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The Hymenoptera associated with spiders in Europe

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The Hymenoptera known to be obligatory parasitoids or predators of spiders or their eggs in Europe form a rather diverse assemblage. Their biologies are briefly reviewed; known host associations are summarized for each genus; and a key is given to the genera of Hymenoptera (other than Pompilidae) involved.

KEY WORDS: – Hymenoptera – Araneae – parasitoid – parasitoid-biology – identification.

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INTRODUCTION

Several groups of Hymenoptera undergo their larval development by feeding on spiders or their eggs. These range from the parasitoids that develop singly or in small broods by feeding on cocooned spider egg masses (Ichneumonidae: certain Pimplinae and Phygadeuontinae; and Pteromalidae: certain *Pteromalus*) to the tiny and highly specialized parasitoids that develop inside individual eggs of spiders (Scelionidae: Baeini and Idrini); and from external parasitoids of mobile spiders themselves (Ichneumonidae: Polysphinctini) to the behaviourally more complex aculeate groups that provision more-or-less chosen locations or constructed cells with one (Pompilidae) or more (certain genera of Sphecidae) spiders as prey. In almost all cases, the species of Hymenoptera that make use of spiders in these various ways are specialists and use no other host or prey groups.

For some ancestral Hymenoptera, attacking spiders appears to have met with at least modest evolutionary success such that, today, series of closely related genera share essentially similar habits. This is true of the family Pompilidae, the rather specialized tribes Polysphinctini, Idrini and Baeini, and also the genera of Pimplinae and some groups of Phygadeuontinae that develop somewhat atypically by feeding on successive eggs inside spider egg cocoons. The latter habit is also found, however, in occasional species or species groups isolated within phygadeuontine (e.g. *Bathythrix, Gelis*) and pteromalid (*Pteromalus*) genera that otherwise attack different sorts of hosts. Still other isolated species (for example, of the eulophid genus *Pediobius*) may be obligatorily associated with spider egg cocoons as secondary parasitoids; that is, attacking the primary parasitoid, in the present case probably after it has finished feeding. Other Hymenoptera, such as the diapriid genus *Basalys*, have sometimes been reared as parasitoids of Diptera feeding as larvae on spider eggs. The occurrence of obligatory secondary parasitism in spider egg cocoons may indicate a fairly long standing and stable primary relationship between parasitoids and this rich source of food, as has been suggested from a consideration of the structure and function of egg sacs themselves (Austin, 1985).

Townes & Townes (1960: 216–219) and Townes (1969: 96–98) trace the evolution of the Polysphinctini (parasitizing mobile spiders) from ancestral habits of attacking spider egg cocoons, in particular those that are in well-defined nests guarded by the parent spider. Habits transitional to those of Polysphinctini are said to be present in extant pimpline genera such as *Clistopyga* and *Zaglyptus*. These include attack on the guarding spider, sometimes before it has laid its eggs, and development on both adult and eggs (Nielson, 1935a), as well as consumption of spiderlings within the egg cocoon rather than the eggs themselves (Bignell, 1898). These suppositions are based on somewhat limited observations, however, and a careful re-investigation of the biology of *Zaglyptus* and especially *Clistopyga* would be most valuable. Detailed observations on the host-stinging and oviposition habits of adult Polysphinctini, which have several morphological peculiarities such as their strongly tapered ovipositors and enlarged 5th tarsal segments and pulvilli, would also be of great interest, especially as the available accounts (Bignell, 1898; Nielsen, 1923) are somewhat different and, in any case, rather incomplete. Polysphinctini are remarkable in being the only Pimplinae known to allow the host some further development

after being attacked, and also for the extreme specialization of their larvae. In addition to ventral protuberances by means of which the larvae fix themselves to a caked saddle of their progressively accumulated exuviae on the host integument (Nielsen, 1923), polysphinctine larvae in their final instars develop more-or-less paired, wart-like dorsal protuberances on several consecutive central body segments, each retractile and furnished with outwards-projecting hooks. These structures differ according to genus (Nielsen, 1923, 1928, 1935a, 1937) and are used by the larva first to grip the silk spun by the host as the parasitoid larva releases its hold on the host itself to finish its feeding, and then to move rather easily among strands of the host's silk as it constructs its cocoon. Final instar larvae of the genera *Zaglyptus* (Nielsen, 1923, 1935a) and *Clistopyga* (Nielsen, 1929) are furnished with broadly similar hook-bearing warts, although *Tromatobia,* which similarly feeds in spider egg cocoons but is arguably more primitive, has less elaborate structures bearing only unhooked spines (Nielsen, 1923). In all cases these structures seem to aid movement and orientation via the host's silk during cocoon formation, albeit in slightly different ways.

Since the last serious attempt to summarize information on parasitism of European spiders (Bristowe, 1941), there has been considerable progress in the taxonomy of the parasitoids involved, especially at the generic level. Generic names of parasitoids used in Bristowe's day often had less clear meanings than in their current restricted senses, and the specific names he gives were gleaned from many sources, some more likely to be reliable than others. Indeed, the difficulty of interpreting much of what is in the literature may be why Foelix (1982), in an otherwise full and thorough account of the biology of spiders, chose to devote only about two pages to the barest outline of Hymenoptera attacking spiders, only a few lines of which referred to parasitoids. However, there is now a sufficiently firm taxonomic base for it to be possible to collect and record information on host–parasitoid associations with more accuracy and purpose, and preliminary results have certainly indicated that most parasitoids of spiders or their eggs can be expected to have discernible host ranges that may be characterized, or restricted, partly by the habitat in which they search for hosts and partly by host taxonomic groupings. The aculeate Hymenoptera that utilize spiders appear to be particularly strongly habitat-specialized as opposed to selecting taxonomically limited groups of spiders, although, of course, in a particular habitat they may regularly encounter only a narrow range of potential prey species. Nevertheless, comparatively few hard data on prey associations have been collected, and undoubtedly much remains to be learned.

One general aim of the present paper is to help and encourage arachnologists to look at parasitism of spiders and their eggs in the course of their fieldwork. To this end we present a section detailing methods and a key which includes all the genera of European Hymenoptera known to contain species that are parasitoids of spiders or their eggs. That biological and host-range information which seems to be reasonably clear-cut is summarized for each genus. Collecting together literature records of parasitism and taking their validity on trust always tends to undermine the really firm, first-hand, evidence available, by adding to it a greater percentage of erroneous records. To guard against this, we have examined available host records critically, discarding several that seem to have been the result of erroneous assumptions and judging that many others are too ambiguous or vague to be usefully included. To a large extent we have

depended on recent fieldwork and reviewing the adult parasitoids preserved in the collections of the British Museum (Natural History) (BMNH) and the National Museums of Scotland (NMS): even then, much of the preserved material has little relevant data, and in only comparatively few cases can host-range information be summarized with much confidence.

REARING AND RECORDING METHODS

The somewhat scanty level of information on particular parasitoids that we are able to present here would be added to enormously if people collecting or studying spiders in the field could be persuaded to cooperate by sending parasitoids reared from spiders or their egg sacs to us. Only then will it be possible to improve substantially on this preliminary treatment. Undoubtedly several species and/or genera not yet known to be associated with spiders might be expected to crop up; Bristowe (1941: 342) mentions finding parasitoid larvae on three spider familes (Gnaphosidae (= Drassidae), Lycosidae and Salticidae) from which we have not seen Polysphinctini reared; and with accurate data, the true host associations of all species will become clearer. We hope to be in a position to define host associations at both specific and generic levels in future publications.

For reared material, ideal data would include name and stage of host, date and place of collection, date of adult parasitoid emergence and details of brood size, and, particularly, a clear indication of the ecological situation or microhabitat from which the parasitized material was collected. If quantitative data are available they should also be noted. Mobile spiders found bearing hymenopterous larvae (Polysphinctini, or just conceivably Pompilidae) will normally need feeding if the adult is to be reared. For parasitoids of egg cocoons, especially, it may not be possible to give the name of the host with certainty, and for all such cases it is always best to express the maximum doubt. Host family names are better than no names at all but, even if 'spider egg cocoon' is all that can be given, the microhabitat information will still be valuable and, indeed, may be crucial from the parasite's point of view. If several identical egg sacs are collected at the same time it is, nevertheless, important that they are kept singly if possible, so that each parasitized sac can be unambiguously associated with the parasitoid(s) that emerge; these host remains should always be individually preserved along with the respective adult parasitoids and their cocoons.

Parasitoids reared in cramped airtight containers are much more liable to succumb through disease and mould formation than those reared under more spacious and less humid conditions: large corked tubes, for example, are usually much better than small plastic stoppered ones. When adult parasitoids emerge they are best left to die naturally in large clean containers, and they must then be allowed to dry out to prevent the mould formation that will certainly take place if they are kept tightly stoppered in small containers. They can be sent through the post dry, in small protected tubes, but need to be loosely wedged and fully isolated, using firm plugs of cotton wool, from anything mobile (e.g. egg sacs, data slips, etc) that would otherwise fragment them as they are shaken in transit. Alternatively, adult parasitoids can be killed (preferably some days after emergence) by dropping them into 70% alcohol (preferably free from

glycerine), and may conveniently be examined or posted in that medium. Please send all parasitoids to Dr M. R. Shaw, Department of Natural History, National Museums of Scotland, Chambers Street, Edinburgh EH1 1JF. First class postage is essential if larvae on living spiders are sent.

