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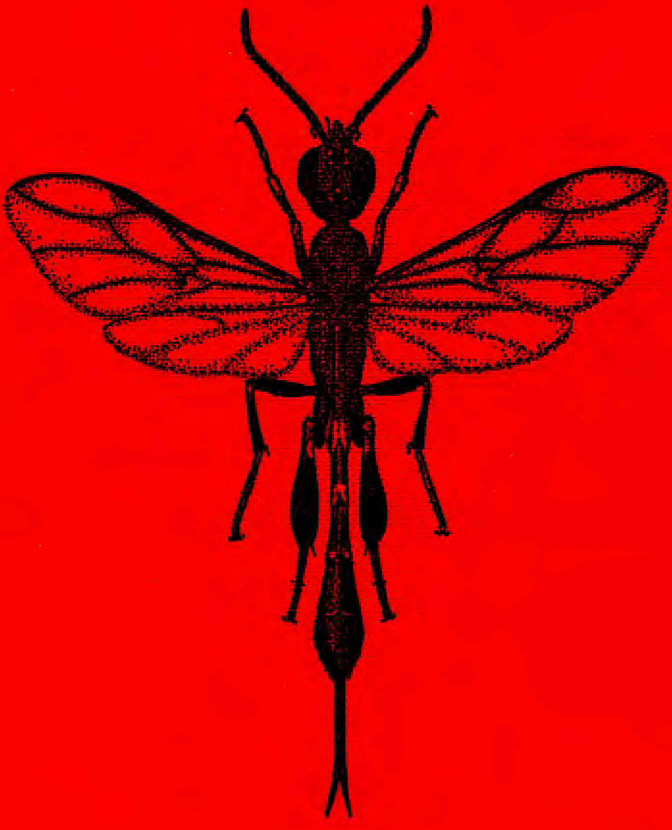
Handbooks for the Identification of British Insects
Vol. VI, Part 1

HYMENOPTERA

INTRODUCTION AND KEY TO FAMILIES

O. W. Richards



ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

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Identification of British Insects

Vol. VI, Part 1

HYMENOPTERA

INTRODUCTION AND KEY TO FAMILIES

Second edition

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CONTENTS

FOREWORD

The author has incorporated new morphological, behavioural, life-history and taxonomic information in this new edition, and brought up-to-date the whole of his text. The original drawings have been retained, but modified where necessary; many are reproduced to a larger scale than in the first edition.

EDITOR
3rd January 1977

CORRIGENDA

Page 3, fig. 7: *for* epicranial suture *read* epicranial sulcus
Page 17, fig. 34: *for* pleural suture *read* pleural sulcus
Page 73, fig. 194: *for* HALICTUS *read* LASIOGLOSSUM

HYMENOPTERA
INTRODUCTION AND KEY TO FAMILIES

OWAIN WESTMACOTT RICHARDS

INTRODUCTION

THE order Hymenoptera possibly contains more species than any other group of British insects. The smaller parasitic species are still not well known but seem to be very numerous. Nixon, for instance, in the 1940's described more than seventy new British species in the genus *Dacnusa*. In the ICHNEUMONIDAE, many genera are thought to contain twice as many British species as have as yet been recorded. There is also a very great deal to discover about the biology of most groups.

The most generalized Hymenoptera are found amongst the sawflies. In this group most of the characters of a primitive winged insect may be found, though not necessarily all combined in one species. The wing-venation alone is always of a peculiar Hymenopterous type which has proved difficult to interpret. The structure of the higher Hymenoptera has become extremely specialized and has presented many problems in morphology. Most of the more important of these have now been solved, though there are still many minor points unsettled. Our knowledge of their structure has grown piecemeal and terminology has often been devised for a single family or group rather than for the whole order. Only rather recently has much attempt been made to unify the nomenclature with that employed in other insect orders. A thorough survey of the structure of the whole order is therefore necessary, together with an attempt to co-ordinate the terms which have been applied to the same structures in different groups.

It may be noted here that the greatest specialization of structure occurs in some of the Parasitica, whereas the greatest specialization of behaviour occurs in the Aculeata. Such insects as the Proctotrupids are much more specialized in structure than a wasp or even a honey-bee, though the social Hymenoptera show the highest peak in the evolution of invertebrate behaviour.

It is a pleasure to acknowledge the help I have received from numerous colleagues in the British Museum (Natural History). Dr Perkins, in particular, has made a number of discoveries in structure or interpretation which have been incorporated without further acknowledgement. He also greatly helped me with the key to the families. Dr M. G. Fitton updated my nomenclature of the Ichneumonidae. The illustrations of whole insects numbered in Roman figures were drawn by Mrs C. A. O'Brien.

COMPARATIVE MORPHOLOGY

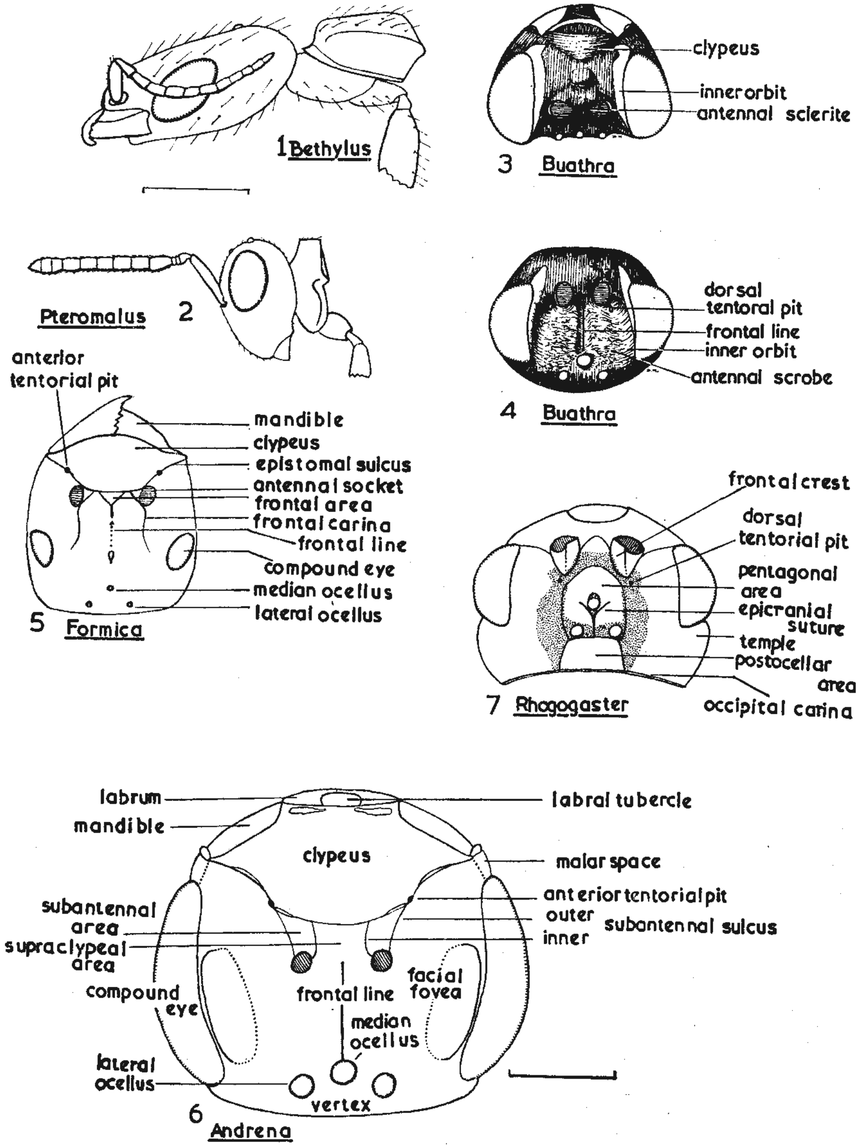
SCULPTURE

The surface of the body in Hymenoptera is often sculptured in a variety of ways (punctate, striate, etc.). The paper by Eady (1968) is useful in explaining the descriptive terms in general use.

HEAD AND ITS APPENDAGES

The head of Hymenoptera is characteristically *orthognathous* (fig. 2) with its long axis vertical and the mouthparts directed downwards, though all stages to a *prognathous* head (fig. 1) with mouthparts directed forwards occur. Its dorsal surface is, therefore, normally directed anteriorly and its ventral one posteriorly. It is probably more convenient to describe the head in the orientation in which it will normally be found when the insect is at rest (or dead).

The most obvious landmarks for the study of a Hymenopterous head are the compound eyes, the antennal sockets, the clypeus, the ocelli, the foramen and the proboscidial fossa. The *compound eyes* (figs 5, 6) in most Hymenoptera occupy the greater part of the side of the head. They are very reduced in many worker ants, though in British forms always represented by at least one facet, and are relatively small in some of the Parasitica. Sometimes numerous hairs arise from between the facets, and not infrequently the inner margin is excised just above the level of the antennal sockets (e.g., *Vespa*). The part of the head within this excision is known as the *ocular sinus*. The front of the head between the eyes is termed the *face*; it is made up of the clypeus, lower face and upper face (see below). Normally, the antennae are articulated in sockets at about the middle of the face, but the exact position of the *antennal sockets* (fig. 5) varies in different groups and they may be situated very low down, near the mandibles. The antennal socket is surrounded by a sulcus defining a narrow *antennal sclerite* (fig. 3); in ICHNEUMONIDAE the shape of this sclerite is of importance in classification and in some genera (e.g., *Tryphon*) is produced into large dorsal processes. The *clypeus* (figs 5, 6) includes the greater part of the face below the antennal sockets in most Symphyta and Aculeata; in ants it may even extend up between them. It is usually smaller and much further removed from the antennal sockets in the Parasitica (figs 3, 15); in such forms the area between the antennal sockets, the clypeus and the compound eyes may be termed the *lower face*. Laterally and dorsally the clypeus is defined by the curved *epistomal sulcus* (fig. 5). On each side, usually near the top of the epistomal suture is a small pit, the *anterior tentorial pit* (figs 5, 6, 14), which is a useful landmark in species whose epistomal sulcus is largely obliterated. The pit marks the point where an arm of the tentorium, the internal skeleton of the head, is invaginated. The ventral margin of the clypeus supports the labrum and, primitively, one articulation of the mandibles (p. 9) is at each outer corner. The *ocelli* (figs 5, 6) lie near the top of the face; they are typically three in number but may be reduced or absent in wingless forms. They vary much in position; the distance from the outer edge of a lateral ocellus to the compound eye is the ocular-ocellar line, *OOL*, and the distance between the inner edges of the two lateral ocelli is the postocellar line, *POL*.



FIGS 1–7. (Scale-line, figs 1–2 = 0.5 mm; 3–7 = 1.0 mm) 1, *Bethylus cephalotes* (Först.) (Bethylidae) ♀. Head and prothorax from left side. Prognathous head. 2, *Pteromalus puparum* (L.) (Pteromalidae) ♀. Head and prothorax from left side. Orthognathous head. 3, *Buathra laborator* (Thunb.) (Ichneumonidae) ♂. Head in anteroventral view (antennae removed). 4, The same, head in antero-dorsal view (antennae removed). 5, *Formica rufa* L. (Formicidae) ☿. Head in anterior view (antennae removed). 6, *Andrena jacobi* Perk. (Andrenidae) ♀. Head in anterior view (antennae removed, hairs omitted). 7, *Rhogogaster viridis* (L.) (Tenthredinidae) ♀. Head in antero-dorsal view (antennae removed).

The ratio *POL*:*OOL* is of importance in the separation of species in several groups; the distance of the lateral ocelli from the back of the head may also be important. The *foramen* (fig. 8) (perhaps more correctly *foramen magnum*) is an approximately circular gap in the skeleton of the back of the head through which the internal organs pass from the head to the thorax, these two parts of the body being attached to one another by the cervical membrane. The *proboscidial fossa* (figs 9, 10, 11) is the hollow in the lower part of the posterior surface of the head into which the mouthparts are received when at rest. Primitively, it is nearly continuous with the foramen but in many forms a bridge (p. 7) is formed which separates them.

When these landmarks have been recognized, it is possible to study the morphology of the head in greater detail. The *labrum* (figs 6, 9, 10), primitively, is hinged to the ventral margin of the clypeus and is a transverse flap of not very different texture. Such a condition is seen, for instance, in *Tenthredo* (TENTHREDINIDAE), *Brachymeria* (CHALCIDIDAE) or *Apis* (APIDAE). But in every group there is a tendency for the line of attachment to move upwards on the under (or inner) side of the clypeus so that much or all of the labrum is hidden. When this happens, the labrum becomes thinner and paler and sometimes (PTEROMALIDAE) acquires an unusual shape. In the sawfly genus *Pamphilius*, the labrum is not only attached well up on the underside of the clypeus but is also bent back when at rest so as to cover the tip of the labium. In many bees, the labrum bears a central projection, the *labral tubercle* (fig. 6). Primitively, the ventral side of the labrum is continuous with the roof of the pharynx, but in some Hymenoptera, especially the higher forms (e.g., ICHNEUMONIDAE, most Aculeata), a second flap, usually membranous, arises from the point where the labrum and pharynx meet. This is the *epipharynx*; it is certainly not present or at least fully developed in all groups, but no comparative study of this point seems to be available.

In some Hymenoptera, two weakly impressed sulci run from the outer and inner edges of the antennal socket to the epistomal suture. These are the *outer* and *inner subantennal sulci* (fig. 6) and when both are present define the *subantennal area* (fig. 6). The area between the inner subantennal sulci and bounded below by the epistomal sulcus, but usually not defined above, is the *supraclypeal area* (fig. 6). This area seems often to be much larger in the Parasitica than in other groups and in such a species as *Metopius dissectorius* (Panzer) forms a big raised plate, widely separating the clypeus from the antennal sockets.

The part of the face above the antennal sockets may be known as the *upper face*. Until the works of Du Porte and of Snodgrass (1947) were published, it was usual to attempt to recognize traces of a Y-shaped 'epicranial suture' on the Hymenopterous head. It is now realized that this sulcus is a larval feature which is probably never carried over into the adult in the Endopterygotes. It is therefore possible to define the *frons* only as the central part of the area between the antennal sockets and the median ocellus. In various Hymenoptera, keels or impressed lines may be developed on parts of the frons and, though these should not be identified with parts of the epicranial sulcus as they sometimes have been in the past, they may require names if they are found to be taxonomically important. Whilst the main central area of the upper face may be quite undifferentiated, it is more often divided by a central keel or groove (the *frontal line*) (figs 4, 5, 6). In ants the frontal line normally forks at about or rather above the level of the antennal sockets and faint branches reach the epistomal sulcus and define the *frontal area* (fig. 5). In some sawflies (e.g., *Nematus ribesii* (Scop.)), somewhat similar sulci are present but do not meet above to form a frontal line. They then appear like inner subantennal sulci which have shifted some way towards the mid-line. The grooves and keels of the head are discussed in more detail by Betrem (1952).

In many sawflies, a pair of more or less distinctly impressed sulci run from the back of the head on each side of the lateral ocelli and down to the antennal sockets. These seem to be of a secondary nature; they define a *postocellar area* (fig. 7) behind the ocelli and a *pentagonal area* (or *frontal area*) (fig. 7) below them. In many Hymenoptera the frons is more or less excavated to receive the basal part of the antennae; these excavations are the *antennal scrobes* (fig. 4). Sometimes their inner edge is strongly raised (=*frontal carina* of ants (fig. 5) or the very similar *frontal crests* (fig. 7) of *Rhogogaster*, TENTHREDINIDAE), sometimes they are separated by an elevated crest on the frontal line (*Cerocephala*, PTEROMALIDAE) or they may be centrally confluent, a division perhaps being indicated by the nature of the surface sculpture. In other genera (e.g., *Helcon*, BRACONIDAE), it is the outer edge of the scrobes which is raised and keel-like. In the CHRYSIDIDAE, the upper margin of the fused scrobes (=*cavitas facialis*) is marked by a transverse keel. The epistomal sulcus sometimes runs close to the compound eyes but it is often well separated from them. The intervening area is then the *inner orbit* (figs 3, 4) which may be considered to run up the whole inner edge of the eye, though above the antennal sockets it is continuous with the frons. In some bees (*Andrena*) or Sphecoids (*Crabro*) the orbit bears a depressed, often pubescent, possibly sensory area, the *facial fovea* (fig. 6).

The top of the head is the *vertex* (figs 5, 6, 8, 9, 10) which bears the lateral ocelli and is usually limited posteriorly by the *occipital sulcus* or *carina* (figs 7, 8, 9, 13). The lower part of this carina, where it approaches[1] the proboscidial fossa, is often termed the *genal carina* and provides important characters for the classification of sawflies and ICHNEUMONIDAE. If the occipital sulcus (or carina) is effaced the vertex will not be marked off from the *occiput* (figs 8, 9, 10, 11, 13) which lies between the occipital sulcus and the *postoccipital sulcus* (fig. 8) which surrounds the foramen. This last sulcus is obliterated in some forms but its position can be roughly fixed by the *posterior tentorial pits* (figs 8, 9, 10) which lie in it below the foramen. These pits are the second main point of origin of the tentorium. A secondary arm of the tentorium joins the surface of the head on each side near the antennae. In the sawflies and Parasitica, this is at a point above the sockets, indicated by a feeble (*Rhogogaster*, TENTHREDINIDAE) or sometimes a deep *dorsal tentorial pit* (figs 4, 7) (*Buathra laborator* (Thunb.), ICHNEUMONIDAE). In Aculeates, it appears that these pits are normally below the antennae. The area between the compound eyes and the occipital sulcus is the *gena*

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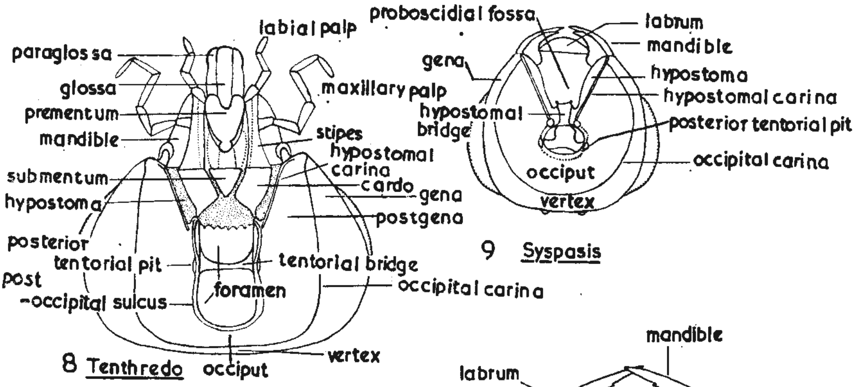
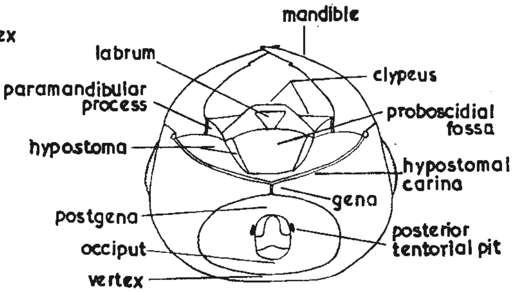
[1] The exact course of the carina ventrally varies; it may run into the hypostomal carina or may run parallel to it and end at the articulation of the mandibles. In some prognathous heads (e.g. *Gasteruption*) the carina (fig. 13) may form a circle round the foramen. It is convenient to treat the carina as following the course of the sulcus, which is nearly always obsolete.

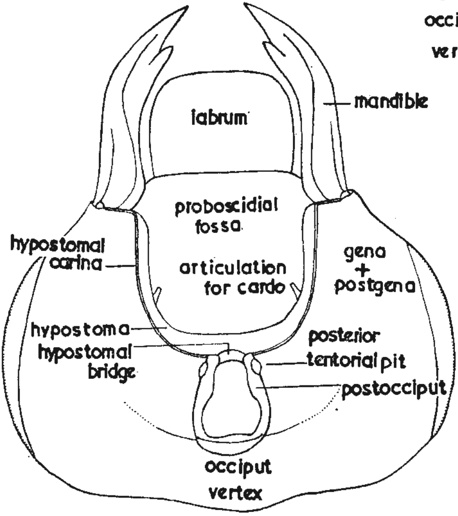


8 Tenthredo

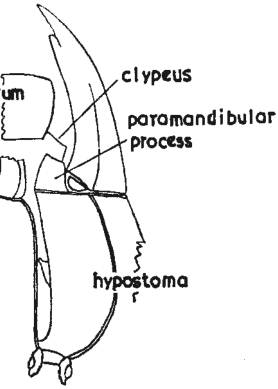
9 Syspasis



10 Tiphia



11 Anthophora



12 Anthophora

Figs 8–12. (Scale-line = 1.0 mm. All heads with maxillae and labium removed) 8, *Tenthredo schaefferi* Klug (Tenthredinidae) ♀. Head in posterior view. 9, *Syspasis lineator* (Fab.) (Ichneumonidae) ♂. Head in ventral view. 10, *Tiphia femorate* Fab. (Tiphiidae) ♀. Head in ventral view. 11, *Anthophora acervorum* (L.) (Apidea) ♀. Head in ventral view. 12, The same, hypostomal region, seen more from right side.

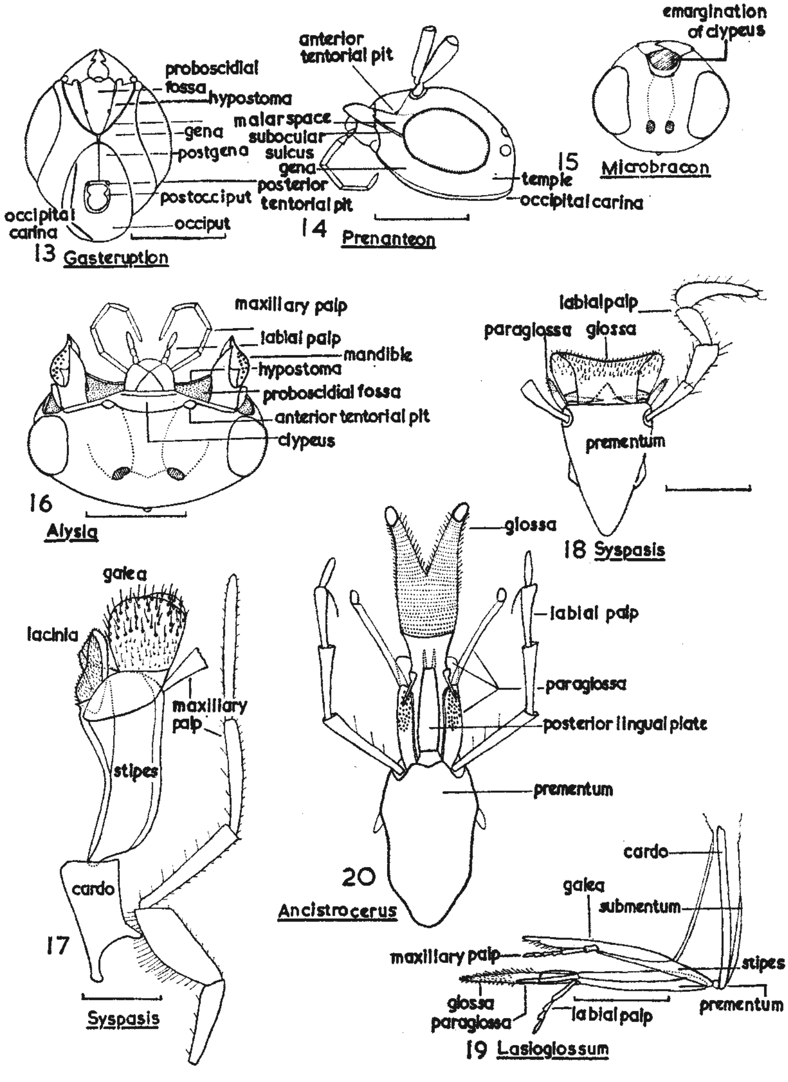
(figs 8, 11); the upper part of the gena is known as the *temple* (figs 7, 14) and the part of the gena immediately adjacent to the compound eye is the *outer orbit*. The area between the occipital and postoccipital sutures is the occiput, already referred to, of which the lower part is called the *postgena* (figs 8, 10, 11, 13), while the *postocciput* ((fig. 11) lies between the postoccipital sulcus and the foramen. The occipital sulcus (or carina) is not rarely absent (e.g., *Nematus*, TENTHREDINIDAE; *Anthophora*, ANTHOPHORIDAE) and the vertex and occiput, gena and postgena are then continuous (fig. 11).

The proboscidial fossa is only a shallow depression in the Symphyta but it is deep, often with its sides nearly vertical, in the Apocrita. A more or less distinct *hypostomal sulcus*, often hardly separated from the *hypostomal carina* (figs 8, 9, 10, 11, 13), arises on each side by the posterior (non-clypeal) articulation of the mandibles and runs upwards and inwards, usually to meet its fellow from the other side below the posterior tentorial pits. The sclerite enclosed within this sulcus is the *hypostoma* (figs 8–13) of which the large central part is membranous. In the Symphyta, the sclerotized part of the hypostoma is very narrow, the membrane therefore nearly approaching the postgena. In the Apocrita, the hypostoma is always broader; it may be in the same plane as the postgena or gena (e.g., *Tiphia*, fig. 10), or slightly inclined towards the fossa (*Gasteruption*, fig. 13), or nearly or quite at right angles to the plane of the postgena (*Syspasis*, fig. 9; APIDAE, figs 11, 12). Dorsally (=posteriorly) the membranous part of the hypostoma is primitively continuous with the membrane of the foramen (fig. 8) (XYELIDAE, TENTHREDINIDAE) but in nearly all Hymenoptera a sclerotized bridge separates them. This bridge can be formed in several ways but, by fusing with the main crosspiece of the tentorium, it plays an important part in strengthening the head. There appear to be at least five types of bridge:

(*a*) A *hypostomal bridge* (fig. 9), composed of the hypostoma only (CEPHIDAE, many ICHNEUMONIDAE).
(*b*) A *postgenal bridge*, produced by the fusion of the postgenae behind the hypostomal bridge (Siricoidea, Megalodontoidea, some ICHNEUMONIDAE).
(*c*) Like (*b*), but with a *postoccipital bridge* in addition (most Apoidea).
(*d*) With a hypostomal and postoccipital bridge (fig. 11) but a forward projection of the latter separates the postgenae (some Apoidea).
(*e*) A *genal bridge* (figs 10, 13), lying immediately behind the hypostomal bridge. This is found when the lower ends of the occipital carina have moved inwards to form a complete circle round the foramen. Behind the genal bridge, there are also postgenal and narrow postoccipital bridges (*Gasteruption*; Bethyloidea).

Species with prognathous heads always have a broad bridge, usually types (*e*) or (*c*), but the bridge is also broad in some orthognathous heads, such as that of *Apis*. Taxonomically, the most important points are the presence or absence of a bridge and the width of the part in the same plane as the gena or postgena.

In some groups, a ventral process of the hypostoma reaches and fuses (Megalodontoidea; *Tiphia*) or nearly fuses ANTHOPHORIDAE with the clypeus. The process may be in the same plane as the gena or (APIDAE) in the plane



FIGS 13–20. (Scale-line, figs 13 and 19 = 1.0 mm; 14–16 = 0.5 mm; 17–18, 20 = 0.25 mm) 13, *Gasteruption jaculator* (L.) (Gasteruptiidae) ♀. Head in ventral view (labium and maxillae removed). 14, *Prenanteon longicornis* (Dalm.) (Dryinidae) ♀. Head from left side, only scape of antennae shown. 15, *Bracon discoideus* Wesm. (Braconidae) ♀. Head in antero-ventral view. 16, *Alysia manducator* (Panz.) (Braconidae) ♀. Head in antero-ventral view (antennae removed). 17, *Syspasis lineator* (Fab.) (Ichneumonidae) ♂. Right maxilla in dorsal view, palp shown detached. 18, The same, labium in ventral view (last three segments of right palp removed). 19, *Lasioglossum leucozonium* (Schrank) (Halictidae) ♀. Labio-maxillary complex from left side. 20, *Ancistrocerus parietum* (L.) (Eumenidae) ♀. Labium in ventral view.

of that part of the hypostoma which forms the side wall of the fossa (i.e., at right angles to the gena). Elsewhere (all other sawflies; Ichneumonoidea) such processes are absent. These *paramandibular processes* (figs 10, 12) separate the fossa in which the mandibles are articulated from the proboscidial fossa; when they are absent there is a ventral gap in the side wall of the fossa and this is closed by a part of the mandibles.

The region between the bottom of the compound eye and the articulation of the mandibles is the *malar space* (figs 6, 14); its length and proportions are of great taxonomic importance. In some groups (e.g., DRYINIDAE; some Chalcidoidea) a well-marked *subocular sulcus* (fig. 14) connects the lower corner of the eye to the mandibular articulation. In the ICHNEUMONIDAE, if the sulcus is not developed, its position is usually marked by a narrow band of dull coriaceous sculpture. The malar space is morphologically of compound origin. In some sawflies it can be seen that the ventro-lateral corners of the clypeus extend into it and provide one articulating point for the mandibles.

The area which is bounded by the clypeus above and the closed mandibles below is sometimes known as the 'mouth opening' or 'peristomium', but both these terms are unfortunate from the morphological point of view. The width of the area can probably be best referred to as the distance between the mandibular condyles and where the area is as high as broad, as in the Cyclostome Braconids (figs 15), this is due to an emargination of the clypeus.

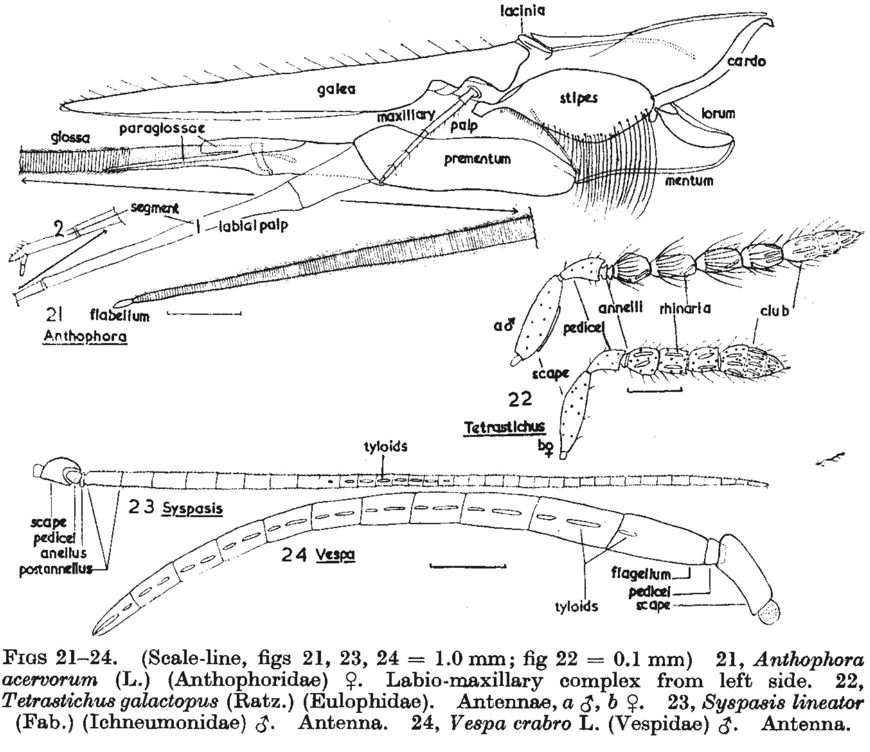
The mouthparts of Hymenoptera show every stage from the simple biting type of most sawfles to the greatly elongate, retractile type of the bees. A considerable lengthening of the mouthparts is clearly useful in any species which requires to obtain quantities of nectar from flowers. It is not surprising, therefore, that some degree of elongation has occurred independently on many occasions and in all the main groups of Hymenoptera; in many ways the most elaborate arrangement is that found in the non-British pollen and honey collecting Masarid wasps where the mouthparts are even more modified than those of the higher bees.

The *mandibles* (figs 5, 6, 8–11), both in position and to a considerable extent in function, stand apart from the labio-maxillary complex. Perhaps because of their use for such purposes as opening the cocoon, killing or handling prey, or making nests, they have not been reduced as in most Lepidoptera or Diptera which have also developed sucking mouthparts. They have remained relatively stout, usually bent inwards, with their tips meeting or crossing when at rest, the distal margin usually more or less toothed. They have a double articulation, an emargination of the mandible fitting over a ball-like condyle of the malar space and a *mandibular condyle* fitting into a hollow in the bottom of the gena. In a number of groups, the arrangement of tooth-like projections on the margin of the mandibles and of grooves on their surface are of taxonomic importance. In one group of the BRACONIDAE (and in two exotic groups of other families) the mandibles are bent outwards instead of inwards. This is known as the *exodont* condition (fig. 16); when it is developed, the principal tearing action of the mandibles takes place when they are opened instead of when they bite against one another. Sexual differences in the mandibles are common in the Aculeate Hymenoptera, where the females mandibles are often shorter and broader, serving as tools for next-construction. Considerable differences are also found elsewhere in the Hymenoptera.

The maxillae and labium are firmly united to one another by membranes and form a single *labio-maxillary complex* (figs 19, 20). When this is lengthened for the collection of nectar it is capable of some degree of retraction and of folding when not in use.

Each *maxilla* (figs 17, 19, 20) consists of a basal piece or *cardo* which articulates with a process of the hypostoma. At the distal (ventral) end of the cardo a *stipes* is articulated. The stipes bears externally at its distal end the *maxillary palpi* which primitively have six segments but frequently have fewer in specialized families or genera. Internally the stipes bears two lobes, a more proximal one, the *lacinia*, and a more distal one, the *galea*. The lacinia is lost or quite rudimentary in all bees. All these structures show a variety of differences in shape, sculpture and spiny covering in different families and genera. Apart from the bees, however, little use has been made of these characters in classification, partly because they require dissection of the specimen and also because the parts may look very different if the viewpoint is a little altered.

The *labium* (figs 18–21) consists of a *submentum*, a *mentum* and a *pre-*



FIGS 21–24. (Scale-line, figs 21, 23, 24 = 1.0 mm; fig 22 = 0.1 mm) 21, *Anthophora acervorum* (L.) (Anthophoridae) ♀. Labio-maxillary complex from left side. 22, *Tetrastichus galactopus* (Ratz.) (Eulophidae). Antennae, *a* ♂, *b* ♀. 23, *Syspasis lineator* (Fab.) (Ichneumonidae) ♂. Antenna. 24, *Vespa crabro* L. (Vespidae) ♂. Antenna.

mentum. The submentum is of the normal insect type, viz., a flat plate, in nearly all sawflies (fig. 8) but in the Apocrita it is usually membranous. In bees, a V-shaped sclerite (the *lorum*, fig. 21) lies in the correct position and has been identified with the submentum. It has an additional connection with the cardo on each side and evidently partly serves to hold the two cardines together. In the MASARIDAE, which also have very long mouthparts, a lorum-like structure is also developed but in this family looks more like a secondary thickening of the membrane. These observations certainly do not prove that the lorum is not a submentum, but the possibility should not be forgotten. In many Hymenoptera, including apparently the sawflies, there is no separate mentum but in the bees a sclerite is found anteriorly to the postmentum (e.g., *Anthophora*, fig. 21) in the position where a mentum should be found. In other bees (e.g. *Andrena*) a mental area is indicated at the proximal end of the prementum by slight notches. The distal end of the prementum bears externally the *labial palpi* which characteristically have four segments though the number may be reduced in particular families or genera. The palpi are sometimes borne on special lobes of the prementum, the *palpigers* (fig. 21), which may look like a basal segment of the palp. Centrally there are three lobes, the outer ones being the *paraglossae* and the inner one the *glossa.* The three lobes together may be collectively referred to as the *ligula.* In primitive forms the paraglossae are about as big as the glossa but they are relatively reduced and sometimes quite rudimentary in higher forms. The primitive insect glossa of two equal lobes does not occur in the Hymenoptera and in the sawflies there is always a single undifferentiated lobe. In the Apocrita (except higher bees), the glossa is apparently always bilobed, even if only obtusely so; the division between them is only deep in forms with a long glossa (some Sphecoids and Vespoids, fig. 20). Most bees, however, especially those with a long glossa, have a single, rather narrow lobe, which in the higher forms usually ends in a small plate or *flabellum* (fig. 21). In the short-tongued bees, such as *Lasioglossum* (fig. 19) and *Andrena,* the lengthening of the proboscis is due to an elongation of the prementum and the glossa remains short. On the posterior (ventral) surface of the glossa a plate may be developed, the *posterior lingual plate* (fig. 20), to the interior surface of which are attached the muscles which move the glossa. This plate provides an important character for the classification of the VESPIDAE. The labial palpi in the higher bees are converted into organs for sheathing the ligula and one or more segments have the shape of an angle-girder, quite unlike the cylindrical distal segments.

