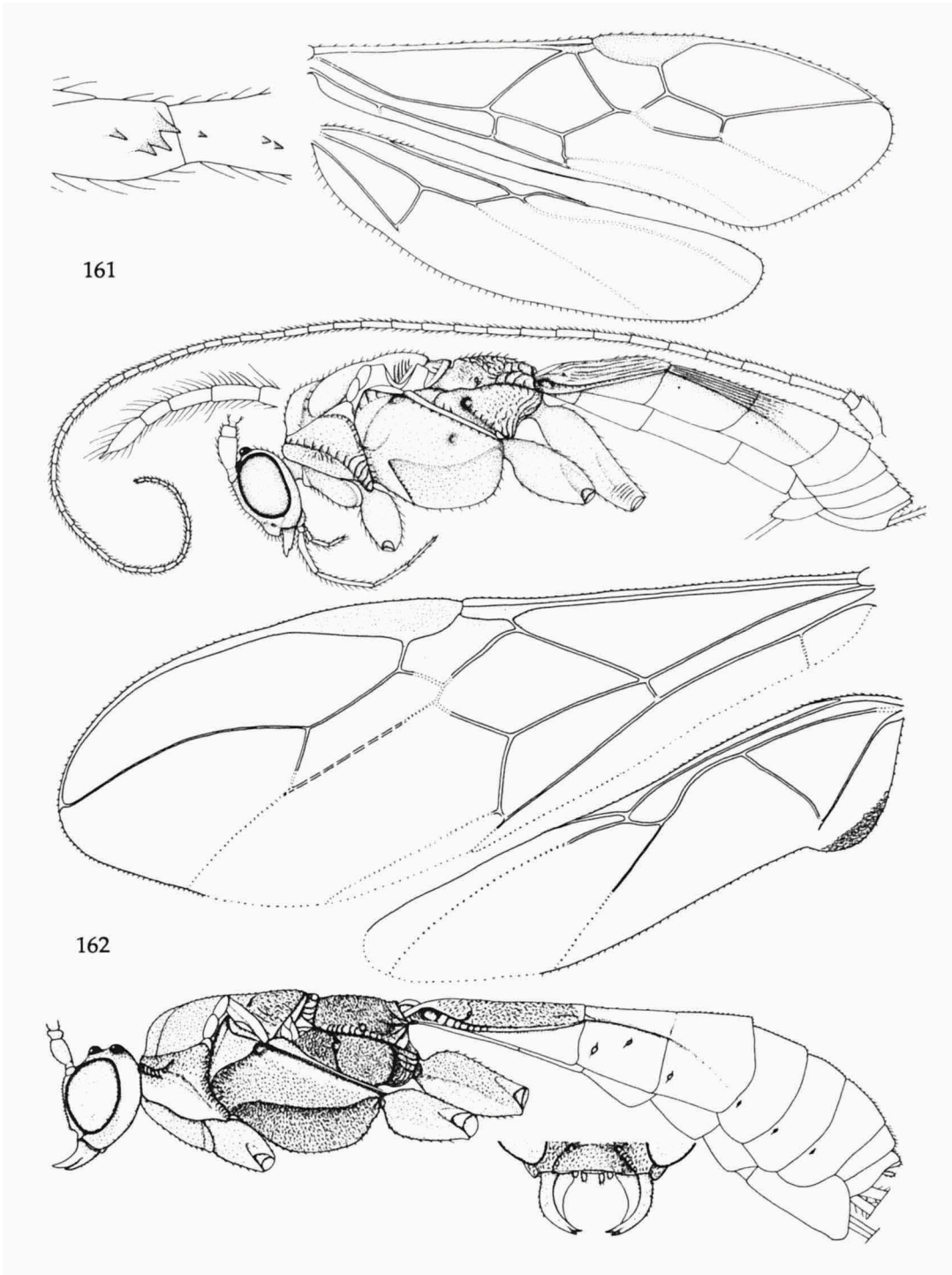


Fig. 161, Macrocentrinae (*Macrocentrus*), ♀; fig. 162, Amicrocentrinae (*Amicrocentrum*), ♀. 161 (including hind trochantellus), 162 (including detail of palpi), habitus and wings.