SYNOPTIC CLASSIFICATION OF THE GENERA OF HYMENOPTERA ASSOCIATED WITH SPIDERS IN EUROPE

Alternative names used for these genera in earlier publications are given in parentheses. These names include those now regarded as synonyms and misidentifications, as well as those no longer applied to the species concerned because of improvements in classification.

Superfamily Ichneumonoidea
- Family Ichneumonidae
  - Subfamily Pimplinae
    - Tribe Ephialtini
      - *Tromatobia*
      - *Zaglyptus*
      - *Clistopyga*
    - Tribe Polysphinctini
      - *Dreisbachia (Laufeia)*
      - *Schizopyga*
      - *Zabrachypus*
      - *Acrodactyla (Colpomeria)*
      - *Piogaster*
      - *Oxyrrhexis*
      - *Polysphincta*
      - *Sinarachna*
      - *Zatypota*
  - Subfamily Phygadeuontinae
    - Tribe Phygadeuontini
      - *Hemiteles (Ocymorus)*
      - *Aclastus (Gnypetomorpha)*
      - *Polyaulon (Thaumatotypus, Thaumatotypidea)*
      - *Gelis (Pezomachus)*
      - *Agasthenes (Hemiteles)*
      - *Gnypetomorpha*
      - *Bathythrix (Ischnurgops)*
    - Tribe Mesostenini
      - *Hidryta*
      - *Idiolispa*
      - *Trychosis (Goniocryptus)*

Superfamily Chalcidoidea
- Family Pteromalidae
  - Subfamily Pteromalinae
    - *Pteromalus (Habrocytus)*
- Family Eulophidae
  - Subfamily Entedontinae
    - *Pediobius (Entedon)*

Superfamily Proctotrupoidea
  Family Diapriidae
    Subfamily Diapriinae
      Tribe Diapriini
        Basalys
  Family Scelionidae
    Subfamily Scelioninae
      Tribe Idrini
        Idris (Acolus)
        Ceratobaeus
      Tribe Baeini
        Baeus
Superfamily Pompiloidea
  Family Pompilidae
Superfamily Sphecoidea
  Family Sphecidae
    Subfamily Sphecinae
      Tribe Sceliphronini
        Chalybion
        Sceliphron (Pelopoeus)
    Subfamily Larrinae
      Tribe Miscophini
        Miscophus
      Tribe Trypoxylonini
        Trypoxylon (Apius)

BIOLOGY AND HOST ASSOCIATIONS

This section has the same arrangement as the synoptic classification above. The names and higher classification of spiders follow Locket, Millidge & Merrett (1974).

Ichneumonidae—Pimplinae

The western Palaearctic Pimplinae have been catalogued by Oehlke (1967) and by Aubert (1969), and together these provide a fairly comprehensive guide to the literature. Keys to species are given by Kasparyan (1981 (in Russian)). Earlier keys to European Pimplinae, at least those associated with spiders, are of very limited value. A handbook to British Pimplinae is in preparation (Fitton, Shaw & Gauld).

Tromatobia

This genus is Holarctic and Neotropic in distribution. Five species are currently recognized in Europe. All are (normally gregarious) parasitoids of spider egg cocoons, and there are many published host records for the commoner species. These chiefly attack araneid cocoons—though not exclusively so, as has been claimed by some authors. In contrast, the rarer species are very poorly known. The ovipositing female appears not to attack spiders guarding their eggs: at any rate, *Tromatobia* species have sometimes been

reared from cocoons under active guard, although detailed observations on interactions at the time of oviposition have not been recorded. We have seen reared material of *T. oculatoria* (Fabricius) from egg cocoons of *Araneus diadematus* Clerck, *A. ?cucurbitinus* Clerck, *Zygiella x-notata* (Clerck), *Philodromus aureolus* (Clerck), *P. cespitum* (Walckenaer) and *Gongylidium rufipes* (Sundevall); and specimens of *T. variabilis* (Holmgren) from *Araneus redii* Scopoli. We have kept egg cocoons of *A. diadematus* and *Z. x-notata* parasitized by *T. oculatoria* under observation during the winter and found that, at least when oviposition takes place late in the autumn, the larvae feed through the winter, chiefly in very early spring, becoming fully fed and constructing their cocoons by late March or early April. In large cocoons, such as those of *A. diadematus*, a proportion of eggs may be left unconsumed and these produce spiderlings in due course. Nielsen (1923, 1937) gives biological information on *T. oculatoria* and *T. ovivora* (Boheman).

Zaglyptus

This small genus has a worldwide distribution and three species occur in Europe. Nielsen (1935a) gives an account of the biology of *Z. varipes* (Gravenhorst) which he found commonly in the egg nests of *Cheiracanthium erraticum* (Walckenaer) and less commonly in those of *Sitticus floricola* (Koch), both among old *Phragmites* flower heads. The female spider is stung to death and normally about two to four (exceptionally up to eight) eggs are laid in the nest. The resulting larvae develop on both the eggs and the dead adult, and can do so even if the female spider had not laid her eggs before being attacked. We have seen material of *Z. varipes* reared from nests of *Clubiona reclusa* (Pickard-Cambridge) in *Rubus* and *Rumex* leaves. To judge from literature records and the circumstances in which adults have been collected, the other British species, *Z. multicolor* (Gravenhorst), may be more associated with arboreal hosts, but we have seen broods labelled as being reared from nests of *Enoplognatha ovata* (Clerck) in curled *Rubus* leaves.

Clistopyga

Clistopyga is a very widely distributed genus, though absent from Australia. There are four species in Europe. Very little biological information on this genus is available: Nielsen (1929) records finding two larvae of *C. incitator* (Fabricius) in a single egg cocoon of *Segestria senoculata* (Linnaeus) in a hole in a stone wall, and from this and the morphology of the adult it has not unreasonably been presumed that the hosts are egg cocoons hidden away in crevices. Adults of *C. incitator* are often seen on tree trunks, where one (abnormally small) female has been observed repeatedly probing, and completely disappearing backwards into, the spinnings of *Salticus zebraneus* (Koch) in chinks, though eggs of neither parasitoid nor spider could afterwards be found. We can also record once rearing *C. rufator* Holmgren, from one of two cocoons found in an egg cocoon of *Clubiona juvenis* Simon in a curled dead *Phragmites* leaf. The female spider was found dead in the same retreat but seemed not to have been fed upon. It should not necessarily be assumed that the ovipositing female *C. rufator* had killed it because female *Clubiona* species seem often to waste away beside their eggs, especially if the latter fail. Indeed, the structure of the ovipositor of *Clistopyga* suggests that attendant spiders may not be stung.

Dreisbachia

A small genus with species widely scattered around the world. One, *D. pictifrons* (Thomson) (= *bridgmani* (Bignell)), occurs in Europe. Several specimens have been reared from immature *Clubiona* species in damp bushy places: interestingly (for adults have 'primitive' wing-venation more typical of their presumed ancestry), the egg is placed on the cephalothorax, in a dorsolateral position about level with the second or third pair of legs. Thus oviposition on the cephalothorax may be a primitive feature in Polysphinctini—the only other European genus known to have this habit is *Schizopyga*. The frail cocoons of the two genera are similar, too, in being relatively unspecialized and made in the host's retreat. The type specimen of *Pimpla bridgmani* was supposedly reared from *Drassodes lapidosus* (Walckenaer), and this single rearing appears to have given rise to many citations in the literature. However, the type preserved in the BMNH is without host remains and the possibility that the host was a misidentified clubionid cannot be ruled out.

Schizopyga

It is easy to regard *Schizopyga* as a primitive polysphinctine genus on the basis of Nielsen's (1935a) biological observations on *S. podagrica* (Gravenhorst) (which name, however, has often been misapplied within *Schizopyga*) as a parasitoid of *Cheiracanthium erraticum* (Walckenaer) in July/August. Thus the hosts are nest makers and seem to be attacked only in their nests. The adult parasitoid bites through the silk to oviposit on the spider (frequently a mature female) within, laying an egg more or less dorsally at the posterior of the cephalothorax, near to the petiole. However, immature spiders in nests are also parasitized. *Schizopyga* is a relatively small Holarctic genus with four species in Europe. We have seen reared specimens of two species: *S. circulator* (Panzer) from *Clubiona terrestris* Westring, *C. neglecta* Pickard-Cambridge and *C. trivialis* Koch; and *S. frigida* Cresson from *C. terrestris* and *C. lutescens* Westring. Several of the host individuals involved have been males (Nielsen's (1935a) comment that practically all parasitized hosts are females may have been a result of his investigating chiefly the nests made by mature females for egg-laying), and the winter is passed by *S. frigida*, at least, on mobile often sub-adult hosts which feed actively in spring.

Zabrachypus

A small Holarctic genus with one species occurring in Europe. There are no host records.