The membrane which forms the anterior (dorsal) surface of the prementum slopes up to the slit-like entrance to the pharynx (the true mouth) which lies immediately below the line along which the epipharynx is attached. There are a number of plates involved in the support of the mouth which will be found described in the works of Duncan (1939), Michener (1944), Ulrich (1924) and others. Immediately beneath the mouth opening a pouch is sometimes invaginated (apparently only in Aculeates), the *infrabuccal pouch*; the top of the pouch may be produced into a projecting lip, resembling but smaller than the epipharynx. The pouch is known to play an important part in the life of ants and wasps which store both food and waste matter in it and there is some evidence that it is especially well-developed in those Sphecoids which build mud nests.

The *antennae* (figs 22–24) provide characters of the greatest value in classification. The more generalized members of both the Symphyta and Apocrita have them of a relatively simple type. The first segment or *scape* is usually thicker and often longer than the others; its base is widened into a ball to articulate in the socket. The second segment or *pedicel* is small, often a little conical in shape, and with the scape forms a ball and socket joint for the distal part of the antenna, the *flagellum.*[2] In the primitive condition, the flagellum consists of a large number (20–75) of segments, all very much alike in structure (sometimes a little thinner distally), and variable in number even within the species. There is a tendency for the flagellum of the male to be longer than that of the female, consisting of longer and more numerous segments. In both suborders there has been a tendency to reduce the number and to differentiate the form of the flagella segments. In the higher sawflies there are characteristically 9 antennal segments (scape, pedicel, 7 flagellar) but *Arge* has only 3, all the flagellar segments being fused. In other genera the segments may have apico-lateral processes (pectinate) or the distal ones may form a club (clavate) or show other specializations. In such Apocrita as the ICHNEUMONIDAE or BRACONIDAE the usual type of antenna is also the many-segmented one. In the first named family and less obviously in the second a very short segment, the *annellus* (fig. 23), lies between the pedicel and the flagellum. In the more specialized Parasitica the number of segments is reduced (usually 11–15) and their form becomes differentiated. The most specialized antenna occurs in females of the Chalcidoidea (fig. 22*b*) where the following parts may be recognized: scape, pedicel, anelli (0–4 segments), *funicle* and club. The club consists of a number of thicker segments (in Chalcids usually 3), often partially or completely fused with one another. In the groups of the Parasitica in which the female antenna is clubbed that of the male (fig. 22*a*) is not or only slightly so modified. In the Aculeata, antennae with 20–30 segments are only found in the non-British BETHYLIDAE sub-family SCLEROGIBBINAE. In the vast majority of species there are 12 segments in the female and 13 in the male. Fewer segments occur sporadically in many families and reduction is especially common in the ants (Formicidae). The condyle of the scape has been called the *radicle* in Ichneumonids in which it has some taxonomic importance.

In descriptions, it is usually preferable to refer to, say, the fourth antennal rather than to the second flagellar segment since this eliminates any chance of confusion, but in some of the most differentiated types of antennae it may be convenient to number the different groups of segments separately. Care must be taken in some genera not to overlook the pedicel which may be much withdrawn into the scape (e.g., in the bee *Nomada*). In the ICHNEUMONIDAE the annellus (fig. 23) is fused with the first flagellar segment or *postannellus* and is usually but not always omitted from the count. Probably the least ambiguous way of referred to the number of segments would be to record: postannellus + *n* segments.

The surface of the antennae is closely covered with sense-organs of various types. These are sometimes taxonomically important, especially when large enough to be visible without great magnification. In many species (e.g.,

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[2] Some authors count the pedicel in enumerating the flagellar segments.

Ichneumonidae, *Ichneumon*, *Diplazon*, *Helictes*; Vespidae, *Vespula*) the males have longitudinal prominences or keels on a number of flagellar segments. These have been called *tyloids* (fig. 24) in the Ichneumonidae and Vespidae, and the term might well be extended to cover all structures of this type, including those where the tyloids are recessed. Longitudinal, groove-like structures on the segments are known as *rhinaria*. They sometimes look like flattened, procumbent bristles. In some Parasitica (Cynipids, Chalcids, Proctotrupids) where they are large they may be taxonomically useful (fig. 22).

THORAX

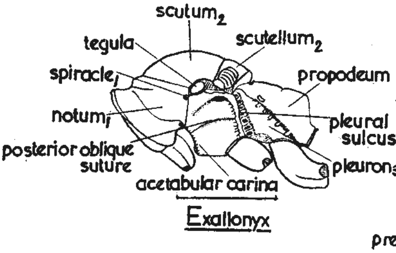
The thorax consists of three segments of which the two hinder ones normally bear wings. In the suborder Apocrita the first abdominal segment (propodeum) has become firmly attached to the thorax and is connected to the rest of the abdomen by a narrow petiole. It is convenient in higher forms to consider the propodeum in conjunction with the thorax; Michener (1944:167) has proposed the term 'mesosoma' for the thorax + propodeum; this is almost equivalent to 'holmus' of Haupt (1938).

The earliest students of Hymenoptera failed to recognize the homologies of the parts of the thorax, especially in the Apocrita. A system of nomenclature, therefore, grew up which, although incorrect, is still used to a considerable extent in taxonomic work. Most of the more obvious errors in the thoracic nomenclature used by taxonomists have been corrected by Snodgrass (1910, 1935). There is still some disagreement about the interpretation of the sternal region. In a paper by Richards (1956), the views of Weber (1933), Ferris (1940) and Michener (1944) have been summarized and a somewhat different scheme suggested. Matsuda (1960), however, believes, probably correctly, that nearly all the areas which I called mesosternal are really pleural. There remain a number of genera in which it is difficult to decide whether a sulcus or carina is one of the original ones or a new structure of secondary origin. As a matter of policy, to keep the number of terms as low as possible, somewhat slender evidence for the identification of areas or sulci has been accepted. It may be noted that many features of the thorax are difficult to make out in wingless species and the special study made by Reid (1941) may be referred to.

PROTHORAX

The *pronotum* is rather closely attached to the mesonotum, while the *propleura* (figs 32, 42, 46) are loosely attached to their notum and appear more like proximal segments of the legs. In a few sawflies (e.g., Snodgrass, 1910: figs 12, 13) each propleuron is divided into an episternum and epimeron, but much more often there is a single plate. The pronotum is often provided with keels, furrows, tubercles, etc., of great systematic importance. It is commonly divided by a transverse furrow into an anterior, sometimes rather neck-like part and a more posterior part at a rather higher level, in the plane of the mesonotum. In many Ichneumonidae, this furrow is crossed on each side by an oblique keel, the *epomia* (fig. 34). The anterior margin of the posterior part may pass into the furrow in a smooth curve or be raised into a transverse keel or *crista* (figs 43, 44, 47) (Zikàn, 1935:

144). The subtriangular areas on each side of the dorsal aspect of the pronotum are termed the *humeri*. In less specialized Hymenoptera (Symphyta, some CHALCIDIDAE), the first thoracic spiracle (figs 29, 37) opens on a small cuticular ring lying in the membrane between the postero-lateral margin of the pronotum and the top of the mesepisternum. In the TENTHREDINIDAE, the hind margin of the pronotum is characteristically reflexed (fig. 28) inwards just in front of the spiracle. In the Aculeata, the pronotum



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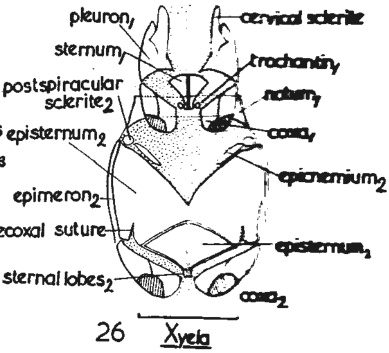

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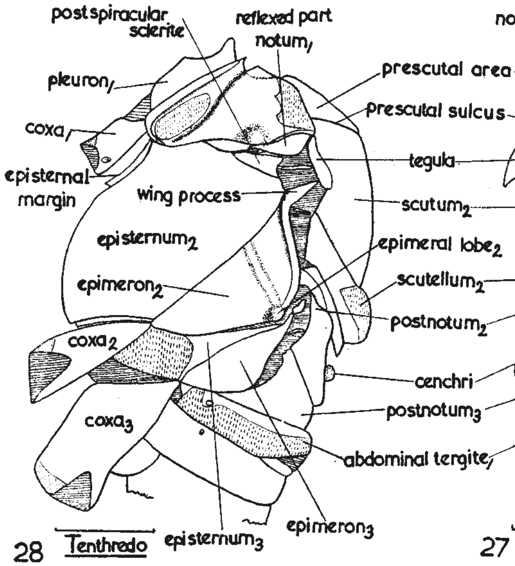

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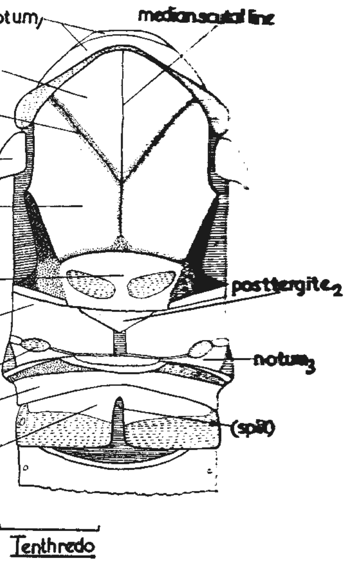

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FIGS 25–28. (Scale-lines = 1.0 mm, except in fig. 26 where it is 0.5 mm) 25, ***Exallonyx niger*** (Panz.) (Proctotrupidae) ♀. Thorax and propodeum, seen from the left. 26, *Xyela julii* (Bréb.) (Xyelidae) ♂. Pro- and mesosternal regions. 27, *Tenthredo perkinsi* (Mor.) (Tenthredinidae) ♀. Thorax and base of abdomen in dorsal view. 28, The same, seen from the left side.

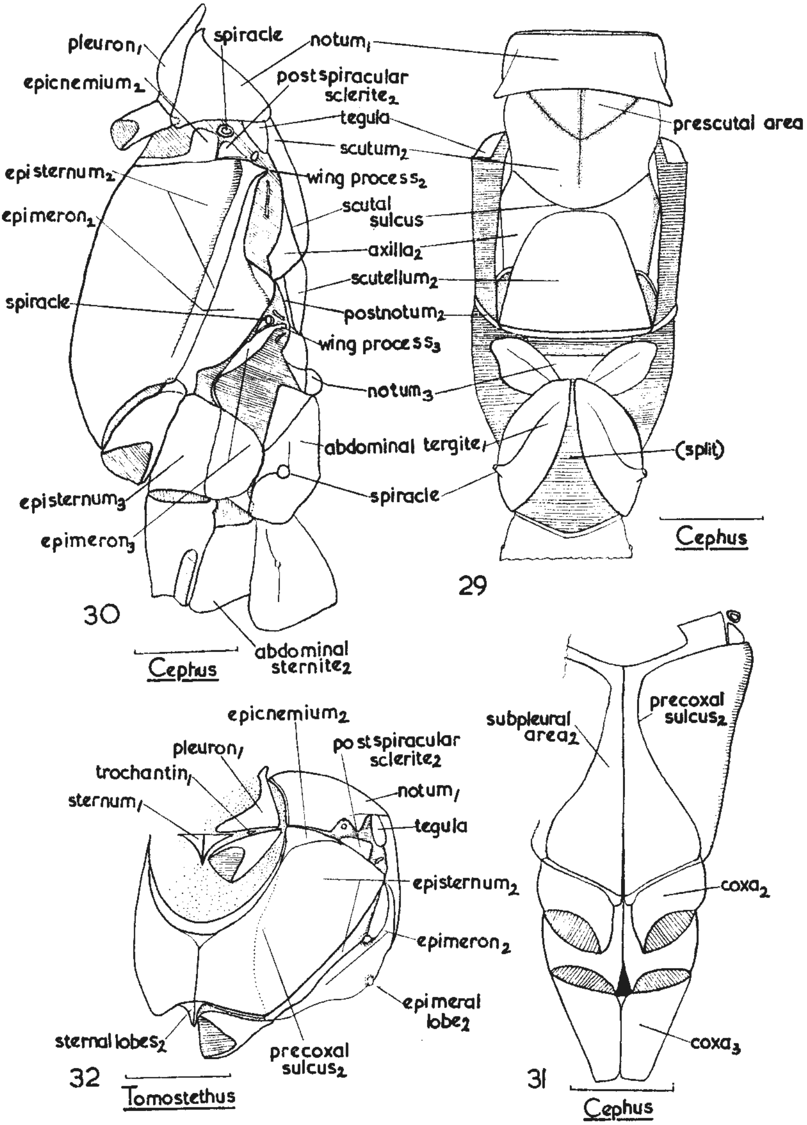
at this point is produced backwards and swollen into *pronotal tubercles* (figs 42, 43, 44, 47) which cover the spiracle. In the ICHNEUMONIDAE and in the Cynipoidea, the postero-lateral corner of the pronotum is emarginate and the spiracle is surrounded by the pronotum on three sides. In some Proctotrupoidea (e.g., PROCTOTRUPIDAE) (fig. 25), the pronotum has fused with the postspiracular sclerite (p. 20) so that the spiracle seems to open on the pronotum. In the Aculeata, the pronotal tubercles may reach back as far as the tegulae (e.g., POMPILIDAE) (fig. 42) or be widely separated from them (e.g., Sphecoidea, fig. 44; Apoidea, fig. 47).

In its primitive condition, the ventral corners of the pronotum are widely rounded and its postero-lateral margin only loosely overlaps the mesepisternum (Symphyta, except Tenthredinoidea; Chalcidoidea; some Aculeata, as Bethyloidea, Pompiloidea). In all the more specialized Hymenoptera, the ventral corners are more or less acutely pointed and the postero-lateral margin is closely and almost or quite immovably coadapted to the mesepisternum. In the most specialized condition (CIMBICIDAE, PROTOTRUPIDAE, GASTERUPTIIDAE), the pronotum extends round to the mid-ventral line and is there fused to form a complete ring. Wingless forms, such as *Gelis* ♀ (ICHNEUMONIDAE) and many worker FORMICIDAE, may show the pronotum in an apparently primitive condition whereas the corresponding winged form has the notum coadapted and ventrally produced.

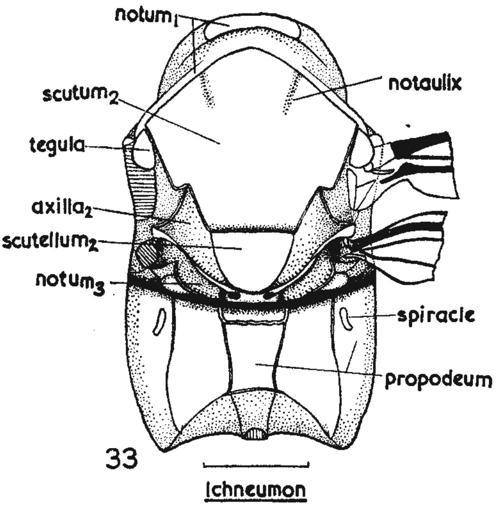
The anterior margin of the pronotum defines a horseshoe-shaped area (in the most specialized type, a ring) which is directed almost ventrally, with a slight anterior tilt. The anterior part of the horseshoe is filled by the head and the cervical membranes, the posterior part by the propleura, lying side by side, and by the *cervical sclerites* (fig. 26) which, except in some Symphyta, are completely fused to the anterior part of the pleuron. In the primitive condition (most Symphyta), the inner margins of the propleura diverge a little posteriorly and the *prosternum* (figs 26, 32) lies in the gap so formed; in a few Symphyta, there may also be traces of a trochantin (figs 26, 32) between the coxa and the sternum or pleuron. In some XYELIDAE (Ross, 1937 : fig. 129), the prosternum is made up of an anterior basisternum with a median longitudinal furrow and a separate, much more posterior spinisternum which is produced inward into a lamella. In the higher sawflies, the spinisternum seems to fuse with the anterior margin of the mesothorax and this may explain the existence of a pit in that position in some Aculeata (Duncan, 1939 : 54, *Vespula*; Michener, 1944 : 176, *Anthophora*; and also fig. 46, *Mimumesa*. In the more specialized Hymenoptera, the propleura are contiguous throughout and the prosternum is only visible by dissection. For this reason it is rarely referred to in taxonomic literature.

MESOTHORAX

The second thoracic segment is much the largest since it contains the principle flight-muscles. Dorsally, the segment is covered by the *mesonotum* which is divided into two principal sclerites, the *scutum* and the *scutellum* (figs 27, 29, 41, 43); taxonomists often reserve the term mesonotum for the scutum alone. From the front margin of the scutum two sulci, the *notaulices* (incorrectly *prescutal sulci*, Compere and Rosen, 1970) (figs 27, 34, 36, 37) often converge backwards, defining a V-shaped *prescutal area* (wrongly



FIGS 29–32. (Scale-lines = 0.5 mm) 29, *Cephus cultratus* Eversm. (Cephidae) ♀. Thorax and base of abdomen in dorsal view. 30, The same, seen from the left side. The contraction between the first and second abdominal segments, shown in figs 29–30, is the first indication of the condition universal in the Apocrita. The reduction of the top of the metepisternum in this species indicates the development seen later in the Ichneumonidae. 31, The same, mesosternal region in ventral view. 32, *Tomostethus nigritus* (Fab.) (Tenthredinidae). Pro- and mesothorax seen from the left side and beneath.



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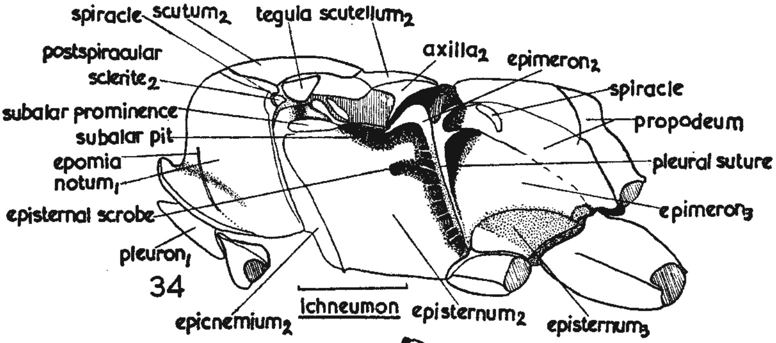

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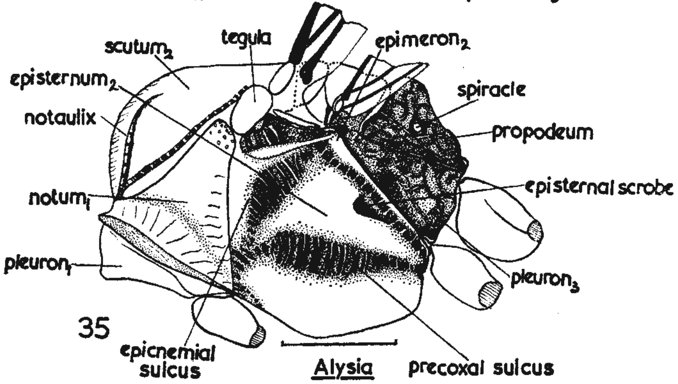

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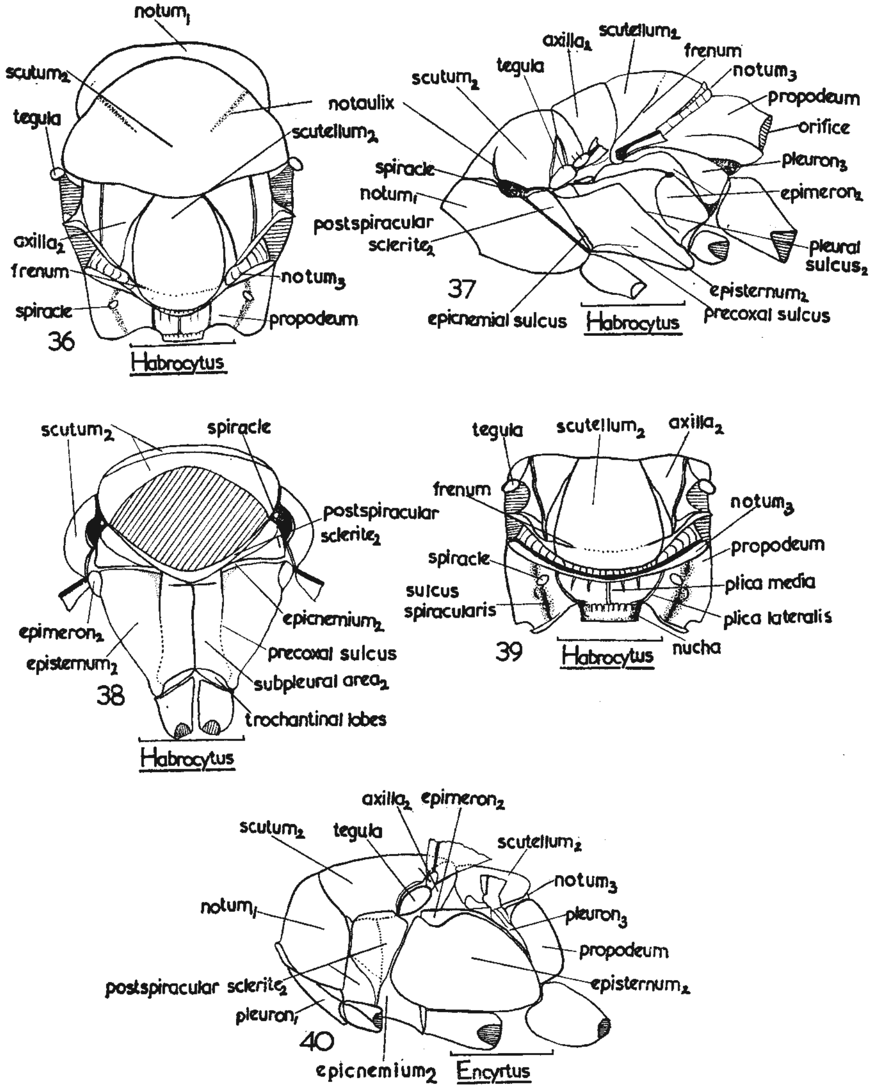
FIGS 33–35. (Scale-line in figs 33–34 = 1.0 mm, in fig. 35 = 0.5 mm) 33, *Ichneumon sarcitorius* Linn. (Ichneumonidae) ♀. Thorax and propodeum in dorsal view. For areas of the propodeum see fig. 48. 34, The same, seen from the left. 35, *Alysia manducator* (Panz.) (Braconidae) ♀. Thorax and propodeum seen from the left. The epicnemial and precoxal sulci are engulfed in much larger depressions.

prescutum) (figs 27, 30). The sulci are deep and strong in sawflies (weak in SIRICIDAE) and meet at about the centre of the thorax. In other forms (some CYNIPIDAE, some BETHYLIDAE), they extend back to the hind margin of the scutum without meeting; in many groups, they are weak and very incomplete or even absent. There is often present a *median scutal line* (figs 27, 43) which longitudinally bisects the prescutal region. On each side of the scutellum are two more or less triangular areas, the *axillae* (figs 29, 30, 33, 36, 40, 41, 43), which belong morphologically to the scutum though taxonomists usually treat them as part of the scutellum. The true *scutellar sulcus* runs behind the axillae and, on its central part, in front of the scutellum. The *scutal sulcus* (fig. 48) divides the scutum from the axillae and is coincident centrally with the scutellar sulcus. Arising on each side of the scutal sulcus may be a pair of *parapsidal furrows* or sulci (figs 41, 43) which extend forward about half way across the scutum but they are often absent. The scutal areas lateral to the parapsidal sulci are the *parapsides.* In many sawflies (*Tenthredo, Arge,* etc.) there is a postnotum (figs 27, 28) behind the scutellum. The hind margin of the scutellum is continuous with the hind margin (axillary cord) of the forewing and the postnotum is a plate laid down in the intersegmental region between the second and third thoracic segments; it is treated as the fourth plate of the mesonotum. In a few sawflies Ross (1937 : 25, fig. 120) has recognized a 'post-tergite' forming a narrow posterior plate of the scutellum. The central area of the postnotum is what is termed the *postscutellum* in sawflies but not in Apocrita. In higher groups the postnotum is invaginated and is invisible externally. In some Chalcidoids the posterior third of the scutellum is often differentiated by sculpture and may be marked off by a faint or even strong line, the *frenum* (figs 36, 37, 39); there are some grounds for thinking that this posterior area is really the postnotum.

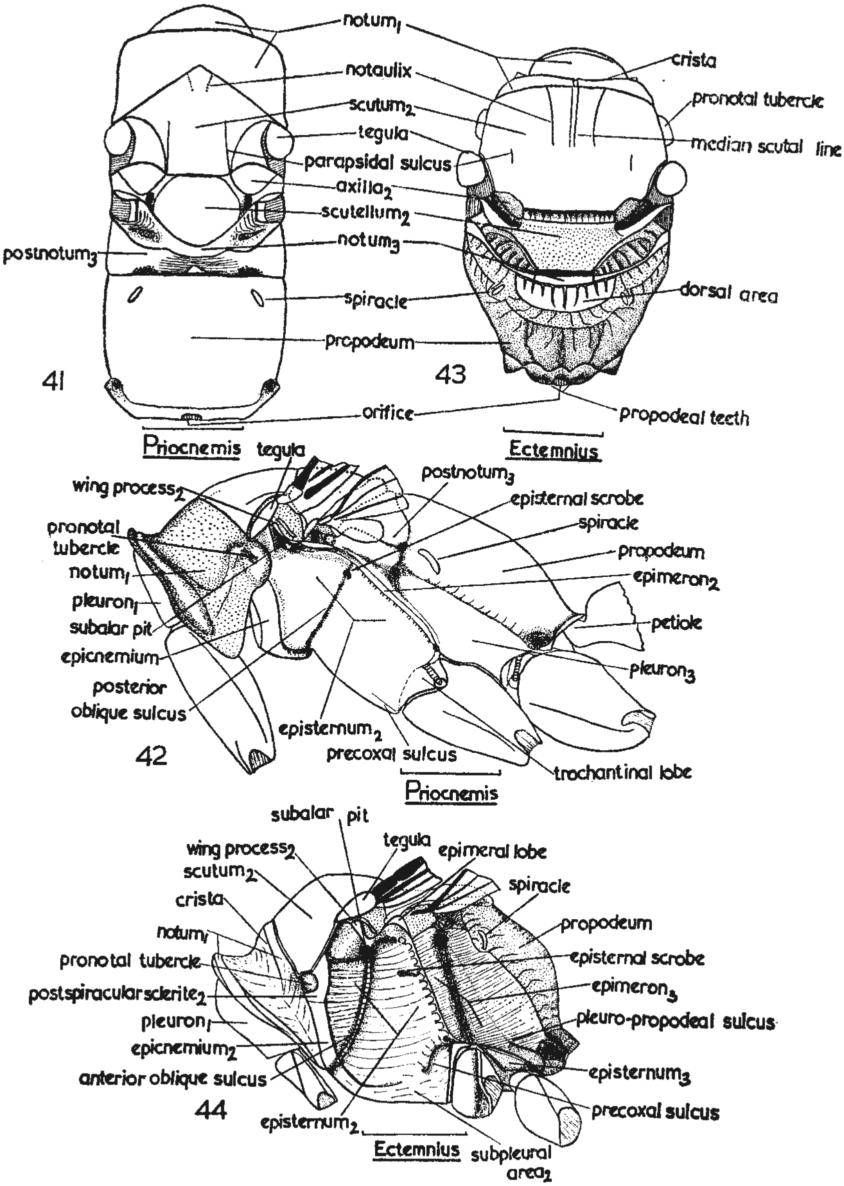
The sternal and pleural regions of the thorax are so intimately connected that it is convenient to treat them together. The lateral aspect of the mesothorax or pleuron is primarily divided into an anterior *mesepisternum* (figs 28, 30, 37, 45, 46) and a posterior *mesepimeron* (figs 28, 30, 34, 37, 40, 45, 46, 47) by the *pleural sulcus* which runs obliquely forwards and upwards from the lateral articulation of the mid coxa to the *wing-process* (figs 28, 42, 44) beneath the forewings. The epimeron is quite large in sawflies (e.g., *Tenthredo*) and most Chalcidoids but in most Apocrita it is reduced to a narrow posterior strip, often marked off only by a row of punctures. In the ENCYRTIDAE (Chalcidoidea), the mesepisternum is enormously developed and completely conceals all but the most dorsal part of the epimeron. The postero-dorsal corner of the epimeron is nearly always produced into a rounded, convex lobe (figs 28, 32, 44) which more or less overlaps the second thoracic spiracle (fig. 29) in the same way as the pronotal tubercles do the first. This lobe is a useful landmark. The *mesosternum* is relatively well developed in EUPELMIDAE (Chalcidoidea), where it exhibits a longitudinal *median sternal groove = mesolcus* (figs 45, 46), and in CHRYSIDIDAE (Bethyloidea) (Richards, 1956: 103, fig. 4). But the area which was called mesosternum in *Xyela* (Richards, loc. cit., fig. 1) is probably part of the mesepisternum (Matsuda, 1960). Just in front of each mid coxa is a transverse area marked off by a sulcus. It seems from its structure in *Urocerus* (SIRICIDAE) that this area is the *trochantin* and that the sulcus cutting it off (sometimes deep, sometimes very faint) is the *trochantinal sulcus* (figs 42, 45, 46). In most species the median part of the trochantin is indistinguishably fused with the *mesosternal lobe* (figs 26, 32). In many ICHNEUMONIDAE and BRACONIDAE these lobes lie largely in a plane at right



FIGS 36–40. (Scale-line = 0.5 mm) 36, *Habrocytus elevatus* (Walk.) (Pteromalidae) ♂. Thorax and propodeum in dorsal view. 37, The same, seen from the left. 38, The same. Mesothorax in ventral view (prothorax removed). 39, The same. Scutellum and propodeum seen posterodorsally. 40, *Encyrtus scutellatus* (Swed.) (Encyrtidae) ♂. Thorax seen from the left side.

angles to the ventral surface, the mid coxae being directed posteriorly rather than ventrally. In a few genera (e.g., *Ammophila*, SPHECIDAE) the mesosternum is in the same plane as and is solidly fused to the metasternum. In most Hymenoptera a *precoxal sulcus* or carina (figs 26, 31, 32, 35, 37, 42, 44, 45, 47) runs from the bottom of the pleural sulcus, at first parallel with the trochantinal sulcus and then bending sharply forwards to end on the front margin of the mesepisternum. The precoxal sulcus is often discontinuous and when its central part is represented only by a very short line or tubercle it has been called by Michener the *mesopleural signum* (fig. 46). The extreme anterior part of the sulcus is deep in some ICHNEUMONIDAE and in them has been called the *sternaulus.* The area between the precoxal sulcus and the median sternal groove is commonly called the *mesosternum* by taxonomists. Michener, on the supposition that the true mesosternum is really represented by little more than the groove, calls it the *subpleural area.* In fact, apart from an example such as *Eupelmus* already quoted, it seems impossible to say where the lateral boundaries of the mesosternum lie and the normal taxonomic nomenclature seems to be harmless.

In many sawflies, the antero-dorsal corner of the mesepisternum is cut away and a small *postspiracular sclerite* (figs 26, 28, 29, 32, 34, 37, 40, 44, 45, 46, 47) lies in the emargination. In most Chalcidoidea, also, the postspiracular sclerite is conspicuous and may even extend downwards and fuse with its fellow from the other side. In most higher Hymenoptera, however, the sclerite is indistinguishable and seems to be fused with the episternum or (see p. 14) the pronotum. An *epicnemial sulcus* (or carina) usually runs from the region of the postspiracular sclerite down to near the end of the precoxal sulcus, cutting off an anterior *epicnemium* (=prepectus) (figs 26, 30, 32, 35, 37, 40, 42, 44, 45, 46, 47). Sometimes the epicnemial sulcus is continuous with the front of the prexoxal sulcus, sometimes the two sulci cross, or they may not meet at all. The epicnemia of the two sides occasionally fuse across the mid line (e.g., *Tomostethus*, TENTHREDINIDAE; *Gasteruption*). Frequently, the front of the subpleural areas is more or less depressed to receive the backwardly projecting fore coxae. The posterior margin of this depression is sometimes defined by an *acetabular carina* (figs 25, 46) which may be difficult to distinguish from the bottom of the epicnemial carina. In many Apocrita, the part of the mesepisternum just below the wing-process is raised into a *subalar prominence* (fig. 34) below which lies the *subalar pit* (figs 34, 42, 44, 47). What may be a similar prominence is indicated in *Cephus*. In many Sphecoids and in some bees, the subalar pit is connected by an *anterior oblique sulcus* (figs 44, 45, 46, 47) (sometimes confused with the epicnemial sulcus) to the ventral end of the epicnemium. This sulcus defines an *anterior plate* of the mesepisternum. Another sulcus, the *scrobal sulcus* (figs 46, 47), in many Aculeates connects the anterior oblique sulcus to the *episternal scrobe* (figs 34, 42, 44), a pit found in many Apocrita (not in *Metopius*, ICHNEUMONIDAE, nor in any Symphyta) near the centre of the hind margin of the mesepisternum. The area lying above the scrobal sulcus is the *hypo-epimeral area* (fig. 47) which has sometimes been confused with the upper part of the epimeron. In the ICHNEUMONIDAE, the hypoepimeral area is not defined but a shining patch known as the *speculum* often occurs in the same position. In most POMPILIDAE and many DRYINIDAE (possibly also some Sphecoids), the



FIGS 41–44. (Scale-line = 1.0 mm) 41, *Priocnemis perturbator* (Harr.) (Pompilidae) ♀. Thorax and propodeum in dorsal view. 24, The same, seen from the left side. 43, *Ectemnius lapidarius* (Panz.) (= *chrysostomus* (Lep. and Br.)) (Sphecidae) ♀. Thorax and propodeum in dorsal view. 44, The same, seen from the left side.

anterior oblique sulcus is not present but a *posterior oblique sulcus* (figs 25, 42) starts from a similar point at the bottom of the epicnemium and runs up to the episternal scrobe. In forms with coarse sculpture or with very specialized structure, few of these sulci may be complete or easy to trace and some of them may be absent. It is also nearly certain that these are additional secondary sulci or carinae in particular specialized genera.

METATHORAX

The metathorax, which bears the relatively small hind wings, is always smaller and less differentiated than the mesothorax. Dorsally, the *metanotum* consists of a single central area, usually defined by lateral depressions (figs 27, 28, 30, 33, 36, 37, 40, 41, 43, 48). This central area (Perkins, 1959: 2) is what most taxonomists (not Kohl or Kieffer) have termed the 'postscutellum' in the Apocrita. As that term has been used for quite a different structure, namely the corresponding area of the mesopostnotum in the Symphyta, it seems that this usage in the Apocrita should be dropped. Ross (1937: fig. 120) has recognized a metascutellum in *Macroxyela.* In all Symphyta except the CEPHIDAE, it bears two rounded prominences, the *cenchri* (figs 27, 28), which have a roughened surface to engage the forewings (see p. 28) when they are folded over the abdomen. The *metapostnotum* (figs 27, 28, 41) is fully visible in many Symphyta though even in this suborder it is often very narrow or lies in a vertical rather than a horizontal plane. In the Apocrita, it is usually invaginated and invisible except for lateral vestiges but it is well developed in the POMPILIDAE and is probably incorporated in the furrow which runs along the anterior margin of the propodeum in many ICHNEUMONIDAE. In some sawflies (e.g., *Tenthredo*, fig. 28), the *metapleural sulcus* divides the metapleuron into the nearly equal *metepisternum* and *metepimeron.* More often the division of the pleuron is very unequal (e.g., *Cephus*, fig. 29) and it seems from a comparative study that the metepisternum is only properly developed ventrally and that it has been reduced above to a narrow strip[3] or even invaginated in front of the pleuron, just as the mesepimeron has been crowded out behind the mesopleuron. In or near the posterior margin of the mesepimeron, in its upper part, is a deep pit; sometimes another pit is also found lower down. A secondary suture going obliquely through the upper pit may divide the metepimeron secondarily into two (e.g., *Vespula*). It is usual to refer merely to the 'metapleuron' since its detailed morphology is so uncertain. Even its boundary from the propodeum may be almost obliterated, as in *Ectemnius* (fig. 44). In the metasternal region, it is sometimes possible to recognize a precoxal sulcus, subpleural areas (e.g., *Ectemnius*, fig. 45) and a bilobed, pit-bearing central plate which probably represents the *metasternum* (figs 45, 46) and trochantins.