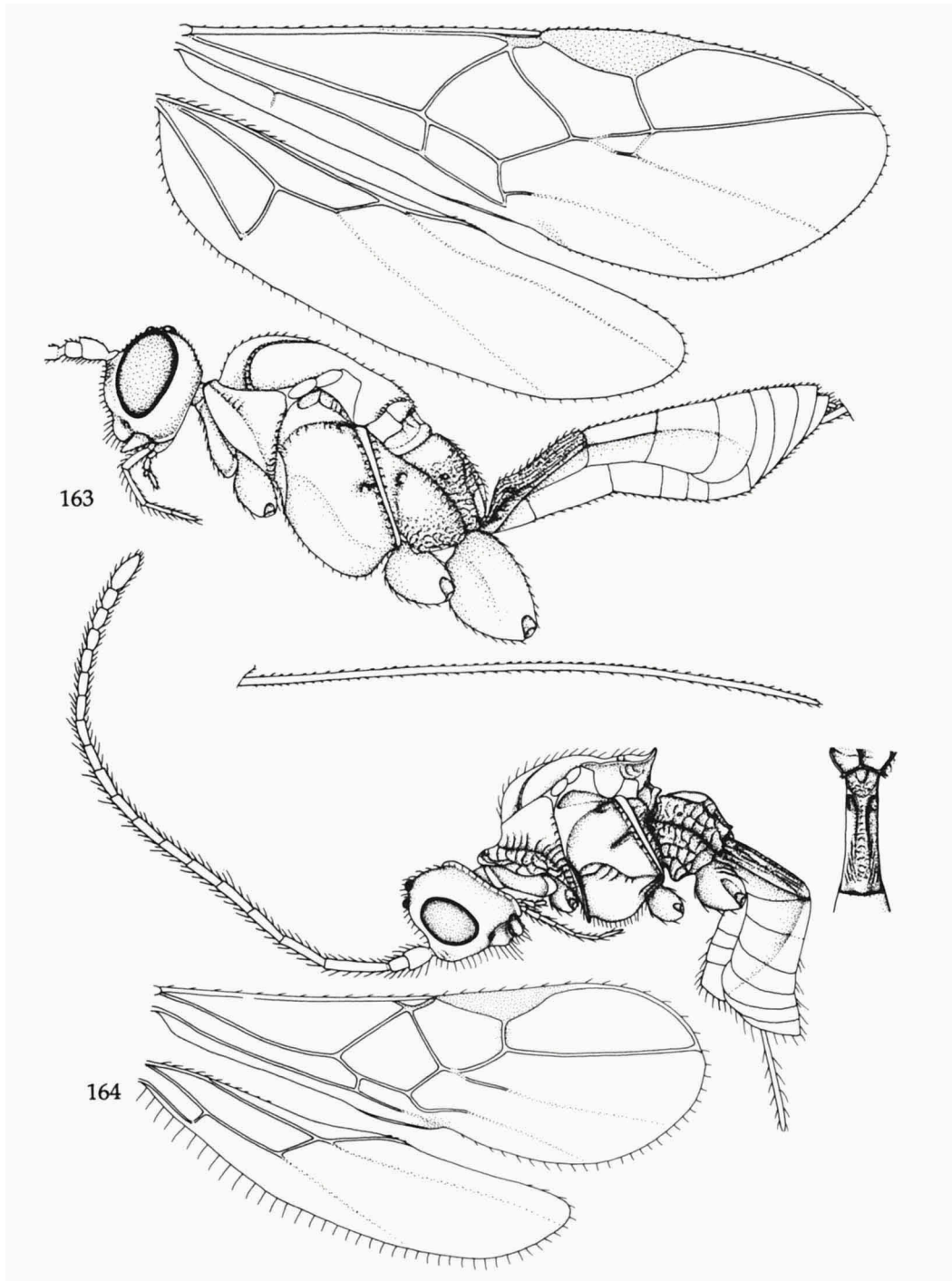


Fig. 163, Microtypinae (*Microtypus*), ♀; fig. 164, Blacinae (*Blacus*), ♀. 163, 164 (including dorsal aspect of first metasomal tergite), habitus and wings.