Acrodactyla

Acrodactyla is a genus of moderate size found in the Holarctic and through the Oriental region to Australia. Six species occur in Europe. *Acrodactyla degener* (Haliday) is (in Britain) an abundant parasitoid of certain linyphiids, particularly in woodland but occuring also in open places such as field crops. We have seen reared material from hosts confidently identified as *Lepthyphantes tenuis* (Blackwell), *L. zimmermanni* Bertkau, *L. minutus* (Blackwell), *L. mengei* Kulczynski, *Kaestneria dorsalis* (Wider), *Linyphia triangularis* (Clerck) and *L. peltata* Wider, and Nielsen (1923) records observations on this species as a parasite of *L. zimmermanni* (= *zebrinus*) on tree trunks under the name *Polysphincta pallipes* (cf. Nielsen, 1928). We have seen several specimens of

A. quadrisculpta (Gravenhorst) reared from *Tetragnatha* species (see also Nielsen, 1937). *Acrodactyla madida* (Haliday) (= *clypeata* (Holmgren)) lacks the characteristic cocoon structure of the above two *Acrodactyla* species (which is papery and spindle shaped with a square cross section), and also departs from the usual polysphinctine habit of overwintering as a small larva on the host. Instead it overwinters as a prepupa in a tougher and more cylindrical rough brownish cocoon. We have seen several specimens reared from *Meta segmentata* (Clerck) (or possibly *mengei* (Blackwall))—and this host is also recorded by Nielsen (1923)—but also one from a host confidently determined as *Lepthyphantes* sp. and another from ?theridiid sp.

Piogaster

A small genus with three species in Europe, one in Japan and one in California. All are rare in collections and there are no host records. Circumstantial evidence suggests that some, at least, are arboreal.

Oxyrrhexis

The genus includes only one species, *O. carbonator* (Gravenhorst), which has a Holarctic distribution. We have not seen any reared material. There are several hosts recorded in the literature, but the name *carbonator* has been so widely misapplied that only *Steatoda borealis* (Hentz), from which it has been recorded three times in North America (Townes & Townes, 1960), seems credible.

Polysphincta

Most of the pimpline species associated with spiders have at some time been referred to '*Polysphincta*'. The name is now restricted to a rather small group, which is widely distributed in the northern hemisphere and South America. Four species occur in Europe. *Polysphincta tuberosa* Gravenhorst is (in Britain) a fairly common parasitoid of *Araneus* species occurring on trees and bushes. Most of the reared material seen has been from *A. cucurbitinus* Clerck, but we have also seen specimens from *A. quadratus* Clerck and *A. diadematus* Clerck. Nielsen (1923) concluded that the species is bivoltine in Denmark and suggested a well-defined alternation between *A. quadratus* and *A. redii* Scopoli as hosts. Other species of *Polysphincta* are very poorly known, though Nielsen (1923) gives an account of the biology of *P. nielseni* Roman as a parasite of *Cyclosa conica* (Pallas).

Sinarachna

The genus comprises seven species widely distributed in the northern hemisphere, of which four occur in Europe. We have seen several specimens of *S. nigricornis* (Holmgren) reared from *Araneus diadematus* Clerck collected from trees and bushes and a single specimen from '?*Theridion*'. The egg is positioned dorsolaterally on the abdomen, unusually remote from the petiolar region. Nielsen (1928) gives details of the biology of *S. nigricornis* (as *pallipes* var. *nigricornis*), and in the same paper records *S. pallipes* (Holmgren) as a parasite of *Achaearanea lunata* (Clerck). The somewhat aberrant species *S. anomala* (Holmgren) has several times been recorded in the literature from species of *Dictyna*, which is noteworthy in that cribellate spiders do not otherwise seem to be attacked by Polysphinctini (cf. Bristow, 1941: 344).

Zatypota

This is a moderately large genus, almost worldwide in distribution. Four, or possibly five, species occur in Europe, and we have seen reared material of four. In every case the host has been a theridiid: *Z. albicoxa* (Walker) (= *eximia* (Schmiedeknecht)) from *Achaearanea simulans* (Thorell) and *A. lunata* (Clerck); *Z. bohemani* (Holmgren) from *Theridion mystaceum* Koch; *Z. ?discolor* (Holmgren) (= *percontatoria* sensu Kasparyan, 1981) from *T. sisyphium* (Clerck); and *Z. percontatoria* (Müller) (= *gracilis* sensu Kasparyan, 1981) from *T. tinctum* (Walckenaer), *T. varians* Hahn and *T. simile* Koch. Nielsen (1923) gives biological notes for three species.

Ichneumonidae —Phygadeuontinae

Hemiteles

The name *Hemiteles* has traditionally been applied to a large, unnatural assemblage of species. It is now restricted to a very small Holarctic group, all species of which are presumed to parasitize spider egg cocoons. Three European species are recognized and keyed by Horstmann (1974). Published host records exist for two of these but, because of the confused taxonomic history, bare records are particularly difficult to accept. We have reliable records only of *H. similis* (Gmelin), which in Britain is commonly reared from the egg cocoons of *Zygiella x-notata* (Clerck), and perhaps other species, collected from window frames of outbuildings and similar situations. We have seen no material reared from non-spider hosts and consider all such records to be very dubious. The larvae of *H. similis* live gregariously and usually spin their dark cocoons conspicuously visible through the host's silk. Broods seen by us range from three to 13 individuals and include both sexes.

Aclastus

This is a moderately large genus, almost worldwide in distribution. According to Horstmann (1980) the species occur, often in large numbers, in damp areas. They attack linyphiids and amaurobiids. Horstmann (1980) has revised the eleven European species. There are very few published host records. Horstmann (1980) notes that *A. minutus* (Bridgman), which has been recorded from *Erigone arctica* (White) and *Leptorhoptrum robustum* (Westring) (Linyphiidae), is one of the commonest species of Ichneumonidae on the North Sea coast of Germany. We have seen only one species reared from reliably named host material: *A. micator* (Gravenhorst) from egg sacs of *Amaurobius fenestralis* (Ström) (Amaurobiidae) found under bark of *Ulmus*. Broods consisted of from one to five individuals, including both sexes, and in the case of one brood of two about eight spiderlings also hatched.

Polyaulon

A small genus occurring in Europe and North America. Females of some species are wingless. There is only one host record for the genus: the single British species, *P. paradoxus* (Zetterstedt), has been once reared from unidentified spider eggs (Bristowe, 1941: 351; Kerrich, 1942). Its small round cocoons (or possibly those of its host?) have also been found beneath rotten logs, often hanging on rootlets (Evans, 1969).

Gelis

This is a large Holarctic genus. Some species are fully-winged but many have ant-like micropterous and wingless forms. A lot of taxonomic problems remain to be solved and at present there is no really satisfactory way of identifying species. Hosts are small cocoons or cocoon-like structures of a wide range of insect groups and also the egg sacs of spiders. The species associated with spider egg cocoons appear to attack them exclusively. Some are solitary and others are gregarious. Among the reared material we have seen, we are reasonably confident of the identity of the following *Gelis* species: *G. fasciitincta* (Dalla Torre) from *Agroeca* species (probably *proxima* (Pickard-Cambridge)); *G. melanocephalus* (Schrank) from *Agroeca (brunnea* (Blackwell) or *proxima*) and *Araneus redii* Scopoli; *G. zonatus* (Foerster) from *Agroeca (brunnea* or *proxima*); *G. micrurus* (Foerster) from *Pardosa pullata* (Clerck), *P. nigriceps* (Thorell) and *P. lugubris* (Walckenaer); *G. bicolor* (Villers) from *Theridion pallens* Blackwall and *Steatoda albomaculata* (Degeer); *G. rugifer* (Thomson) from *Clubiona reclusa* Pickard-Cambridge; *G. picipes* (Gravenhorst) from *Zelotes* species; *G. aquisgranensis* (Foerster) from a gnaphosid; and *G. rufulus* (Foerster) and *G. intermedius* (Foerster) from unidentified egg sacs. In addition, we have seen material of several other species reared from spider egg sacs, including those determined as *Dictyna* species, *Enoplognatha ovata* (Clerck), *Theridion 'denticulatum* (Walckenaer)', *Euophrys frontalis* (Walckenaer), *Ero tuberculata* (Degeer), *Pisaura mirabilis* (Clerck), *Zygiella x-notata* (Clerck), *Araneus cornutus* Clerck and *Tibellus oblongus* (Walckenaer).

Agasthenes

This small genus has been revised by Townes (1983). The single species which occurs in Europe, *A. varitarsus* (Gravenhorst), has been reared from the egg sacs of *Tetragnatha extensa* (Linnaeus) on reeds (Kerrich, 1942; Smith, 1957; both as *Hemiteles stagnalis* (Thomson)).

Gnypetomorpha

The name *Gnypetomorpha* has often been applied incorrectly to *Aclastus*. In its correct sense *Gnypetomorpha* comprises two, possibly three, species which occur in the Palaearctic. The two European species are found in Britain. Two males of *G. obscura* (Bridgman) were reared by Bridgman (1883) from egg bags of a spider found in a rolled-up *Urtica* leaf, protected by the spider herself; one male developed from each bag. *Gnypetomorpha sisyphii* (Verhoeff) was reared from *Theridion sisyphium* (Clerck) (Verhoeff, 1891), and there is also a record (presumably incorrect) from *Apanteles* sp. (Hym., Braconidae) (Hedwig, 1944).

Bathythrix

This is a large genus, almost worldwide in distribution. The 21 European species have been revised recently by Sawoniewicz (1980) who records them as solitary parasites of the cocoons of parasitic wasps, sawflies and beetles, the egg cocoons of spiders and the puparia of hoverflies. One species, *B. fragilis* (Gravenhorst), regularly attacks the egg cocoons of *Agroeca brunnea* (Blackwall) (or perhaps *A. proxima* (Pickard-Cambridge)) and has also been reared from the nests of various sphecid wasps in *Rubus* stems (Danks, 1971). The disparity between these hosts is puzzling because most other *Bathythrix* species appear to

have rather restricted host associations; despite the wide host-range of the genus overall. Danks's and earlier records from aculeate Hymenoptera, and Danks's suggestion that *B. fragilis* as currently recognized might include two species, appear not to have been investigated by Sawoniewicz. We have also seen a single small male *Bathythrix* reared from the egg sac of *Tetragnatha extensa* (Linnaeus) (Smith, 1957, as *Ischnurgops* sp.); it belongs to *B. decipiens* (Gravenhorst), a species which we have seen reared from cocoons of the whirlygig beetle *Gyrinus colymbus* Erichson similarly found exposed on waterside vegetation.