PROPODEUM

The *propodeum* is the name given to the first abdominal segment in the Apocrita. This segment is modified even in the Symphyta; the tergite is

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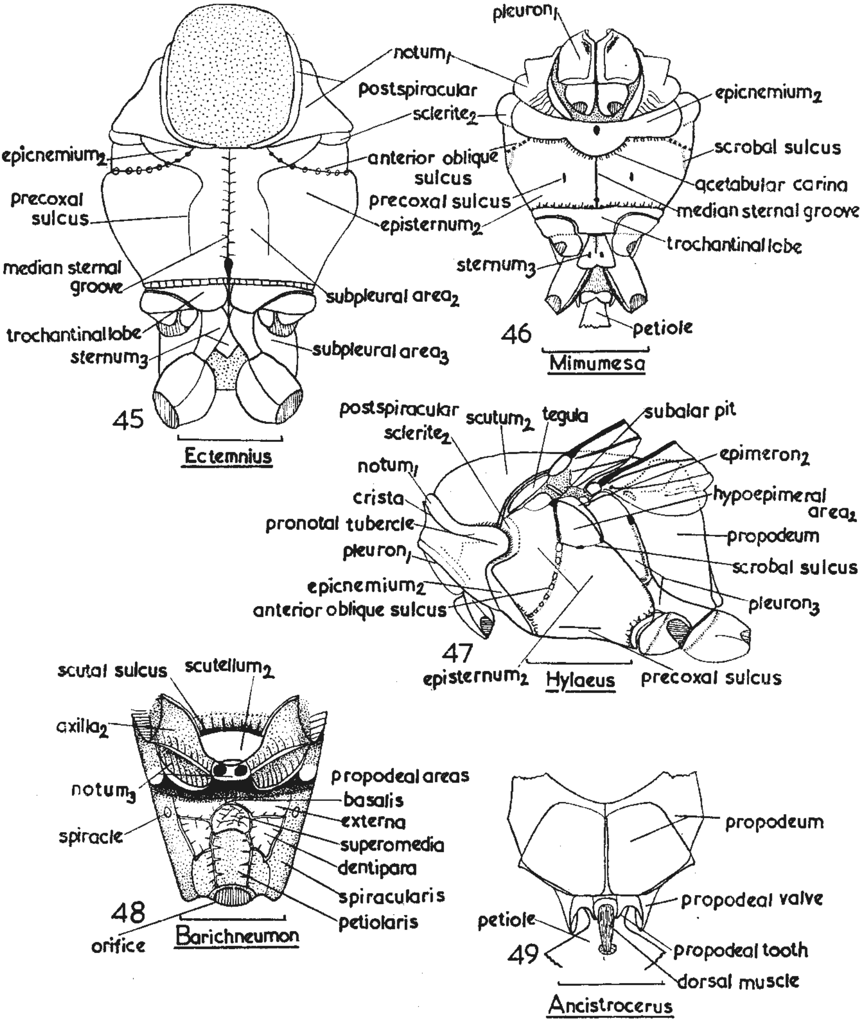
[3] This interpretation differs from that offered by Michener (1944) for *Anthophora* but the question is not so far of much taxonomic importance.

commonly split (figs 27, 30) longitudinally and in the CEPHIDAE the articulation between it and the rest of the abdomen is somewhat constricted. The first sternite is always much reduced and is often unrecognizable. In the Apocrita, the tergite consists of a large plate, often domed, bearing two



FIGS 45–49. (Scale line = 1.0 mm) 45, *Ectemnius lapidarius* (Panz.) (= *chrysostomus* (Lep. and Br.)) (Sphecidae) ♀. Thorax in ventral view (propleuron removed). 46, *Mimumesa spooneri* Rich. (Sphecidae) ♀. Thorax in ventral view. The precoxal suture is represented by a 'pleural signum'. 47, *Hylaeus signatus* (Panz.) (Colletidae) ♀. Thorax and propodeum from the left side. 48, *Barichneumon heracliana* (Bridgm.) (Ichneumonidae) ♂. Propodeum and part of thorax in dorsal view. 49, *Ancistrocerus oviventris* (Wesm.) (Eumenidae) ♀. Articulation of second abdominal segment to propodeum in dorsal view.

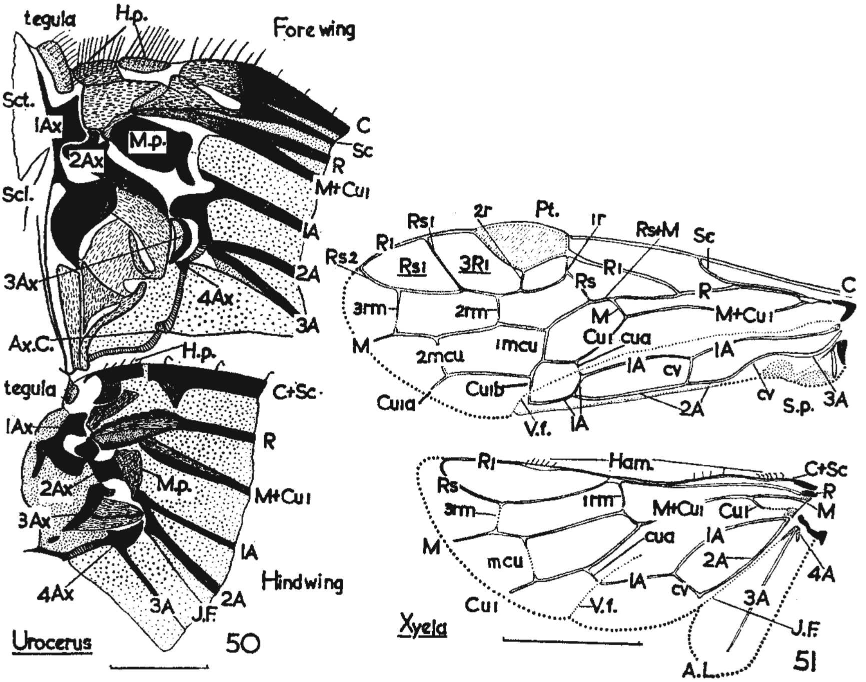
often conspicuous spiracles (figs 41, 43). The sternite is sometimes visible (e.g. *Ammophila*) but often absent. The spiracles usually lie near the lateral margin of the tergite and provide some evidence as to where the boundary between it and the metapimeron lies. The primitive type of propodeum has dorsal, posterior and lateral surfaces but the dorsal surface may become short or completely obliterated (EURYTOMIDAE, VESPIDAE, some APIDAE) and the whole segment is much reduced in many Chalcidoidea (e.g., ENCYRTIDAE). In many ICHNEUMONIDAE, the surface is areolated, i.e., has a regular pattern of raised keels, defining areas to which names have been given. The names of the more important of them are shown in fig. 48. The lower outer corner of the *area dentipara* is often produced into a tubercle or tooth, the *dentiparal tubercle*, *tooth* or *spine*. The outer keel defining the *area spiracularis* seems to be the boundary between the propodeum and the metepimeron; thus the so-called *area lateralis* is the lower part of the metepimeron and the *area juxtacoxalis* of the metepisternum. In many Aculeata, a curved keel or furrow, or a difference of sculpture, defines a *dorsal area* (=*area cordiformis*) (fig. 43) of the propodeum. In the Chalcids, particularly the PTEROMALIDAE, a different set of keels has been developed and C. G. Thomson's nomenclature may be used. There is a (fig. 39) median keel (*plica media*) and often another one on each side of it (*plica lateralis*); outside these is a furrow (*sulcus spiracularis*) in which the spiracles lie. The abdomen is often borne on a slight projection or *nucha*. In the very modified thorax of the CHRYSIDIDAE, the central part of the metanotum is often fused with the propodeum. In *Chrysis*, there are strong tooth-like projections from the top of the metapleuron and from the propodeum. These teeth approach closely without fusing and the spiracle can be seen from the side and, to a smaller extent, from above. In *Omalus* and its allies, the two teeth are fused *below* the spiracle which lies wholly on the dorsal aspect of the propodeum.

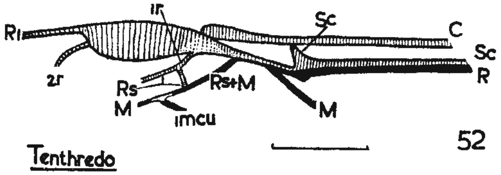
The second abdominal segment, in the Apocrita, is articulated by its petiole to the propodeum with a double ball-and-socket joint. The internal organs enter the petiole somewhat ventrally and above the point where they leave the propodeum is a small, usually circular, *orifice of the propodeum* (fig. 49), through which passes the *dorsal muscle* (of the petiole) (fig. 49) which enters a small swelling at or near the anterior end of the petiole. Two *propodeal teeth* (figs 43, 49) usually project on each side of the orifice and in some Aculeata (e.g., *Odynerus*) there may be a pair of raised *propodeal valves* (fig. 49) outside the teeth. The detailed mechanism of these structures in the Honey bee is described by Snodgrass (1942).

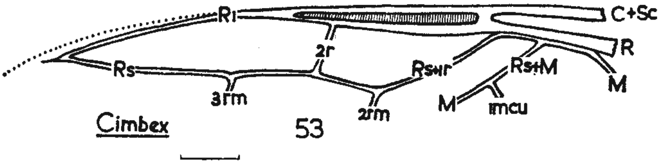
The Evanioidea and, to a less extent, certain other groups in the Parasitica are peculiar in that the articulation of the gaster is high up on the propodeum, near the metanotum. The gap thus developed between the two sides of the propodeum by the upward displacement of the orifice is closed by secondary sclerotization.

WINGS

Hymenoptera characteristically have two pairs of wings, the fore and hind ones on each side being held together by a row of hooks or *hamuli*, arising from the front edge of the hind wing and engaging with the down-







FIGS 50–53. (All except fig. 50 are of left wings. Scale-lines = 1.0 mm. Longitudinal veins are shown with a capital letter, cross-veins in small letters.) 50, Axillary region of *Urocerus gigas* (L.). 1–4 *Ax.*, axillary sclerites. *Ax. C.*, axillary cord. *H.p.*, humeral plate. *M.p.*, median plate. *Scl.*, mesoscutellum. *Sct.*, mesoscutum. 51, Fore and hind wings of *Xyela julii* (Bréb.) (Xyelidae). *A.L.*, anal lobe. *Ham.*, hamuli. *J. F.*, jugal fold. *S.p.*, scaly patch. *V.f.*, vannal fold. 52, Pterostigmal region of forewing of *Tenthredo arcuata* Först. (Tenthredinidae). Black veins are shown dark and yellowish ones are cross-hatched. 53, The same of *Cimbex femorata* (L.) (Cimbicidae).

folded hind margin of the forewing. In more primitive types the hamuli arise at a number of points from the articulation of the wing to the R_1 vein, but in higher forms they tend to form a compact group at the most distal site. There is a suggestion (Richards, 1949) that their number may be related to the amount of flying undertaken, occasionally their number is of some taxonomic importance, e.g., in *Sphecodes* (Apoidea).

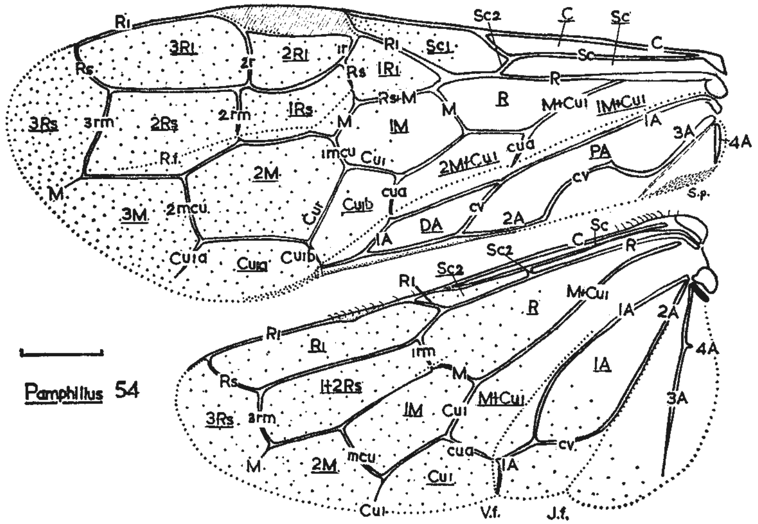
The wings are very rarely somewhat reduced in sawflies but a more or less extreme reduction occurs in many families of the Apocrita, especially and often to a greater extent in the female.

The surface of the wing can be divided into three areas, the anterior *remigium* and the posterior *vannus*, separated by the *vannal fold* (*v.f.*) (figs 51, 54) which is an important landmark. The third area, the *jugum*, is scarcely developed in the forewing of Hymenoptera but is seen in what is usually called the *anal lobe* of the hind wing. When the wing is outstretched the front margin of the wing is the *costal margin*, the hind margin is the *dorsal margin*, and the tip of the wing is the *apex*. The membrane is supported by a series of *veins* which articulate with the thorax by means of the *axillary sclerites* (1–4*Ax.*); these are shown in *Urocerus gigas* (L.) (SIRICIDAE) (fig. 50). These sclerites are of importance in the folding of the wing and assist in recognizing the wing-veins which tend to articulate with particular sclerites. Besides the axillary sclerites 1–4, the *tegula*, the *humeral plate* (*H.p.*) and the *median plate* (*M.p.*) will be noticed. The usual arrangement is that *C* articulates with *H.p.*; *Sc* with 1*Ax.*; *R* with 2*Ax.*; *M* with *M.p.*; 1*A* with 3*Ax.* Unfortunately, the development of the axillary sclerites is so variable and their contours so ill-defined that they are less helpful than might be hoped in interpreting the veins. The tegula is normally a much larger structure than it is in *Urocerus* where it can only be seen after maceration. Its colour, shape or sculpture are frequently of taxonomic importance. The humeral plate is often of a different colour from the rest of the costa and in the ICHNEUMONIDAE is often termed the *radix*. The axillary sclerites are normally hidden by the tegula, but the median plate is often prominent and its colour may be of taxonomic importance (e.g., *Nomada*, Apoidea).

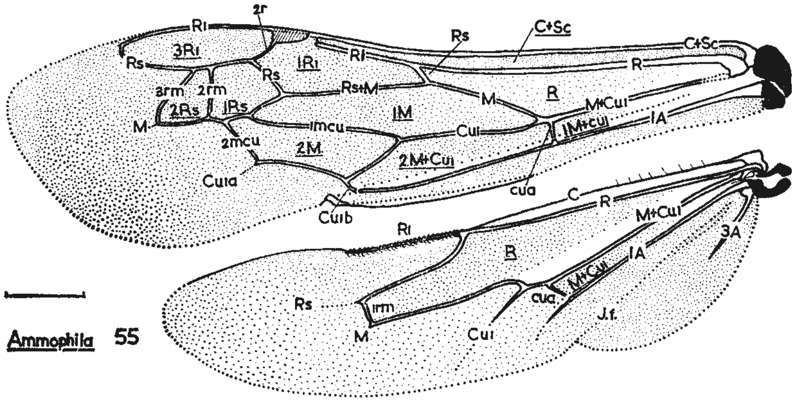
The wing-veins provide the most important single character for the classification of the order but there is, unfortunately, no universally accepted system for labelling them and the *cells* which they enclose. The Jurinean system which most systematists employ (see Rohwer and Gahan, 1916, for a review of the subject up to that date) has no relation to the modifications of the Comstock-Needham system used for other orders. Moreover, hardly two writers on the same family use all the names in quite the same sense. The scheme proposed by Ross (1936) for the sawflies and since adopted by a number of other entomologists (Burks, 1938; Duncan, 1939; Michener, 1944; Lanham, 1951; Eady, 1974) is probably the most successful attempt to establish a universally applicable system. For the British fauna, the most practical arrangement seems to be to describe Ross's scheme and to relate it to the systems in widest systematic use. Any full discussion of the problem would involve going outside the British fauna; little time will be spent therefore in attempting to justify proposed homologies.

The most complete venation of any British species is found in *Xyela julii* (Bréb.) (Symphyta, XYELIDAE) (fig. 51), though a few extra veins are found in wings which are otherwise less complete. A detailed commentary on this species will make it possible to deal more shortly with other wings.

(1) The *pterostigma* is of rather uniform texture but there is a suggestion that it is bounded by veins, the cell being filled in by a thickening of the membrane. This origin for the pterostigma is much more obvious in *Cimbex* (CIMBICIDAE, fig. 53) and male *Mutilla* (MUTILLIDAE, fig. 59). The anterior



Pamphilius 54



Ammophila 55

FIGS 54–55. (Left wings are shown. The longitudinal veins are shown with a capital letter, the cross-veins with small letters and abbreviations for cells are underlined. The scale lines represent 1.0 mm.) 54, The fore and hind wings of *Pamphilius* sp. (Pamphiliidae). *J.f.*, jugal fold. *S.p.*, scaly patch. *V.f.*, vannal fold. 55, The same of *Ammophila sabulosa* (L.) (Sphecidae). *J.f.*, jugal fold.

margin of the pterostigma is supposed to be formed by a branch of the *subcosta* (*Sc*) and the posterior margin by the first branch of the *radius* (R_1). Apart from a few primitive sawflies, *Xyela, Pamphilius* (PAMPHILIIDAE, fig. 54), *Sc* is usually fused with *R*. But Mr R. B. Benson has pointed out that in such genera as *Tenthredo* (TENTHREDINIDAE, fig. 52), the apparent radius is bicoloured and the paler anterior part probably represents *Sc* and is produced into a stub ($=Sc_1$) a little before the pterostigma. In *Urocerus* (fig. 50), *Sc* is distinct near the base of the wing but soon runs into *R*. A distinct *Sc* has been noted by Dr J. F. Perkins in the Sphecoid, *Astata* (fig. 61), and in this case runs into the *costa* (*C*). R_1 runs along the posterior margin of the pterostigma and then for a variable distance along the costal margin of the wing. In Parasitica, the part of R_1 beyond the pterostigma is often called the *metacarp*.

(2) The *radial sector* (*Rs*) has two branches (Rs_1, Rs_2) in the XYELIDAE but in no other sawflies. It appears that the primitive stock of the Apocrita must also have had a branched *Rs*, and a vein corresponding to Rs_2 is seen in *Astata, Mutilla* and probably *Andricus* (CYNIPIDAE, fig. 62).

(3) In *Xyela julii*, the *media*, just after it leaves $M + Cu_1$ fuses with *Rs* for a short distance. In some exotic XYELIDAE this fusion does not take place and the two veins are connected by a short cross-vein (1*r–m*). This is why the two more distal radio-median cross-veins of the British species are labelled 2*r–m* and 3*r–m*.

(4) The series of veins in the posterior part of the wing are the *cubitus* (1 and 2) (very reduced in all Hymenoptera) and the *anals* (1–4). Snodgrass has proposed that the 1*A* should be called the postcubitus and the remaining anal veins the vannals and jugals, but the change in the old nomenclature seems to have insufficient advantages to be adopted here.

(5) There is no trace of Cu_2 in this wing, but in some exotic Symphyta it is visible proximally, running in the vannal fold.

(6) The proximal part of Cu_1 is only visible in the hind wing but in some non-British XYELIDAE and ARGIDAE, it is developed in a similar way in the forewing also. Cu_1 leaves *M* somewhere about the middle of the wing and ultimately forks into two branches Cu_{1a} and Cu_{1b}.

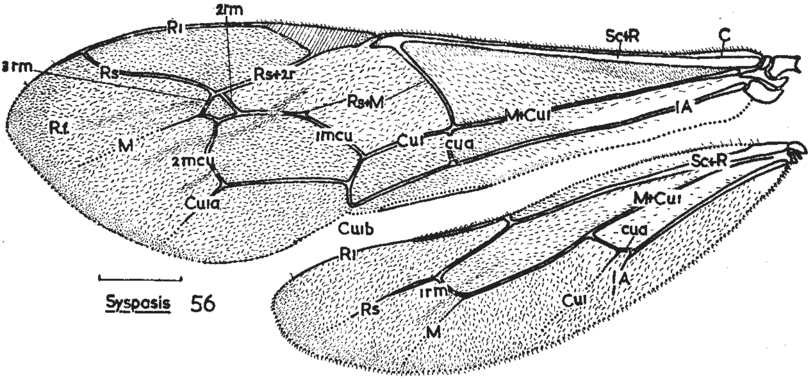
(7) The first anal vein (1*A*) takes a rather similar course in all Hymenoptera in which the venation is not greatly reduced, running just behind the vannal fold. The peculiar sinuous course of $3A + cv + 2A$ is analysed in detail by Ross (1936: plate 2, figs 14–19).

In *Xyela*, only one cross-vein, *cu–a*, connects Cu_1 to 1*A*, but in *Pamphilius* (fig. 54) and some other genera there are two such cross-veins.

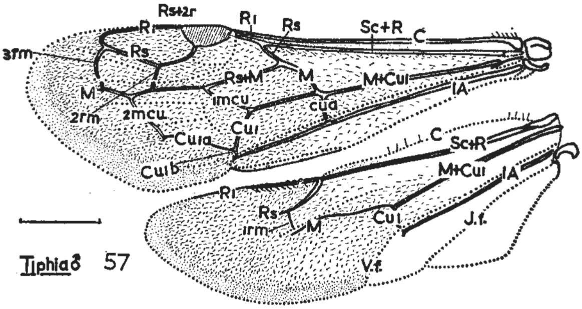
(8) The inflected hind margin (=frenal fold) which engages with the hamuli is shown in all the figures of forewings by drawing a continuous, not a dotted, margin.

(9) The forewings of all sawflies, except the CEPHIDAE, have a scaly patch behind 3*A* (*S.p.* in figs 51, 54). When the wings are folded over the abdomen this engages with the cenchri and helps to hold the wings in position.

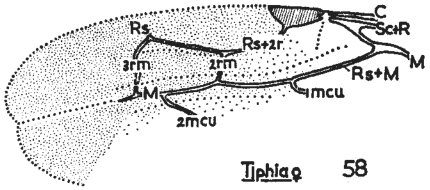
(10) Short gaps or short stretches where the vein is decolorized are known as *fenestrae*. They most often occur where veins, especially cross-veins, are crossed by the folds. In *Xyela*, they are seen in 1*r*, in the second abscissa of *Rs*, in 2*r–m*, 3*r–m*, in the third abscissa of *M*, and in *cu–a* and Cu_{1b}. The



Syspasis 56



Tiphia♂ 57



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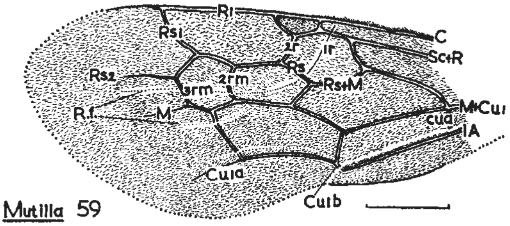


Mutilla 59

FIGS 56–59. (Left wings are shown. The longitudinal veins are shown with a capital letter, the cross veins with a small one. The scale lines represent 1.0 mm.) 56, The fore and hind wings of *Syspasis lineator* (F.) (Ichneumonidae). 57, The same of *Tiphia femorata* F. (Tiphiidae) ♂. *J.f.*, jugal fold. *V.f.*, vannal fold. 58, The same, part of forewing of ♀. 59, Distal part of forewing of *Mutilla europaca* L. (Mutillidae) ♂. *R.f.*, radial fold.

fenestra in 1*r* probably indicates the general tendency for the reduction of this vein which is absent or rudimentary (*Astata*, fig. 61) in most specialized wings. The fenestrae in *Rs*, 2*r–m* and 3*r–m* correspond to what is a well-marked *radial fold* in some wings. It seems that the radial fold may bifurcate (ICHNEUMONIDAE, fig. 56; *Mutilla*, fig. 59; *Bracon*, fig. 63) and the fenestra in *M* is due to the posterior branch of the radial fold. The vannal fold, with the fenestrae in *cu–a* and Cu_{1b}, is very regularly developed. It seems that the development of folds and of fenestrae may have more taxonomic importance than has as yet been given to it, but the size and position of the fenestrae in 2*m–cu* is already used as a generic character in some ICHNEUMONIDAE.

(11) The vannal fold usually runs out at a small indentation of the wing margin, the *preaxillary excision*. The anal lobe or jugum, marked off by a slight jugal fold and supported by vein 4*A*, is very small.

(12) The cells of the wing are referred to by the name of the principal vein which forms their costal or proximo-costal boundary. They are labelled in figs 54–55.

(13) Riegel (1949), from studies of exotic BRACONIDAE, has suggested (and Dr J. F. Perkins has found some evidence from other groups to support him) that *M* may really have left $M + Cu_1$ at about the point where that vein is gently curved in *Xyela* and joined *Rs* just beyond the point where R_1 leaves *R*. This piece of *M* is never more than suggested by a stub or angulation, but if it really existed it would mean the following changes in the labelling of fig. 51: distal part of $M + Cu_1$ would become Cu_1; first free abscissa of *M* would become 1*m–cu*; and 1*m–cu* and 2*m–cu* would become 2 and 3*m–cu* respectively. This theory has been regarded as too uncertain to be accepted and it is not of much importance for British species.

(14) The venation of the hind wing is simpler and more reduced than that of the forewing. It will be seen that in *Xyela* (fig. 50), and *Pamphilius* (fig. 54), there are at least two well-developed groups of hamuli. In higher forms (figs 55–57, 60, 62), the proximal group of hamuli is reduced or absent. *Rs* is never more than one-branched, Cu_1 is unbranched, and 3*A* lies in the pronounced anal lobe. Traces of the two branches of the radial fold and of the vannal fold are visible.

(15) It will be noted that according to this scheme, which follows Ross, the anal lobe is supported by 4*A* in the forewing but by 3*A* and 4*A* in the hind. It seems likely that this region requires more study.

The other figures are of a selection of British genera showing various stages of reduction from the more complete Symphytan type.

Pamphilius (fig. 54) is not very different from *Xyela*. In the forewing, it lacks one branch of *Rs*, but there is a second *cu-a* cross-vein and the arrangement of 2*A*, 3*A* and their connecting cross-vein is less specialized. In the hind wing Sc_2 is preserved but the base of Cu_1 is lost and the 1*A* reaches the margin.

The forewing of *Ammophila sabulosa* (L.) (SPHECIDAE, fig. 55) shows especially the loss of *Sc*, of 1*r* and of all the anal veins except 1*A*. In the hind wing, *Sc*, the distal part of *Rs*, an *r–m* and *m–cu* cross-vein, and 2*A* are lost. *Astata boops* (Schrk.) (fig. 61), another Sphecoid, is less specialized, retaining part of *Sc*, a trace of 1*r*, a trace of Rr_2, and an anal vein behind 1*A*. It should be noted that in the Apocrita a single R_1 cell is formed by the loss of $1r$, whereas in the Symphyta NEMATINAE a similar single cell is formed by the loss of $2r$.

Syspasis lineator (F.) ICHNEUMONIDAE (fig. 56) not only lacks *Sc* but the costal cell is nearly obliterated; not only $1r$ but also the middle abscissae of $Rs + M$ and *Rs* are lost. The composite, stub-bearing vein (stub $= Rs + M =$ *ramellus*), which taxonomists sometimes call the '*disco-cubital*', is made up of $1m\text{–}cu + (Rs + M) + M$. In the hind wing, *C* is almost lost but the venation otherwise resembles *Ammophila*. It is taxonomically important whether Cu_1 is nearer $M + Cu$ or $1A$ ('nervellus intercepted above or below the middle'); also whether the composite vein $Cu_1 + cu\text{–}a$ is directed outwards as in the figure, is perpendicular to $M + Cu_1$, or is directed to the base of the wing (nervellus 'postfurcal', 'opposite', or 'antefurcal').

Tiphia femorata F. (TIPHIIDAE, figs 57, 58) is an aculeate showing considerably more reduction than *Ammophila*. The middle abscissa of *Rs* and, in the female, part of the distal one are missing. In the hind wing the distal part of Cu_1 is lost.

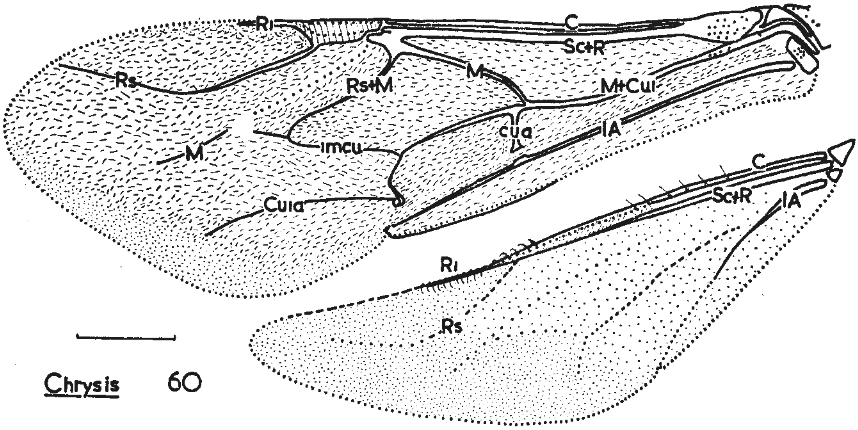
Chrysis ignita (L.) (CHRYSIDIDAE, fig. 60), in the forewing is still more reduced but the homologies are easily seen. The hind wing has little definite venation left and the preaxillary excision and the anal lobe are only weakly indicated.

Bracon hebetor Say (BRACONIDAE, fig. 63) shows the characteristic difference between this family and the ICHNEUMONIDAE. The middle abscissa of $Rs + M$ is preserved (in most Braconids) and the first abscissa of *Rs* is present, but the cross-vein $2m\text{–}cu$ is absent. In the hind wing (fig. 159) the cross-vein $r\text{–}m$ meets $Sc + R$ and not *Rs* as it does in the ICHNEUMONIDAE (fig. 56).

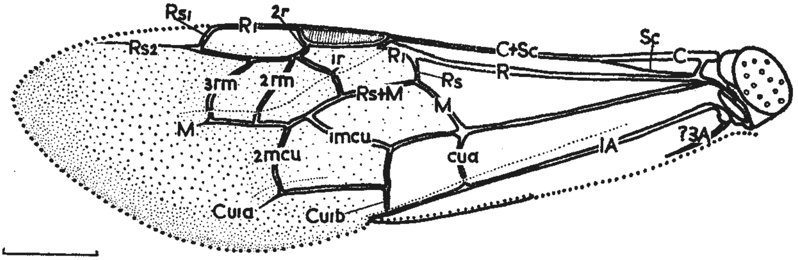
Andricus kollari (Htg.) (CYNIPIDAE, fig. 62) is an example of a peculiar type, on the whole very reduced but retaining, apparently, traces of two branches of *Rs*. The absence of the costa and of the pterostigma is characteristic.

The other wings which are illustrated are examples of peculiar specialized types which might well cause difficulty, *Gasteruption assectator* (L.) (GASTERUPTIIDAE, fig. 64), *Neoneurus bistigmaticus* (Morl.) (BRACONIDAE, fig. 65), *Helorus coruscus* Hal. (Proctotrupoidea, HELORIDAE, fig. 66), and *Neorhacodes enslini* (Ruschka) (ICHNEUMONIDAE, fig. 67). The last-named is one of the few members of its family in which cross-vein $2m\text{–}cu$ is absent or almost so (as in a Braconid) and the close fusion of *Rs* and *M* is peculiar. In *Chalcis sispes* (L.) (CHALCIDIDAE), the venation is so reduced that it is probably convenient to retain the usual systematic nomenclature (as also in some Proctotrupoids), viz., $Sc + R =$ *submarginal vein*; 1st and 2nd parts of $R_1 =$ *marginal* and *postmarginal veins* and $2r + Rs =$ *stigmal vein*. The remaining venation is more or less visible in Chalcidoids, depending on the species and on the lighting.

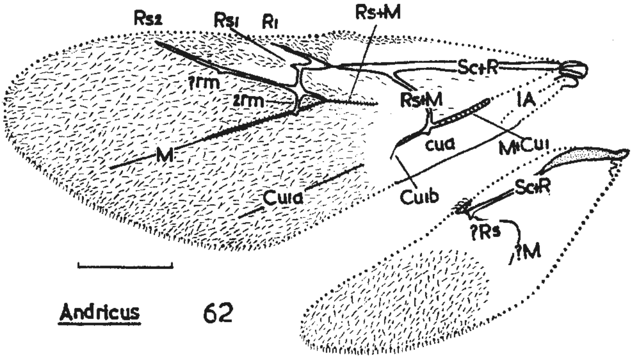
To supplement this account, the synonyms of the terms used for veins and cells in a number of standard works have been listed (see pp. 95–97). Michener (1944:180), who has applied Ross's system with minor modifications to the bees, has suggested certain compromises with the older taxonomic nomenclature which will probably prove useful in the more specialized wings such as those of Aculeata. The cell $2R_1$, radial cell of most taxonomists but the *marginal cell* of others, might retain the latter name. The three cells



Chrysis 60

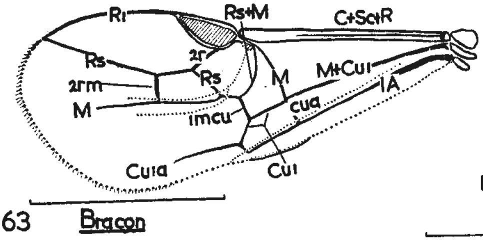


Astata 61



Andricus 62

FIGS 60–62. (Left wings are shown. The longitudinal veins are shown with capital letters, the cross-veins with small ones. The scale lines represent 1.0 mm.) 60, Fore and hind wings of *Chrysis ignita* (L.) (Chrysididae). 61, Forewing of *Astata boops* (Schrk.) (Astatidae). 62, Fore and hind wings of *Andricus kollari* (Htg.) (Cynipidae), agamic ♀.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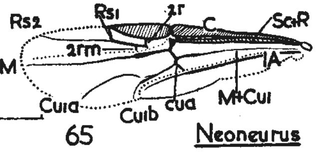
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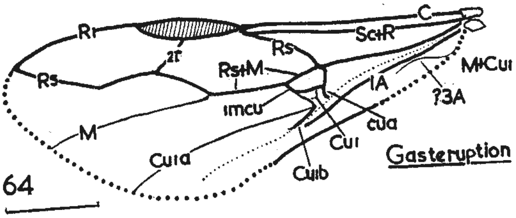
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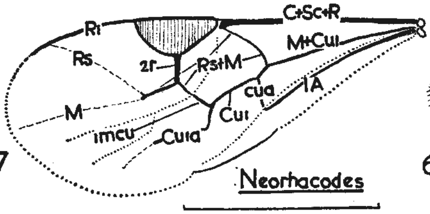
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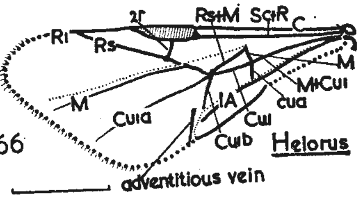
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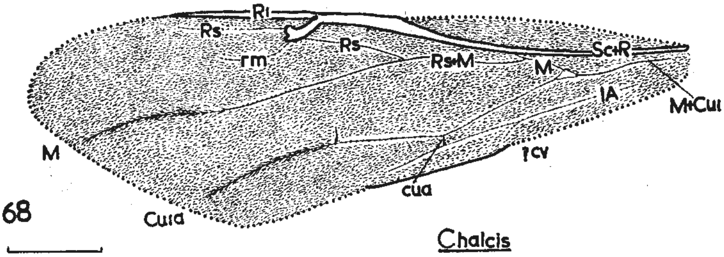
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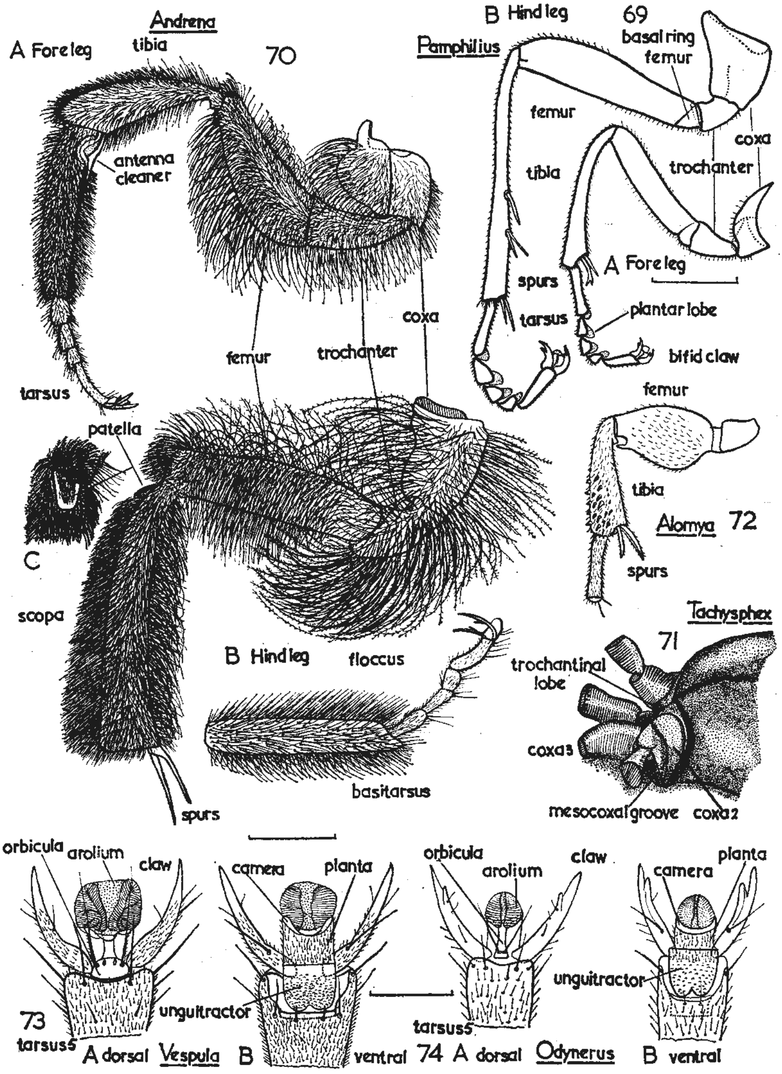
FIGS 63–68. (Left forewings are shown. The longitudinal veins are shown with capital letters, the cross-veins with small ones. The scale lines represent 1.0 mm.) 63, *Bracon hebetor* Say (Braconidae). 64, *Gasteruption assectator* (L.) (Gasteruptiidae). 65, *Neoneurus bistigmaticus* (Morley) (Braconidae). 66, *Helorus coruscus* Hal. (Heloridae). 67, *Neorhacodes enslini* (Ruschka) (Ichneumonidae). 68, *Chalcis sispes* (L.) (Chalcididae).