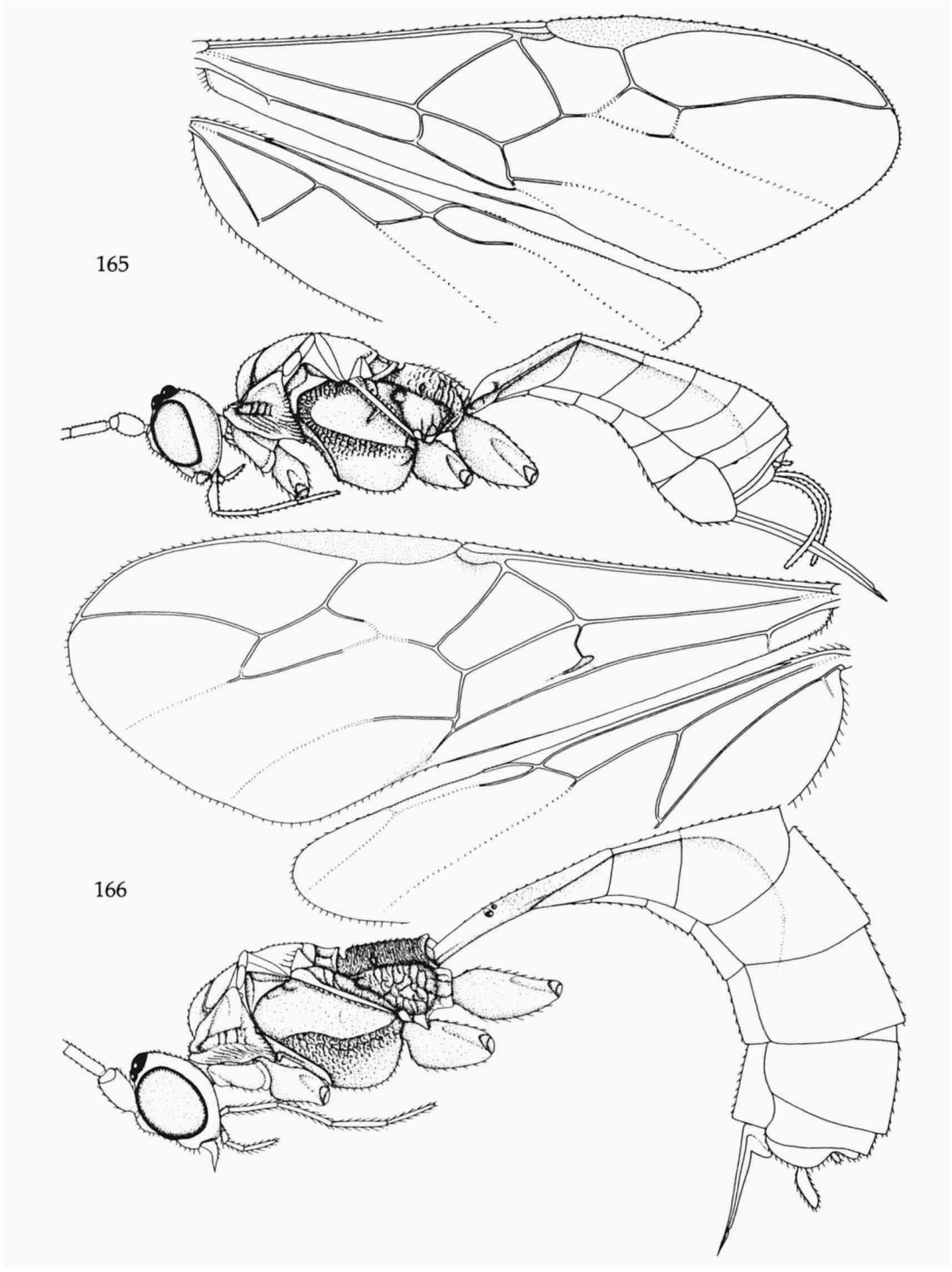


Fig. 165, Homolobinae (*Homolobus*), ♀; fig. 166, Xiphozelinae (*Xiphozele*), ♀. 165, 166, habitus and wings.