Hidryta

The three European species of this small Holarctic genus are keyed by Horstmann (1984). We have seen material of the only British species, *H. sordida* (Tschek), reared from *Pardosa pullata* (Clerck), and Edgar (1971) has investigated its biology as a parasitoid of *P. lugubris* (Walckenaer). He found it to be bivoltine, developing singly in the egg sacs of both generations of the host and overwintering as a prepupa in one. A Japanese species is known also to be bivoltine and to overwinter in *Pardosa* egg cocoons (Nishida, 1982).

Idiolispa

This is a small Holarctic genus. The probably single European species, *I. analis* (Gravenhorst), occurs as far east as Japan and in North America. *Idiolispa, Hidryta* and *Trychosis* seem to form a natural group, which Townes (1970: 146) says "parasitize egg cocoons of spiders", but the only published host record for *Idiolispa* refers to the moths *Lymantria dispar* (Linnaeus) and *L. monacha* (Linnaeus) (Leonardi, 1928). We regard this record as very dubious, however, and we have seen a reared specimen "ex lycosid cocoon 30.vi.64", but unfortunately with no other data.

Trychosis

Trychosis is a moderately large genus with most species in the Holarctic, but with some in the Oriental and one in the Neotropic regions. The European species have been studied by van Rossem (1966, 1971), who recognized 10 species. Although not all have been reared, it is supposed that spider egg cocoons are attacked exclusively and that records of rearings from Lepidoptera are erroneous. We have reliable host records for the following species: *T. tristator* (Tschek), 14 rearings from *Pisaura mirabilis* (Clerck) and one from *Oxyopes heterophthalmus* (Latreille); and *T. legator* (Thunberg) from *Xysticus ulmi* (Hahn), *Thomisus onustus* Walckenaer and *?Cheiracanthium* sp. In most cases only one parasite emerges from an egg sac. However, a small brood of three males (which have proved impossible to determine to species, in NMS) emerged from a group of cocoons found in a tetrahedrally folded leaf of *Salix aurita,* possibly constructed by a clubionid. Some observations on the biology of *Trychosis* species are reported by Nielsen (1935b).

Pteromalidae

Pteromalus

This large genus has previously been subdivided into two genera, *Pteromalus* and *Habrocytus* (Graham, 1969), but since recombined. We have seen material of

one species, *P. platyphilus* Walker, reared from the egg sacs of *Dictyna arundinacea* (Linnaeus) in Surrey and Aberdeenshire. Other species of Pteromalidae may be more loosely associated with spiders, as explained in the notes given for *Basalys*. The Pteromalidae of north west Europe are monographed by Graham (1969).

Eulophidae

Pediobius

There are more than 40 species of this genus in Europe, revised by Bouček (1965). Two species are associated with spiders: *P. grunini* (Nikolskaya) is known from Czechoslovakia and western Kazakhstan, U.S.S.R.; and *P. brachycerus* (Thomson) is widely distributed throughout Europe, including Britain. Both species are gregarious secondary parasitoids (hyperparasites). We have seen *P. brachycerus* reared from an unidentified ichneumonid in the egg sac of *Araneus cornutus* Clerck; from *Agasthenes varitarsus* in the egg sac of *Tetragnatha extensa* (Linnaeus) (see Smith, 1957); and from the egg sac of an unidentified *Tetragnatha* species, in which it is presumed to have been hyperparasitic. Bouček (1965) records it from a "*Polysphincta*" [?misident.] pupating in the egg sac of *Argiope bruennichi* (Scopoli) and refers to literature records of further reared material not seen by him. The type series of *P. grunini* was reared from a puparium of *Ogcodes fumatus* (Erichson) (Diptera: Acroceridae) in the abdomen of a *Clubiona* sp. (see Bouček, 1965).

Diapriidae

Basalys

Although we are not aware of any other records suggesting that the genus *Basalys* is at all regularly associated with spiders, we include it here on the strength of a series of *B. pedisequa* (Kieffer) which we have seen reared from phorid puparia found in a spider's egg cocoon under bark. The Diptera whose larvae feed on spiders or their eggs are beyond the scope of this paper (see Bristowe, 1941: 362–370; also Irwin, 1979), but it is to be expected that their puparia would be prone to parasitism on a more-or-less facultative basis by a number of diapriids, pteromalids and even phygadeuontine ichneumonids that are regular or specialist parasitoids of Diptera puparia, and seem often to attack whichever of a suitable size are present in the environment in which they search. Nixon (1957, 1980) provides keys to the British genera and species of Diapriidae.

Scelionidae

Idris

There are 19 species recorded from Europe which have been revised recently by Huggert (1979). He gives hosts for only two species: *I. flavicornis* Foerster has been reared from the eggs of *Arctosa perita* (Latreille) and *Pardosa* species (*P. nigriceps* (Thorell), *P. pullata* (Clerck), *P. purbeckensis* (Pickard-Cambridge) and *P. monticola* (Clerck)) in Denmark and The Netherlands; and *I. flavoclavatus* (Kieffer) has been bred from the eggs of *Segestria senoculata* (Linnaeus) in Sweden. The biology of *I. flavicornis* is described by Kessler & Fokkinga (1973).

Ceratobaeus

Only one species is known from Europe (Italy), *C. pedestris* (Kieffer). It is redescribed by Huggert (1979), but nothing is known of its biology. *Ceratobaeus* is treated as a subgenus by Huggert (1979), but more recently it has been retained as a separate genus (Austin, 1984a; Galloway & Austin, 1984). Austin (1984b) discusses the biology of non-European species.

Baeus

The only species known from Europe is *B. seminulum* Haliday, which was redescribed by Kieffer (1926). Its biology has been studied by Vachon (1955). It is widely distributed throughout western Europe, including Britain, and has been recorded from the eggs of *Dysdera erythrina* (Walckenaer), *Tegenaria picta* Simon and *Microphantes* species in France, and *Theridion* species in France and Germany (Vachon, 1955; Kieffer, 1926). Outside Europe, *Baeus* is strongly associated with two spider families, Araneidae and Theridiidae (Austin, 1985).

Pompilidae

This is a large family of aculeate wasps with some 27 genera in Europe. Wolf (1972) has provided keys to the north west European fauna, and M. C. Day (BMNH) presently has a handbook to the British species in preparation.

All Pompilidae prey on adult or juvenile spiders, though a few use prey collected by other pompilids. Many species excavate nests in the ground, some use the occupied or vacant nests of other pompilids, while a few construct their own mud nests, often in association with man's domestic situations. Nests usually comprise a single cell, though sometimes several cells are built together. A single spider is stung and paralysed, the cell may have been prepared in advance, or it may be excavated afterwards. In the latter event, the prey is often temporarily hidden. Some species do not use nests but rather sting and oviposit onto brooding spiders or only temporarily paralysed hunting spiders, in much the same way as do some polysphinctine Ichneumonidae. There is little or no evidence for highly developed prey-species specificity, though some genera undoubtedly specialize on spiders in orb-webs, others on free hunting spiders and others again on those living in burrows. Richards & Hamm (1939) and Bristowe (1941, 1948) discuss the biology and prey of British species. Day (1981) gives a comprehensive account of the biology of *Pompilus cinereus* (Fabricius).

Sphecidae

Chalybion

A single species, *Chalybion femoratum* (Fabricius), has been recorded from southern Europe. Members of this genus use pre-existing holes and cavities in which to build their mud nests, or they utilize the abandoned mud nests of other wasps such as *Sceliphron* and *Trypoxylon*. Nests comprise several cells which are stocked with multiple prey. Bohart & Menke (1976) discuss the biology and systematics of this genus.

Sceliphron

Three species are known from Europe; *S. destillatorium* (Illiger), *S. spirifex* (Linnaeus) and the introduced *S. caementarium* (Drury) from the West Indies. No

species is recorded from Britain. Members of the genus are often referred to as "mud dauber wasps" as they construct free nests with collected mud. Nests consist of several continuous tubes or cells which are provisioned with many small spiders of various families. The taxonomy of the genus is dealt with by van der Vecht (1961), van der Vecht & Breugel (1968) and Bohart & Menke (1976): the latter include references to the biology of non-European species.

Miscophus

There are 20 species of *Miscophus* known from Europe. These are revised in a series of papers by Andrade (1952–1960: see Bohart & Menke, 1976, for details). Two species are recorded from Britain: *M. concolor* Dahlbom and *M. ater* Lepeletier (Richards, 1980). *Miscophus* species dig nests in loose sandy soil using the large spines on their fore tarsi as a rake. Nests are frequently unicellular, and are stocked with a moderate to large number of small, often juvenile, spiders. Prey records are few, although papers on the biology of non-European species are given in Bohart & Menke (1976).