FIGS 69–74. (Figs 69–72 scale-line = 1.0 mm. Figs 73–74 = 0.25 mm.) 69, *A* Fore leg, *B* Hind leg of *Pamphilius varius* (Lep.) (Pamphiliidae) ♀, antero-ventral view. 70, *A* Fore leg, *B* Hind leg, *C* base of hind tibia of *Andrena fulva* (Müller) (Andrenidae) ♀, *A* and *B* posterior, *C* dorsal view. 71, Left mid coxa of *Tachysphex pompiliformis* (Panz.) (Sphecidae) ♀, ventro-lateral view. 72, Mid leg (less part of tarsus) of *Alomya debellator* (F.) (Ichneumonidae) ♀, anterior view. 73, *A* dorsal, *B* ventral view pretarsus of *Vespula vulgaris* (L.) (Vespidae) ☿. 74, The same of *Odynerus spinipes* (L.) (Eumenidae) ♀.

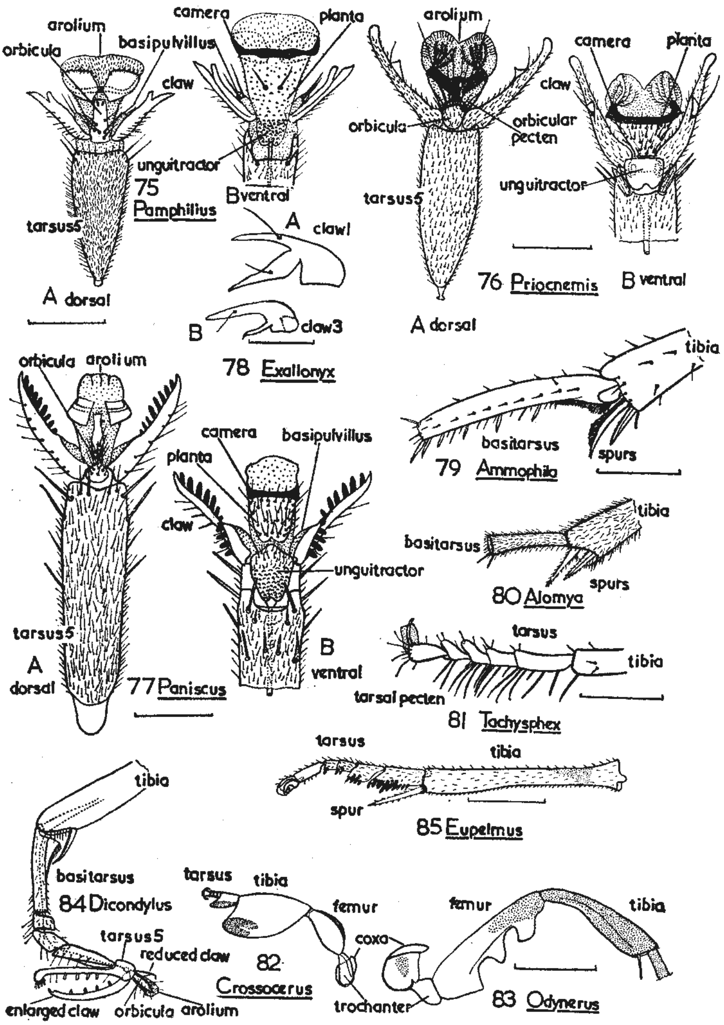
R_1, $1Rs$ and $2Rs$, the cubital cells of many taxonomists but *submarginal cells* of others, might retain the latter name. Michener's suggestion of the name intercubiti 1–3 for the cubital cross-veins of taxonomists (=1st abscissa *Rs*, *2r–m*, *3r–m*) seems less happy. The length of the abscissa of R_1 before the pterostigma is often very important. It is the *parastigma* of Schmiedeknecht (=*prestigma* of Michener) (fig. 55, *Ammophila*). The terms synonymized on pp. 95–97 were obtained from the following works: FORMICIDAE, Donisthorpe (1927: fig. 8); Symphyta, Enslin (1912: fig. 7); BETHYLIDAE, Kieffer (1914*a*, figs 4–6); PROCTOTRUPIDAE, Kieffer (1914*b*, fig. 3); BRACONIDAE, Marshall (1889: plate 1) and Schmiedeknecht (1930: fig. 45); ICHNEUMONIDAE, Morley (1903 : p. xxxvi) and Schmiedeknecht (1930: fig. 21); Aculeata, Saunders (1896 : plate 1) and Schmiedeknecht (1930: figs 8 and 9).

Note: veins = nerves = nervures; × -vein = cross-vein. Synonyms such as medius = median = medialis are not listed separately. Nervus recurrens, etc., are listed under recurrens.

LEGS

The legs, of which there is a pair for each thoracic segment, consist of a *coxa*, *trochanter*, *femur*, *tibia* and segmented *tarsus* (figs 69, 70). The coxa is short and stout and its principal articulation (p. 18) is with the pleuron; in a few primitive types there is also a less important articulation with the trochantin. In many Aculeata (fig. 71, *Tachysphex*) and in the EVANIIDAE and GASTERUPTIIDAE, the mid coxa is crossed by a deep furrow, the *mesocoxal groove* (Michener, 1944 : 181). The trochanter is a small segment which allows the femur to be directed in a generally dorsal direction even when the distal end of the coxa is directed ventrally. In the Symphyta (fig. 69) and some Apocrita (ICHNEUMONIDAE, fig. 72), there is a trochantellus, an apparent second segment to the trochanter which is really a piece cut off the proximal end of the femur (Snodgrass, 1935 : 197). A few Aculeata, VESPIDAE and Nyssoninae (SPHECIDAE), have more or less distinct traces of this proximal piece or *basal ring* of the *femur*. The tarsus nearly always consists of five segments, but four in many Chalcidoids and three in the Trichogrammatidae. The last tarsal segment bears the *claws* and associated parts which together form the pretarsus. The claws may be simple (fig. 73), or bifid (figs 69, 74, 75, 78), or with one or more subapical teeth (fig. 76), or pectinate (fig. 77). Between the claws, lies the foot-pad or *arolium* (pulvillus of some authors) in whose dorsal surface is a plate, the *orbicula*. In the POMPILIDAE, the size of the orbicula and the development of a row of bristles on it (the *orbicular pecten*, fig. 76A) are taxonomically important. Ventrally, between the claws and the last tarsal segment is the *unguitractor*, a plate to which the muscle of the pretarsus is attached by a tendon. Small sclerites called *auxiliae* are usually figured on each side of the apex of the unguitractor but it seems uncertain whether these are really separate from the unguitractor. At the base of the claws, in some Symphyta (fig. 75B) and also apparently in some ICHNEUMONIDAE (fig. 77B) is a membranous lobe, the *basipulvillus*, of which the auxiliae are supposed to be reduced remnants. Beneath the arolium there is a bristly surface, the *planta*,[4] and a supporting sclerotized ring, the *camera*.

[4] This term has also been applied to the first segment of the hind tarsi in *Apis*.



FIGS 75–85. (Figs 75–77, 84–85, scale-line = 0.25 mm. Fig. 78, scale-line = 0.5 mm. Figs 79–83, scale-line = 1.0 mm.) 75, *A* dorsal, *B* ventral view of pretarsus of *Pamphilius inanitus* (Vill.) (Pamphiliidae) ♀. 76, The same of *Priocnemis perturbator* (Harris) (Pompilidae) ♀. 77, The same of *Netelia testacea* Grav. (wrongly labelled *Paniscus* on drawing) (Ichneumonidae) ♀. 78, Claw of fore (*A*) and hind leg (*B*) of *Exallonyx niger* (Panz.) (Proctotrupidae) ♀. 79, Apex of hind tibia of *Ammophila sabulosa* (L.) (Sphecidae) ♀, anterior view of right leg. 80, The same of *Alomya debellator* (F.) (Ichneumonidae) ♀. 81, Left fore tarsus of *Tachysphex pompiliformis* (Panz.) (Sphecidae) ♀, dorsal view. 82, Fore leg of *Crossocerus palmipes* (L.) (Sphecidae) ♂, postero-dorsal view. 83, Mid leg (except tarsus) of *Odynerus spinipes* (L.) (Eumenidae) ♂, posterodosal view. 84, Fore leg of *Dicondylus bicolor* (Hal. *in* Curt.) (Dryinidae) ♀, anterior view. 85, Mid tibia and tarsus of *Eupelmus urozonus* (Deg.) (Eupelmidae) ♀, anterior view.

The tibiae are provided with articulated spurs on the ventral side. Typically, the three legs have 2, 2, 2 spurs (Symphyta) or 1, 2, 2 spurs (Apocrita) at the apex of the tibia, but some Symphyta have 1–4 spurs (fig. 69) near the middle of the tibia also. In particular groups, or even species, some of the spurs may be lost. In the Symphyta, one of the apical spurs of the fore tibia is usually larger than the other and more or less modified into an antenna-cleaner (fig. 69A); the unmodified spur is usually smaller and sometimes lost. In the Apocrita, the fore tibia has only one apical spur (except the Ceraphronoidea which have two) and this is modified, together with the ventral side of the first segment of the tarsus (=*basitarsus* 1) into an antenna-cleaner (fig. 70A). Terms for the parts of this structure have been explained by Michener (1944 : 182). A parallel but slightly different modification of the hind tibia and its larger apical spur forms another cleaning apparatus in the Sphecoids and other groups (fig. 79).

In most Symphyta (fig. 69), each segment of the tarsi ends in a membranous pad, the *plantar lobe*, rather like an arolium. Similar but much smaller structures occur in some Apocrita, e.g., TRIGONALIDAE, POMPILIDAE.

The legs are often conspicuously modified for special habits or modes of life. Thus species which burrow often have enlarged femora and spiny tibiae (*Alomya* ♀, ICHNEUMONIDAE, fig. 72) or long spines on the front tarsi, forming a *tarsal pecten* (*Tachysphex* ♀, SPHECIDAE, fig. 81). In the Apoidea, all the hairs are branched to collect and hold pollen and a dense brush of such hairs on the hind legs of several groups forms a scopa[5] (*Andrena* ♀, ANDRENIDAE, fig. 70B). *Andrena* also has, in many species, a *floccus* or curled tuft of hairs on the trochanter and a plate or *patella* (fig. 70B) at the base of the hind tibia. The latter structure is said to be pressed against the side of the burrow to support the bee. It is less developed in male bees and is absent in forms not burrowing in the soil and in parasitic species. The hind basitarsus of the Apoidea is also usually considerably broadened (fig. 70B), especially in the social species (*Bombus* ☿, Bombinae, fig. 86). In these, also, the hind tibia is externally flattened or concave and fringed by long bristles forming the *corbicle* or pollen-basket. On the inner side of the apex of the tibia a row of stout spines forms the *tibial pecten* and the inner dorsal angle of the basitarsus is produced into an *auricle*. The functions of these structures are explained by Sladen (1912: 20, fig. 5).

Other striking modifications of the legs are those which enable males to seize females, such as broadened front tarsi (*Crossocerus*, Crabroninae, fig. 82) or the toothed mid femur of some *Odynerus* (VESPIDAE, fig. 83), which grip the wings of the female. The front tarsi of most female Dryinids (fig. 84) is formed into a *chela* for gripping the homopterous prey, the fifth segment and one claw being enlarged, while the other claw is reduced or absent. In the ENCYRTIDAE and EUPELMIDAE (Chalcidoidea, fig. 85), one spur and the basitarsus of the mid leg are enlarged for jumping.

ABDOMEN

The abdomen normally consists of ten segments but this number may not be visible without careful study or dissection. Each is normally made up of

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[5] Some ICHNEUMONINAE ♀ also have a so-called scopa of unknown function on the hind coxa.

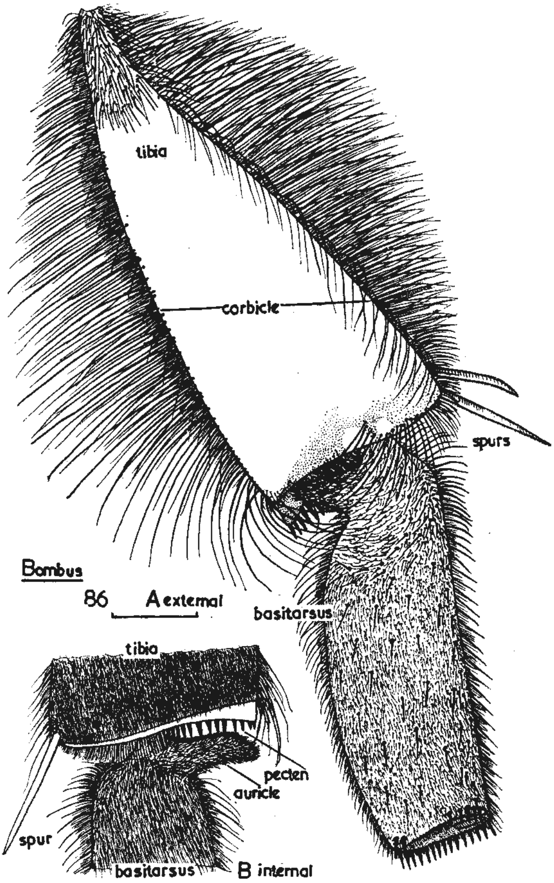
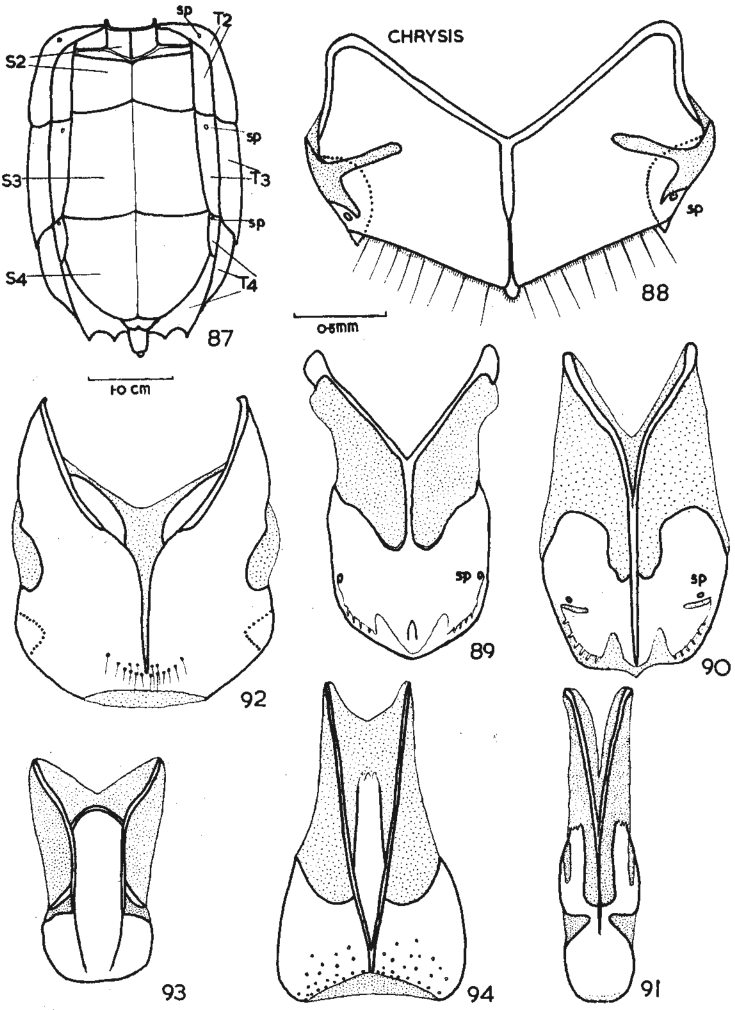


FIG. 86. (Scale-line = 1.0 mm.) *A*, Hind tibia and basitarsus of *Bombus terrestris* (L.) (Apidae) ☿, external view. *B*, Articulation of tibia and basitarsus, internal view.

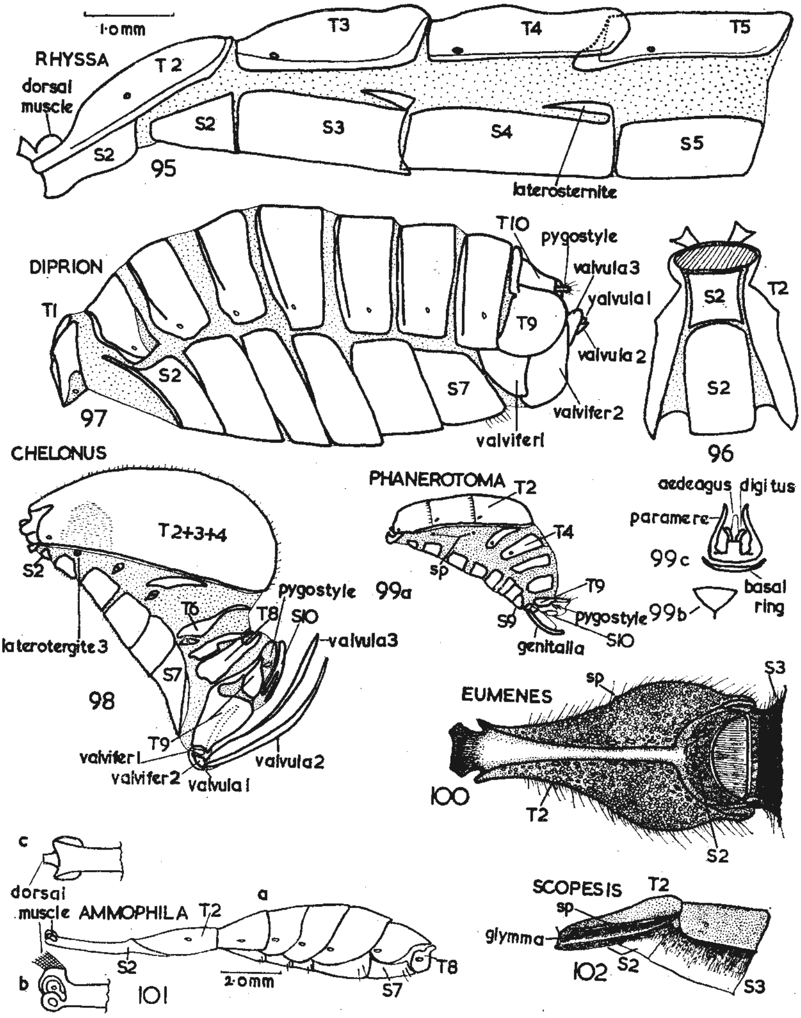
a dorsal plate or *tergite* and a ventral plate or *sternite*. Special sclerites are not developed in the pleural membranes and the spiracular openings lie at the sides of the tergites. At least the ninth tergite and, in the female, the eighth and ninth sternites are strongly modified. In some groups (e.g., CHRYSIDIDAE, segments 2–4, fig. 87; SCELIONIDAE, 2–6; PLATYGASTERIDAE, 3–7; Chalcidoidea, segment 8, fig. 108), a lateral piece of the tergite is well marked off or even completely detached from the main dorsal part of the tergite to form a *laterotergite*. Analogous *laterosternites* are detached from the sides of the sternal plates in many ICHNEUMONIDAE (fig. 95).

In the Symphyta (fig. 97), the first seven segments are normally developed, except that the first sternite is membranous. The eighth tergite is also normal and *spiracles* or stigmata are visible at the sides of the first eight



FIGS 87–94. (The anterior end of each figure is directed towards the top of the page. Figs 88–94 all to the same scale. Small numbers refer to abdominal segments. *T* = tergite; *S* = sternite; *sp* = spiracle.) *Chrysis ignita* (L.) (Chrysididae) ♀. 87, Ventral view of gaster, pubescence and punctures omitted. 88, Abdominal tergite 5, dorsal. 89, Tergite 6. 90, Tergite 7. 91, Tergite 8. 92, Abdominal sternite 5, ventral. 93, Sternite 6. 94, Sternite 7.

tergites. The more posterior parts are modified in connection with the ovipositor or male genitalia, as described below. Ten tergites and nine sternites are recognizable and the tenth tergite bears a pair of small, lateral, piliferous processes, the *pygostyles* (figs 98, 99, 109, 118, 123, 124, 135, 148), sometimes described as cerci. Where the tenth segment is membranous or fused with the ninth, the pygostyles may become attached to the latter. In



FIGS 95–102. (All figs to same scale, except fig. 101. Small numbers refer to abdominal segments. *T* = tergite; *S* = sternite; *sp* = spiracle.) 95, *Rhyssa persuasoria* (L.) (Ichneumonidae) ♂. Base of gaster, left side. 96, Ventral. 97, *Diprion pini* (L.) (Diprionidae) ♀. Gaster, left side. 98, *Chelonus inanitus* (L.) (Braconidae) ♀. Gaster, left side. 99, *Phanerotoma* sp. (Braconidae) ♂, (*a*) gaster, left side, (*b*) abdominal sternite 9, ventral, (*c*) genitalia, ventral. 100, *Eumenes coarctatus* (L.) (Eumenidae) ♀. Petiole, ventral. 101, *Ammophila sabulosa* (L.) (Sphecidae) ♀. (*a*) Gaster, left side, (*b*) base of petiole, left side, (*c*) base of petiole, ventral. 102, *Scopesis bicolor* (Grav.) (Ichneumonidae) ♀. Base of gaster, left side.

general, the tergites of the Symphyta overlap one another very little compared with those of the Apocrita.

In the Apocrita, where the first abdominal segment is modified into the propodeum which is functionally part of the thorax, the usual practice has been to start to number the abdominal segments at the second. This system is very confusing when the morphology of the genitalia is discussed and it seems preferable to have some term for the post-propodeal part of the abdomen. Michener (1944 : 184) has proposed the term 'metasoma' but gaster has been widely used in ants and was adopted by Kerrich and Hedicke (1940 : 185) in the Cynipoidea. The only complication arises from a difference of practice in the treatment of the narrowed first segment or petiole. In the ICHNEUMONIDAE (fig. 114), for instance, the narrow part of the first gastral segment is termed the petiole and the broader, posterior part of the same segment, the *postpetiole*. In the ants, on the other hand, the abdomen is usually described as made up of an epinotum (=propodeum), a scale or petiole (or, in the Myrmicinae, two petiolar segments), and a gaster. Thus in the ants, the gaster may include either the last eight or, in the Myrmicinae, the last seven segments. It is proposed here to use the term *gaster* for all the segments behind the propodeum. The *petiole* is the narrowed anterior stalk, whether composed of part of a segment, or of one segment, or of two. A *dorsal muscle of the petiole* (figs 95, 101) can usually be seen to leave the orifice of the propodeum and to enter a small swelling near the anterior end of the petiole. Oeser (1971) describes the detailed articulation of the petiole to the propodeum in *Ammophila* (SPHECIDAE).

The number of pairs of functional spiracles is clearly of major importance in classification but it is still very little explored, particularly in the Proctotrupoid groups. There is also the difficulty that ring-like structures in the correct position may have no connection with the tracheal system though they are probably a stage in the reduction of a spiracle. As in the Symphyta, most of the Apocrita have eight pairs of functional spiracles. The known examples in British families of reduction are listed below and it will be seen

Hymenoptera with reduced numbers of spiracles

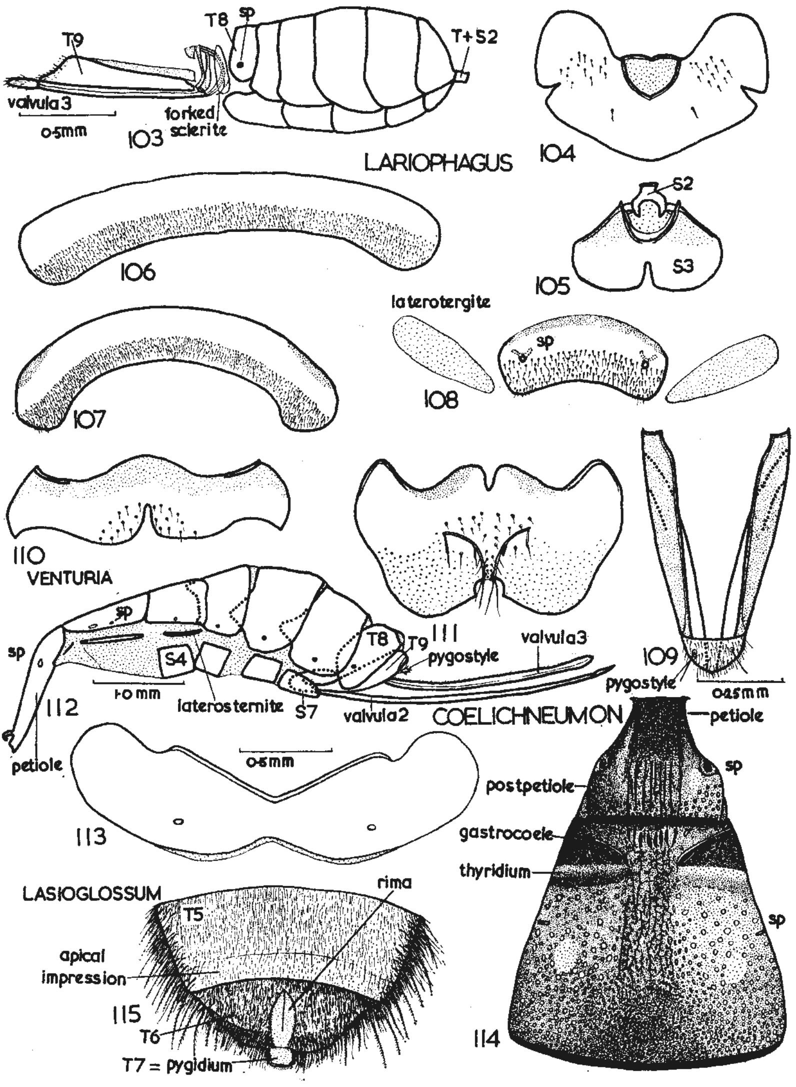
Taxonomic group	Abdominal segments with spiracles
Bethyloidea (Bethylidae[a], Embolemidae ♂, Chrysididae, Cleptinae, Chrysidinae[b])	1–7
Braconidae, Sigalphinae[c], Scelionidae[d]	1–6
Chalcidoidea, Cynipoidea, Evanioidea, Diapriidae	1 and 8
Proctotrupidae, Ceraphronidae, Platygasteridae	1 only

[a] According to van Emden (1931), *Cephalonomia* ♂ has 8 pairs. The same number is found in the DRYINIDAE which are usually placed near the Bethylids but *Bethylus* itself has 7 pairs, as has *Cephalonomia* ♀.

[b] In the CHRYSIDIDAE, spiracles 3–4 are in the ventrally placed laterotergites and spiracles 6 and 7 are certainly non-functional (Dr G. T. Tonapi, *personal communication*).

[c] Spiracles 3–6 are in detached laterotergites.

[d] Whether any of spiracles 2–6 are functional in the SCELIONIDAE requires further study.



FIGS 103–115. (The anterior ends of tergites and sternites are directed towards the top of the page. Figs 112, 114–115 are to the same scale. Small numbers refer, to abdominal segments. *T* = tergite; *S* = sternite; *Sp.* = spiracle.) 103, *Lariophagus distinguendus* (Först.) (Pteromalidae) ♀. Gaster from the right. 104, Abdominal tergite 3, dorsal. 105, Abdominal segment 2 and sternite 3, ventral. 106, Tergite 6, dorsal. 107, Tergite 7. 108, Tergite 8. 109, Tergite 9. 110, Abdominal sternite 6, ventral. 111, Sternite 7. 112, *Venturia canescens* (Grav.) (Ichneumonidae) ♀. Gaster from the left. 113, The same, abdominal tergite 8, dorsal. 114, *Coelichneumon leucocerus* (Grav.) (Ichneumonidae) ♂. Abdominal tergites 2 and 3, dorsal. 115, *Lasioglossum calceatum* (Scop.) (Halictidae) ♀. Abdominal tergites 5–7, dorsal.

that generally the number is fixed for a superfamily but that the Proctotrupoid groups seem to be unusually diverse.

In many Chalcidoidea (some PTEROMALIDAE, fig. 103, ENCYRTIDAE), the first segment of the gaster is reduced to a very small ring, which has not usually been enumerated by taxonomists, though it can be shown to be a segment by counting the sclerites up to the ovipositor. In *Chalcis* itself and some other genera, the corresponding segment forms a relatively long petiole. In some ICHNEUMONIDAE (*Rhyssa,* fig. 96) and in CHRYSIDIDAE (fig. 87) and BETHYLIDAE (fig. 120), the first sternal plate of the gaster is transversely divided. In most Apocrita there is a tendency for the first tergite of the gaster to contribute more to the petiole than does the corresponding sternite. In *Eumenes* (fig. 100) (EUMENIDAE), the first gastral tergite fuses anteriorly along the mid ventral line and the sternite is only easily visible more posteriorly. A similar arrangement occurs in most ICHNEUMONIDAE and in them the sternites of the first two or three gastral segments may be membranous. In the dry condition, the *abdominal membrane* (fig. 112) collapses and stands out as a vertical longitudinal fold. The extent of this membrane, how far forward it reaches into the first gastral tergite, and the relative lengths of the membranes of the first two or three segments, are all characters of taxonomic importance. It seems that the first gastral sternite must always be present anteriorly even if enclosed by the tergite, since processes from it form the hinge between the gaster and the propodeum. In such Sphecoids as *Ammophila* (fig. 101) there is a reverse arrangement and the anterior part of the petiole is formed by the sternite alone and the tergite has shifted backwards. In the ICHNEUMONIDAE (fig. 102), furrows are often seen on each lateral aspects of the petiole and these are known as *glymmae.* In the same family (fig. 114), depressions, often of a special shape or with peculiar sculpture, near the anterior margin of the second gastral tergite are known as *gastrocoeli*; when the posterior part of the gastrocoeli forms a smooth, dull area, this is known as a *thyridium.* The posterior margin of the gastral tergites is often differently sculptured from the more anterior part and in most Aculeates this forms the distinct *apical impression* (fig. 115). In the type of pattern familiar in many bees, the apical impression is more or less fully occupied by a band of pubescence. In one large group of bees, the MEGACHILIDAE (except parasitic species), the gastral sternites 1–6 are covered in the female with dense outstanding hairs which collect pollen. These form the *ventral scopa.* The sixth gastral tergite of the female in many Aculeates has a central *pygidial area* or plate, defined at the side by keels. The whole structure is often termed the *pygidium* (fig. 115). In many Halictidae (fig. 115, T6) (Apoidea), the fifth gastral tergite of the female has a smooth central line defined by pubescence and known as the *rima.*

The number of tergites and sternites which are normally developed is a very important character in classification though difficult to make out in the smaller Parasitica. It is convenient to deal with the sexes separately and with the female first. In this sex, 7 abdominal tergites (6 gastral) are nearly always normally developed. Exceptions are found in some Chalcidoidea (tergite 2 reduced), CHRYSIDIDAE (Chrysidinae tergites 5–7 retracted within 4, Cleptinae tergites 6–7 retracted within 5), and some PROCTOTRUPIDAE and BRACONIDAE in which some of the tergites are fused. An extreme modification occurs in the Braconid Sigalphinae (figs 98, 99), where the greater part of the first three gastral tergites is fused into a *carapace.* Within this, the spiracle-bearing laterotergites 3–6 and most of the rest of the abdomen are retracted. The carapace of the allied genus *Phanerotoma* (fig. 99) shows signs of the fusion of three plates and those of gastral tergites 3 and 4 may have hyaline spots which look like spiracles. Nevertheless, the true spiracles lie in the hidden laterotergites, as in *Chelonus.* In some males of *Chelonus,* there is an oval opening before the end of the carapace and this has been described as a copulatory opening. It is evidently no more than a depression of problematic function, for both the anus and genitalia lie ventrally to it.

There are considerable differences in the modifications of the last tergites and these seem to have great importance in classification. When the eighth and ninth tergites are more or less retracted and desclerotized, as in the Aculeata, the whole ovipositor becomes retracted with them and is only visible when in use. In most of the Parasitica, the eighth and ninth tergites are wholly or partly exposed and the ovipositor is therefore not so much retracted. There are, however, two arrangements: one in which there is little retraction (e.g., ICHNEUMONIDAE, fig. 112) and one in which the anterior part of the ovipositor has moved far forwards and may be partly hidden (e.g., Chalcidoidea, fig. 103, and especially Proctotrupidae, figs 116–119).

If the ovipositor is unusually long it may merely project far beyond the abdomen, as in the Pimplinae (ICHNEUMONIDAE) or in some TORYMIDAE (Chalcicoidea). A number of extraordinary devices has been developed to protect the ovipositor when not in use. It may merely be curved over the body as in *Leucospis* (CHALCIDIDAE) or more or less spirally coiled inside the abdomen as in most Cynipoidea and, in particular, in *Ibalia* (Chrystal, 1930). In *Orussus* (Symphyta), the ovipositor is looped inside the abdomen (Rohwer and Cushman, 1917). In many SCELIONIDAE and in some PLATYGASTERIDAE (Scelionoidea), the ovipositor is highly modified and enclosed in a membranous sac. When not too long, the retracted sac merely traverses the whole length of the abdomen, as in *Scelio,* but in such genera as *Inostemma* the first gastral tergite is produced into a horn which may extend over the thorax and head. The sac containing the ovipositor can be retracted inside this process. The morphology of this structure has been partially elucidated by Baumann (1939). Finally, in some non-British Mymarids (*Idiocentrus* Gahan) a somewhat similar though more sclerotized sac projects forwards from under the abdomen and may extend as far forwards as the underside of the head.

The modifications of the last tergite can be keyed as follows:

1 Tergite 8 (seventh gastral) fully exposed and resembling tergite 7. (More or less retracted in the TRIGONALIDAE but fully pigmented)........................2

– Tergite 8 with at most a small central piece exposed and sclerotized. Tergite 9 entirely retracted and depigmented. Tergite 10 not separately developed. Pygostyles absent except in SCELIONIDAE....................................5

2 Tergite 9 (eighth gastral) with its central portion exposed but its sides retracted and sometimes partly depigmented. Pygostyles present. (In *Agriotypus* and *Phrudus* more retracted)..3

– Tergite 9 entirely retracted and depigmented...................................4

3 Tergite 10 (ninth gastral) separately developed, even if small......Symphyta (except *Orussus*), ICHNEUMONOIDEA (except Sigalphinae), Evanioidea, some Proctotrupoids (CERAPHRONIDAE (fig. 123), DIAPRIIDAE, PROCTOTRUPIDAE).