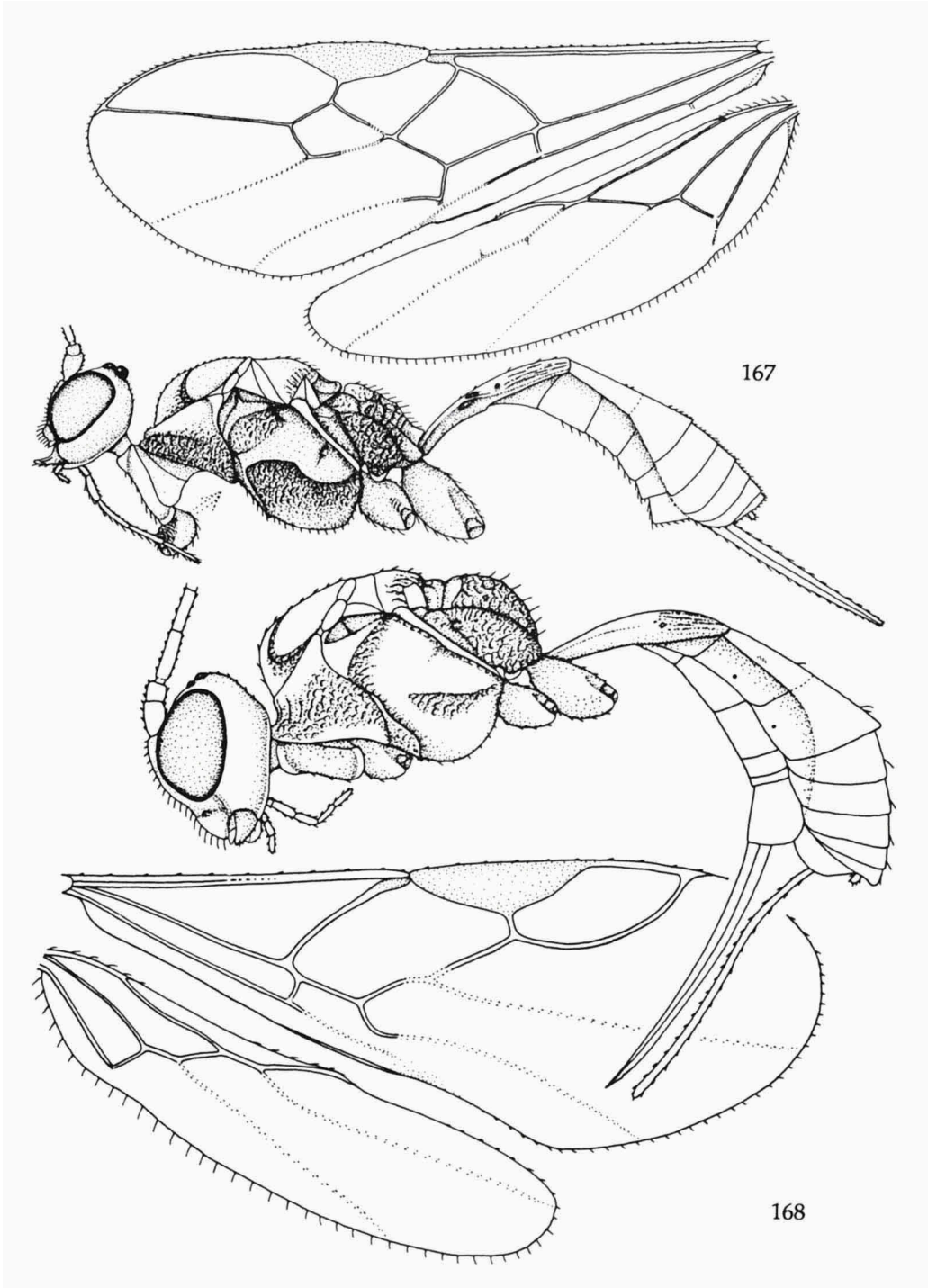


Fig. 167, Meteorini (*Zele*), ♀; fig. 168, Euphorinae s.s. (*Microctonus*), ♀. 