Trypoxylon

There are nine European species of this genus, four of which are known from Britain: *T. clavicerum* Lepeletier, *T. figulus* (Linnaeus), *T. attenuatum* Smith and *T. medium* de Beaumont (Richards, 1980; Pulawski, 1984). Gussakovskij (1936) has revised the Palaearctic species. The majority nest in pre-existing cavities (e.g. the broken ends of plant stems, beetle burrows, old nests of bees or other mud wasps, and small holes in buildings), but a few non-European species construct their own mud nests in sheltered situations. Nests are divided into several to many cells which are stocked with many small spiders. The genus as a whole shows no highly developed prey specificity, but some species may preferentially hunt for spiders in a particular habitat. Hamm & Richards (1930) and Bristowe (1948) give accounts of the biology of British species.

KEY TO ADULTS OF HYMENOPTERA ASSOCIATED WITH SPIDERS IN EUROPE

In addition to parasitoids, the genera of Sphecidae that provision their cells with spiders are included in the key, but the large family Pompilidae is accommodated only at the family level. The adults of the Hymenoptera that are keyed differ from other insects that might be found associated with spiders or their egg sacs by having biting mouthparts and two pairs of membranous wings or, if apterous or brachypterous, having the characteristic appearance of *Baeus* (Fig. 50) or else looking ant-like.

Terminology used in the key follows Richards (1977) but we hope that reference to the figures will render it self-explanatory.

1 Antenna with at least 16 segments. (Family Ichneumonidae) . 2
— Antenna with at most 14 segments (Figs 43, 50, 51, 54, 55, 59). 29

2 Tergite 1 of gaster (Figs 1, 2) much narrower anteriorly than posteriorly or relatively long and narrow; with the spiracles at or behind the midlength; anteriorly (Fig. 4) without a depression around the dorsal muscle and without a lateral pit (glymma). (Subfamily Phygadeuontinae) 3

— Tergite 1 of gaster (Fig. 3) relatively short, broad anteriorly; with the spiracles in front of the midlength; anteriorly (Fig. 5) with the dorsolateral carinae enclosing laterally a depression around the dorsal muscle and with a lateral pit (glymma) on the outer side of the carina, adjacent to the depression. (Subfamily Pimplinae) 16

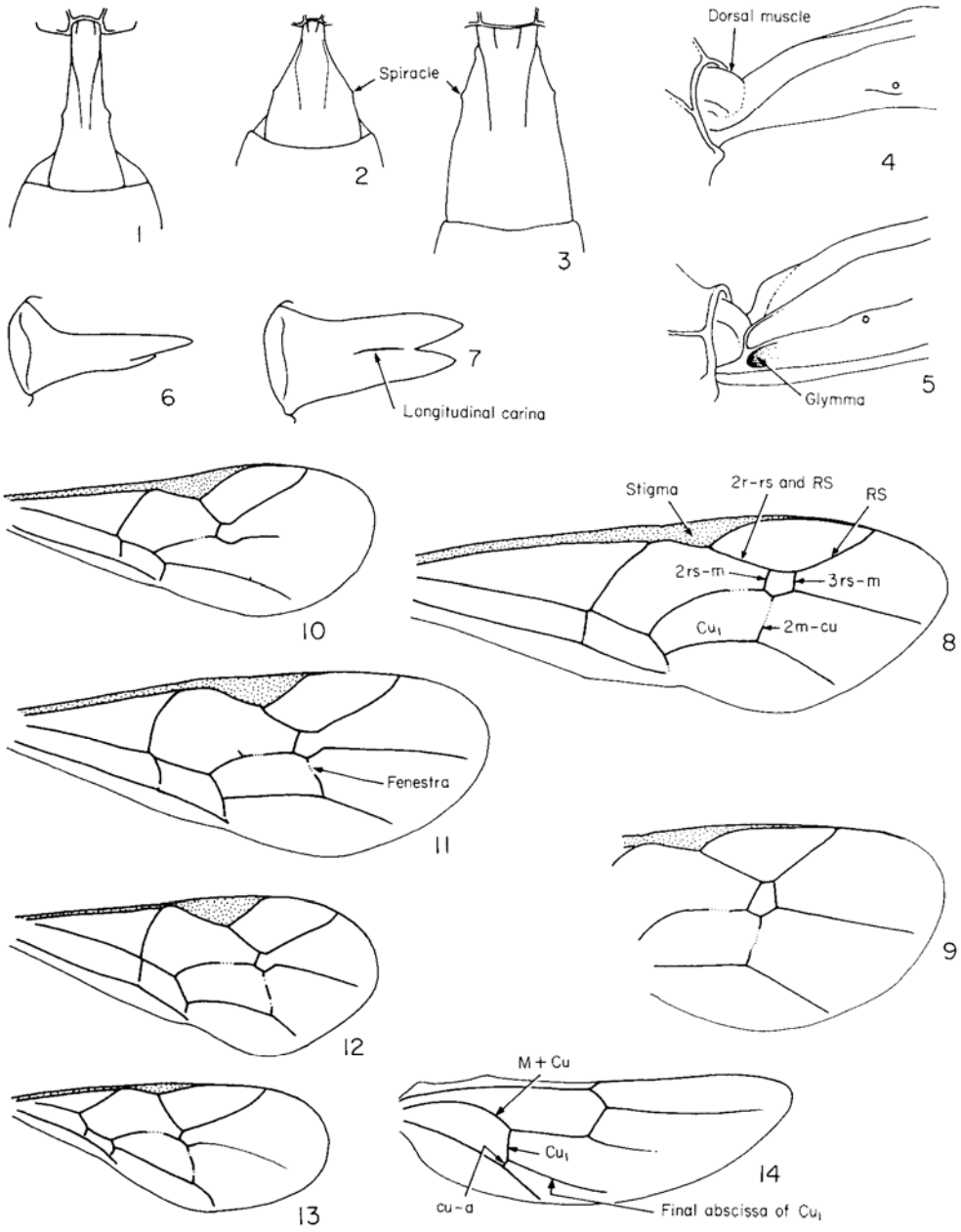
3 Wingless or with vestigial wings, obviously not capable of flight 4
— Wings fully developed, apparently capable of flight . . . 6

4 Mandible (Fig. 6) very narrow distally, with the small lower tooth obliquely behind the upper one. Vestigial wings present. (Tergites 2 and 3 of gaster separated by a complete suture. Length 2.5–2.7 mm.)
Aclastus (part, brachypterous specimens of one species)
— Mandible (Fig. 7) relatively wide distally, with the lower tooth directly below the upper one. Minute, vestigial wings present or wings completely absent 5

5 Eyes small, their horizontal diameter much less than the width of the adjacent temple (Fig. 23). Mandible with proximal part of outer surface not inflated. Tergites 2 and 3 of gaster fused, with no trace of a suture between them, (the large syntergum thus formed has two pairs of spiracles); without a crease defining the laterotergite. (Length 2.0–3.1 mm.)
Polyaulon (part, apterous females)
— Eyes larger, their horizontal diameter greater than the width of the adjacent temple (Fig. 22). Mandible with proximal part of outer surface more or less inflated. Tergites 2 and 3 of gaster separated by a complete suture or partially or completely fused; with a crease separating the laterotergite, which is usually inflexed. (Length 1.7–5.3 mm.)
Gelis (part, wingless and micropterous males and females)

6 Fore wing (Fig. 8) with vein 2m-cu present, with a single fenestra and sloping to make an angle of more than 90° where it meets vein Cu_1; stigma narrow; vein 2r-rs&RS between the stigma and vein 2rs-m at least 0.65 times as long as vein RS between vein 3rs-m (which is always present) and the wing margin 7
— Fore wing (Figs 10, 11, 12) with vein 2m-cu absent or present, if present with two or one fenestrae, if with one sloping to make an angle of 90° or less where it meets vein CU_1; stigma wide or very narrow; vein 2r-rs&RS between the stigma and vein 2rs-m at most 0.60 times as long as vein RS between vein 3rs-m (or if it is absent the position it would occupy) and the wing margin . 9

7 Epicnemial carina (Fig. 15) extending dorsally only to about the level of the middle of the hind lateral margin of the pronotum. Epomia (Fig. 15) usually strong. (Length 6.1–11.5 mm. Fore wing length 4.4–8.5 mm.) . . . *Trychosis*



Figures 1–14. Fig. 1, dorsal view of tergite 1 of gaster of *Aclastus*. Fig. 2, dorsal view of tergite 1 of gaster of *Gnypetomorpha*. Fig. 3, dorsal view of tergite 1 of gaster of *Dreisbachia*. Fig. 4, dorsolateral view of anterior part of tergite 1 of gaster of *Aclastus*. Fig. 5, dorsolateral view of anterior part of tergite 1 of gaster of *Dreisbachia*. Fig. 6, mandible of *Aclastus*. Fig. 7, mandible of *Hemiteles*. Fig. 8, fore wing of *Idiolispa* (venation labelled as in key). Fig. 9, part of fore wing of *Hidryta*. Fig. 10, fore wing of *Gnypetomorpha*. Fig. 11, fore wing of *Hemiteles*. Fig. 12, fore wing of *Gelis*. Fig. 13, fore wing of *Polyaulon*. Fig. 14, hind wing of *Hemiteles*.