– Tergite 10 indistinguishably fused with tergite 9 or membranous......Chalcidoidea

4 Tergite 10 separately developed. Pygostyles present.................... *Orussus*

– Tergite 10 membranous. Tergite 9 sclerotized at sides. Pygostyles present TRIGONALIDAE

– Tergite 10 indistinguishably fused with tergite 9 or membranous. Pygostyles absent Cynipoidea, DRYINIDAE

5 Tergite 8 a single plate without spiracles, either partly exposed and pigmented (BETHYLIDAE, fig. 122) or entirely retracted and depigmented (CHRYSIDIDAE, fig. 91, CLEPTINAE). Spiracles on segments 1–7 (figs 87–90)........Bethyloidea

– Tergite 8 entirely retracted, more or less depigmented and divided into two plates which may be joined by a narrow anterior sclerotized band; or else the tergite entirely membranous...6

6 Tergite 8 completely divided (=spiracular plates). Spiracles on tergites 1–8 Apoidea

– Tergite 8 (fig. 130) formed of two plates connected by a narrow anterior sclerotized band. Spiracles on tergites 1–8........................ Sphecoidea, Vespoidea

– Tergites 8 and 9 entirely membranous. Spiracles on tergites 1–6. Pygostyles present .... SCELIONIDAE

There are two ways of interpreting the last abdominal segments and particularly the ovipositors of female Hymenoptera, that of Snodgrass (1935) based on a comparison with the condition in *Machilis* and that of Scudder (1961*a*, *b*) based on a comparison with *Lepisma*. It is possible, however, to use Snodgrass's nomenclature while regarding the comparison with *Lepisma* as better founded. I have taken this course, partly because Oeser (1961) in his very detailed study of a range of Hymenopterous ovipositors also uses Snodgrass's nomenclature.

On the ventral side of the abdomen, the last visible sternite is usually the seventh. In the Symphyta, the central part of the margin is more or less marked off as a lobe and the sternite is known as the *hypopygium*. In all Hymenoptera (figs 118, 119, 121, 123, 124–6, 127–8, 131), the eighth sternite is reduced and membranous but on each side is found a *first valvifer* (triangular plate), to which is attached the lone *first valvula*. The valvifer is probably of the nature of an appendage base and the first valvulae are the active part of the ovipositor, forming the saw in the Symphyta, the effective ovipositor in the Parasitica, and the lancets of the sting in the Aculeata. The sternite of the ninth segment is also reduced and on each side is found a *second valvifer* (oblong plate) to the anterior end of which is attached the *second valvula*. The second valvulae of each side are immovably joined to one another and form a sheath (sting-sheath) for the first valvulae. The fused second valvulae have along most of their length a pair of ridges or rails projecting into corresponding grooves in the first valvulae. Thus the latter can move in and out without being detached from the sheath. These two pairs of valvulae together constitute the *terebra*. In the sawflies, both pairs of valvulae are normally provided with transverse raised keels which terminate below in the serrations of the saw (figs 124–5). In the Apocrita, the second valvulae normally bear analogous 'barbs' (fig. 127) but the first valvulae are smooth. The barbs are specially well developed in *Apis*. The *third valvulae* (gonostyli, ovipositor sheaths, sting palps) each arise from the posterior end of the second valvifer. They are usually softer than the other valvulae and more or less covered with bristles. In at least some genera (*Bethylus* (fig. 121), *Cleptes*, *Tiphia*, *Myrmica*) each third valvula seems to be two-segmented. How far the second valvifer consists of an appendage-base (coxite) and how far of the ninth sternite itself seems to be doubtful. In a few groups (Formicinae and Dolichoderinae in the ants, and the TRIGONALIDAE) the parts of the ovipositor are much reduced.

Nomenclature of the ovipositor

Snodgrass (1935)	Scudder (1961b)
1st valvifer	Gonangulum
1st valvula	1st gonapophysis
2nd valvifer	2nd gonocoxa
2nd valvula	2nd gonapophysis
3rd valvula	Gonoplac
—	1st gonocoxa (usually absent in Hymenoptera)

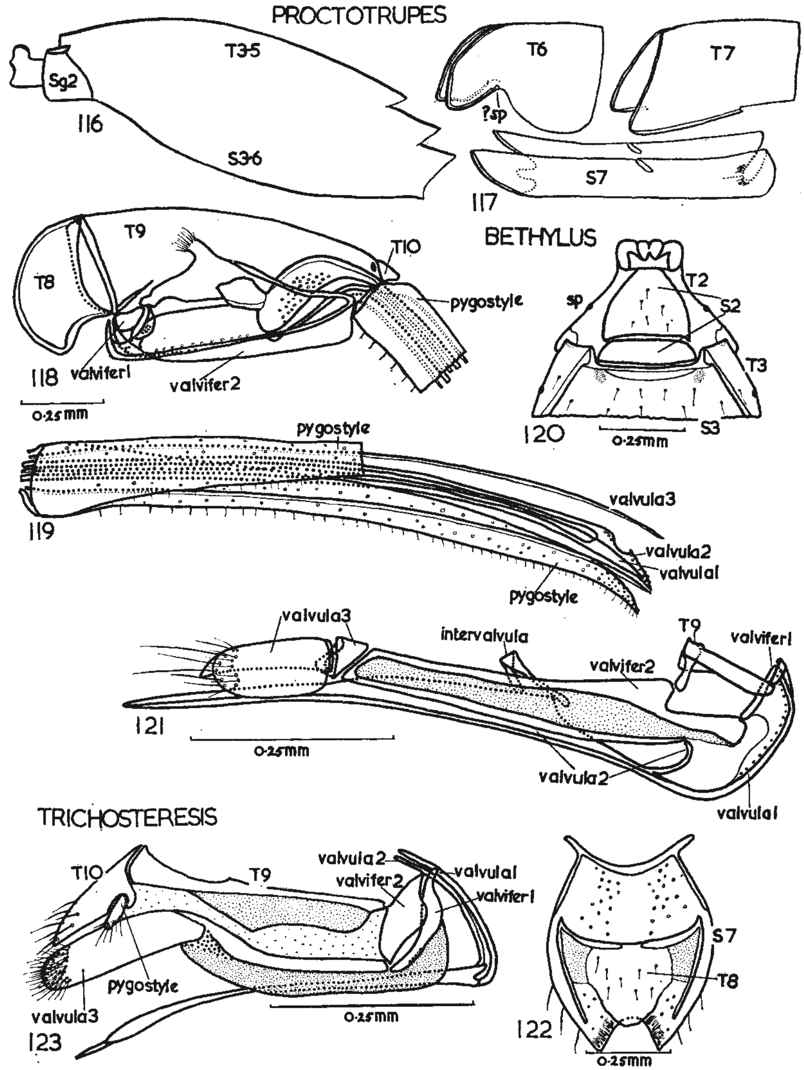
Scudder (1961*b*:36) suggests that the laterotergite of segment 8 (cf. fig. 108, *Lariophagus*) which seems to be present in most Chalcidoids may represent the first gonocoxa of other orders but probably more study, particularly of the musculature, would be required before accepting this.

In the Symphyta and Parasitica, the female genital orifice lies at the base of the first valvifer and the eggs pass down the ovipositor, often being greatly elongated in the process. In a few Parasitica (p. 53) the eggs remain attached to the ovipositor by their pedicels until they hatch. In the Aculeata, the genital orifice is anterior to the first valvifers which no longer act as an ovipositor. Unfortunately, this fundamental difference between the Parasitica and the Aculeata is difficult to verify and in many forms of special interest, such as the BETHYLIDAE, DRYINIDAE and many Proctotrupoidea, no data on this point are available.

The ovipositor and the modified last abdominal plates have not so far proved so useful in separating species as have the corresponding parts of the male. In the Tenthredinoidea, the form of the hypopygium, of the saw, and less often of the third valvulae may be highly specific. In the Parasitica with protruding ovipositor, the colour, length, and sometimes shape of the valvulae are often of importance. There are specific modifications of the inner part of the second valvifer in some *Bombus* (APIDAE) and in several groups (e.g., Chalcidoidea) there are specific modifications of the seventh sternite (fig. 111) (sixth gastral).

Snodgrass (1941) has published an extensive survey of the male genitalia of the Hymenoptera in a paper which includes much information on the abdomen in general.

In the male, the first eight tergites (7 gastral) are exposed and usually normally developed. In a few Apoidea the eighth tergite is largely concealed by the seventh. The first sternite is rarely visible as a definite sclerite but the next six (up to sternite 7 = sixth gastral) are nearly always fully developed though sometimes of specialized shape (figs 141–5) (e.g., Sphecoidea, Apoidea). Exceptions occur in the PROCTOTRUPIDAE, where several sternites may be fused; in the CHRYSIDIDAE and some BRACONIDAE where, as in the female, a number of posterior segments may be retracted and of specialized structure, and in the Apoidea where sternite 7 may be widely overlapped by sternite 6 or even 5. The condition of the remaining sclerites is tabulated below, so far as existing information allows.



Figs 116–123. (*T* = tergite; *S* = sternite; *Sg* = segment; *sp* = spiracle.) 116, *Proctotrupes gravidator* (L.) (Proctotrupidae) ♀. Abdominal segments 2–5 and sternite 6 from the left. 117, Abdominal tergite 6 and segment 7. 118, Abdominal tergites 8–10 and base of ovipositor. 119, Distal part of ovipositor. 120, *Bethylus cephalotes* (Först.) (Bethylidae) ♀. Abdominal segments 2–3, ventral view. 121, Ovipositor from the right. 122, Abdominal tergite 8 and sternite 7, dorsal view. 123, *Trichosteresis glabra* (Boh.) (Ceraphronidae) ♀. Abdominal segments 9–10 and ovipositor from the right.

1 Tergite 10 developed as a separate plate even if longitudinally divided, clearly separated from tergite 9 at least by a well-marked sulcus. Pygostyles present.
  A. Tergite 9 consisting of a single plate, but largely concealed ... Cephidae, Xiphydriidae
  B. Tergite 9 consisting of two plates at most joined by a narrow sclerotized bridge.
    (*a*) Tergite 10 formed of a single plate or longitudinally divided into two but not inserted between the plates of tergite 9 .... Most Symphyta
    (*b*) Tergite 10 consisting of a single plate let in between the plates of tergite 9, or else divided and each half joined with each half of tergite 9 ... Most Ichneumonidae

2 Tergite 10 not separately developed,[6] either indistinguishably fused with tergite 9 or membranous. Sometimes (Vespoidea, Apoidea) a small sub-anal plate (? sternite 10) is present.
  A. Tergite 9 more or less exposed, undivided. Pygostyles present .... Chalcidoidea, Braconidae (except *Chelonus*, etc.), *Gasteruption*, *Aulacus*, *Scelio*, some Ichneumonidae (Ophioninae).
  B. Tergite 9 concealed and divided, halves sometimes narrowly connected anteriorly, sometimes very small and reduced.
    (*a*) Pygostyles present ...... Proctotrupidae, Pompilidae (figs 147–150), most Formicidae, Mutillidae, Tiphiidae, some Sphecoidea (Sphecinae, etc.), Braconidae (*Chelonus*, etc.).
    (*b*) Pygostyles absent .... *Evania*, Cynipoidea, some Formicidae, Scoliidae, Chrysididae, Bethylidae, Vespidae, some Sphecoidea, Apoidea.

Some of the smaller Parasitica would no doubt repay study from this point of view.

The external genitalia of the male are attached to the hind margin of the ninth segment. They have a common plan which can easily be recognized in most genera but the nomenclature of the parts has led to prolonged controversy. Snodgrass and nearly all workers who have studied the development of the organ deny that it includes any abdominal appendages. According to them its parts are developed from the original penis or 'phallus' by secondary sclerotization in its wall. Many other workers (e.g., Peck, 1937; Michener, 1944, 1944*a*), from a comparative study of the structures found in adults of different orders, conclude that the outer parts of the genitalia are derived from abdominal appendages and only the inner part corresponds to the aedeagus. One fundamental difficulty is that the buds of the appendages of the ninth sternite appear in the embryo but disappear before the larva hatches. When much later, at about the time of pupation, the genitalia begin to develop as buds on the ninth sternite, it is impossible to decide whether they are the same structures as before. As it is impossible at the moment to resolve this controversy, two sets of terms will be given, Snodgrass's and the most convenient selection from the terms used by those who take the opposite views. Earlier workers devised an extraordinary number of terms and these are partly listed in the papers already quoted and especially in Boulangé's (1924) valuable work on the Symphyta. There is at least a certain convenience in using Snodgrass's terms since his work provides the only survey of the structures in all families.

On the view that the male genitalia are partly made up of abdominal appendages, the gonocardo is generally held to be a fused pair of coxites, the gonostipes and gonosquama to be derived from styli, and the volsella to have been secondarily differentiated from the inner side of the appendage.

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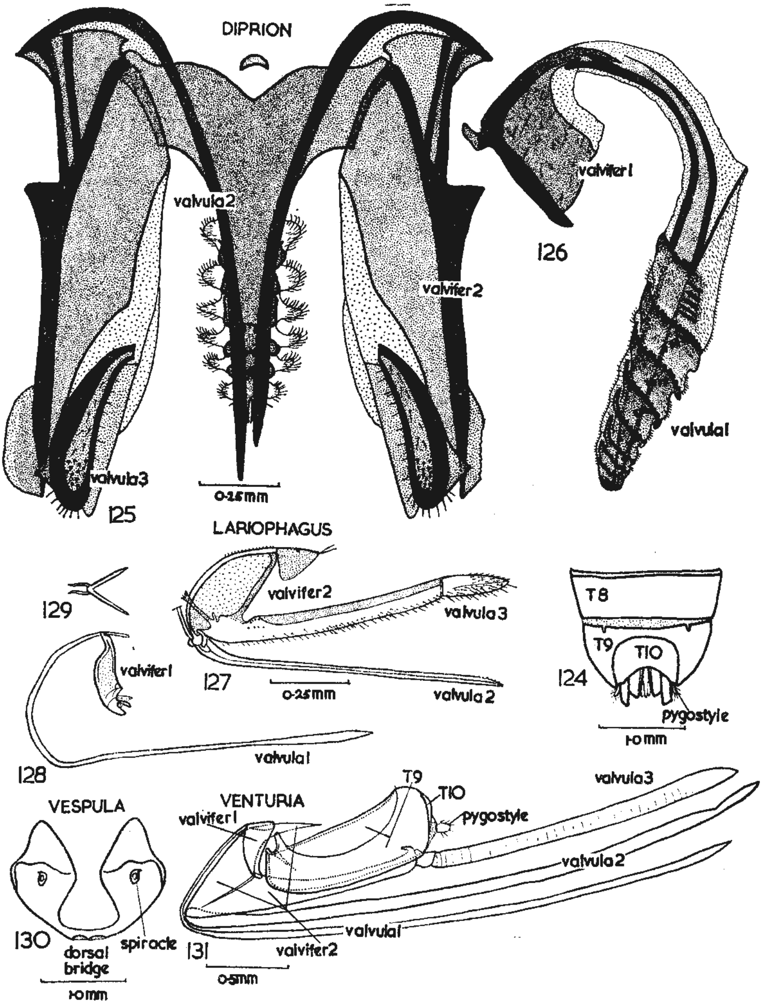
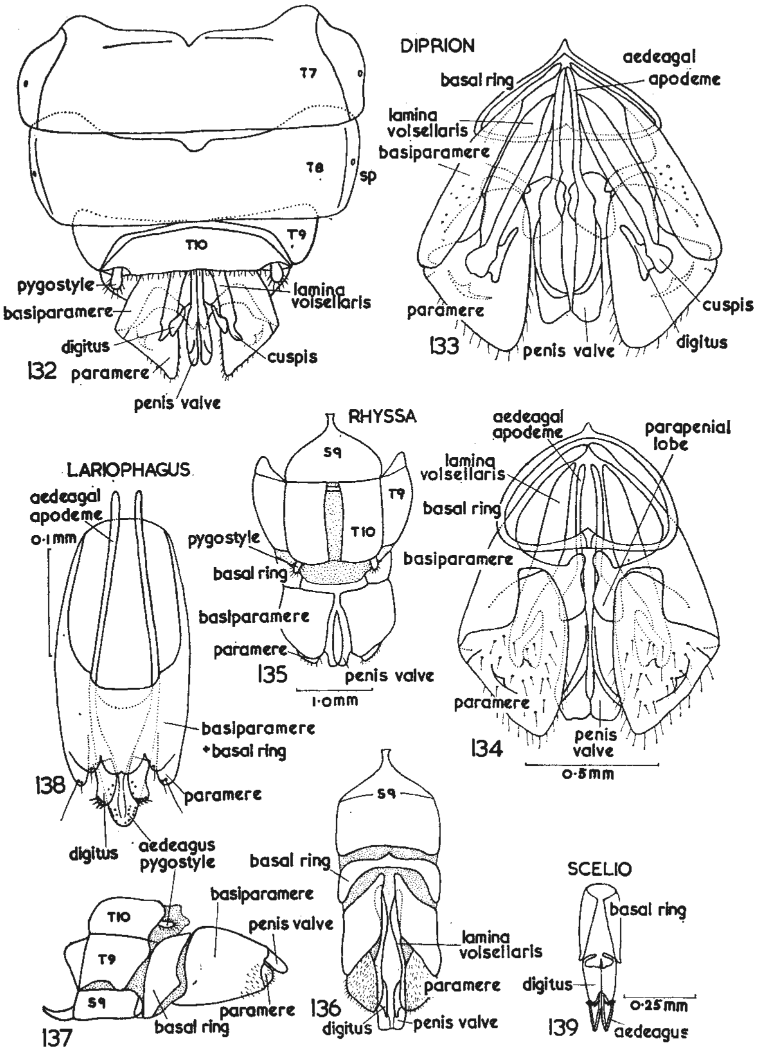
[6] According to Peck (1947 : 225) some Chalcidoidea have a distinct tergite 10.

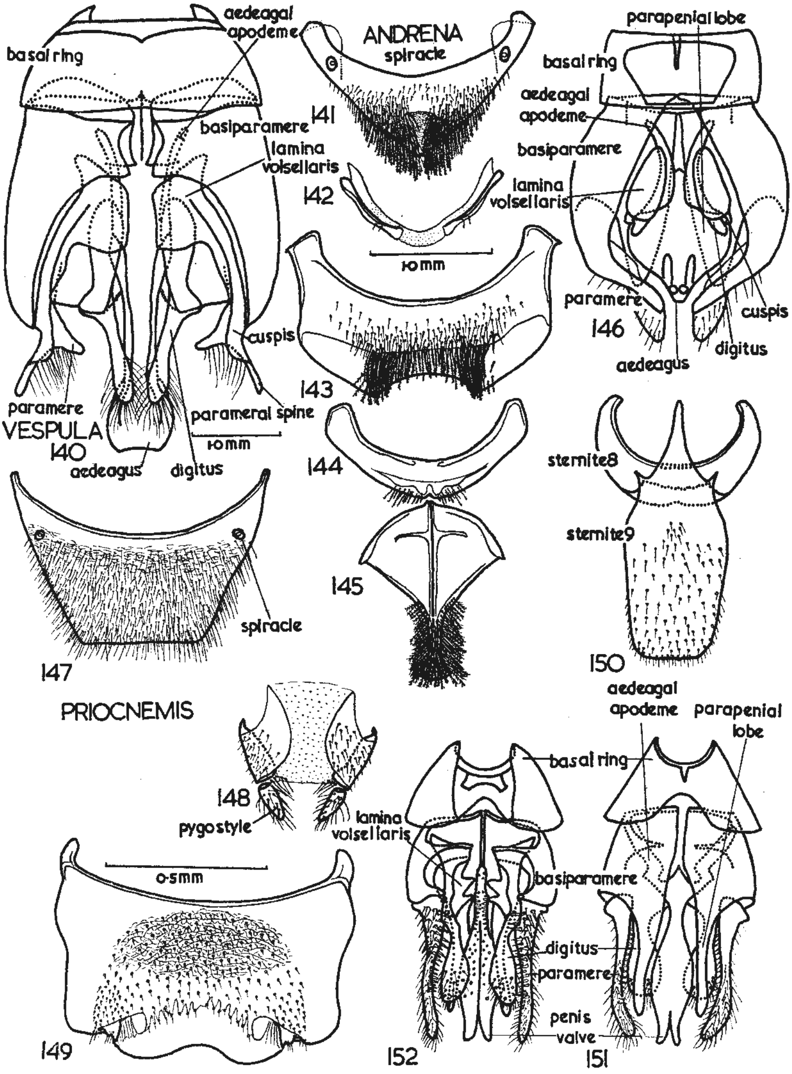
The gonostipes, gonosquama and volsella are together sometimes termed the gonoforceps. In particular families, the various parts may show extensive modification, especially by fusion or reduction. The parameres are often not distinct from the basiparameres. In the NEMATINAE and in the POMPILIDAE (figs 151–2), the basiparameres are produced into parapenial lobes,



FIGS 124–131. (Small numbers refer to abdominal segments. *T* = tergite; *S* = sternite.) 124, *Diprion pini* (L.) (Diprionidae) ♀. Posterior end of abdomen, dorsal view. 125, Second valvifers and second and third valvulae, dorsal view. 126, Right first valvifer and valvula, right side. 127, *Lariophagus distinguendus* (Först.) (Pteromalidae) ♀. Left second valvifer and second and third valvulae, left side. 128, Left first valvifer and valvula, left side. 129, Forked sclerite. 130, *Vespula germanica* (F.) (Vespidae) ☿. Abominal tergite 8, dorsal view with lateral flaps bent inwards. 131, *Venturia canescens* (Grav.) (Ichneumonidae) ♀. Ovipositor, left side.



FIGS 132–139. (Small numbers refer to abdominal segments. *T* = tergite; *S* = sternite; *sp* = spiracle.) 132–134, *Diprion pini* (L.) (Diprionidae) ♂. 132, Abdominal tergites 7–10 and genitalia, dorsal view. 133, Genitalia (actual dorsal, morphological ventral). 134, Genitalia (actual ventral, morphological dorsal). 135–137, *Rhyssa persuasoria* (L.) (Ichneumonidae) ♂. 135, Abdominal segments 9–10 and genitalia, dorsal view. 136, Ventral view. 137, From the left. 138, *Lariophagus distinguendus* (Först.) (Pteromalidae) ♂. Genitalia, ventral view. 139, *Scelio inermis* (Zett.) (Scelionidae) ♂. Genitalia, ventral view.



FIGS 140–152. (Figs 141–5 are to one scale; Figs 147–152 are to one scale.) 140, *Vespula germanica* (F.) (Vespidae) ♂. Genitalia, ventral view. 141, *Andrena haemorrhoa* (F.) (Andrenidae) ♂. Abdominal tergite 8, dorsal view. 142, Tergite 9. 143, Abdominal sternite 7, ventral view. 144, Sternite 8. 145, Sternite 9. 146, Genitalia, ventral. 147, *Priocnemis exaltata* (F.) (Pompilidae) ♂. Abdominal tergite 8, dorsal view. 148, Tergite 9. 149, Abdominal sternite 7, ventral view. 150, Sternites 8 + 9. 151, Genitalia, dorsal view. 152, Genitalia, ventral view.

Principal terms used in describing the male genitalia

Snodgrass (1941)	Other terms
Basal ring	Cardo or gonocardo
Basiparameres	Stipes or gonostipes
Parameres	Squama, gonosquama
Volsella	Volsella
Lamina volsellaris	Basivolsella
Cuspis	Distivolsella
Digitus	Lacinia or gonolacinia
Aedeagus	Aedeagus
Penis valve	Sagitta or parameres
Aedeagal apodeme	—
Spatha	Spatha

running close to and parallel with the penis valves. The volsella may be much reduced with its three divisions not clearly recognizable, as in most Apoidea. In *Apis* itself, the whole structure is reduced except for the enlarged penis. A very greatly modified structure occurs in many Proctotrupoidoids *sensu lat.* (fig. 139) in which the basiparameres and parameres are reduced or absent and the volsella becomes attached to the sides of the aedeagus. A peculiar feature in most of the more primitive families of the Symphyta is the development of 'cupping disks' on the underside of the parameres. These are membranous areas which can be retracted by special muscles and make it possible for the parameres to grip a smooth surface in the same way as an evacuated rubber cupping disk. Another peculiarity in the Symphyta is that the Tenthredinoidea have the male genitalia inverted (strophandrious), so that what is the dorsal side of other groups is directed ventrally. The lower sawflies have normal genitalia (orthandrious) but both types are known within the family XYELIDAE. Only a few selected types (figs 135–140, 146, 151–2) of male genitalia are illustrated here since the subject has been so fully dealt with by Snodgrass. Detailed information on particular groups will be found in the following works: Symphyta, Boulangé (1924) and Ross (1945); ICHNEUMONIDAE, Peck (1937); Evanioidea, Crosskey (1951); BETHYLIDAE and DRYINIDAE, Richards (1939); Apoidea, Beck (1933) and Michener (1944).

LIFE-HISTORY

Although the majority of species of Hymenoptera are represented by both males and females, facultative and obligate parthenogenesis are both commoner in this order than in any other group of insects. A complete account of sex-determination in the Hymenoptera would be a long and complex story (White, 1954: Chap. xvii) but, briefly, in most species, under natural conditions, unfertilized eggs produce males which are haploid with half the normal complement of chromosomes. Females come from fertilized eggs and are diploid. Regular exceptions to this rule are known in a number of sawflies (Benson, 1950 : 127–9) and Parasitica (e.g., some Cryptinae (ICHNEUMONIDAE), *Rhodites* (CYNIPIDAE)) in which males are very rare or unknown and females are produced parthenogenetically. In the Cynipids with alternating generations (p. 63) one type of female produces both sexes parthenogenetically whereas the other, after fertilization, produces females only. Where there is parthenogenesis and the oviposition-habits of a species are known, it is often possible to obtain eggs in captivity from a single bred or captured female and thus to associate larvae and males with the correct species of female.

Hymenoptera always lay eggs, usually in a protected situation, where the larval food is available, e.g., sawflies in plant tissues, Parasitica and some Aculeata in or on their host, advanced Aculeata in nests with a food-store. Some Tryphoninae (ICHNEUMONIDAE) carry the eggs attached to the ovipositor and a few (e.g., *Polyblastus*) may then place the emerging first stage larva on its host (sawfly larva). A few parasites (e.g., *Perilampus*) lay eggs which produce an active larva which finds its own host and, in some TRIGONALIDAE, the eggs may be laid on leaves and eaten by caterpillars in certain other parasites of which they eventually develop.

The larva is fundamentally of two types, that of the Symphyta in which thoracic and abdominal legs are nearly always present and that of the Apocrita which is a legless maggot, rarely with fleshy processes which some authors have supposed to represent rudiments of thoracic or abdominal legs. Except in the parasitic Orussidae, the anus is open in the Symphyta and faeces are passed at frequent intervals, whereas in the Apocrita (except a few of the ants) the anus is closed until just before pupation when the faeces are ejected in one mass. With their unreduced structure and often conspicuous colour-pattern the larvae of Symphyta usually show good specific differences which, combined with their food-plants, make useful keys for their identification possible. The larvae of many sawflies are superficially like a caterpillar but there is usually at least one more pair of abdominal legs (typically present on segments 2–7 and 10) and none of these legs bear crochets. The larvae of the Apocrita are so reduced that their identification is a matter of considerably difficulty and is usually possible only to the family or genus. First instar larvae are commonly more characteristic of their group than the later stages. A general account of the early stages of many groups of Hymenoptera is given by Clausen (1940). A few groups have been more or less comprehensively dealt with: Short (1952, 1959, 1960, 1970) (families of Parasitica, genera of Ichneumonoids), Evans (1956–59, 1959*b*, *c*, 1964) (Sphecoidea, Pompilidae), Michener (1953) (Apoidea). The larvae of Vespoids (Richards, unpublished) have the opening of the spinneret slit-like, the maxilla has two papillae and the mandibles are tridentate in lower forms. In the Sphecoidea the spinneret usually has paired openings (except Sphecinae & Ampulicinae), the maxillae have two papillae and the mandibles usually have more than two teeth. In the Apoidea, the spinneret opening is slit-like, there is one maxillary papilla and the mandibles are bidentate or unidentate.

The larvae of the Symphyta feed on flowering plants, ferns and a few on horsetails. While most species feed externally on the leaves, leaf-mining, stem-boring and gall-making forms are not rare and the Siricoidea are associated with fungus-impregnated wood. The legless maggot of *Orussus* is usually supposed to be a parasite of wood-boring beetles, though this is not quite certainly established (cf. Cooper, 1954).[7]

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[7] A species of *Guiglia* (Orussidae) in New Zealand is parasitic on an introduced Siricid but perhaps its natural host is a native Xiphydriid (G. B. Rawlings, *personal communication*).

The larvae of Apocrita usually feed on the bodies of other insects, less commonly on those of Arachnids. The larvae of the following British groups eat vegetable materials. Chalcidoidea, TORYMIDAE: *Megastigmus* and some *Syntomaspis* on seeds; EURYTOMIDAE: *Systole* and some *Bruchophagus* on seeds, most *Tetramesa* in galls on Gramineae. Cynipoidea, Cynipinae: most species are gall-makers but those of one section live in galls of other species. Formicidae: most species collect nectar, honey-dew or plant-seeds, and these, together with animal matter, form part of the food of the larvae. Vespoidea: the social species collect nectar and fruit-juices, some of which goes to the larvae whose main food, however, is dead insects. Apoidea: all species live on pollen and nectar but, in parasitic species, the host-egg or young larva may first be destroyed.

It is usual in the Apocrita to contrast the parasitic mode of life of the Parasitica with the predatory life of most Aculeata (except bees). It was O. M. Reuter who first suggested that most of the so-called parasitic insects are more properly described as refined predators and should be known as 'parasitoids'. They retain the mobility and the fully developed sense-organs which tend to be lost in true parasites such as lice. The adult stage is not closely associated with the host, which is nearly always[8] killed by the larva. While it is unnecessary to insist on the use of the term parasitoid it is certainly true that no hard and fast line can be drawn between Parasitica and Aculeata in either structure or function.

The difference between an ovipositor and a sting has already been alluded to (p. 46) but it has not so far led to any very useful criterion. Many Ichneumonids seem to be able to insert an egg into their host without greatly disturbing it. Others, such as the species of *Polysphincta* whose larvae develop externally on spiders, induce a short-lived paralysis. Other parasites, such as many Chalcidoids or species of *Bracon*, induce a permanent paralysis of the host or even kill it before laying an egg upon it. Finally, some groups which lay in spiders' egg-sacs (*Tromatobia*) or in cockroach oothecae (EVANIIDAE) are predatory on a number of eggs, and *Gasteruption assectator* (L.), developing in nests of *Prosopis*, may eat more than one host-larva (Höppner, 1904).

There is a similar variation amongst the Aculeata, though perhaps deep paralysis is the most usual condition of the prey. In many Pompilids, the prey recover completely, and will survive if they are removed from the nest. In a few Pompilids (non-British), no nest is made and the prey recovers and lives a normal life for a time before succumbing to the external parasitic larva. A number of Hymenoptera which are classed as Aculeata are exclusively parasitic. The principal examples in the British fauna are the following: BETHYLIDAE (hosts usually larvae of Lepidoptera or Coleoptera and some rudimentary maternal care of the developmental stages has been recorded); DRYINIDAE (hosts Cicadelloidea or Fulgoroidea, behaviour typically parasitic); TIPHIIDAE (prey beetle larvae or (*Myrmosa*) various Aculeata, behaviour transitional but no nest is made); SAPYGIDAE and MUTILLIDAE (parasitic on other Aculeates except for a few exotic Mutillids

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[8] In the BRACONIDAE Euphorinae, which attack adult beetles, the host is not necessarily killed and Timberlake (1916) experimentally bred two successive generations of an American species from a single ladybird.

which attack Coleoptera and Diptera); CHRYSIDIDAE (prey usually Aculeates, behaviour essentially parasitic); CLEPTINAE (British species attack sawfly larvae, but some exotic ones lay in Phasmid eggs). Of these groups, only the TIPHIIDAE, SAPYGIDAE and MUTILLIDAE are unambiguously Aculeata.

Finally, there is a number of scattered genera of parasitic Aculeata which are examples of a very different type of evolution. In them the host is, with very few exceptions, of the same family and often the parasite seems actually to have evolved from something very like the species which it now parasitizes. In these parasites, it is the food-store of the host rather than the host itself which is parasitized, but the larva or, in the social species, the reproductive capacity of the host is nevertheless destroyed.

The known examples of parasitic Aculeata in the British fauna are shown in Table I. Some of the peculiar examples of temporary parasitism amongst ants are omitted.

TABLE I

Family of parasite	Parasite	Host
Formicidae	*Strongylognathus*	*Tetramorium*
	Anergates	*Tetramorium*
	Sifolinia	*Myrmica*
Pompilidae	*Evagetes*	Pompilini
	Ceropales	*Pompilus, Anoplius*
Vespidae	*Vespula austriaca* (Pz.)	*Vespula rufa* (L.)
Sphecidae	*Nysson*	*Gorytes, Argogorytes*
Halictidae	*Sphecodes*	*Halictus, Andrena*
Megachilidae	*Coelioxys*	*Megachile, Anthophora*
	Stelis	*Anthidium, Osmia*
Anthophoridae	*Melecta*	*Anthophora*
	Epeolus	*Colletes*
	Nomada	*Andrena, Melitta, Halictus, Eucera*
Apidae	*Psithyrus*	*Bombus*

The Parasitica (except some Tryphoninae, p. 53) do no more for their offspring than lay their eggs in or on a host. Most Aculeata make some provision for their protection after hatching by making nests. The papers of Iwata (1942) and Malyshev (1936) review the behaviour of solitary wasps and solitary bees, respectively, and the papers by Nielsen (1932–36) deal with Aculeates as a whole. *Tiphia* and Bethylids make no nests, though the prey of the latter may be moved to a sheltered situation. POMPILIDAE mostly excavate a single cell in the ground (exceptions include *Dipogon* and *Argenioideus* which nest in all sorts of natural cavities, *Auplopus* see below, and *Homonotus* which stings a spider in its own nest). Many Sphecoids and bees and some EUMENIDAE (*Odynerus*) make a similar nest in the ground but more often with a number of cells branching from the bottom of the main burrow. In *Andrena bucephala* (Kby) and *A. ferox* Sm., many females may share a common entrance burrow though they probably have separate nests. The cells may be lined with a coating of saliva (e.g., *Colletes*, COLLETIDAE), perhaps sometimes diluted with water, or with vegetable material (*Macropis*, MELITTIDAE). In another type of nest, mud is used to build cells either freely suspended (*Eumenes*, EUMENIDAE), attached to stones, etc. (*Auplopus*, POMPILIDAE; some *Ancistrocerus*, EUMENIDAE) or in burrows in hollow wood or in hollow stems with mud partitions (some EUMENIDAE; *Trypoxylon*, *Passaloecus*, etc., SPHECIDAE; *Chelostoma*, some *Osmia*, MEGACHILIDAE). More often species which nest in wood or hollow stems separate the cells with wood-particles or pith (many CRABRONINAE, SPHECIDAE; *Anthophora furcata* (Pz), ANTHOPHORIDAE, more rarely with resin (some *Passaloecus*, SPHECIDAE; *Heriades*, MEGACHILIDAE). In one species which nests in rotten wood, *Ectemnius quadricinctus* (F.), several females may have a common entrance burrow to their separate nests. Certain species have peculiar and characteristic nesting habits. *Anthidium manicatum* (L.) (MEGACHILIDAE) builds ill-defined cells in a mass of plant-wood hidden in some natural cavity. Three species of (MEGACHILIDAE), *Osmia bicolor* (Schrk), *O. aurulenta* (Pz) and *Hoplitis spinulosa* (Kby), next in empty snail-shells. The first-named species makes partitions of chewed vegetable matter and hides the shell in a little pile of beechbud-scales, etc. *H. spinulosa* makes partitions of cow-dung. Other species of *Osmia*, such as *O. inermis* (Zett.), make cells of chewed vegetable matter attached to the underside of large stones. The leaf-cutter bees of the genus *Megachile* mostly make beautiful cells out of pieces cut out of leaves; the cells may be in a burrow in the earth (e.g., *M. maritima* (Kby), *M. leachella* Curtis = *argentata*) or in rotten wood (*M. ligniseca* (Kby), *M. versicolor* Smith).

The FORMICIDAE mostly make rather irregular galleries in the earth or in rotten wood or in some natural cavity. Some species (e.g., *Lasius fuliginosus* (Latr.)) make a nest of 'carton', a material composed of chewed wood, earth and saliva. *Formica rufa* and its allies make the familiar mounds of pine-needles and other vegetable fragments, usually in woods, and *Lasius flavus* (F.) usually makes earth mounds in meadows, though in some habitats very little mound is made. Of the other social Hymenoptera (cf. p. 63), a few species of *Halictus* make a comb-like group of cells underground, apparently more by excavation than by building. The VESPIDAE build nests of carton or wasp-paper, usually in cavities in the ground, but in *Vespula norwegica* (F.) hanging in bushes, and in *Vespa crabro* L. usually in hollow trees or sheds. *Bombus* and *Apis* make cells of wax secreted by the female and worker in *Bombus* but by the worker alone in *Apis*. The cells do not form a regular comb in *Bombus* and there are several larvae feeding in each waxen pocket. In this genus, also, the empty cocoons are used to store honey.