167, 168, habitus and wings.

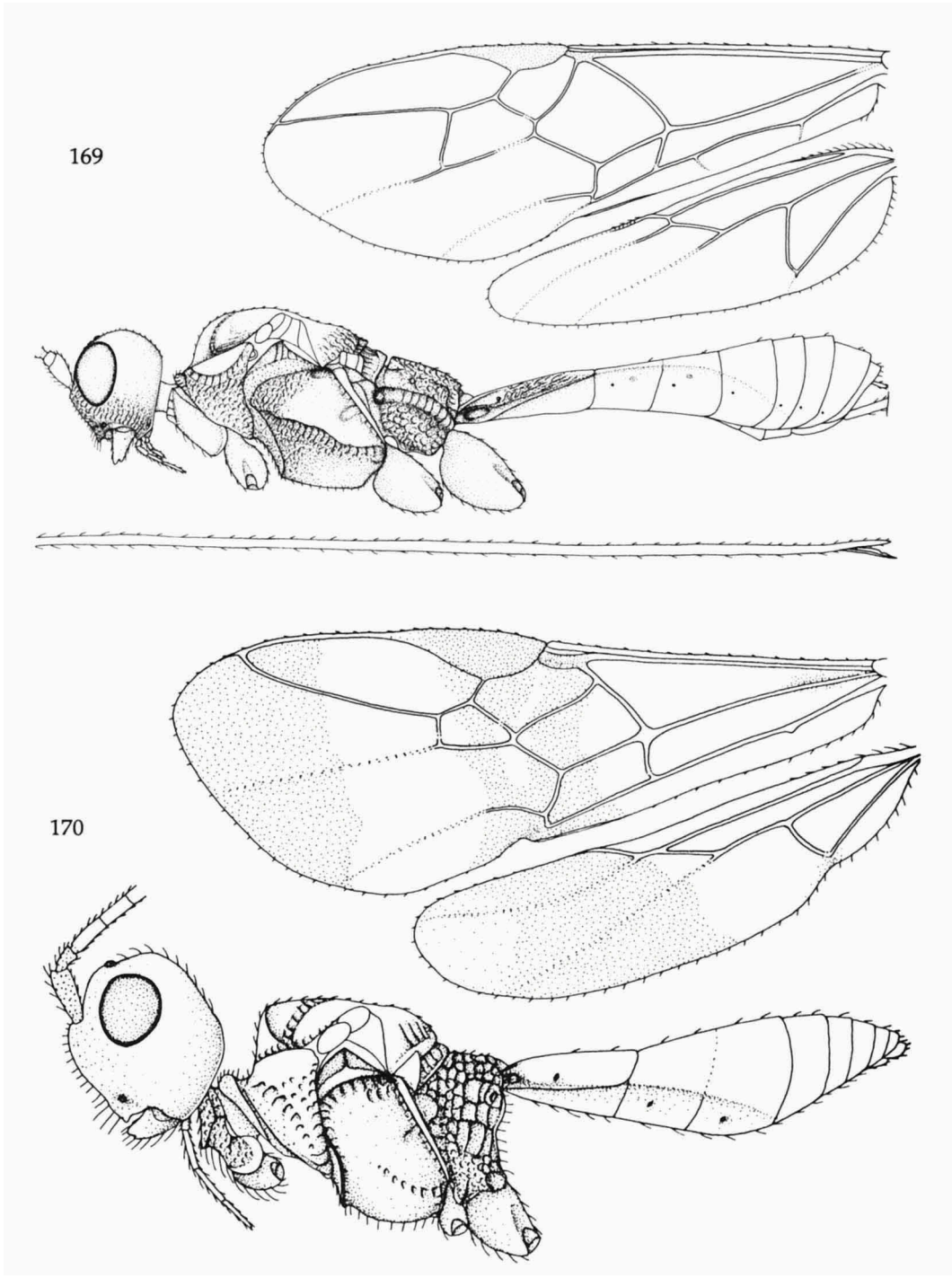
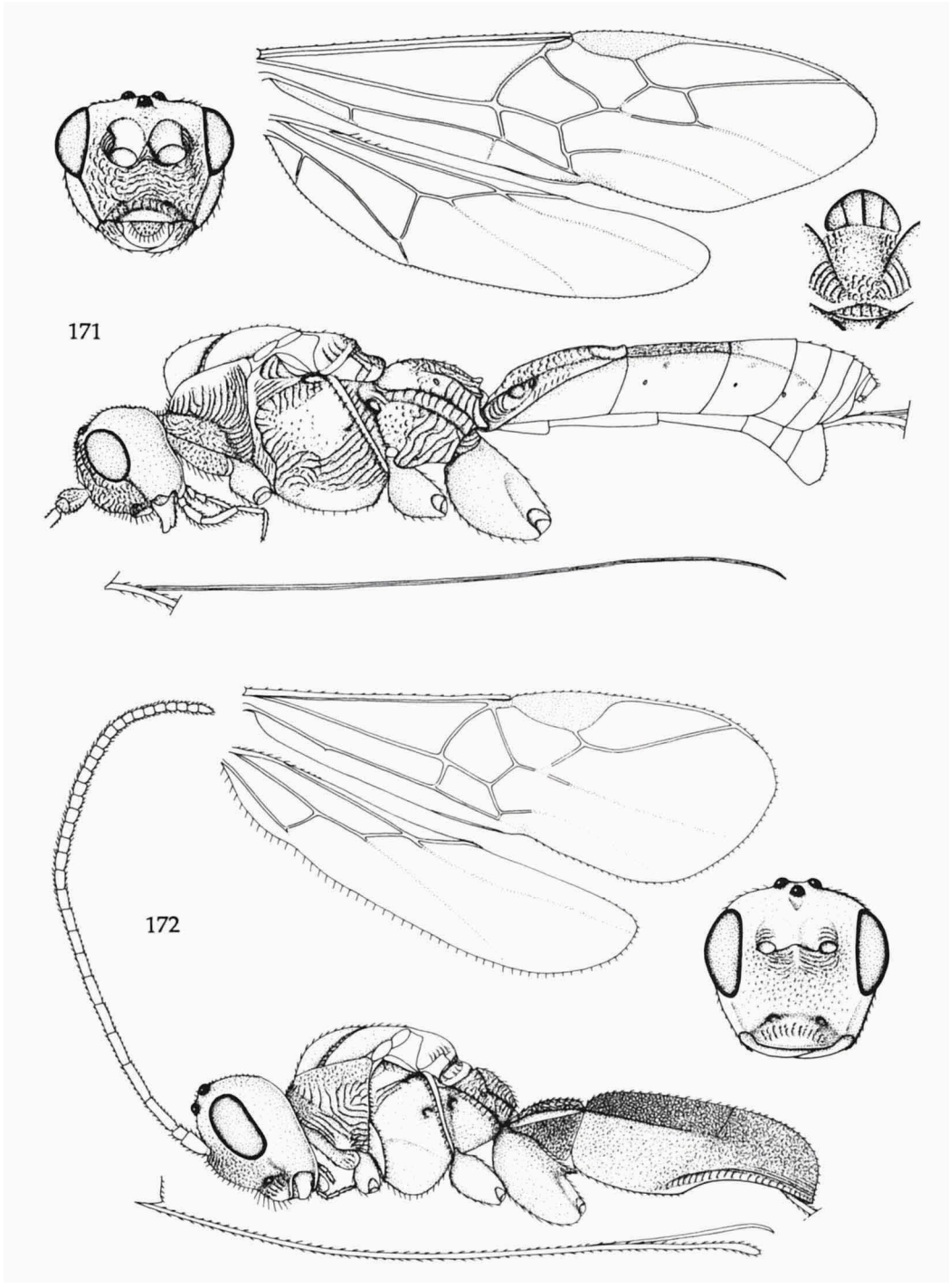