— Epicnemial carina (Fig. 16) extending dorsally almost to the top of the episternum. Epomia usually weak or absent . . . 8

8 Notauli (Fig. 17) well defined, extending to about middle of mesoscutum. Fore wing (Fig. 9) with veins 2rs-m and 3rs-m converging anteriorly. (Length 4–7 mm. Fore wing length 3.1–4.9 mm.) . . . . . *Hidryta*

— Notauli absent or (Fig. 18) weakly defined and short. Fore wing (Fig. 8) with veins 2rs-m and 3rs-m subparallel. (Length 7–10 mm. Fore wing length 5.6–7.4 mm.) . . . *Idiolispa*

9 Fore wing (Fig. 10) with vein 2m-cu absent or almost completely lacking pigment. (Hind wing usually with the final abscissa of vein Cu_1 absent.) 10

— Fore wing (Fig. 11) with vein 2m-cu present and pigmented (except for the fenestra (e)). (Hind wing with the final abscissa of vein Cu_1 present (Fig. 14) or absent.) 11

10 Antenna with more than 18 segments. Tergite 1 of gaster (Fig. 1) narrow, more than 1.8 times as long as posteriorly broad . . . . . *Aclastus* (part, one species)

— Antenna with 16 or 17 segments. Tergite 1 of gaster (Fig. 2) wide, less than 1.4 times as long as posteriorly broad. (Length 2.0–3.0 mm. Fore wing length 1.7–1.9 mm.) . . *Gnypetomorpha*

11 Fore wing (Fig. 11) vein 2m-cu with only one fenestra . . 12

— Fore wing (Fig. 12) vein 2m-cu with two fenestrae (usually widely separated but, even so, sometimes with only a small pigmented section separating them) 14

12 Tergite 2 of gaster (Fig. 19) with the spiracle opening on the laterotergite (care needs to be taken in observing this character because the spiracle is often visible from both the ventral and dorsal aspects through the translucent cuticle), the laterotergite separated by a crease and usually inflexed. (Length 3.6–5.3 mm. Fore wing length 3.0–4.0 mm.) . . . . . *Agasthenes*

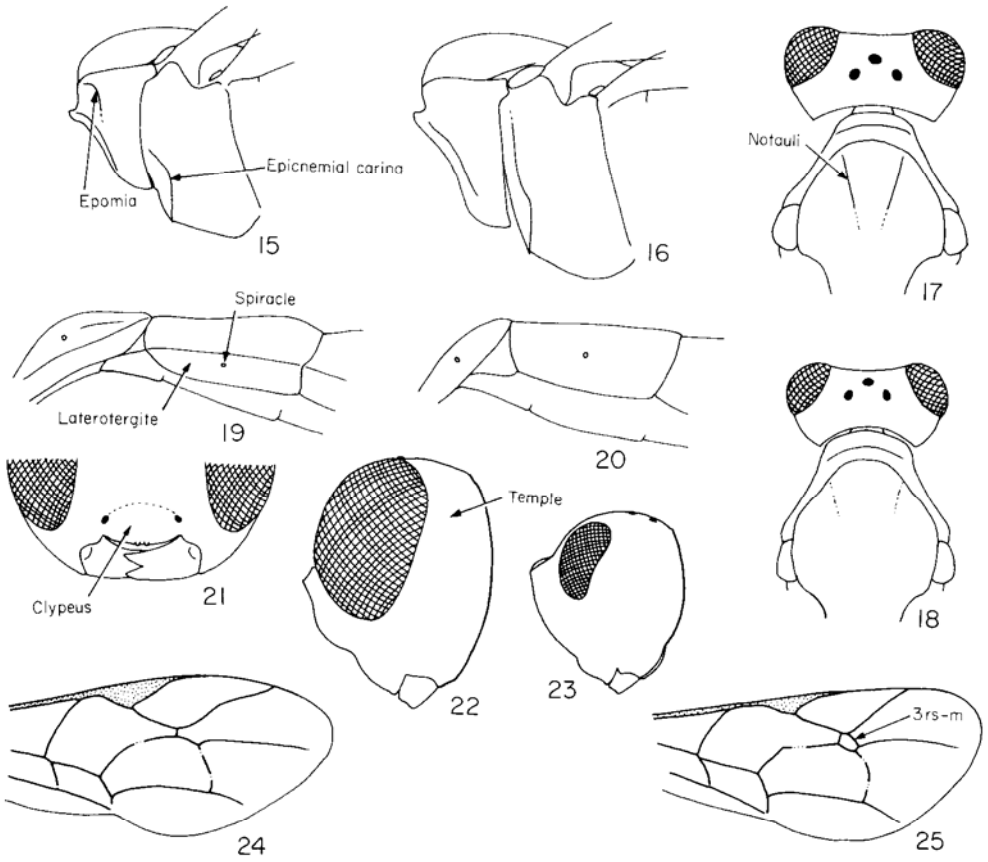
— Tergite 2 of gaster (Fig. 20) with the spiracle on the tergite proper, the laterotergite not defined by a crease. . . . 13

13 Hind wing (Fig. 14) with the final abscissa of vein Cu_1 present. Mandible (Fig. 7) relatively wide distally, with the lower tooth directly below the upper one; with a longitudinal carina on the distal part of the outer surface. (Length 4.0–5.5 mm. Fore wing length 3.1–4.1 mm.). . . . . *Hemiteles*

— Hind wing with the final abscissa of vein Cu_1 absent. Mandible (Fig. 6) very narrow distally, with the small lower tooth obliquely behind the upper one; without a longitudinal carina on the distal part of the outer surface. (Length 2.5–4.5 mm. Fore wing length 2.1–3.5 mm.) . *Aclastus* (part, most species)

14 Apical margin of clypeus (Fig. 21) with a pair of conspicuous tubercles medially. (Length 3.6–7.1 mm. Fore wing length 3.2–5.1 mm.) . . . . . *Bathythrix*

— Apical margin of clypeus simple or with a single tooth medially 15



Figures 15–25. Fig. 15, lateral view of thorax of *Trychosis*. Fig. 16, lateral view of thorax of *Idiolispa*. Fig. 17, dorsal view of mesoscutum of *Hidryta*. Fig. 18, dorsal view of mesoscutum of *Idiolispa*. Fig. 19, ventrolateral view of tergite 2 of gaster of *Agasthenes*. Fig. 20, ventrolateral view of tergite 2 of gaster of *Hemiteles*. Fig. 21, clypeus of *Bathythrix*. Fig. 22, lateral view of head of *Gelis*. Fig. 23, lateral view of head of *Polyaulon*. Fig. 24, fore wing of *Polysphincta*. Fig. 25, fore wing of *Tromatobia*.

15 Eyes larger, their horizontal diameter greater than the width of the adjacent temple (Fig. 22). Mandible with proximal part of outer surface more or less inflated. Fore wing (Fig. 12) usually with stigma wide. (Length 2.5–6.0 mm. Fore wing length 2.2–4.8 mm.) . . . . *Gelis* (part, fully winged specimens)

— Eyes smaller, their horizontal diameter much less than the width of the adjacent temple (Fig. 23). Mandible with proximal part of outer surface not inflated. Fore wing (Fig. 13) with stigma very narrow. (Length 2.0–3.1 mm. Fore wing length 2.0–2.5 mm.) . . . *Polyaulon* (part, fully winged specimens)

16 Fore wing (Fig. 24) with vein 3rs-m absent entirely . . . 17

— Fore wing (Fig. 25) with vein 3rs-m present, although occasionally only weakly pigmented 28

17 Tarsus (Fig. 26) with the fifth segment not greatly broadened; pulvilli not projecting beyond apices of claws. Female with ovipositor in lateral view straight and tapered only at apex

(usually with a nodus) (Figs 29, 30) OR tapered from middle and distinctly upcurved (Fig. 28); lower valve without a central swelling 18

— Tarsus (Fig. 27) with fifth segment conspicuously broadened and usually with pulvilli projecting beyond apices of claws. Female with ovipositor (Fig. 31) in lateral view tapered from the middle to the apex, at most only weakly curved; lower valve with a central swelling 20

18 Female with ovipositor (Fig. 28) in lateral view distinctly upcurved and tapered from middle to apex. Male with antennal segments lacking tyloids AND hind wing (see Fig. 14) with abscissa of Cu_1 between M + Cu and cu-a longer than cu-a. (Length 5.6–9.1 mm. Fore wing length 3.9–6.3 mm.) . *Clistopyga*

— Female with ovipositor (Figs 29, 30) in lateral view straight and tapered only at apex. Male with some of antennal segments 3 to 10 bearing tyloids (Figs 32, 33, 34) AND/OR hind wing with abscissa of Cu_1 between M + Cu and cu-a at most as long as cu-a 19

19 Female with proximal tooth of lower valve of ovipositor (Fig. 29) large, with a long antero-dorsal spine. Male with tyloids on outer side of segments 6 and 7 (Fig. 32) or 8 to 10 (Fig. 33) or 3 to 8 (Fig. 34) of antenna. (Length 4.2–7.7 mm. Fore wing length 3.1–6.2 mm.) . . . . . *Zaglyptus*

— Female with proximal tooth of lower valve of ovipositor (Fig. 30) not enlarged, without an antero-dorsal spine. Male without tyloids on segments of antenna. (Length 4.7–10.1 mm. Fore wing length 3.7–7.8 mm.) . . . *Tromatobia* (part)

20 Clypeus and face (Fig. 35) confluent, forming an evenly convex surface. (Surface of eyes bearing numerous long hairs which are more than three times the diameter of an eye facet in length.) (Length 4.6–9.2 mm. Fore wing length 3.4–7.2 mm.) . *Schizopyga*