There are three or four well-known patterns of behaviour in the nest-making Aculeata. Most POMPILIDAE catch and paralyze their prey before they start looking for a nesting-site or building a nest. The solitary EUMENIDAE and the VESPIDAE build a cell and lay an egg in it before bringing any food. Sphecoids and solitary bees do not lay in a cell until it is stored. The only exceptions are some of the few species which practice progressive provisioning; that is, return to the cell after the egg has hatched to supply the larva with additional food as it is required. Although recorded in a number of EUMENIDAE, Sphecoids and bees, the only example in Britain is *Ammophila pubescens* Curtis (*campestris* auct.). This wasp is quite exceptional because it is capable of simultaneously looking after several nests in different stages (Baerends, 1941). Such behaviour may perhaps be regarded as transitional to truly social behaviour, which may be said to occur when a female builds cells for or feeds offspring which are not her own. In British Hymenoptera, social behaviour is known in the FORMICIDAE (but a few species are parasites), VESPIDAE (Vespinae, one parasitic species), HALICTIDAE (some species of *Halictus* and *Lasioglossum*) and APIDAE (*Bombus* and *Apis*).

One special type of behaviour may be mentioned because it involves immersion in water which would be harmful for almost all other species. A Mymarid, *Caraphractus*, and a Trichogrammatid, *Prestwichia*, are both capable of swimming under water with their legs and rudimentary wings to reach the eggs of water-bugs and water-beetles. *Agriotypus* (ICHNEUMONIDAE) which parasitizes Caddis pupae (*Silo*, etc.) also walks under water but never swims. Some other Ichneumonids and some Braconids which attack aquatic or subaquatic hosts may penetrate the water a short distance.

The nature of the host of the Parasitica and of the prey of Aculeata is a large subject, of great economic importance, and the literature is now immense. Many of the older records must be received with caution because of defects in taxonomy and in observation. The catalogue of parasites being edited by Thompson (1943–1971) is incomplete and is still appearing: it summarizes the greater part of the information about Parasitica, especially those associating with insect pests. Iwata (1942) and others have summarized the information for Aculeata. A much condensed summary is given here in Tables II and III. The parasite is assumed to attack the nymph or adult in Exopterygota and the larva or pupa in the Endopterygota, unless otherwise stated. No host is known for the British Embolemidae but an American genus parasitizes a Fulgoroid. A host-name followed by a second name (in parentheses) indicates that the host itself is a parasite on the insects represented by this second name.

TABLE II Summary of the hosts of British Hymenoptera Parasitica. Single species or individuals sometimes behave differently from what is here recorded

Host	Parasite
Arachnida	
Araneida, adults	Ichneumonidae: Polysphinctini, including *Schizopyga*
Araneida, eggs	Ichneumonidae: some *Gelis*, *Hemiteles*, *Tromatobia*, *Zaglyptus*. Chalcidoidea: some Entedoninae. Scelionoidea: some Scelionidae
Pseudoscorpionida, ? adult	Ichneumonidae: *Obisiphaga stenoptera* (Marsh.)
Acarina, adult	Chalcidoidea: *Ixodiphagus*, *Tetrastichus eriophyes* Taylor
Myriapoda **Chilopoda**	Some Proctotrupidae
Insecta	
ODONATA, eggs	Some Mymaridae
ORTHOPTERA	
Blattidae, eggs	Evaniidae
Acrididae, eggs	Some Scelionidae
Tettigoniidae, eggs	Scelionidae (? *Macroteleia*); Aphelininae (*Centrodora*)
PSOCOPTERA	
Eggs	Some Mymaridae
Nymphs	Braconidae (*Leiophron*)

TABLE II—*continued*

Host	Parasite
THYSANOPTERA	Eulophidae (*Thripoctenus*)
HEMIPTERA	
Eggs	Chalcidoidea: some Encyrtidae, some Tetrastichinae, some Trichogrammatidae, many Mymaridae. Scelionoidea: many Scelionidae
HETEROPTERA	Braconidae: Euphorinae
HOMOPTERA	
Psylloidea	Some Encyrtidae
Aleyrodoidea	Some Aphelininae
Aphidoidea	Aphidiinae; some Encyrtidae, some Aphelininae
Coccoidea	Many Encyrtidae, Eunotinae, some Eupelmidae, some Aphelininae; some Pteromalidae; Platygasteridae: *Allotropa*
MEGALOPTERA	
Sialis, eggs	Some Trichogrammatidae
Raphidia	Ichneumonidae: *Nemeritis raphidiae* Krchb. = *Pyracmon* auctt. Brit.
NEUROPTERA	
Eggs	Some Trichogrammatidae, some Mymaridae
Chrysopa	Ichneumonidae: *Dichrogaster*. Heloridae
Hemerobius	Ichneumonidae: some *Gelis, Charitopes* Cynipoidea: *Aegilips, Anacharis*
COLEOPTERA	Some Braconini, Spathiini, Hecabolini, Pambolini, Doryctini, Triaspidini, *Cenocoelius, Blacus,* some Helconini, some *Meteorus.* Ichneumonidae: Xoridinae, Acaenitinae, *Bathyplectes,* most Tersilochinae, Phrudinae, Poemeniini (=Neoxoridini), some Ephialtini, Anomalonini. Some Chalcididae, some Eurytomidae, some Torymidae, Cleonyminae, some Eupelmidae, some Encyrtidae, some Tridyminae, some Pteromalinae, some Merisinae, some Spalagiinae, some Entedontinae, some Tetrastichinae. Most Proctotrupidae, Diapriidae: *Spilomicrus*
Adults	Braconidae: many Helconinae, *Pygostolus* (Blacinae) and some Euphorinae
Eggs	Some Trichogrammatidae, some Mymaridae
MECOPTERA	
Boreus	Braconidae: *Dyscoletes*
TRICHOPTERA	Ichneumonidae: *Agriotypus* and *Sulcarius*
LEPIDOPTERA	
Eggs	Some Trichogrammatidae, some Mymaridae, many Scelionidae
Larvae and pupae	Most Braconini, Hormiini, Rogadini, some Exothecini, Sigalphini, Microgasterinae, some Helconinae, *Eubadizon, Orgilus,* most *Meteorus*; Ichneumoninae, most Cryptini, most Pimplini, many Ephialtini, most Banchinae (=Lissonotinae), Sphinctini, Phytodietini (=Neteliini), most Thymaridini (=Eclytini), Meto-

TABLE II—*continued*

Host	Parasite
	piinae, Ophioninae, Anomaloninae (=Therioninae), most Campopleginae, most Cremastinae; some Chalcididae, some Eupelmidae, some Encyrtidae, some Pteromalinae, some Elasmidae, most Elachertinae, many Eulophinae, many Entedontinae, many Tetrastichinae
HYMENOPTERA	
Symphyta, Siricoidea	Ichneumonidae: Rhyssini. Ibaliidae. Aulacidae. Chalcidoidea: Pteromalidae: *Xiphydriophagus*
Cephoidea	Some Braconini. Ichneumonidae: some Ephialtini, *Collyria*
Megalodontoidea	Ichneumonidae: *Notopygus*, *Olesicampe auctor* (Grav.)
Tenthredinoidea	Braconidae: Ichneutini, some Braconini. Ichneumonidae: Exenterini, Tryphonini, Adelognathinae, Ctenopalmatinae, some Ephialtini, most *Olesicampe*, *Aptesis*. Chalcidoidea: some *Perilampus*, *Dahlbominus*, some Eurytomidae, some Pteromalinae, some Eupelmidae
Ichneumonidae	Some Cryptinae. Braconidae: some *Syntretus*
Cynipidae	Ichneumonidae: *Orthopelma*; Chalcidoidea; Ormyridae, some *Eurytoma*, some Pteromalinae, *Olynx*
Dryinidae	Diapriidae: *Ismarus*
Formicidae	Braconidae: *Paxylomma*, ?*Neoneurus*, ?*Myiocephalus*. Chalcidoidea: *Eucharis*
Eumenidae	Ichneumonidae: *Acroricnus*
Vespidae	Ichneumonidae: *Sphecophaga*. Pteromalidae: *Dibrachys* sometimes. Eulophidae: *Melittobia*
Sphecidae (*Spilomena*)	Ichneumonidae: *Neorhacodes*
Sphecoidea, Apoidea	Gasteruptiidae. Ichneumonidae: *Perithous*, some *Mastrus*, some *Aritranis*, some *Gambrus*. Braconidae: *Syntretus splendidus* (Alford, 1968). Chalcidoidea: some Eurytomidae, some Torymidae, some Tridyminae, *Melittobia*
Hym. (Heteroptera)	Ichneumonidae: Mesochorinae
Hym. (Aphidoidea)	Cynipoidea: Charipinae. Chalcidoidea: some Encyrtidae, some Pteromalidae, some Ceraphronidae
Hym. (Coccoidea)	Chalcidoidea: some Encyrtidae, some Aphelininae
Hym. (Lepidoptera)	Trigonalidae: ?Pseudogonalos (cf. Clausen, 1940). Ichneumonidae: Mesochorinae. Chalcidoidea: some *Elasmus*, some Tetrastichinae
Hym. (Hymenoptera)	Ichneumonidae: *Pseudorhyssa*, *Euceros*
Eggs	Some Trichogrammatidae
DIPTERA	Braconidae: some Exothecini, Opiinae, Alysiinae. Ichneumonidae: Stilpnina, many Phygadeuontina, Orthocentrinae, Oxytorinae (=Plectiscinae). Cynipoidea: Figitinae, Eucoilinae. Chalcidoidea: some Chalcididae, some Eurytomidae, some Torymidae, some Eupelmidae, some Encyrtidae, most Pireninae, some Tridyminae, most Lamprotatinae, some Pteromalinae, some Merisinae, some Miscogasterinae, some Spalangiinae, *Melittobia*, many Eulophinae, some Entedontinae, some Tetrastichinae. Proctotrupoids: most Diapriidae, many Ceraphronidae, most Platygasteridae
Syrphidae	Ichneumonidae: Diplazontinae. Ceraphronidae *Trichosteresis*
Eggs	Some Trichogrammatidae
SIPHONAPTERA	Chalcicoidea: *Bairamlia*

TABLE III Summary of prey of non-social British Hymenoptera Aculeata

Prey	Predator
ARANEIDA	Pompilidae, *Miscophus*, *Trypoxylon*
ORTHOPTERA	
Blattidae, nymph	*Tachysphex obscuripennis* (Schenck) (=*lativalvis* (Thoms.))
Acrididae	Other *Tachysphex*
PSOCOPTERA	*Rhopalum*
EPHEMEROPTERA	*Crossocerus* (*Blepharipus*) *walkeri* (Shuck.)
THYSANOPTERA	*Spilomena*
HEMIPTERA	
Heteroptera, nymph and adult	*Astata*, *Dinetus*, most *Lindenius albilabris* (F.)
Auchenorrhyncha, nymphs or adults	Dryinidae
Auchenorrhyncha, adult	*Argogorytes*, *Psenini*, *Gorytes*, *Didineis*
Typhlocybidae	*Crossocerus* (*Blepharipus*) *ambiguus* (Dahlb.), *Aphelopus*
Psyllidae	*Psenulus concolor* (Dahlb.)
Aphididae	*Stigmus*, *Pemphredon*, *Cemonus*, *Diodontus*, *Passaloecus*, *Psenulus atratus* (F.)
LEPIDOPTERA	
Larvae	Bethylidae: (*Bethylus*, *Goniozus*); most Eumenidae. Sphecidae: *Ammophila*, *Podalonia*
Adults	*Lestica* (? sometimes), *Hoplocrabro* (sometimes)
TRICHOPTERA, adult	*Hoplocrabro* (sometimes)
COLEOPTERA	
Adults	Some *Cerceris*
Larvae	Most Bethylidae
Cicindelidae, larva	*Methocha*
Scarabaeidae, larva	*Tiphia*
Chrysomelidae, adult	*Entomognathus*
Chrysomelidae, larva	*Symmorphus*
HYMENOPTERA	
Tenthredinidae, larva	Chrysididae (Cleptinae)
Parasitica, adult	*Lindenius armatus* (V.d.L.)
Aculeata, larva	Chrysididae, Sapygidae, *Myrmosa*, *Mutillidae*
Apoidea, adult	*Philanthus*, some *Cerceris*
DIPTERA	*Crabro*, *Crossocerus* (except some spp. of subgenera *Blepharipus* and *Hoplocrabro*), *Ectemnius*, *Lestica* (*Clypeocrabro*) usually, some *Lindenius*, *Mellinus*, *Oxybelus*, *Rhopalum* (*Corynopus*)

From the biological point of view Hymenopterous parasites may be classified in several ways. They may be *internal* or *external* parasites according as most of their development takes place inside or outside the host. In the former case, the egg is almost always inserted into the host, but there are a few exceptions. They can be *solitary* or *gregarious* according as one or more than one larva can successfully develop on one host. While gregarious species may exceptionally develop solitarily, only one larva of a solitary species survives in a host if there is a second oviposition. Most ICHNEUMON-

IDAE are solitary parasites (exceptions are some *Gelis*, some *Hemiteles*, some *Agrothereutes*, some *Ephialtes* (*Iseropus*), some *Netelia* (=*Paniscus*), some *Gambrus*; these are all parasites of prepupae or pupae, often in the host cocoon). Many species of the other groups of Parasitica are gregarious. In the BRACONIDAE, the two types of behaviour are about equally common. In Aculeata, it is very unusual for more than one egg to be laid on a single host or in one cell. Some species of *Tiphia* lay more than one egg on Scarabaeid larvae and the Bethylids, a group transitional to the Parasitica, are often gregarious parasites. A special type of gregarious parasitism is known as *polyembryony*; it arises not from multiple oviposition but from the development and later separation of cell-groups derived from a single embryo. The process is described and illustrated in Imms (1957: 192) and further details are given by Clausen (1940). Amongst British species it occurs in BRACONIDAE (some *Macrocentrus*), ENCYRTIDAE (*Ageniaspis*, *Litomastix*, some *Copidosoma*) and in *Platygaster zosine* Walker PLATYGASTERIDAE; in the first two families the hosts are caterpillars, in the third CECIDOMYIIDAE. It is characteristic that unisexual broods are produced, bisexual broods being the result of more than one oviposition. Parasitism is described as *direct* or primary when the egg or larva is in or on the host; *hyperparasitic* or secondary when the egg or larva is in or on another parasite. This usage is convenient, though the behaviour of an *Apanteles* which lays its eggs directly inside a caterpillar and of a *Mesochorus* or *Tetrastichus* which locates the *Apanteles* larva inside its host seem rather different. But there are so many varieties of behaviour that the difference is one of ecological rather than behavioural significance. Thus the term hyperparasite tends to be used for any parasite of a parasite, even when the parasitism is really direct on the pupa of its parasite-host in its cocoon and not inside the body of a primary host. Tertiary parasitism is also known; it is just possible that it is obligatory in some species of *Pediobius* (=*Pleurotropis*) (EULOPHIDAE) (Clausen). The term *multiparasitism* is commonly used to describe the situation when primary parasites of two or more species are simultaneously present in one host. It normally leads to the death of all but one or sometimes of all the parasites. *Superparasitism* occurs when more parasites of one species are present than can develop successfully, e.g., more than one of a solitary species. This also leads to the death of all or all but one of the parasites in solitary species. In gregarious parasites it may lead to some mortality or to stunting. Finally, there are wide differences in the way in which the life-history of host and parasite fit together. The basic types are illustrated by a few chosen examples in Table IV, but there may be more elaborate co-adaptation of life-cycles when there is more than one generation a year. Later generations may attack a different instar or species (e.g., some species of *Apanteles*) and the host's diapause may control that of its parasite (e.g., SYRPHIDAE and *Diplazon*, Schneider, 1950).

The majority of mature hymenopterous larvae spin a cocoon with silk from the labial glands. The silk is often impregnated with dark material, making the cocoon brown and parchment-like. It seems that this impregnation is often faecal material which has collected in the gut and (in the Apocrita) is voided only at pupation. Most Chalcidoidea spin no cocoon and the pupa is more or less obtect, with a thickened integument and the sheaths of the appendages soldered to the body. *Euplectrus*, however, makes a cocoon

TABLE IV Stages of hosts in relation to parasites

Parasite	Host	Host stage laid in	Host stage when parasite leaves
Trichogramma	Lepidoptera	Egg	Egg
Chelonus	Lepidoptera	Egg	Larva
Ibalia	Siricidae	Egg	Larva
Diplazon	Syrphidae	Egg	Puparium
Apanteles	Lepidoptera	Larva	Larva
Some *Leiophron*	Miridae	Nymph	Nymph
Exochus	Lepidoptera	Larva	Pupa
Pimpla	Lepidoptera	Pupa	Pupa
Dibrachys	Lepidoptera	Pupa	Pupa
Some *Leiophron*	Heteroptera	Nymph	Adult
Perilitus	Chrysomelidae	Adult	Adult

but the silk is secreted by the malpighian tubes (Clausen, 1940 : 153). A number of the FORMICIDAE spin no cocoons and in some species pupae with and without cocoons are found in the same nest. In Sphecoids, cocoons are usually spun but are absent or reduced to a small cap in a few genera (*Stigmus, Psenulus*). In the Apoidea, many genera spin cocoons and others do not (e.g., *Anthophora, Halictus*) and the phenomenon is of some taxonomic importance. When Hymenoptera are bred the cocoon should always be preserved, for not only is it often specifically recognizable but it contains the last larval exuviae which show most of the essential characters of the mature larva. In Sphecoids, also, the cocoon may include recognizable fragments of prey.

Most adult Hymenoptera seem to feed to some extent on nectar or honeydew. There is not much information about many of the small parasitic species but when reared in captivity they seem to require some form of syrup if they are to complete normal oviposition. A few sawflies (Benson, 1950:79) are regularly predacious on other insects. In the Apocrita, many Parasitica suck the juices of their hosts as well as ovipositing on them. This is usually done by feeding at punctures made with the ovipositor. Sometimes a considerable number of hosts may be killed in this way without any eggs being laid. In the Aculeata, Mutillids are said (Clausen, 1940) to kill more prey by feeding than by oviposition; such a habit is rarely recorded in Sphecoids but it is known in *Mellinus* and also in the Dryinids (Bethyloidea) and Pompilids.

Besides the variation which at all times constitutes one of the difficulties of taxonomy, there are certain special types of variation which are very characteristic of the Hymenoptera, though not confined to this order. Sexual dimorphism is often very great and separate keys for the identification of each sex are often necessary. Parasitic Hymenoptera often vary greatly in size, perhaps especially when the host is a wood-borer (see figs 5 and 6 of *Sirex* and its parasite *Thalessa* in Bischoff, 1927). Some of this variation is proved to depend on the size of the host or, in gregarious parasites, on the number per host (Salt, 1941). In *Gelis corruptor* (Först.) the size of the host also determines whether the male is macropterous or micropterous (Salt, 1952). The females are always wingless. In the Chalcid, *Trichogramma semblidis* (Auriv.), the females are winged but the males are winged if bred from Lepidopterous eggs but wingless if bred from those of *Sialis* (Megaloptera). These wingless males also differ in the structure of the legs and antennae (Salt, 1937). Another type of variation is that related to season. Species which have more than one generation a year may occur in two distinct forms. In British bees, this is well-known in some species of *Andrena* (Perkins, 1919); the seasonal differences are usually in the colour of the pubescence or the cuticle, but they may also occur in surface sculpture. In the males of *Andrena rosae* (Pz.) and *A. trimmerana* (Kby) a tooth on the postgena of the early brood is absent in the summer brood. *A. trimmerana*, however, has an additional tooth on the mandible in the summer brood. In the Ichneumonid *Sphecophaga*, adults appearing in the spring and early summer are fully winged while those appearing in late summer are usually micropterous (Perkins, 1937). The supposed dimorphism in cocoons in this genus (Clausen, 1940:81) is, at least as far as the British fauna is concerned, due to the confusion of two species. Seasonal alary dimorphism is known in some Chalcids (? any British) but similar variation in many ENCYRTIDAE and in the Cerocephalinae (PTEROMALIDAE) is not at present understood and is not seasonal.

A further type of variation which is seasonal, but also something more, is the alternation of generations in the Cynipinae. In the double-brooded oak-inhabiting genera, the generation which emerges in autumn, winter or early spring (depending on the species) from galls which developed during summer and autumn consists of females only. These agamic (symbol ♉) females lay parthenogenetic eggs and the very different type of gall produced matures in the spring or early summer. From these galls emerge the sexual generation (♂♀). The sexual generation is often so different in structure from the agamic one that in the past they were put in different genera. The gall is not only of a different structure and appearance but often also on a different part of the tree. The extreme of this development is seen in *Andricus kollari* (Htg.) in which the agamic females emerge in the autumn from marble galls on our native species of oak but the sexual generation emerges in the spring from galls on *Quercus cerris* (Marsden-Jones, 1953).

Finally, a special type of variation is seen in the worker caste (symbol ☿ or ♀) of social Hymenoptera. In *Halictus* and *Lasioglossum*, the difference is very slight but the workers of *L. malachurum* (Kby) were at one time regarded as a separate species. In wasps and bumblebees the difference is mostly in size and the queens and workers may intergrade; there is sometimes also an average difference in colour-pattern. In *Apis*, the differences are much more profound since the queen lacks pollen-collecting apparatus and wax-glands. In ants the differences are still greater and may affect almost any part of the body, according to the genus. The absence of the wings in the workers and the consequent modifications of the thorax are only the most conspicuous differences. Worker ants themselves are often highly variable but they are not dimorphic with a soldier caste (symbol ♃) in any British species. It has long been known that specific differences are much better shown in the queens of wasps and bumblebees than they are in workers. In ants, the workers because they are the caste most frequently collected have been treated as the basic type for taxonomic purposes. It is now clear, however, that in them, too, the specific characters are often better shown in the queen.

KEY TO THE FAMILIES OF BRITISH HYMENOPTERA

(An alternative key to the families of British Chalcidoidea will be found in Ferrière & Kerrich (1958). Oehlke's key (1969) to the families and subfamilies of German Hymenoptera is also useful.)

1 Abdomen broadly attached to the thorax, no marked constriction between first and second abdominal segments. Cenchri present except in CEPHIDAE, in which the first abdominal tergite is centrally divided by a membranous slit (fig. 29). Front tibia usually with two apical spurs. A closed anal cell often present in the forewing. Larva with gut continuous; thoracic (except *Orussus*) and, generally, abdominal legs present. (Another key to the families is given by Benson, 1951, *Handbk Ident. Br. Insects* **6** (*2a*))..................Suborder **Symphyta**....2

– Abdomen deeply constricted between the first segment (propodeum) and the second (first of gaster) except in a few minute Chalcidoidea with very reduced wing-venation. Cenchri never present and first abdominal tergite never with a membranous slit extending to its base. Fore tibia with only one apical spur except 2 in the Ceraphronoidea. Forewing with no closed anal cell. Larva with rectum not connected to front part of gut before pupation (except sometimes in last instar); legs absent......................Suborder **Apocrita**......10

2 Antennae with three segments of normal thickness, third very long and made up of several fused, followed by a thread-like flagellum of at least 9 segments. Head without an hypostomal bridge. Forewing (fig. 51) with *Rs* forked (always in British spp.). Male genitalia strophandrious (in British spp., orthandrious in some American spp.), parameres with cupping disks and with articulation to parameral plates..................Superfamily **Xyeloidea**, Family XYELIDAE

– Antennae not of this type, *Rs* in forewing not forked..........................3

3 Antennae with 11 or more segments except in ♀ ORUSSIDAE, in which segment 9 is swollen and longer than any of the others. Head with an hypostomal bridge. Male genitalia orthandrious..4

– Antennae with 10 segments or less except in the DIPRIONIDAE, which have the antennae serrate or pectinate. (*Athalia*, *Fenella* and *Heterarthrus*, TENTHREDINIDAE, may have 10–15 antennal segments but lack the following characters which are found in some or all of the families under couplet 4: pronotum with hind margin straight, insect more than 11.0 mm long, fore tibia with 1 (not 2) apical spur, antennae inserted below the eyes and the apparent clypeus). Head without an hypostomal bridge (the CIMBICIDAE, in which a bridge-like condition may appear to be present, have capitate antennae). Male genitalia strophandrious, parameres without cupping disks..Superfamily **Tenthredinoidea**....9

4 Antennae not inserted on ventral side of head; cenchri present. In ♂ genitalia, the parameres with cupping disks and articulated to parameral plates........5

– Either antennae inserted ventrally beneath eyes and below the apparent clypeus (Orussoidea) or cenchri absent (Cephoidea). In ♂ genitalia, parameres without cupping disks and not articulated but fused to parameral plates..............8

5 Pronotum with the hind margin almost straight, the emargination being no deeper than the length of the tegula. Abdomen strongly flattened dorso-ventrally.... ....Superfamily **Megalodontoidea**....6

– Pronotum with the hind margin deeply emarginate, more deeply than length of tegula. Abdomen cylindrical..................Superfamily **Siricoidea**....7

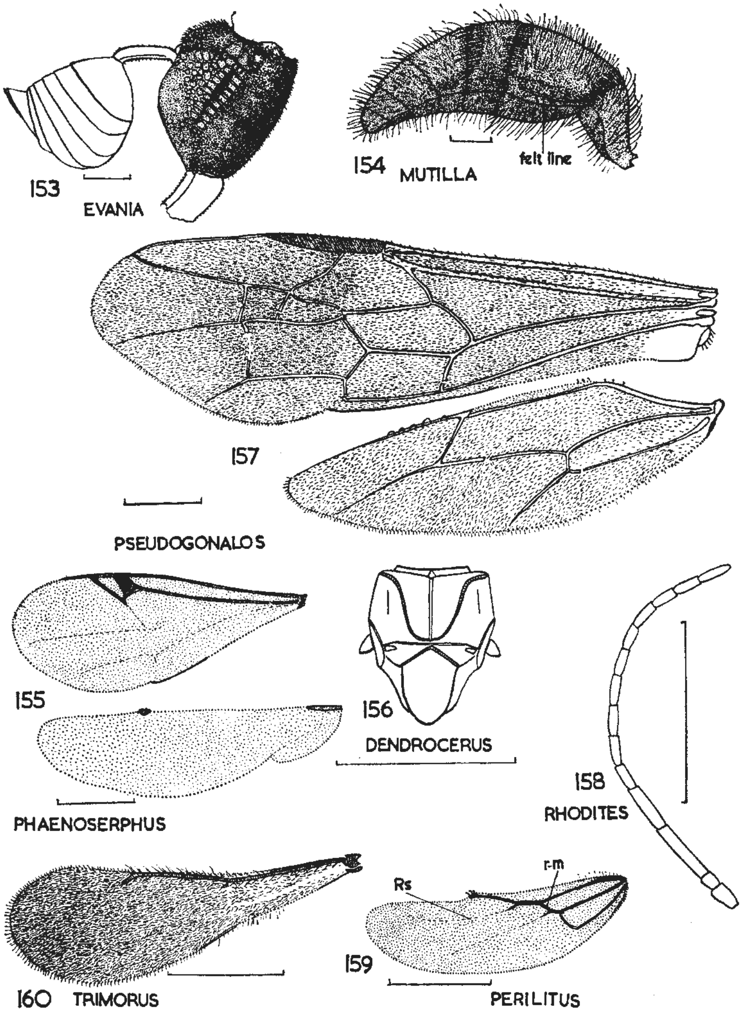
6 Antenna flabellate. Forewing without a separate *Sc*. Second abdominal tergite not medially divided. (Doubtfully British)..........Fam. MEGALODONTIDAE

– Antennae setaceous. Forewing (fig. 54) with a separate *Sc*. Second abdominal tergite divided medially..............................Fam. PAMPHILIIDAE

7 Forewing with first abscissa of *Rs* directed towards base of wing, last abscissa recurved. Mesoscutum much longer than scutellum; tegula minute, hidden. Neck short...Fam. SIRICIDAE

– Forewing with first abscissa of *Rs* directed towards apex of wing, last abscissa not recurved. Mesoscutum hardly longer than scutellum with axillae; tegula normal though rather small. Neck long.................Fam. XIPHYDRIIDAE

8 Antennae with 11 linear segments in ♂; 10 segments in ♀, with ninth large and tenth very small. No constriction between first and second abdominal segments. Forewing with no enclosed anal cell; hind wing without cross-veins *r–m* or *m–cu*. (Doubtfully British)........Superfamily **Orussoidea**, Fam. ORUSSIDAE



Figs 153–160. (Scale-line = 1.0 mm) 153, *Evania appendigaster* (L.) Evaniidae) ♀. Propodeum and gaster from the right. 154, *Mutilla europaea* (L.) (Mutillidae) ♂. Gaster from the right. 155, *Phaenoserphus calcar* (Hal.) (Proctotrupidae). Left wings. 156, *Dendrocerus* sp. (Ceraphronidae). Thorax from above. 157, *Pseudogonalos hahni* (Spin.) (Trigonalidae) ♀. Left wings. 158, *Rhodites rosae* (L.) (Cynipidae) ♀. Left antenna. 159, *Perilitus rutilus* (Nees) (Braconidae). Left hind wing. 160, *Trimorus* sp. (Scelionidae). Left forewing.

– Antennae with 16–30 segments, filiform or slightly clavate. A slight constriction between first and second abdominal segments. Forewing with a closed anal cell; hind wing with cross-veins *r–m* and *m–cu* present .... Superfamily **Cephoidea**, Fam. CEPHIDAE

9 Antenna with three segments, third very long. Forewing with cross-vein *2r* absent .... Fam. ARGIDAE

– Antenna with four segments, third very long, fourth minute. Forewing with cross-vein *2r* present, cell *IM* of a peculiar pyriform shape .... Fam. BLASTICOTOMIDAE

– Antenna with 4–5 segments followed by a very strongly marked club which may show traces of segmentation. Sides of abdomen carinate. Forewing with cross-vein *2r* present .... Fam. CIMBICIDAE

– Antenna typically with 9 segments, rarely with as few as 7 or with 10–15. Sides of abdomen not carinate. Forewing often with cross-vein *2r* present .... Fam. TENTHREDINIDAE

– Antennae with 13 or more segments, serrate in ♀, pectinate in ♂. Forewing with cross-vein *2r* absent .... Fam. DIPRIONIDAE

10 Wings fully developed 11

— Wings very reduced or absent 62

11 Hind wings without an anal or vannal lobe, except in the EVANIIDAE, in which the gaster is attached at the top of the propodeum (fig. 153), in most BRACONIDAE Microgasterinae, in which the antennae have 18 segments and some PROCTOTRUPIDAE, in which the venation of the forewing is characteristic (fig. 155). Costa of hind wing not or imperfectly developed except (apparently) in some Evanioidea and Proctotrupoidea. Hind femur with a trochantellus except in some Cynipoids, Chalcidoids and Proctotrupoids. Last visible tergite and sternite of ♀ not apposed except in Proctotrupoids, some Cynipoids and, less distinctly, Trigonaloids; the ovipositor, which is often elongate, is partly exposed, at least in ventral view, except in EVANIIDAE, most Cynipoids and most Proctotrupoids; in the TRIGONALIDAE the ovipositor is reduced; tergite 8 fully exposed and resembling 7 except in a few BRACONIDAE and Proctotrupoids .... Section **Parasitica**.... 12

— Hind wing with an anal or vannal lobe, except in the FORMICIDAE, in which the segment of the gaster forms a scale or node and in ♂ MUTILLIDAE which have a felt line (fig. 154) on the second gastral tergite and in the Vespinae; the lobe is defined only by a small excision in the CHRYSIDIDAE and CLEPTIDAE. Costal vein of hind wing often developed. Hind femur without a trochantellus though in a few groups the base of the femur may be ringed by a sulcus. Last visible tergite and sternite of ♀ apposed, except in *Ceropales* (POMPILIDAE) and a few parasitic bees (e.g., *Melecta*); ovipositor (sting) entirely hidden, tergite 8 retracted and partly desclerotized (except DRYINIDAE). Antennae with 13 segments or less .... Section **Aculeata**.... 42

12 Gaster attached near the top of the propodeum. Forewing with costal cell wide, pterostigma present. Hind wing with a strong vein along its fore margin and with no enclosed cells (sometimes one such cell in non-British species). Abdomen with spiracles on segments 1 and 8, pygostyles present. Antennae with 13 or 14 segments .... Superfamily **Evanioidea**.... 17

— Gaster normally attached near the bottom of the propodeum. (If the gaster is attached about half-way up the propodeum—*Cenocaelius* and *Paxylomma* (BRACONIDAE)—the costal cell in the forewing is obliterated) 13

13 Forewing with a pterostigma and antennae usually with more than 16 segments, scape short (except *Streblocera*). Hind wing with at least two enclosed cells except *Neorhacodes* (ICHNEUMONIDAE (fig. 67)) and some BRACONIDAE, which have the costa and radius fused in the forewing up to the pterostigma and sometimes about 20 antennal segments or (*Paxylomma*) the first two segments of gaster much longer than broad and the hind basitarsus thickened. Trochantellus distinct, at least on hind leg. Spiracles on abdominal segments 1–8, or BRACONIDAE, Sigalphinae (*Chelonus*, etc.) 1–6. Pygostyles present 14

— Antennae with not more than 16 segments. Forewing with no true pterostigma except in the HELORIDAE, and PROCTOTRUPIDAE, in which the costal cell is wide (figs 66, 155), and the CERAPHRONIDAE (fig. 168), in which the axillae are on the same level as the central part of the scutellum (fig. 156); venation generally reduced. Hind wing with no enclosed cells except in some DIAPRIIDAE and

IBALIIDAE, in which either the head is greatly produced forwards or the costal cell of the forewing is wide. Trochantellus often indistinct or absent. In female, tergites 9 and 10 indistinguishably fused, except in some PROCTOTRUPIDAE and CERAPHRONIDAE..15

14 Forewing (fig. 157) with costal cell wide, $Rs + M$ complete and cross-veins 3 *r–m*, 2 *r–m*, *Rs* and 2 *m–cu* present. Tarsi with plantar lobes. Last visible tergite and sternite almost apposed, ovipositor reduced and hidden, abdominal tergite 9 in ♀ retracted with the central part membranous.

Tergite 10 not separately developed. Mandibles with four large teeth on the right, three on the left one. Antennae with more than 20 segments in the one British species)..............Superfamily **Trigonaloidea**, Fam. TRIGONALIDAE

— Forewing with costal cell almost or quite obliterated, at least one of cross-veins *3r–m*, *2r–m*, *Rs* and *2m–cu* absent. Tarsi without plantar lobes. Last visible tergite and sternite of ♀ abdomen not clearly apposed, ovipositor usually clearly exserted and abdominal tergite 9 often not retracted..Superfamily **Ichneumonoidea**....19

15 Either forewing with a well-developed costa or the edge of the gaster sharp and down-curved, or the head much produced forwards and the antennae inserted on a shelf-like process. Pronotum either obtuse below but with a narrow posteroventral process which meets its fellow from the other side beneath the fore coxae, or the pronotum is fully coadapted to the mesepisternum. Gaster rarely compressed, spiracles on abdominal segments 1, 1 and 8, or 1–6. Last visible tergite and sternite of ♀ apposed, pygostyles present; ovipositor hidden except in the PROCTOTRUPIDAE, in which it projects inside the enlarged pygostyles (figs 118–119). Antennal scape usually long, if short then a pterostigma is present...................................Proctotrupoid groups....20

— Forewing with no pterostigma; proximal part of costa not developed, except weakly in the IBALIIDAE, which have a short antennal scape. Abdomen with spiracles on segments 1 and 8, last visible tergite and sternite of ♀ not apposed; ovipositor exposed, at least below, except in most Cynipoids in which the gaster is usually compressed laterally..16

16 Pronotum lateroventrally pointed and closely coadapted to the mesepisternum, posteriorly extending back to the tegulae. Forewing (figs 62, 169, 171) with cell R_1 more or less complete. Antennae (fig. 158) with scape short and with 12–16 segments. Trochantellus usually not developed. Abdomen in ♀ with tergite 9 retracted and desclerotized. Gaster usually compressed laterally, pygostyles absent..........................Superfamily **Cynipoidea**....26

— Pronotum lateroventrally rounded, not closely coadapted to the mesepisternum, posteriorly usually distinctly separated from the tegulae (figs 36–37). Forewing with cell R_1 not defined by proper veins or absent. Antennal scape usually long (fig. 22) (not clearly so in some MYMARIDAE); antennae with 13 segments or less. Trochantellus often present. Abdomen rarely compressed, with pygostyles, in ♀ central portion of tergite 9 exposed and pigmented..Superfamily **Chalcidoidea**....28

17 Hind wing with an anal lobe. Forewing not longitudinally folded, cross-vein 2 *m–cu* and 2 *r–m* absent. Antennae inserted well above the clypeus, with 13 segments. Gaster (fig. 153) short, compressed, with a long, abrupt petiole and a short, often hidden, ovipositor. Propleura not meeting dorsally and forming a neck...Fam. EVANIIDAE

— Hind wing with no anal lobe. Antennae with 13 segments in ♂, 14 in ♀. Gaster long, gradually clavate, ovipositor exserted, often long. Propleura meeting above and forming a neck..18

18 Forewing not longitudinally folded, with cross-veins 2 *m–cu* and 2 *r–m* present. Antennae inserted just above the clypeus...................Fam. AULACIDAE

— Forewing longitudinally folded, with cross-veins 2 *m–cu* and 2 *r–m* absent (fig. 64). Antennae inserted well above the clypeus..............Fam. GASTERUPTIIDAE

19 Forewing (fig. 56) with cross-vein 2 *m–cu* almost invariably present, $Rs + M$ interrupted. Hind wing with cross-vein *r–m* meeting *Rs* after that vein leaves $Sc + R$. (Including *Agriotypus*[9] and *Neorhacodes*; the latter would run to the

[9] *Agriotypus* is here treated as forming a subfamily of the Ichneumonidae, but Mason 1971) gives grounds for treating it as a Proctotrupoid family, perhaps near *Helorus*.