Fig. 169, Brulleiini (*Brulleia*), ♀; fig. 170, Cenocoeliinae (*Capitonius*), ♂. 169, 170, habitus and wings.



Figs. 171, 172, Helconinae s.s. (*Helcon*, and *Polydegmon*, respectively), ♀♀. 171 (including scutellum), 172, habitus, wings and frontal aspect of head.

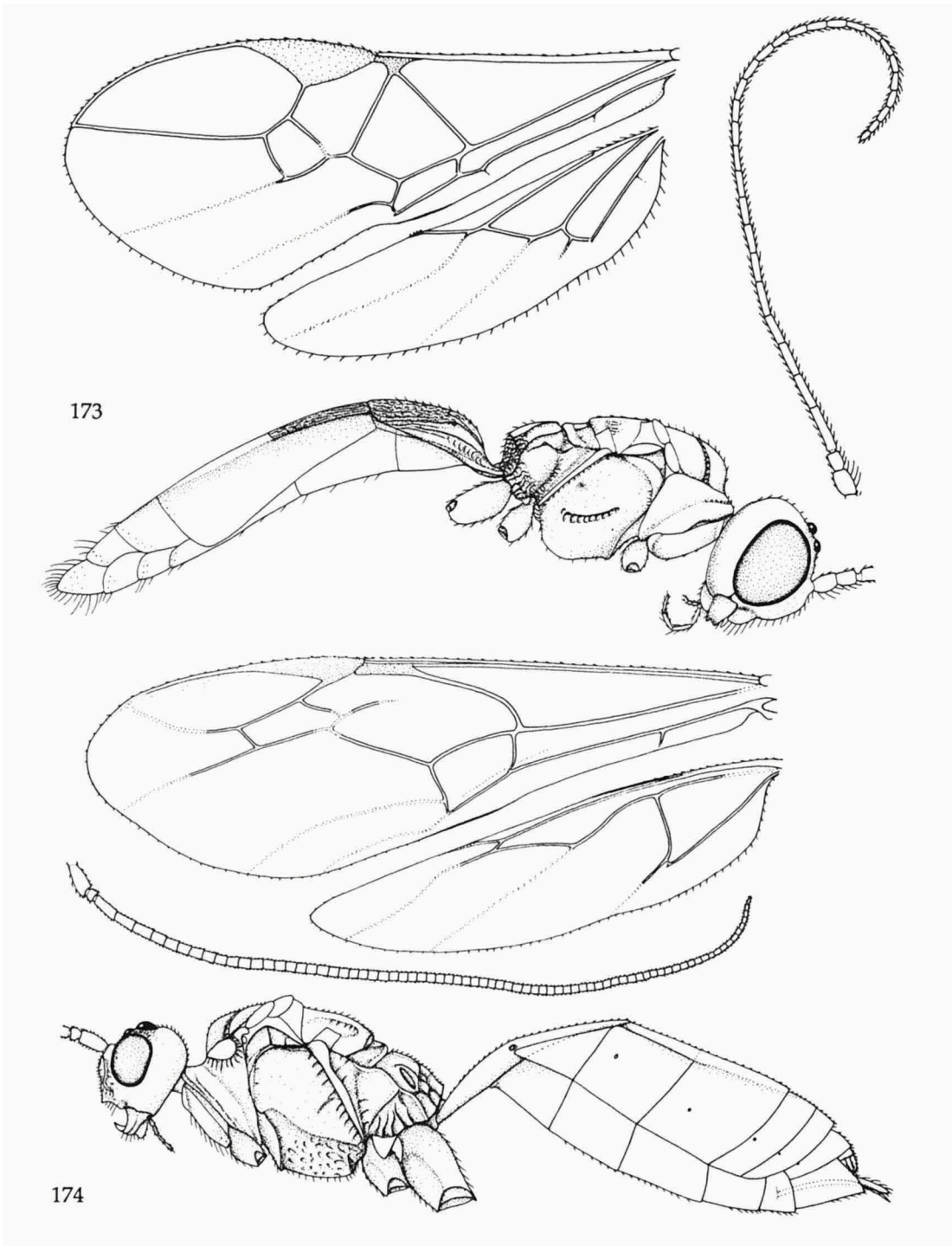


Fig. 173, Meteorideinae (*Meteoridea*), ♀; fig. 174, Cercobarconinae (*Rhamphobarcon*), ♀. 173, 174, habitus and wings.