— Clypeus and face (Fig. 36) separated by a distinct transverse impression. (Surface of eyes usually with only sparse, short hairs.) 21

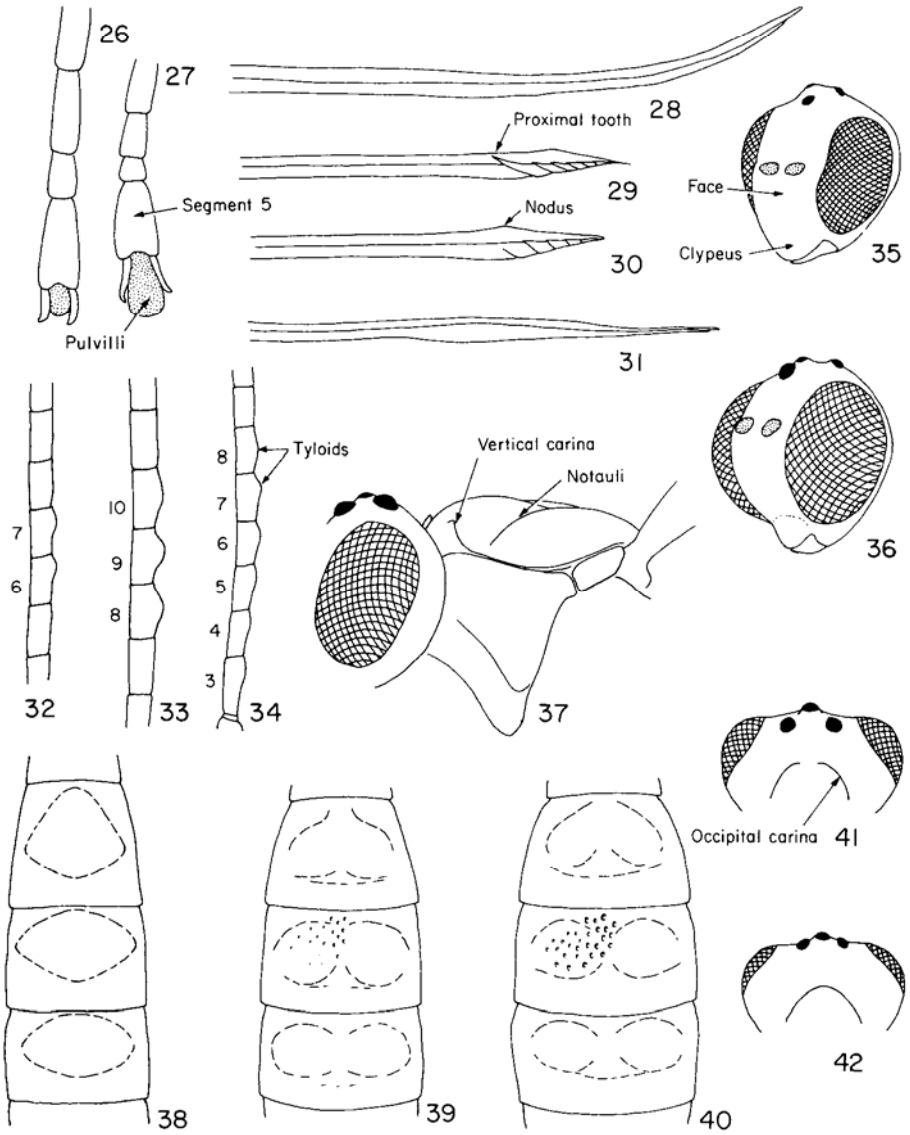
21 Mesoscutum (Fig. 37) with a vertical carina on each side in front of the notauli. (Length 3.4–5.8 mm. Fore wing length 2.8–4.3 mm.) . . . . . *Acrodactyla* (part, most species)

— Mesoscutum without distinct vertical carinae 22

22 Notaulus absent. Gaster with tergites 2 to 4 evenly convex. (Length 4.6–6.7 mm. Fore wing length 3.8–5.0 mm.) . *Piogaster*

— Notaulus (see Figs 17, 18) present. Gaster with tergites 2 to 4 (Figs 38, 39, 40) bearing diagonal or transverse grooves (rather weak in one species of *Acrodatyla*) 23

23 Hind wing with final abscissa of vein Cu_1 present (see Fig. 14) AND/OR mesoscutum with some areas entirely bare and the remainder with only sparse hairs AND/OR tergite 2 of gaster with coriaceous sculpture or strongly punctured centrally . . 24



Figures 26–42. Fig. 26, part of hind tarsus of *Tromatobia*. Fig. 27, part of hind tarsus of *Dreisbachia*. Fig. 28, lateral view of ovipositor of *Clistopyga*. Fig. 29, lateral view of ovipositor of *Zaglyptus*. Fig. 30, lateral view of ovipositor of *Tromatobia*. Fig. 31, lateral view of ovipositor of *Sinarachna*. Fig. 32, part of right antenna of male *Zaglyptus multicolor*. Fig. 33, part of right antenna of male *Zaglyptus varipes*. Fig. 34, part of right antenna of male *Zaglyptus rufescens*. Fig. 35, anterolateral view of head of *Schizopyga*. Fig. 36, anterolateral view of head of *Acrodactyla*. Fig. 37, anterolateral view of mesoscutum of *Acrodactyla*. Fig. 38, dorsal view of tergites 2 to 4 of gaster of *Zatypota*. Fig. 39, dorsal view of tergites 2 to 4 of gaster of *Polysphincta*. Fig. 40, dorsal view of tergites 2 to 4 of gaster of *Oxyrrhexis*. Fig. 41, posterior view of upper part of head of *Sinarachna*. Fig. 42, posterior view of upper part of head of *Acrodactyla*.

— Hind wing with final abscissa of vein Cu_1 absent (or sometimes very weakly indicated) AND mesoscutum with an even covering of hairs AND tergite 2 of gaster smooth and polished centrally . 27

24 Tergites of gaster (particularly 2–4) (Fig. 38) with the central area evenly convex, with almost no punctures, but ranging from coriaceous to smooth and polished; bounded by well defined posterior transverse and anterolateral diagonal grooves. (Length 3.5–5.2 mm. Fore wing length 2.9–4.5 mm.) . . . *Zatypota*

— Tergites of gaster (particularly 2–4) (Figs 39, 40) with a pair of very poorly to strongly developed rounded swellings, covered with fine to strong punctures, especially medially; bounded by weak depressions 25

25 Surface of eyes bearing numerous conspicuous, relatively long hairs. (Length 4.3–7.0 mm. Fore wing length 3.4–5.5 mm.) *Zabrachypus*

— Surface of eyes almost bare 26

26 Tergites of gaster (Fig. 39) with relatively fewer and much finer punctures on the sublateral swellings than medially. Female with ovipositor projecting beyond apex of gaster by at least 0.7 times length of hind tibia. (Length 4.8–13.0 mm. Fore wing length 3.9–9.2 mm.) . . . . . *Polysphincta*

— Tergites of gaster (Fig. 40) with relatively strong punctures on the sublateral swellings and even stronger punctures medially. Female with ovipositor projecting beyond apex of gaster by at most 0.5 times length of hind tibia. (Length 4.7–10.1 mm. Fore wing length 3.8–7.5 mm.) . . . . . *Oxyrrhexis*

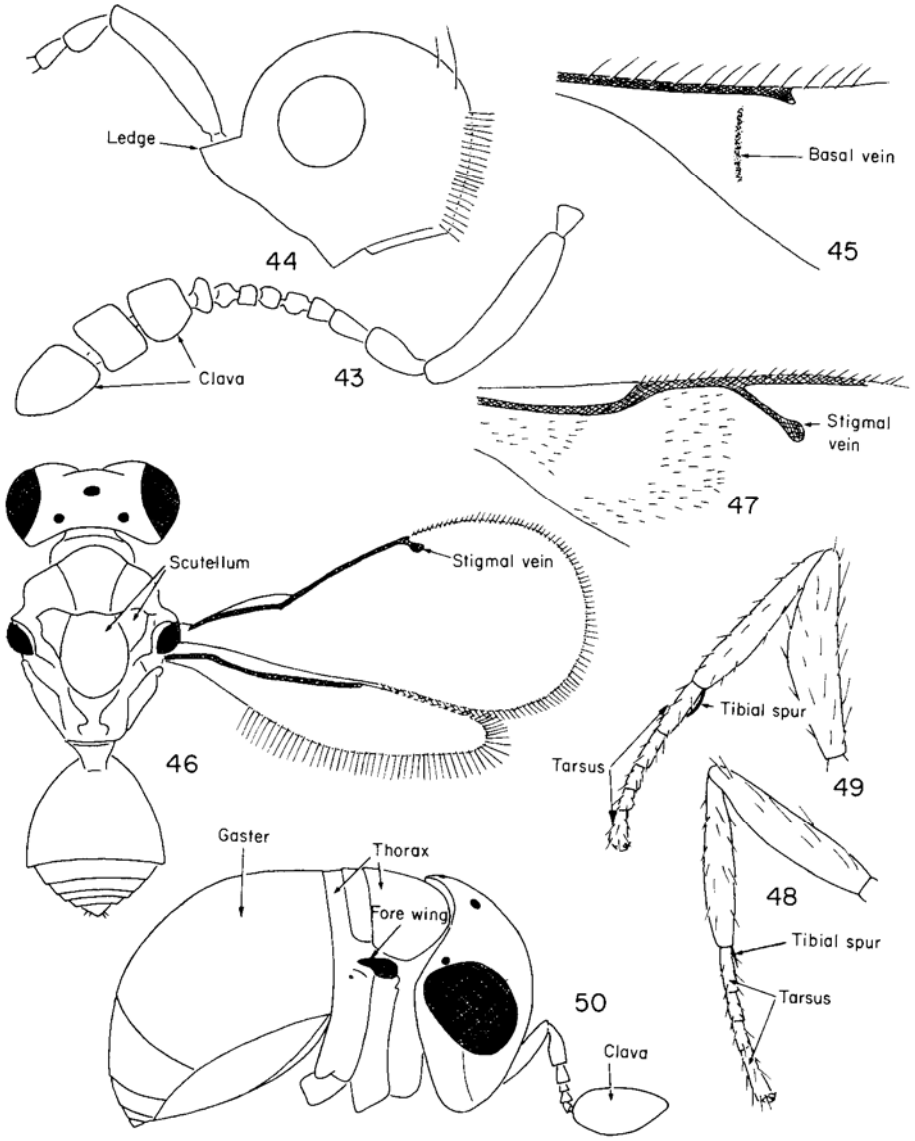
27 Occipital carina (Fig. 41) interrupted mediodorsally. Tergite 1 of gaster less than 1.5 as long as broad. (Length 3.4–5.6 mm. Fore wing length 2.7–4.3 mm.) . . . . . *Sinarachna*