BRACONIDAE but the forewing (fig. 67) is characteristic)..Fam. ICHNEUMONIDAE

— Forewing (fig. 63) without cross-vein 2 $m\text{–}cu$. Hind wing (fig. 159) with cross-vein $r\text{–}m$ meeting $Sc + R$ before the separation of Rs. (Includes Alysiinae, Aphidiinae and Paxylommatinae)....................................Fam. BRACONIDAE

20 Sides of gaster acute or distinctly margined. Antennae with not more than 12 segments. Front tibia with one spur........Superfamily **Scelionoidea**....21

— Sides of gaster rounded or if, in some Belytinae, more acute, the antennae have 14–15 segments..22

21 Antennae with 10 or rarely fewer segments. Forewing without marginal or stigmal veins, often also without a submarginal vein..........Fam. PLATYGASTERIDAE

— Antennae with 11 or 12 segments, or with 7–8 and an unsegmented club; if with 10, the stigmal vein is present (fig. 160).....................Fam. SCELIONIDAE

22 Fore tibia with two spurs. Antennae inserted very low down, at clypeal margin, with 9–11 segments, scape very long. Radial cell in forewing not enclosed, pterostigma sometimes developed. Scutellum usually with a frenum and with axillae in same plane as main surface....Superfamily **Ceraphronoidea**....23

— Front tibia with one spur. Antennae inserted near middle of face, with 11–15 segments, scape usually short. Radial cell in forewing normally closed. Scutellum without a frenum and axillae not in same plane as main surface........ ....Superfamily **Proctotrupoidea**....24

23 Tibial spurs 2, 1, 2; all spurs pectinate; large one of fore tibia not bifid. Antennae with 9–10 segments ♀, 10–11, ♂. Gastral petiole visible as a short ring, tergite 6 with an oval patch of dense reticulation................Fam. CERAPHRONIDAE

— Tibial spurs 2, 2, 2; the large, pectinate one of fore tibia, bifid. Antennae with 11 segments in both sexes. Gastral petiole shorter, usually hidden by the next segment, tergite 6 without a patch of dense reticulation....Fam. MEGASPILIDAE

24 Forewing (fig. 161) with no true pterostigma, though the parastigma is sometimes thickened or else the gaster is long petiolate. Antennae with 11–15 segments inserted (fig. 162) far above the clypeus on a frontal shelf or strong prominence (except in *Ismarus* in which they are inserted normally (fig. 163) at about the middle of face, but this genus has venation of forewing much as in fig. 161 and an enclosed cell in the hind wing)........................Fam. DIAPRIIDAE

— Forewing with a pterostigma. Antennae not inserted on a frontal shelf, usually nearer the clypeus or at middle of face..25

25 Antennae with 15 segments. Venation (fig. 66) characteristic. Gaster long, petiolate..Fam. HELORIDAE

— Antennae with 13 segments, inserted at middle of face, scape short (fig. 164). Forewing with a closed, normally very small, radial cell (fig. 155). Ovipositor (figs 118–119) long................................Fam. PROTOTRUPIDAE

26 Larger species, cell R_1 closed in forewing and nine times as long as broad (fig. 169). Hind basitarsus twice as long as remaining segments together (fig. 170). Largest segment of gaster one of 4–6, two or more small tergal plates preceding the large one...Fam. IBALIIDAE

— Smaller species, cell R_1 not always fully closed, less elongate. Hind basitarsus normal. Largest segment of gaster 2 or 3, or these fused, at most one small tergal plate preceding the large one (fig. 175).............................27

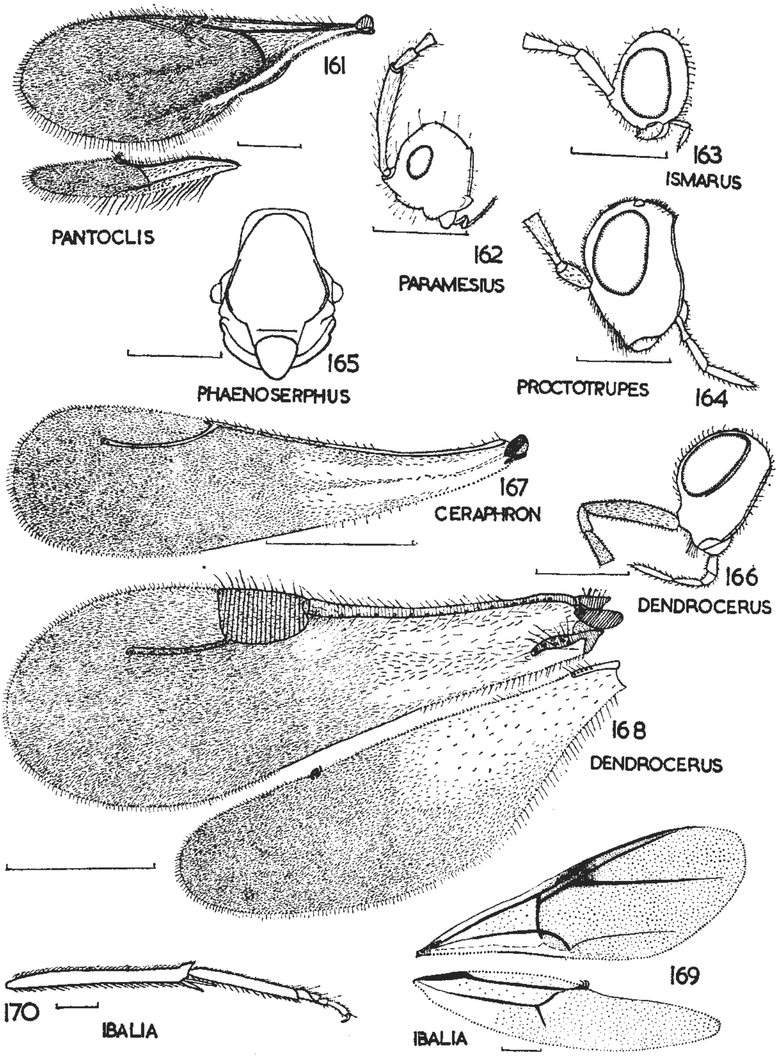
27 $Rs + M$, when present in forewing, directed towards $M + Cu$ rather than $Sc + R$ (fig. 171). If the second or second and third tergites are long and form half the gaster, the scutellum has an apical cup-like depression (fig. 172). Gaster sometimes long petiolate (fig. 173). (Including Eucoilinae and Anacharitinae).. ....Fam. FIGITIDAE

— $Rs + M$, when present in forewing, directed towards the mid point between $M + Cu$ and $Sc + R$ (fig. 62). Second or second and third tergites usually the largest and forming one-half of the gaster, which is never long petiolate (fig. 174). (Including Charipinae).........................Fam. CYNIPIDAE

28 Hind wings linear, base forming a stalk, wings with long fringes (fig. 176). Ovipositor sometimes issuing almost at tip of abdomen. Antennae without annelli. (Including Mymaromminae) (fig. 176).....................Fam. MYMARIDAE

— Not as above...29

29 Axillae advanced strongly in front of anterior margin of the scutellum and usually in front of the tegulae (fig. 177). Tarsi usually with 3 or 4 segments........30



FIGS 161–170. (Scale-lines, figs 161–168 = 0.5 mm, figs 169–170 = 1.0 mm) 161, *Pantoclis* sp. (Diapriidae). Left wings. 162, *Paramesius* sp. (Diapriidae) ♀. Head from the left. 163, *Ismarus halidayi* Först. (Diapriidae) ♂. Head from the left. 174, *Proctotrupes gravidator* (L.) (Proctotrupidae) ♀. Head from the left. 165, *Phaenoserphus calcar* (Hal.) (Proctotrupidae). ♂. Thorax from above. 166, *Dendrocerus* sp. (Ceraphronidae) ♀. Head from the left. 167, *Ceraphron* sp. (Ceraphronidae). Left forewing. 168, *Dendrocerus* sp. (Ceraphronidae). Left wings. 169, *Ibalia leucospoides* (Hochenw.) (Ibaliidae) ♀. Right wings. 170, Same species ♀. Left hind tibia and tarsus.

— Axillae not or little advanced in front of anterior margin of scutellum (figs. 36, 185). Tarsi with 5 segments..........33

30 Hind coxa much enlarged, hind femur compressed. Tarsi 4-segmented. Marginal wing-vein long..........Fam. ELASMIDAE

— Hind coxa not enlarged..........31

31 Mid coxa with base lying before the mid line of the mesopleuron (fig. 40), and lying in a groove on the under side of the thorax..........Fam. ENCYRTIDAE

— Mid coxa lying well behind the mid line of the mesopleuron, with no groove on the underside of the thorax..........32

32 Tarsi usually with 4 segments but with 5 in most Aphelininae and a few females of other groups. Forewing narrower, pubescence not in rows or lines (fig. 179)..........Fam. EULOPHIDAE

— Tarsi with 3 segments. Forewing very broad, pubescence usually in rows or lines, marginal and stigmal veins forming a single curve (fig. 178)..........Fam. TRICHOGRAMMATIDAE

33 Mesepisternum little sculptured, large and almost completely covering the mesepimeron (fig. 40) (except in some ♂ EUPELMIDAE). Mid tibial spur usually enlarged (fig. 85) (spur enlarged in the above ♂ which have a short pronotum)..........34

— Mesepisternum not enlarged, of about the same width as the mesepimeron. Mid titial spur rarely longer than the bigger hind tibial one (except in some Cleonyminae which have a long pronotum)..........35

34 Mesonotum in ♀ with centre of scutum depressed or flat, notaulices impressed at least anteriorly and usually long. Males with scutum usually convex and notaulices often much shorter but in them the mesepisternum is not enlarged. Marginal vein of forewing long..........Fam. EUPELMIDAE

— Mesoscutum more or less convex, notaulices not more than feebly indicated. Mesepimeron enlarged. Marginal vein in forewing as long as submarginal. Scutellum transversely linear. Mid tibia with long bristles...Fam. THYSANIDAE

35 Mandibles sickle-shaped, usually with 1 or 2 inner teeth. Thorax very convex, scutellum usually produced backwards. Gaster compressed, usually with a long petiole. (Doubtfully British)..........Fam. EUCHARITIDAE

— Mandible stout, with 3 or 4 teeth at apex. Thorax rarely so formed..........36

36 Hind coxa large, 2–3 times longer than the front one (fig. 180)..........37

— Hind coxa not so conspicuously longer than the front one (fig. 181)..........39

37 Hind femur with a row of teeth beneath (fig. 182)..........Fam. CHALCIDIDAE

— Hind femur with at most one tooth (fig. 183) beneath..........38

38 Notaulices present. Gaster not coarsely punctured, ovipositor usually long and exserted..........Fam. TORYMIDAE (except Megastigminae)

— Notaulices very feeble or absent. Gaster usually with rows of coarse punctures, ovipositor short..........Fam. ORMYRIDAE

39 Pronotum short, transversely linear, or elongate but much narrowed in front: Mesoscutum usually reticulate. Colours usually metallic. (Including Miscogasterinae, Spalangiinae and Cleonyminae; the elongate pronotum and flattened dorsal side of the gaster in the last named subfamily are sometimes regarded as family characters)..........Fam. PTEROMALIDAE

— Pronotum wide, quadrate (figs 181, 185–6), scarcely narrower than the mesoscutum, which is often coarsely punctured..........40

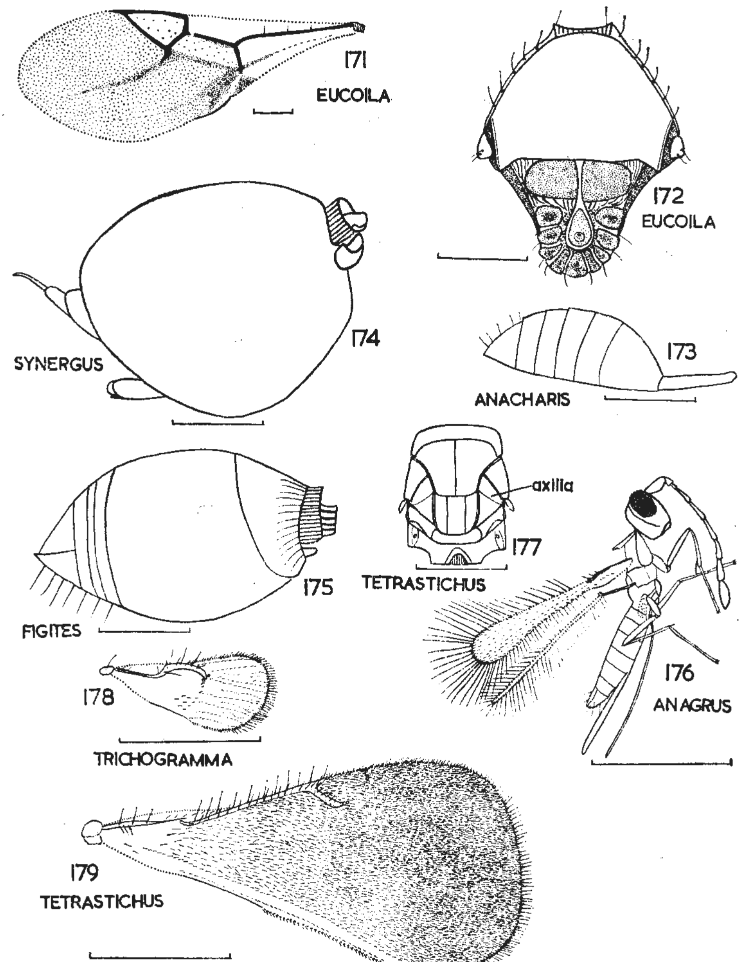
40 Stigmal vein thickened into a very large knob (fig. 184), ovipositor elongate; otherwise rather like the EURYTOMIDAE ...Fam. TORYMIDAE, subfam. Megastigminae

— Stigmal vein not so thickened, ovipositor short..........41

41 Gaster in ♂ long petiolate and antennae more or less verticillate (fig. 185). Gaster in ♀ rounded or ovate, more or less compressed, second tergite never very large, last sternite usually produced (fig. 186). Colours black or yellowish..........Fam. EURYTOMIDAE

— Gaster small, subtriangular, short petiolate, second or fused second and third tergites covering most of its surface. Antennae not verticillate. Thorax large but short. Colours more or less metallic. (Fig. XII)......Fam. PERILAMPIDAE

42 Hind wings with no cells enclosed by veins. Pronotum obtuse below and not closely coadapted to the mesepisternum. Abdominal spiracles on segments 1–7 or 1–8 (DRYINIDAE). ♂ and ♀ with the same number of antennal segments..........Superfamily **Bethyloidea**....49



Figs 171–179. (Scale-line = 0.5 mm) 171, *Eucoila* sp. (Figitidae) ♀. Left forewing. 172, The same species, thorax from above. 173, *Anacharis* sp. (Figitidae) ♂. Gaster from the right. 174, *Synergus* sp. (Cynipidae) ♀, gaster from the right. 175, *Figites* sp. (Figitidae) ♀, gaster from the right. 176, *Anagrus incarnatus* Hal. (Mymaridae) ♀, from the right. 177, *Tetrastichus rapo* (Walk.) (Eulophidae) ♀, thorax from above. 178, *Trichogramma evanescens* Westw., right forewing. 179, *Tetrastichus* sp. (Eulophidae), right forewing.

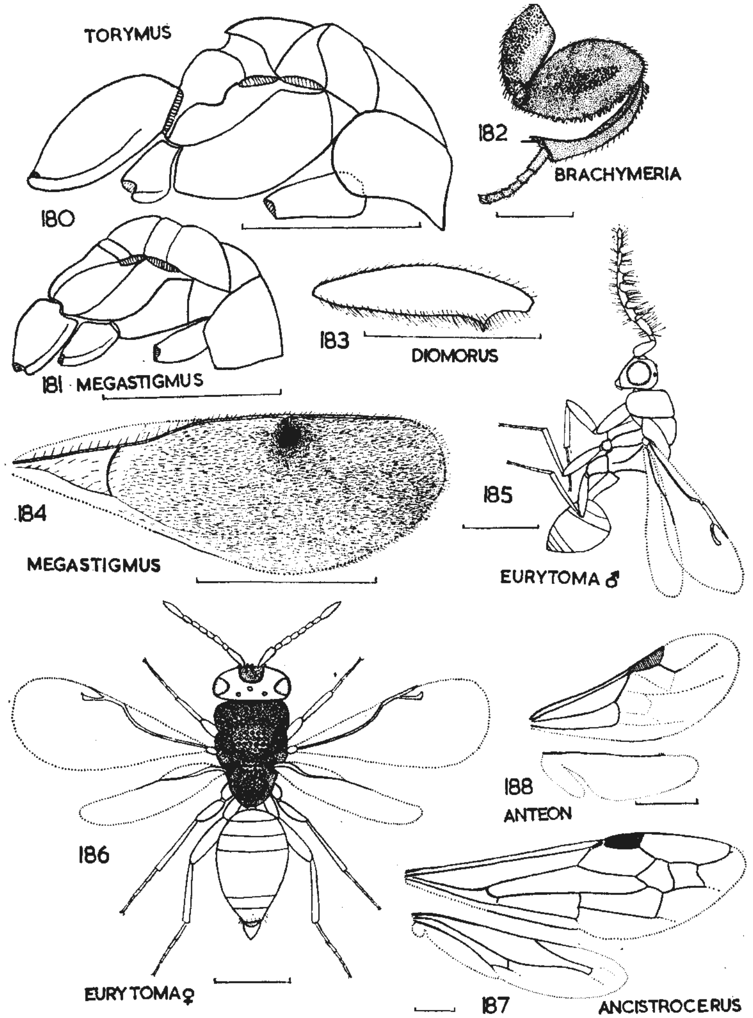
— Hind wing with one or more cells enclosed by veins. Abdominal spiracles on segments 1–8. Nearly always more antennal segments in ♂ than in ♀......43

43 Hind wing without an anal lobe and first segment of gaster forming a scale or node, or the first two segments nodiform and the second segment deeply separated from the third both above and below....Superfamily **Scolioidea**, Fam. FORMICIDAE

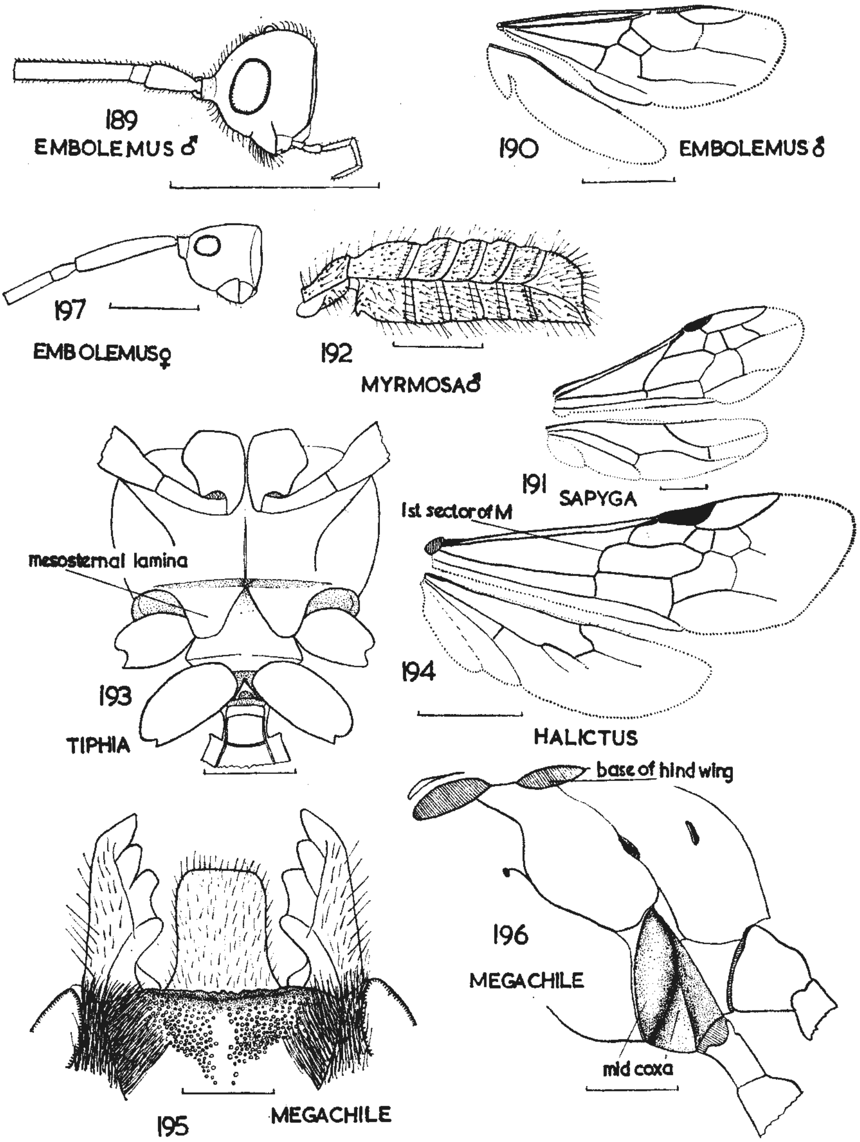
— Hind wings with an anal lobe except in the MUTILLIDAE, in which there is a felt-line (fig. 154) at the side of the second segment of gaster. First segment of gaster not scale-like; if nodiform, then the next segment is closely coadapted to the third 44

44 Pronotum produced back to or almost to the tegulae with no conspicuous lobe concealing the anterior thoracic spiracle (fig. 42) 45

— Pronotum not produced back to the tegulae but usually forming at a lower level a conspicuous lobe (figs 44, 47) over the anterior thoracic spiracle 48



FIGS 180–188. (Scale-lines = 1.0 mm) 180, *Torymus bedeguaris* (L.) (Torymidae) ♀, thorax and coxae from the right. 181, *Megastigmus dorsalis* (F.) (Torymidae) ♀, thorax and coxae from the right. 182, *Brachymeria minuta* (L.) (Chalcididae) ♂, left hind leg. 183, *Diomorus armatus* (F.) (Torymidae) ♀, left hind femur. 184, *Megastigmus dorsalis* (F.) (Torymidae), right forewing. 185, *Eurytoma rosae* Nees (Eurytomidae) ♂, left side. 186, ♀, Dorsal view. 187, *Ancistrocerus parietum* (L.) (Eumenidae) ♂, right wings. 188, *Anteon flavicorne* (Dalm.) (Dryinidae), right wings.



FIGS 189–197. (Scale-lines = 1.0 mm) 189, *Embolemus raddii* Westw. (Embolemidae) ♂, head from the left. 190, The same, right wings. 191, *Sapyga clavicornis* (L.) (Sapygidae) ♀, right wings. 192, *Myrmosa atra* Panz. (Tiphiidae) ♂, gaster from the right. 193, *Tiphia femorata* Fab. (Tiphiidae) ♀, mesosternal region, ventral view. 194, *Lasioglossum morio* (F.) (Halictidae), right wings. 195, *Megachile willughbiella* (Kby) (Megachilidae) ♀, labrum and apex of clypeus. 196, The same, mid coxa and adjacent pleuron. 197, *Embolemus ruddii* Westw. (Embolemidae) ♀, head from the left.

45 Forewing (fig. 187) usually (always in British spp.) longitudinally folded in repose, cell *M* + *Rs* + *M* long, longer than cell *M*. Glossa and paraglossa ending in pigmented pads (fig. 20). Eyes emarginate ....Superfamily **Vespoidea**....46

— Forewing not longitudinally folded in repose, cell *M* + *Rs* + *M* shorter. Glossa and paraglossa without these pads. Eyes usually not emarginate..........47

46 Mandibles long, crossing one another when at rest. Mid tibia with one spur. Tarsal claws bifid. Hind wing with an anal lobe. Solitary species...Fam. EUMENIDAE

— Mandibles short and broad, lying transversely, one above the other. Mid tibia with two spurs. Tarsal claws simple. Hind wing (in the Vespinae) with no anal lobe. Social species...................................Fam. VESPIDAE

47 Mesopleuron divided obliquely by a suture running from near upper posterior corner, downwards and forwards (fig. 42). Pronotum obtuse below and loosely overlapping the mesopleuron (fig. 42). Legs long, hind femur especially so.................................Superfamily **Pompiloidea**, Fam. POMPILIDAE

— Mesopleuron not so divided. Pronotum usually acute below (not in *Tiphia*) and coadapted to the mesopleuron. Legs usually short and stout...Superfamily **Scolioidea**....53

48 Pubescence simple. Hind tarsi not broadened......................................Superfamily **Sphecoidea**, Fam. SPHECIDAE

— Pubescence, at least in part (e.g., near anterior thoracic spiracles), plumose or branched. Hind tarsi usually more or less widened and often densely pubescent (fig. 70).....................................Superfamily **Apoidea**....55

49 Antennae with 10 segments......................................50

— Antennae with 12–13 segments....................................51

50 Antennae not inserted on a prominence but near to dorsal margin of clypeus (fig. 14). Female with chelate fore tarsi (fig. 84) (except *Aphelopus*), sometimes apterous or brachypterous (cf. fig. 188)..................Fam. DRYINIDAE

— Antennae inserted on a prominence high above the clypeus (fig. 189). Female apterous. Male winged with relatively complete venation (fig. 190)...Fam. EMBOLEMIDAE

51 Gaster with 7 exposed segments. Colours rarely metallic (not in British spp.). Pronotum usually parallel-sided. Head more or less prognathous (fig. 1)...Fam. BETHYLIDAE

— Gaster with 3–5 exposed segments. Colours largely metallic (always in British spp.). Head orthognathous. Antennae with 13 segments.................52

52 Gaster with 3 exposed segments (fig. 87), venter concave. Pronotum short but wide. Propodeum normally with sharp lateral keels or teeth. Sculpture usually coarse................................Fam. CHRYSIDIDAE (Chrysidinae)

— Gaster with 4–5 exposed segments, venter a little convex. Pronotum elongate, somewhat narrowed anteriorly. Sculpture finer; colours not entirely metallic...Fam. CHRYSIDIDAE (Cleptinae)

53 Second gastral tergite with lateral felt-lines (fig. 154). Female apterous. Male hind wing without an anal lobe (forewing, fig. 59), body usually well punctured and with conspicuous patches of pubescence................Fam. MUTILLIDAE

— Second gastral tergite without lateral felt-lines. Male hind wings with an anal lobe and body often smooth, shining and nearly bare.....................54

54 First and second gastral tergites not separated by a constriction, first and second sternites with only a feeble constriction between them. Mesosternum simple. Female winged (fig. 191)...................................Fam. SAPYGIDAE

— First and second gastral segments separated by a deep constriction (fig. 192) and/or the mesosternum with two laminae which overlie or project between the bases of the mid coxae (fig. 193). Female often apterous. (Including Methochinae and Myrmosinae)...Fam. TIPHIIDAE

55[10] Antennal socket connected with fronto-clypeal suture by two sutures (fig. 6). Glossa acute, labial palpi with segments alike or the first alone elongate and flattened. Mid coxa externally much shorter than distance from its summit to posterior wing-base (as in fig. 47). Females and many males with a pygidial area (fig. 115)..Fam. ANDRENIDAE

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[10] The key to the families of Apoidea follows Michener and is not easy to use. For the small British fauna it will probably be better to use a key direct to genera.

— Antennal socket connected with fronto-clypeal suture by a single suture. Labial palpi variable but rarely with first segment alone elongate..................56

56 Forewing with first sector of *M* curved (fig. 194). Mentum and submentum virtually absent (fig. 19), labial palpi usually with all segments similar. Mesepisternum usually with a complete anterior oblique suture. Metanotum horizontal. Mid coxa externally much shorter than distance from its summit to posterior wing-base..Fam. Halictidae

— Forewing with first sector of *M* straight. Mentum and submentum present....57

57 Glossa bilobed. Submentum elongate, not V-shaped. Anterior oblique suture present on mesepisternum (fig. 47). Mid coxa externally much shorter than distance from its summit to posterior wing-base...........Fam. Colletidae

— Glossa acute, often elongate. Submentum V-shaped. Anterior oblique suture very rarely complete, usually absent...58

58 Labial palpi with segments similar and cylindrical. Galea short. Mid coxa, except in *Macropis*, much shorter than distance from its summit to posterior wing-base..Fam. Melittidae

— Labial palpi with first two segments elongate and sheathing (fig. 21). Galea very elongate (fig. 21). Mid coxa, except in a few parasitic Apidae, two-thirds as long as distance from its summit to posterior wing-base (fig. 196)...........59

59 Labrum longer than broad and widened to a broad articulation with clypeus (fig. 195). Subantennal suture at outer edge of socket. Forewing with two submarginal cells, usually of about the same length. Last gastral tergite nearly always without a pygidial area. Scopa, when present, on gastral sternites.... ....Fam. Megachilidae

— Labrum usually broader than long; if not, narrowed basally to a short articulation with clypeus. Subantennal suture at inner edge of socket. Forewing usually with 3, rarely with 1 or 2 submarginal cells; if 2, the second is usually much shorter than first. Pygidial area often present. Scopa, when present, on hind legs, rarely also on gastral sternites.....................................60

60 Scopa of female forming a corbicle on the hind tibia and inner apical margin of tibia with a pecten (fig. 86) (except in *Psithyrus*). Pygidial plate absent. Social species...Fam. Apidae

— Scopa of female not forming a corbicle on the hind tibia which has no apical pecten 61

61 Pygidial plate nearly always present in ♀ and usually in ♂. Clypeus protruberant, lateral portions seen from below bent posteriorly and lying parallel to long axis. Fore coxa a little broader than long...................Fam. Anthophoridae

— Pygidial plate absent. Clypeus not protruberant, lateral portions seen from beneath transverse rather than longitudinal. Fore coxa transverse............ ....Fam. Xylocopidae

62 Gastral sternites considerably membranous, tending to dry into a longitudinal fold. Antennae often multiarticulate..63

— Gastral sternites fully sclerotized..64

63 Gaster with tergites 2 and 3 fused, not overlapping, its petiole usually broad, if narrow then its dorsal surface is straight in profile. (Either a circular space between clypeus and mandible (as in fig. 15) or mandibles exodont, fig. 16). Tegulae present..Fam. Braconidae

— Gaster with tergites 2 and 3 usually separate and overlapping; if fused, the gaster is long petiolate and the dorsal surface of the petiole is curved in profile. No circular space between clypeus and mandibles, latter not exodont. Tegulae often absent..Fam. Ichneumonidae

64 First or first and second segments of gaster scale-like or nodiform, well-separated from posterior part of gaster..............................Fam. Formicidae

— The gastral petiole is not scale-like nor composed of two nodiform segments....65

65 Head pyriform, long axis vertical, the 10-segmented antennae, which are as long as whole body, arise from a prominence (fig. 197). Gaster not long petiolate. Females..Fam. Embolemidae

— Head differently formed, or otherwise different...............................66

66 Pronotum not extending back to the tegulae; tegulae absent in some Trichogrammatidae, but these have only 3 tarsal segments. Pronotum not coadapted to the mesepisternum which has a distinct postspiracular sclerite............. .... Superfamily **Chalcidoidea**....28

— Pronotum extending back to the tegulae if the latter are present. Tarsi always 5-segmented. Postspiracular sclerite not distinctly developed..............67

67 Antennae with 10 segments or fewer..68

— Antennae with more than 10 segments..69

68 Females with chelate fore tarsi (fig. 84) and 10 antennal segments. Pronotum not coadapted to the mesepisternum..........................Fam. DRYINIDAE

— Fore tarsi not chelate. Pronotum more or less distinctly coadapted to the mesosternum 20

69 Gaster compressed laterally, conspicuously deeper than broad, integument mostly smooth and shining, except for base..........Superfamily **Cynipoidea**....27

— Gaster not compressed laterally. Integument often more sculptured and pubescent..70

70 Head more or less markedly longer than broad, more or less clearly prognathous. Thoracic sutures usually more complete..................Fam. BETHYLIDAE

— Head more or less globular or at least orthognathous.......................71

71 Antennae not with 12 segments or, if with 12, they arise from a prominence and the gaster is long petiolate or its sides are acutely margined.................20

— Females. Antennae with 12 segments and other characters different............ ....Superfamily **Scolioidea**....72

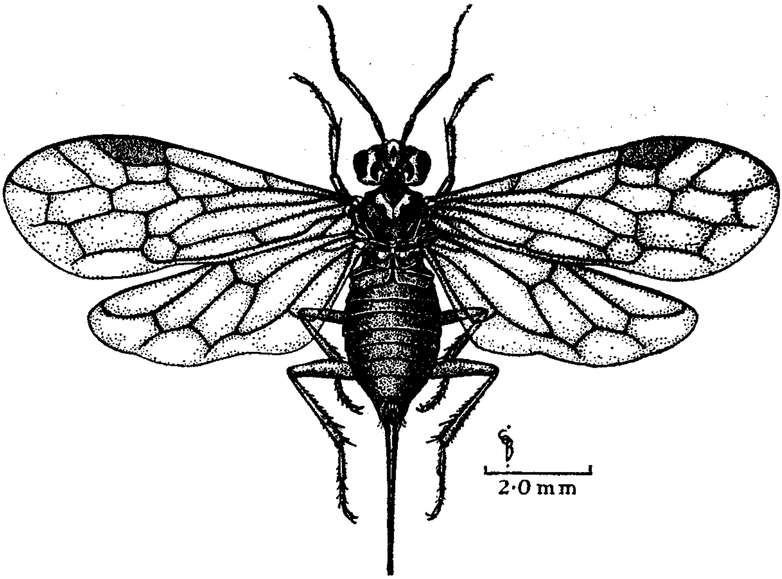
72 Pronotum fused to the mesonotum. Gastral tergite 2 with a lateral felt-line.... ....Fam. MUTILLIDAE

— Pronotum separate from mesonotum. Gastral tergite 2 without a lateral felt-line ....Fam. TIPHIIDAE

RELATIONSHIPS AMONGST THE FAMILIES OF HYMENOPTERA

Very few precise ideas on the phylogeny of the Hymenoptera can as yet be put forward. Clearly the Symphyta include the most primitive living types and amongst them the XYELIDAE and the other Orthandria show ancestral features. No one family seems to be markedly more primitive than the others. The ORUSSIDAE, and especially the CEPHIDAE, show certain approaches to the Apocrita; in the first family, however, this may be due to convergence.

It is difficult to say even as much as this about the Apocrita. Perhaps on the whole the Ichneumonids are as generalized a group as any but the Chalcids have a much less specialized thorax. There are no grounds for regarding the Braconids as forming a link between the two suborders. In most respects they are more specialized than the Ichneumonids. The TIPHIIDAE probably include the most primitive Aculeates but it seems difficult to draw any hard and fast line between Aculeates and Parasitica. Oeser (1961), basing his views on the structure of the ovipositor, would separate out the Aculeata *s.s.* with abdominal segment 7 strongly retracted and the Parasitica (Terebrantes) with it exposed. The Bethyloidea, though Aculeata *s.l.*, are on a separate line from the other superfamilies. It may be noted that some authors consider that the Sphecoids and Apoids might well be united; many would maintain a superfamily FORMICOIDEA, though primitive ants are very like some Tiphiids in structure. Brothers (1975) has put forward new views on the phylogeny of the Aculeata but these are not yet generally accepted.