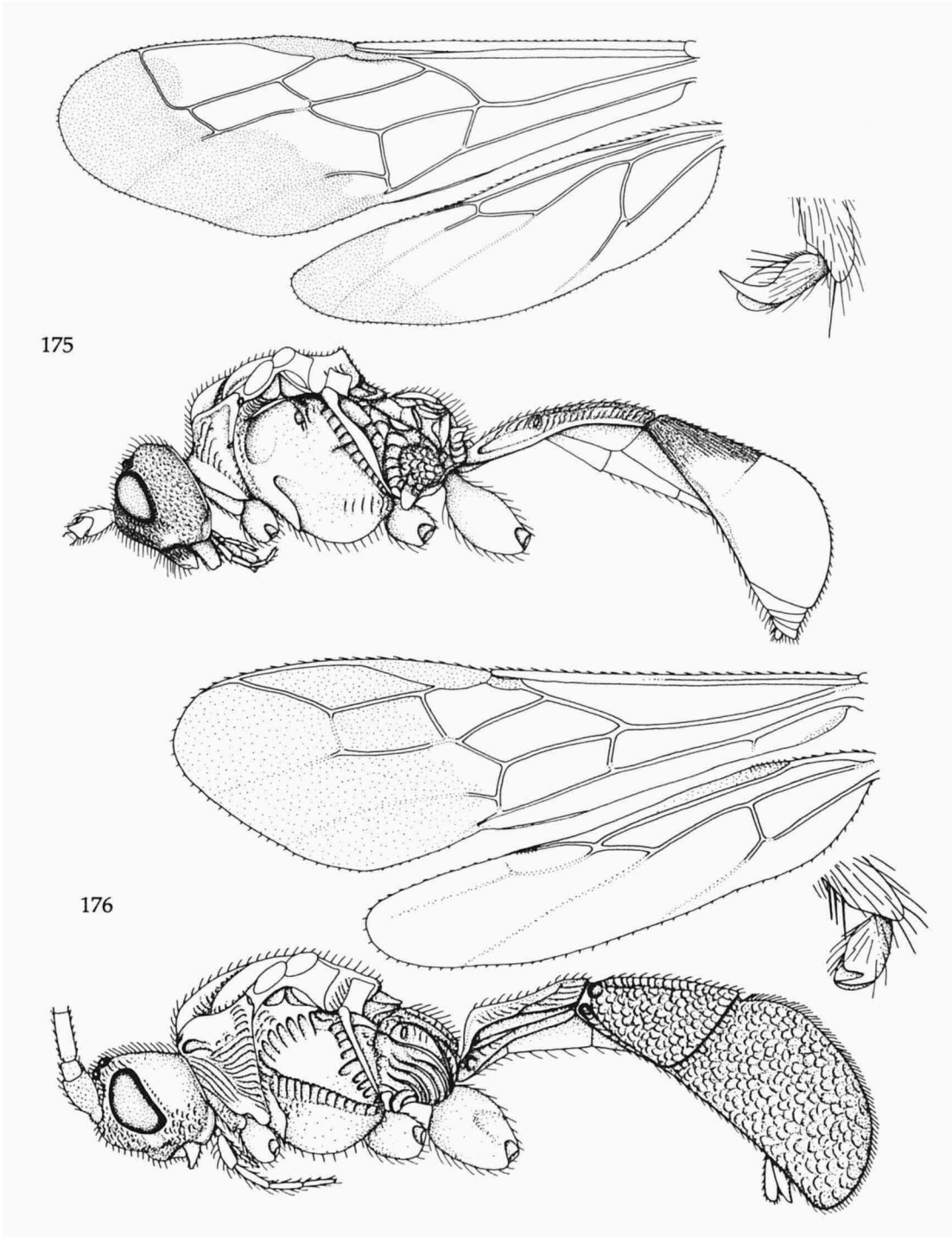


Fig. 175, Trachypetinae (*Trachypetus*), ♂; fig. 176, Sigalphinae (*Sigalphus*), ♀. 175, 176, habitus, wings and tarsal claw.