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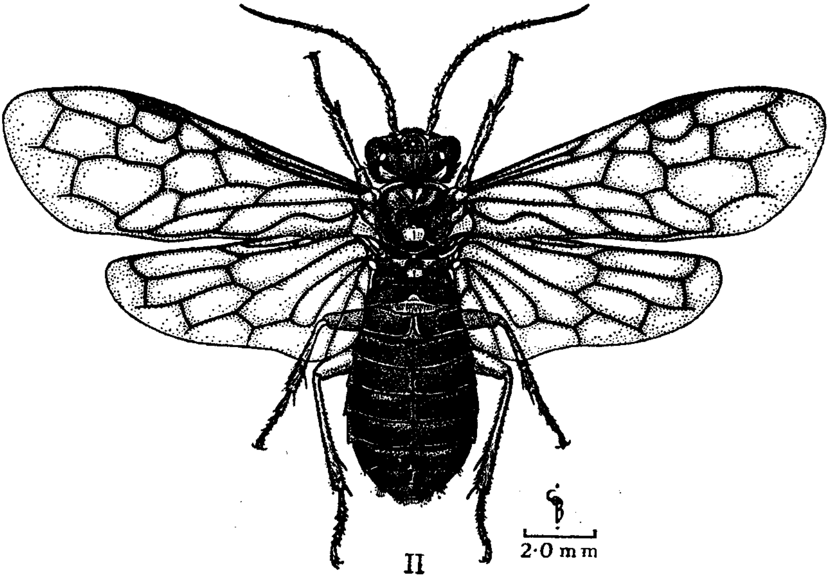
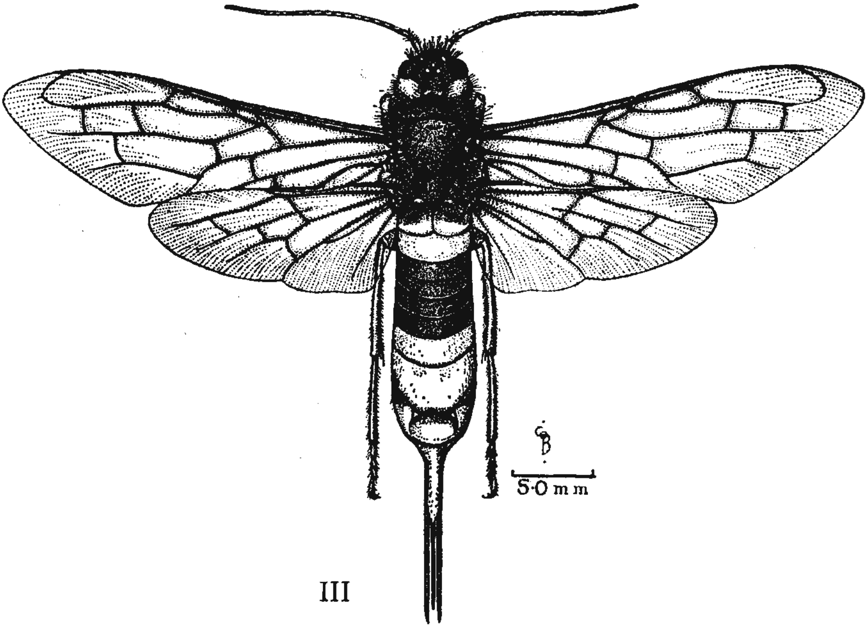


II

FIG. I. *Xyela julii* (Bréb.) ♀ (Xyelidae).
FIG. II. *Pamphilius sylvaticus* (L.) ♀ (Pamphiliidae).



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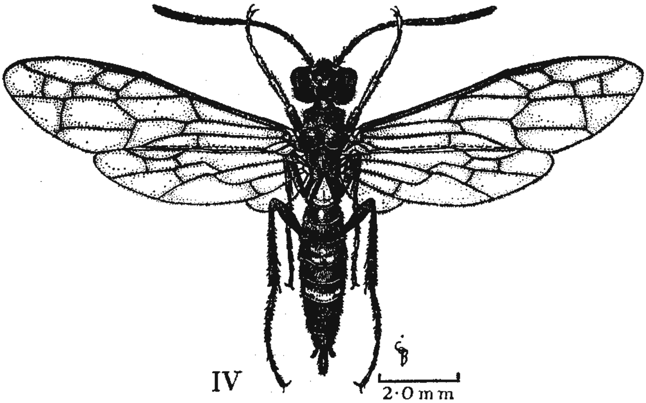

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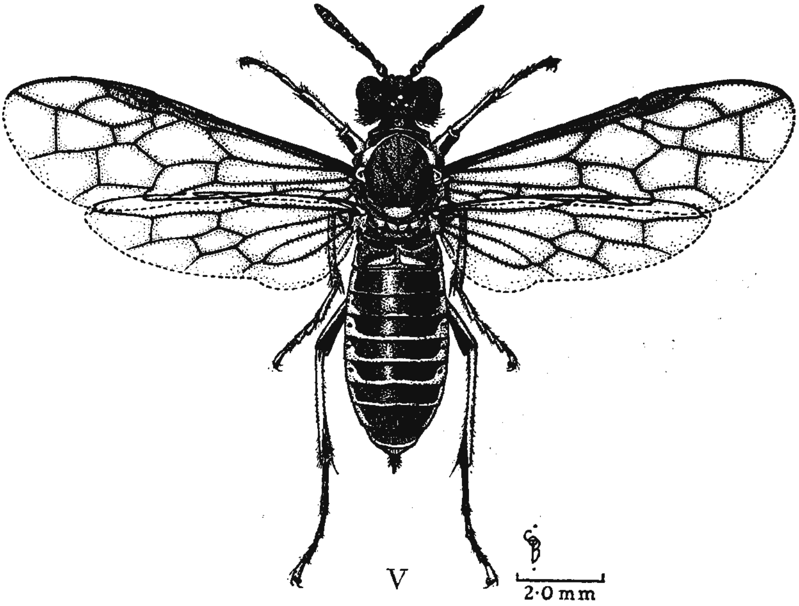
Fig. III. *Urocerus gigas* (L.) ♀ (Siricidae).
Fig. IV. *Cephus pygmaeus* (L.) ♀ (Cephidae).



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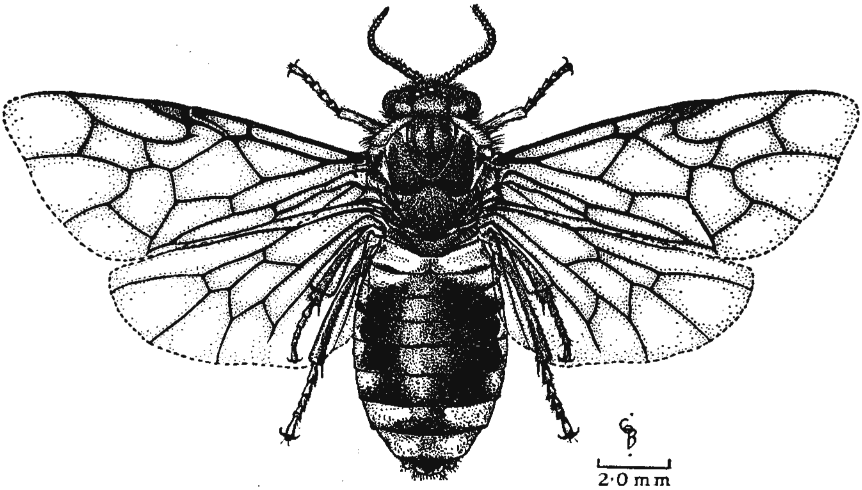

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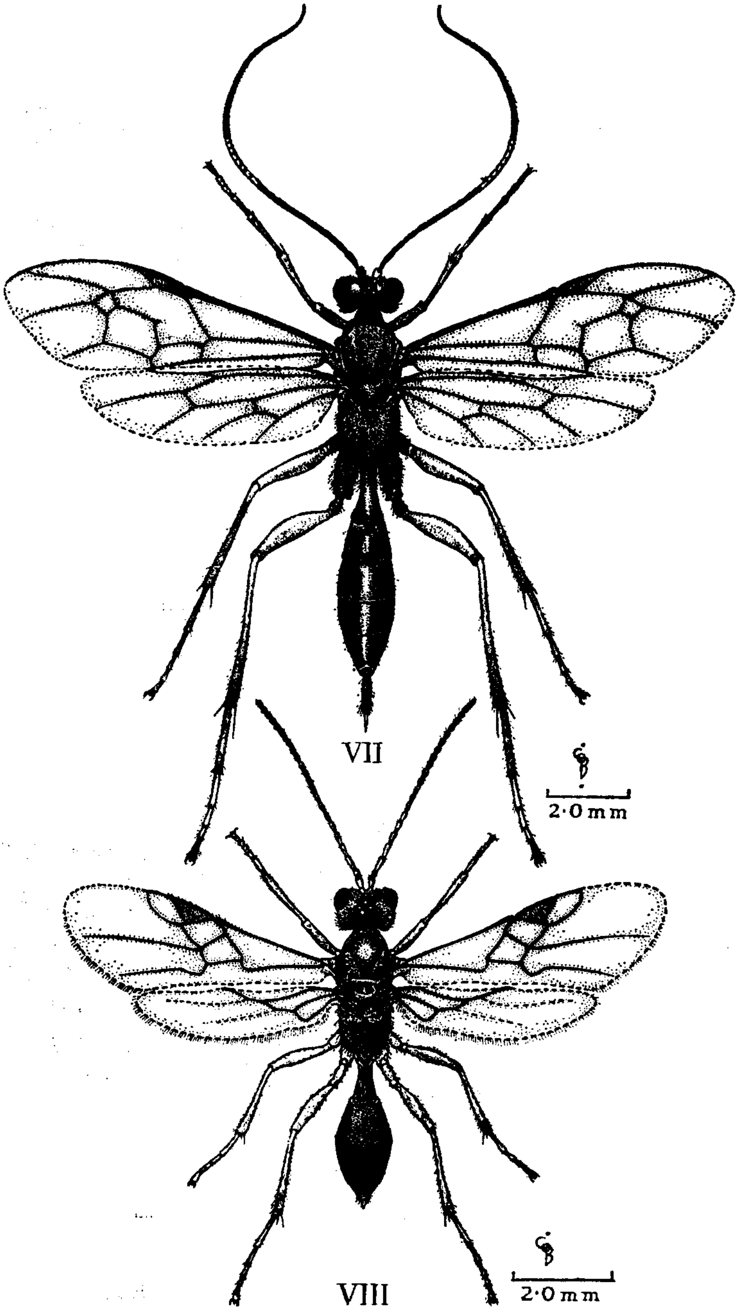
FIG. V. *Tenthredo arcuata* Först. ♀ (Tenthredinidae).
FIG. VI. *Diprion pini* (L.) ♀ (Diprionidae).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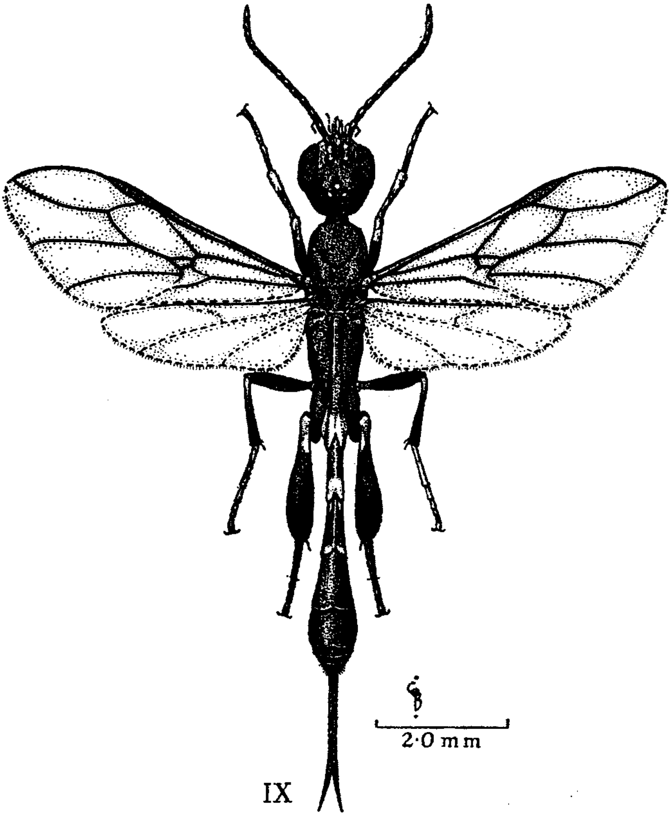
VIII

Fig. VII. *Exetastes atrator* (Forster) ♀ (Ichneumonidae).
Fig. VIII. *Leiophron pallipes* (Curt.) ♀ (Braconidae).



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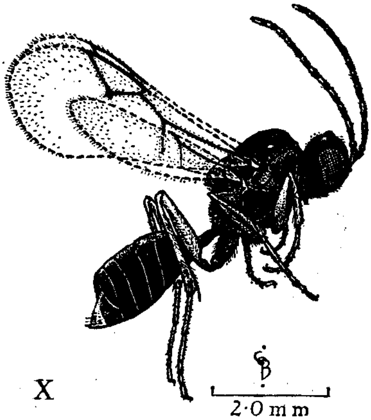
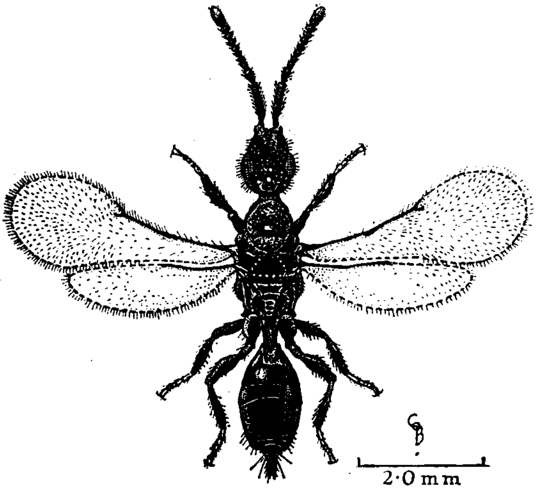


X

FIG. IX. *Gasteruption assectator* (L.) ♀ (Gasteruptiidae).
FIG. X. *Anacharis ensifera* Walk. ♀ (Figitidae).



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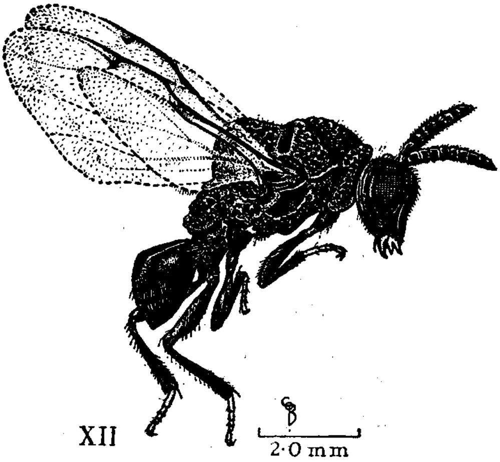

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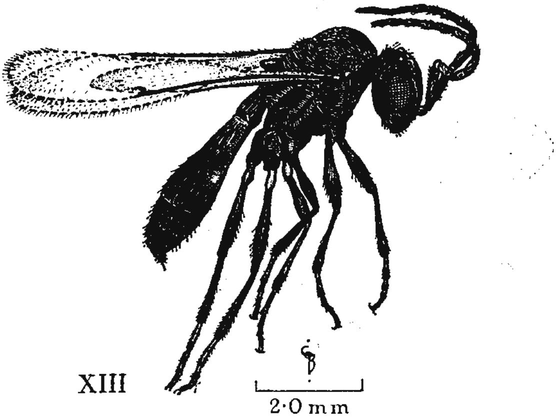
Fig. XI. *Spalangia nigra* Latr. ♀ (Pteromalidae).
Fig. XII. *Perilampus aeneus* (Rossi) ♀ (Perilampidae).



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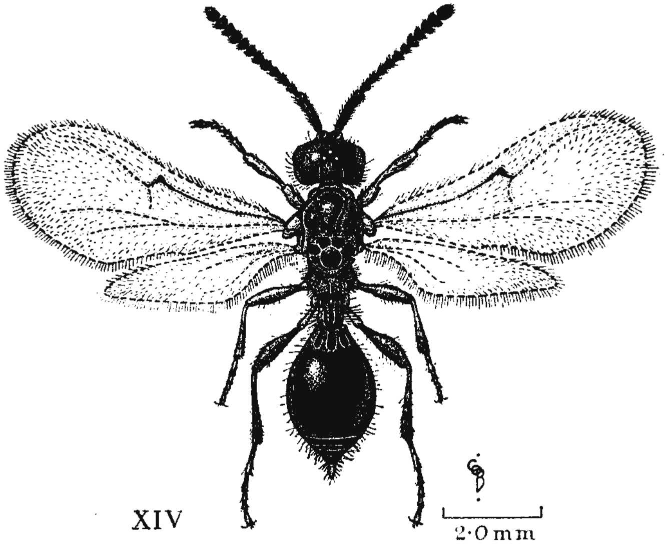
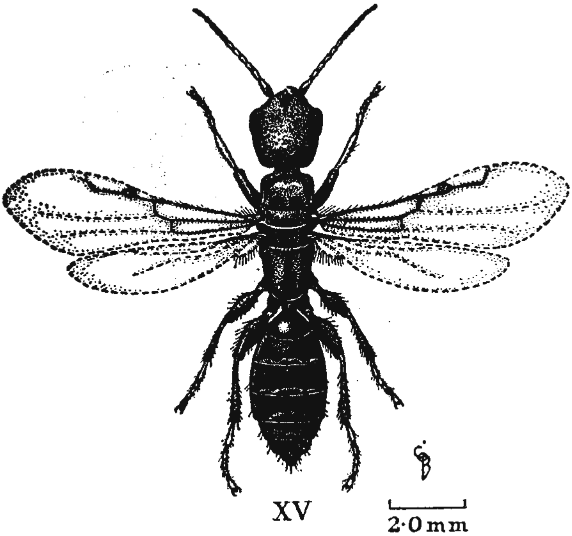


XIV

FIG. XIII. *Hoplogryon elatior* (Hal. *in* Curt.) ♂ (Scelionidae).
FIG. XIV. *Aneurhynchus ruficornis* Thoms. ♀ (Diapriidae).



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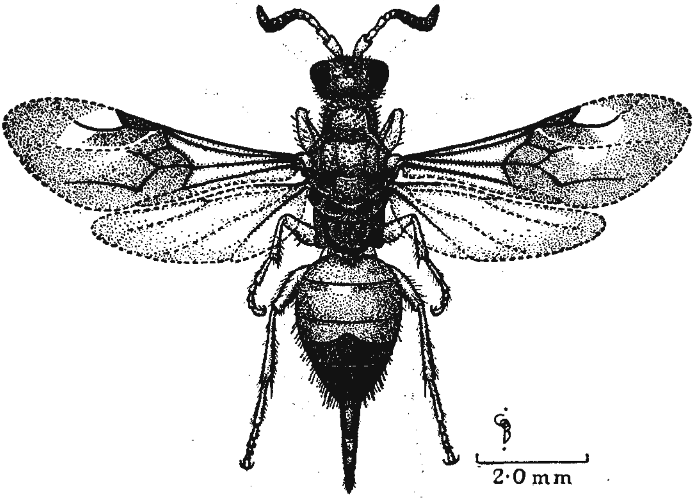
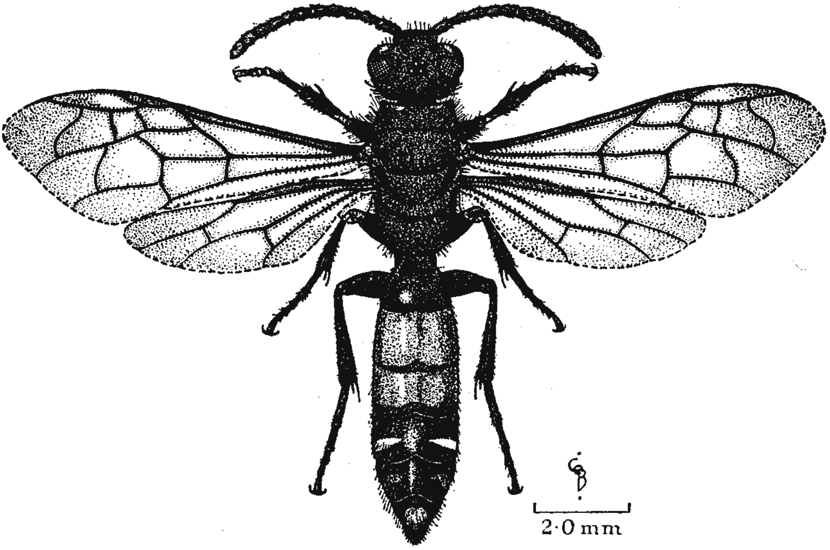


XVI

FIG. XV. *Bethylus cephalotes* (Först.) ♀ (Bethylidae).
FIG. XVI. *Cleptes semiaurata* (L.) ♀ (Chrysididae, Cleptinae).



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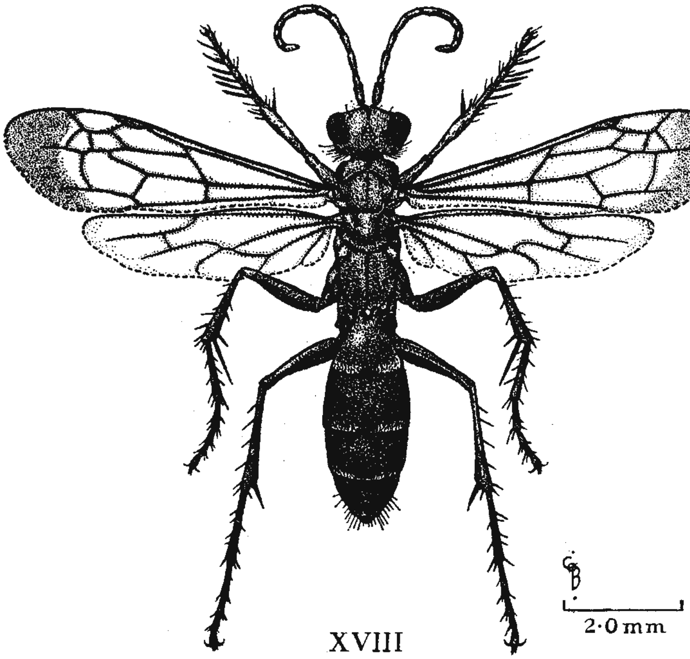
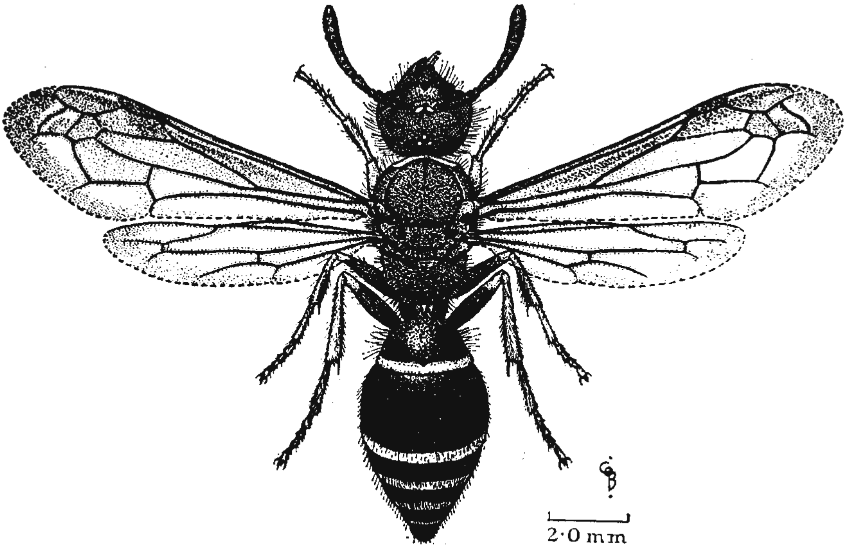


XVIII

FIG. XVII. *Sapyga quinquepunctata* (Fab.) ♀ (Sapygidae).
FIG. XVIII. *Pompilus cinereus* (Fab.) ♀ (Pompilidae).



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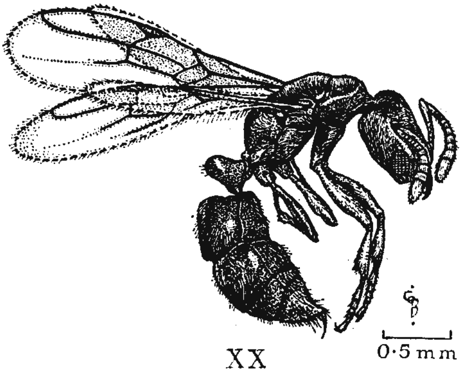
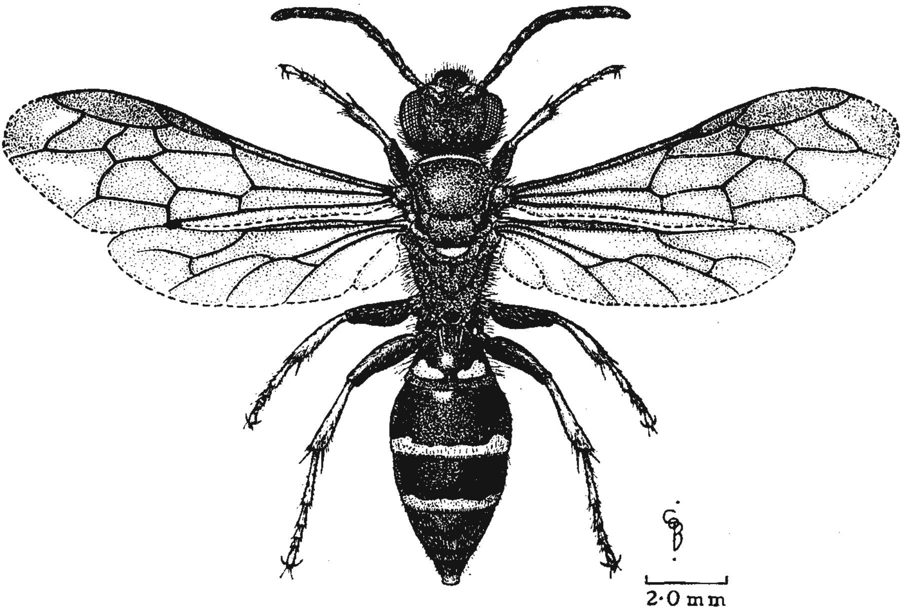


XX

FIG. XIX. *Odynerus spinipes* (L.) ♀ (Eumenidae).
FIG. XX. *Hypoponera punctatissima* Roger ♀ (Formicidae).



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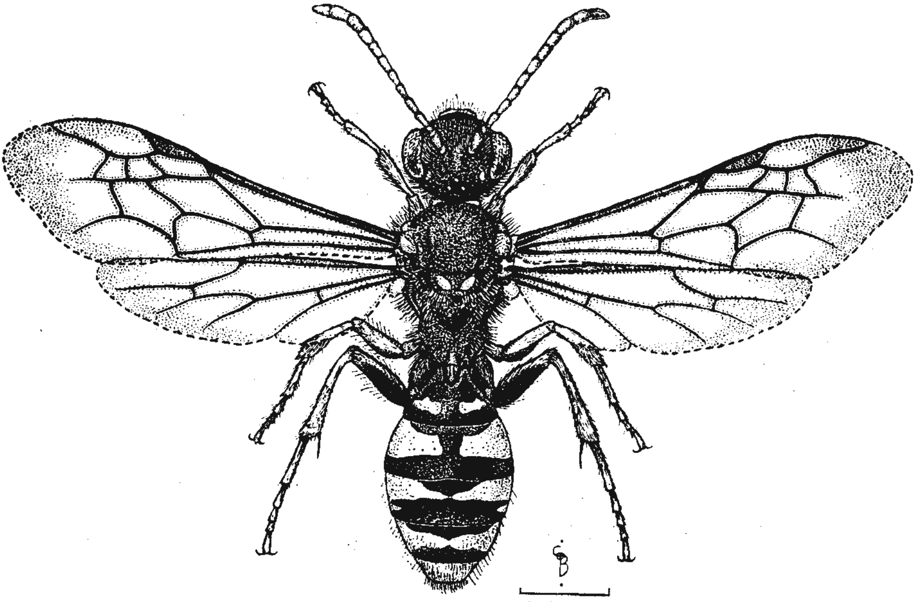

XXII

FIG. XXI. *Argogorytes mystaceus* (L.) ♀ (Sphecidae).
FIG. XXII. *Nomada marshamella* (Kby) ♀ (Apidae).

LITERATURE ON BRITISH HYMENOPTERA

In this series of Handbooks, Benson (1951–58) has dealt with the British Symphyta in three parts. The following parts have appeared on the Parasitica: Askew (1968), Chalcidoidea, Elasmidae & Eulophidae (Elachertinae, Eulophinae, Euderinae); Eady & Quinlan (1963), Cynipoidea, key to the families and subfamilies, Cynipinae (including galls); Ferrière & Kerrich (1958), Chalcidoidea, keys to the families and to Agaontidae, Leucospidae, Chalcididae, Eucharitidae, Perilampidae, Cleonymidae, Thysanidae; Nixon (1957), Proctotrupoidea, Diapriidae (Belytinae); Perkins (1959–60), Ichneumonoidea, Ichneumonidae, keys to subfamilies and Ichneumonidae (Ichneumoninae, Alomyinae, Agriotypinae, Lycoriinae). Graham (1969) has published keys to Chalcidoidea, Pteromalidae of northwestern Europe. In the Aculeata, Bolton & Collingwood (1975) have dealt with the British ants, and Perkins (1976) the Dryinids and Bethylids.

The only other works which are sufficiently up-to-date are Crosskey (1951) on the Evanioidea; Richards (1939) on the Bethylidae, Embolemidae and Dryinidae (a short supplement has been published, Richards (1948), but few new species have been added); and Nixon on the Proctotrupidae (1938). None of the older works, such as Morley on the Ichneumonidae or even Donisthorpe on the Formicidae, is now reliable without the use of supplementary literature. There are a few important papers dealing with large genera or tribes, such as Beirne (1941) on the Diplazonini and Nixon (1943–45) on the Braconidae (Dacnusini). Nixon (1972, 1973, 1974, 1976) has completed a revision of the large Braconid genus *Apanteles*. Most British Hymenopterists have made extensive use of Schmiedeknecht (1930), which contains a great deal of information.

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TERMS AND ABBREVIATIONS

(a) General

(b) Wing-veins and cells

The works using the terms synonymized are listed on p. 35

(1) Forewing veins

Areal ×*-vein:* 1st = 2 *cu–a*, 2nd = Cu_{1b}
Basal: $Rs + M$ or M. Upper = $Rs + M$, lower = *cu–a*
Brachial: 1*A*
Brachial ×*-vein:* 1 *cu–a*
Clavus: Mainly 2*r* (Chalcidoids)
Costa: C or $C + Sc + R$ in some Ichneumonids and Braconids
Cubital: M (Symphyta); $M + Cu_1$ (Schmiedeknecht for Parasitica); $Rs + M$ proximally and M distally (Donisthorpe, Marshall, Saunders); distal part of M (Kieffer)
Cubital ×*-vein:* (Symphyta). 1st = *Rs*, 2nd = 2*r–m*, 3rd = 3*r–m*
Cubital, external: M (Morley)

Cubital, internal: $1m$–$cu + Rs + M$ (Morley)
Disco-cubitalis: $1m$–$cu + Rs + M$ (Schmiedeknecht, Ichneumonidae)
Discoidal: $Rs + M$
Humeral: $2 + 3A$
Intercostal: Sc
Intercostal ×*-vein:* Sc_2
Lanceolate cell ×*-vein:* cv
Marginal: 1st part R_1 (Chalcidoids) or 2_r+Rs (Aculeata, Saunders)
Medial: $M + Cu_1$; or Cu_1 (Morley); or 1st part $= M + Cu_1$, 2nd part $= Cu_1$ (Donisthorpe)
Medial ×*-vein:* 1st $= 1m$–cu (Symphyta, Formicidae); $Cu_1 + Cu_{1b}$ (Morley, Ichneumonidae); 2nd $= 2m$–cu
Metacarp: R_1 distal to pterostigma
Nervulus: Cu–a
Nervus parallelus: Cu_{1a}
Parastigma: Thickened part of R_1 before pterostigma
Posterior: $1A$ (Morley, Saunders); Cu_{1a} (Marshall)
Postmarginal: R_1 (Chalcidoids)
Radial: $1r + Rs$ or $2r + Rs$ (Symphyta); $2r + Rs$ (Apocrita). 1st abscissa $= 2r + Rs$ (Ichneumonidae) or $2r$ (Braconidae). 2nd and 3rd abscissae = parts of Rs
Radial ×*-vein:* $2r$ (Symphyta)
Ramellus: Stub of $Rs + M$ (Ichneumonidae)
Recurrent: $2m$–cu (Schmiedeknecht, Ichneumonidae); or 1st $= 1\mathrm{M}$–cu, 2nd $= 2m$–cu (Aculeata)
Spurius: Anterior $= M$. Posterior $= Cu_{1a}$ (Schmiedeknecht, Ichneumonidae).
Stigmal: Mainly $2r$ (Chalcidoids)
Subcosta: $Sc + R$
Submarginal: $Sc + R$ (Chalcidoids)
Transverso-medialis: Cu–a (Formicidae)

(2) Forewing cells

Anal: Cu_{1a} (Morley); $1A$ (Marshall)
Apical: 1st $= 3M$, 2nd $= Cu_{1a}$
Appendiculate: Rs_1
Areola: $1Rs$
Basal: 1st (upper) $= R$, 2nd (lower) $= M + Cu_1$, 3rd $= 1A$
Brachialis: Cu_{1b}
Costal: C (Formicidae); $Sc + R$ (Marshall)
Cubital: 1st $= 1R_1$ (most Symphyta), or $1 + 2R_1 + 1M$ (Ichneumonidae), or $1 + 2R_1$ (most Apocrita). 2nd $= 1Rs$. 3rd $= 2Rs$ or $2 + 3Rs$ (Ichneumonidae). 4th $= 3Rs$ (Symphyta)
Discoidal: $1M$ (Braconidae, Formicidae). 1st $= 1M$ (most Aculeata, Bethylids, Braconids, Saunders and Marshall); or $2M$ (Morley and Schmiedeknecht, Ichneumonids and Braconids). 2nd $= 2M$ (most Aculeata), or Cu_{1b} (Bethylids), or Cu_1 (Marshall, Saunders), or Cu_{1b} (Morley, Schmiedeknecht). 3rd $= 3M$ (Morley, Schmiedeknecht)
Disco-cubital: $1 + 2R_1 + 1M$ (Ichneumonidae)
Lanceolate: $1A$ (Symphyta)
Marginal: $3R_1$
Medial: $M + Cu_1$ (Marshall) or $Sc + R$ (Aculeata)
Posterior: 1st $= 2M$, 2nd $= Cu_{1a}$
Radial: $3R_1$
Subcostal: C
Submarginal: 1st $= 1 + 2R_1$, 2nd $= 1Rs$, 3rd $= 2Rs$
Submedial: $M + Cu_1$

(3) Hind wing veins

Abscissula: Rs
Anal: $1A$
Anterior: R
Anal ×*-vein:* Cu–a

Axillary: $3 + 4A$ (Symphyta); or c–v (Marshall)
Basal: M
Brachial: $1A$ (Symphyta; Schmiedeknecht, Ichneumonidae), or M $+ Cu_1$ (Schmiedeknecht, Braconidae)
Costal: C
Cubital: M (Symphyta); or $M + Cu_1$ (Schmiedeknecht, Ichneumonidae); or R (Schmiedeknecht, Braconidae); or distal part of M (Marshall)
Cubital ×-vein: $3r$–m
Discoidal: M
Humeral: $2A$ (Symphyta); or ? $3A$ (Morley)
Medial: $M + Cu_1$ or $M + Cu_1 + M$
Medial ×-vein: $1m$–cu
Medio-discoidal: Cu_1
Metacarp: R_1
Nervellus: Cu_1 (Morley); or $Cu_1 + cu$–a (Schmiedeknecht)
Nervellus antefurcal: Internal angle between $M + Cu_1$ and Cu_1 obtuse
Nervellus opposite: This angle rectangular
Nervellus postfurcal: This angle acute
Posterior: $1A$
Radial: Rs
Recurrent: $3r$–m (Schmiedeknecht). 1st $= Cu_1 + cu$–a (Morley); 2nd $= 3r$–m (Morley)
Recurrent ×-vein: $1m$–cu
Subcosta: R
Transverso-discoidal: $3r$–m

(4) Hind wing cells

Anal: $1A$ (or DA)
Appendiculate: ? Rs_1
Axillary: PA
Basal: 2nd $= R$, 3rd $= M + Cu_1$
Brachial: C
Costal: C (Morley) or R (Marshall)
Cubital: $1 + 2Rs$ (Symphyta); or Rs (Morley, Marshall)
Discoidal: 1st $= M$, 2nd $= Cu_1$
Medial: $M + Cu_1$ (Marshall). Anterior $= 1 + 2Rs$ (Symphyta). Posterior $= 1M$ (Symphyta)
Pobrachial: $M + Cu_1$
Posterior: M
Praebrachial: R
Radial: R_1

GENERAL INDEX

Superfamilies are not listed unless they contain more than one family.

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