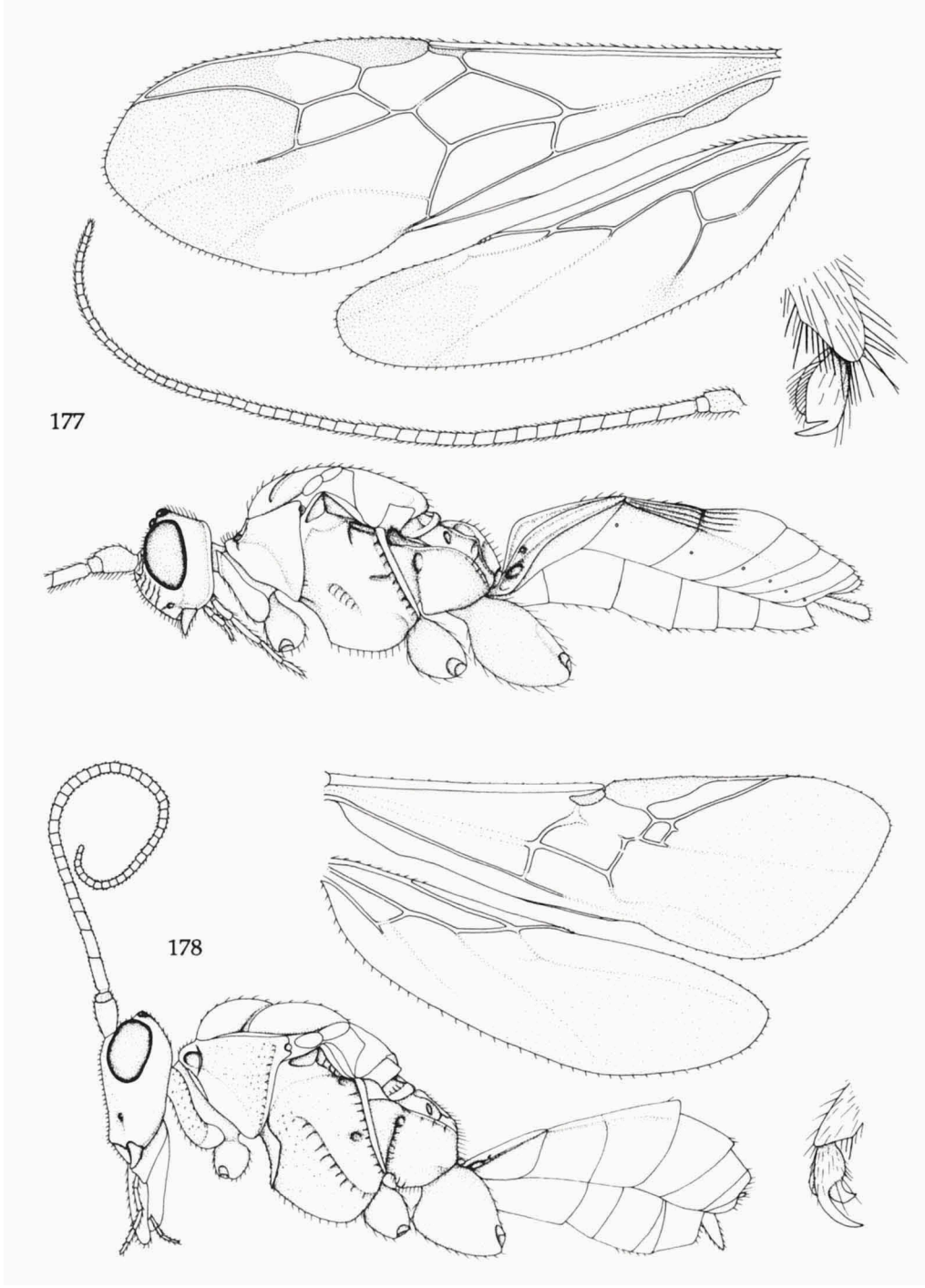


Fig. 177, Pselaphaninae (*Pselaphanus*), ♀; fig. 178, Agathidinae (*Monophrys*), ♀. 177, 178, habitus, wings and tarsal claw.

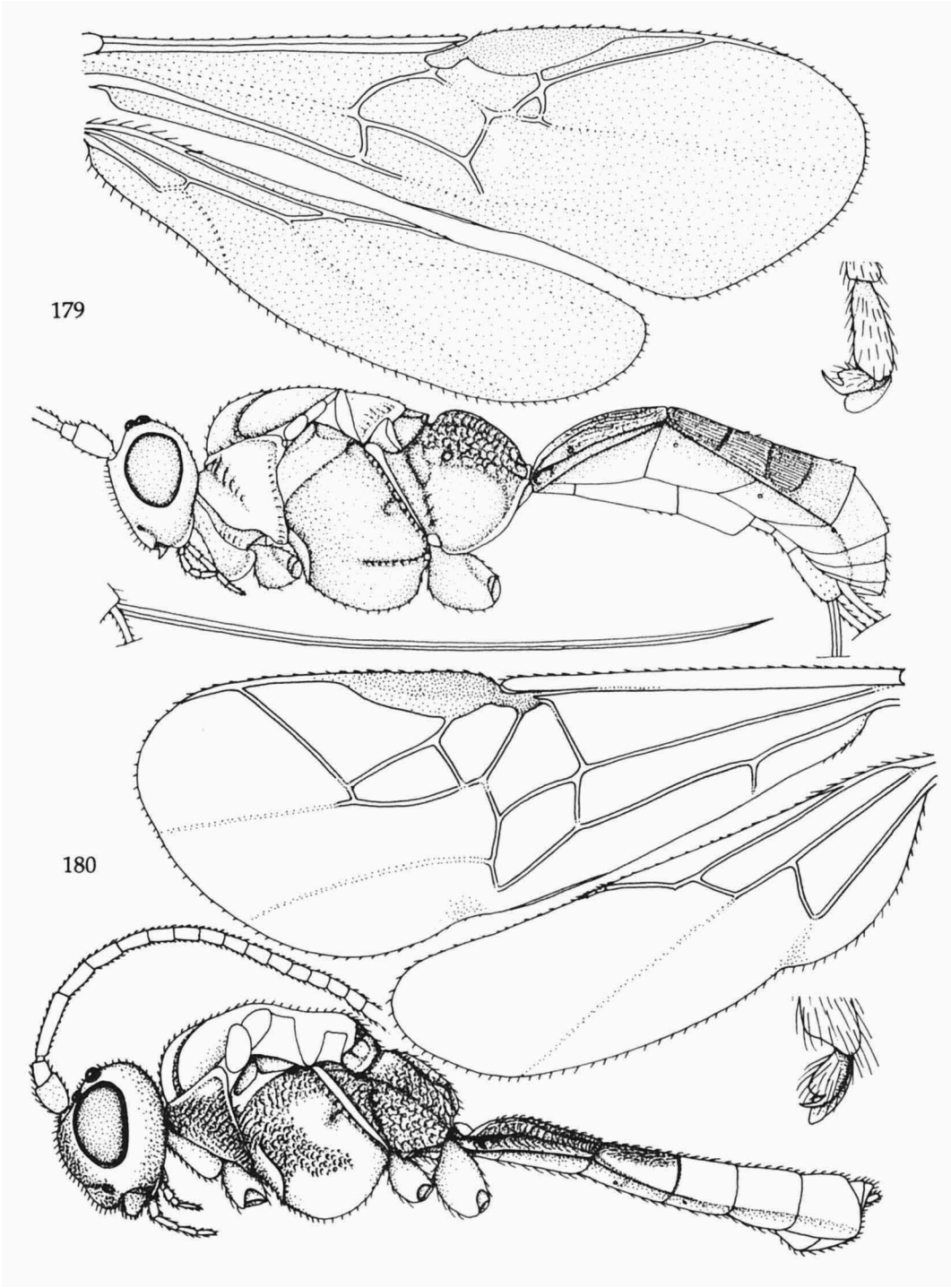


Fig. 179, Agathidinae (*Bassus*), ♀; fig. 180, Ichneutinae (*Ichneutes*), ♀. 179, 180, habitus, wings and tarsal claw.