— Occipital carina (Fig. 42) complete mediodorsally. Tergite 1 of gaster more than 1.7 as long as broad. (Length 4.0–5.8 mm. Fore wing length 3.7–5.2 mm.) . *Acrodactyla* (part, one species)

28 Female with ovipositor (Fig. 31) in lateral view tapered from middle to apex. Tarsus (Fig. 27) with fifth segment conspicuously broadened. (Length 5.1–7.7 mm. Fore wing length 3.7–5.7 mm.) . . . . . *Dreisbachia*

— Female with ovipositor (Fig. 30) in lateral view tapered only at apex. Tarsus (Fig. 26) with fifth segment not greatly broadened. (Length 4.7–10.1 mm. Fore wing length 3.7–7.8 mm.) *Tromatobia* (part)

29 Wings without any closed cells, venation reduced to only a few veins along anterior margin (Figs 46, 51); some forms with membranous wings absent (Fig. 50) or reduced to reach only half distance along gaster. (Small insects, less than 2.0 mm in length. Virtually all species associated with spider egg sacs) . 30



Figures 43–50. Fig. 43, antenna of female *Basalys*. Fig. 44, lateral view of head of *Basalys*. Fig. 45, section of fore wing of male *Basalys*. Fig. 46, dorsal view of *Pediobius*. Fig. 47, section of fore wing of *Pteromalus*. Fig. 48, fore leg of *Pediobius*. Fig. 49, fore leg of *Pteromalus*. Fig. 50, dorsolateral view of female *Baeus*.

— Wings with relatively complete venation containing several closed cells; always fully winged (Figs 59, 66). (Medium to large in size, 5–25 mm in length. Predators of adult and juvenile spiders) 38

30 Antennae inserted onto prominent ledge with protrudes from face (Fig. 44) . . . . . Family Diapriidae
(Only one genus certainly associated with spiders, *Basalys*;

characterized as follows. Notauli absent. Female brachypterous, wings reaching at most to middle of second segment of gaster; antenna 12-segmented, with very sharply differentiated 3-segmented clava (Fig. 43). Male fully winged, basal vein present (Fig. 45); antenna 14-segmented, without clava.)

— Surface of face smoothly rounded, without a protruding ledge (Figs 46, 51) 31

31 Scutellum bulging medially to form distinct medial and lateral parts, posterior margin rounded (Fig. 46). Body metallic blue or green in colour. 32

— Scutellum not so divided (Figs 50, 51), dorsal surface flattened, posterior margin either rounded or pointed. Body dull brown or black in colour. (Family Scelionidae) 33

32 Tarsi 4-segmented; fore tibia with apical spur short and straight (Fig. 48) . . . . . Family Eulophidae
(Only one genus certainly associated with spiders, *Pediobius*; which has the stigmal vein in fore wing very short, almost knob-like (Fig. 46).)

— Tarsi 5-segmented; fore tibia with apical spur long and curved (Fig. 49) . . . . . Family Pteromalidae
(Only one genus certainly associated with spiders, *Pteromalus*, which can be further distinguished from *Pediobius* by its long stigmal vein (Fig. 47).)

33 Antenna with 7 segments, last segment expanded into a large distinct clava (Figs 50, 51) (females). 34

— Antenna 11- or 12-segmented, last segment or segments not swollen into a clava (Figs 54, 55) (males). 36

34 Wings completely absent. Body squat and oval; gaster appearing to be fused to thorax (Fig. 50) . . . . . *Baeus* (females)

— Wings fully developed or reduced in size, never completely absent. Gaster clearly divided from thorax (Figs 51, 52, 53) . 35

35 First tergite of gaster raised dorsally into a hump; gaster elongate, tapering posteriorly (Fig. 53) . . *Ceratobaeus* (females)

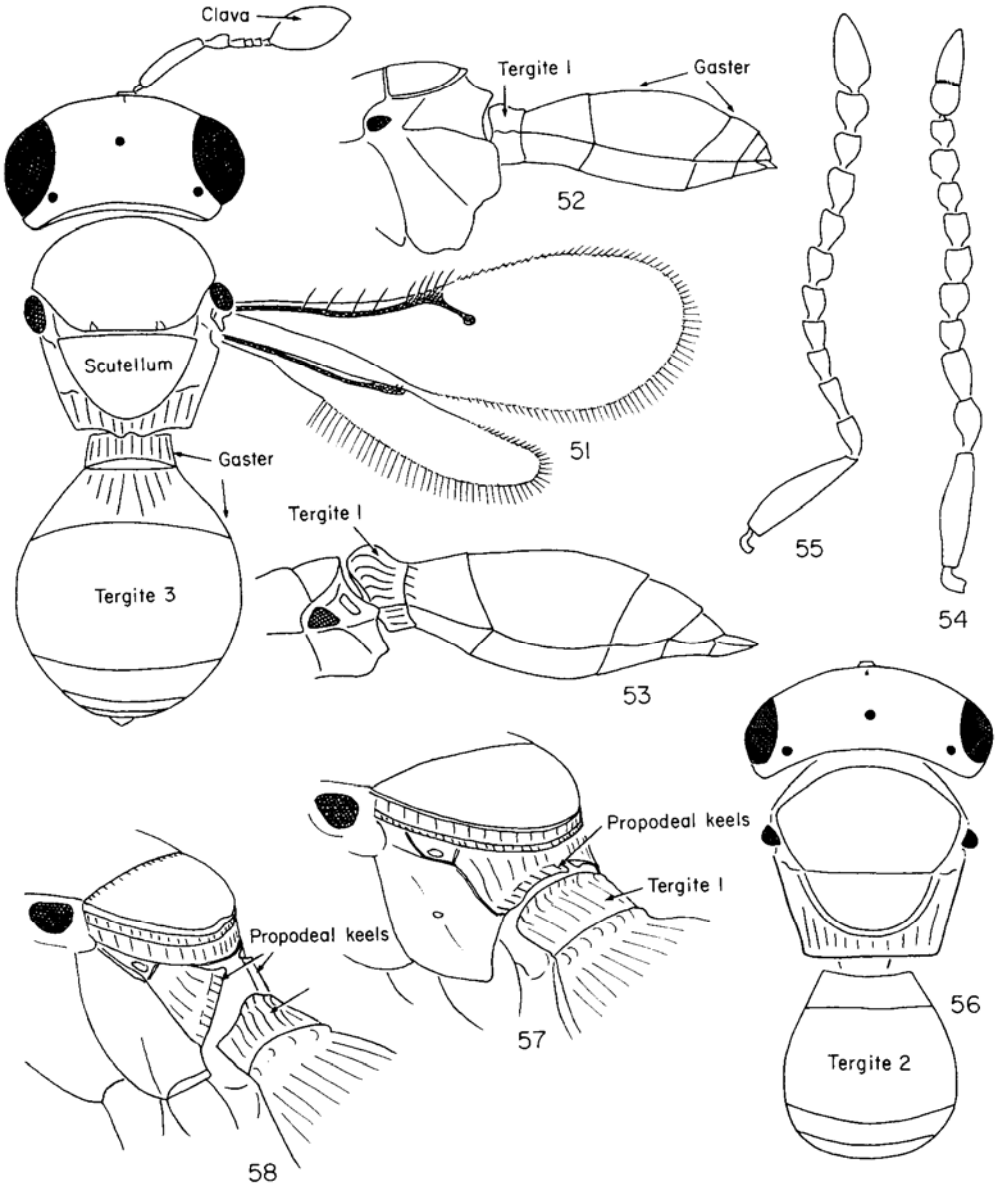
— First tergite of gaster flattened dorsally; gaster usually oval in shape, long and tapering posteriorly (Figs 51, 52) . *Idris* (females)

36 Second tergite of gaster by far the largest (Fig. 56). Antenna with 12 free segments (Fig. 55). . . . . *Baeus* (males)

— Third tergite of gaster by far the largest (see Fig. 51). Antenna with either 10 or 11 free segments, last 2 segments wholly or partly fused (Fig. 54) 37

37 First tergite of gaster flattened, though anterior lip often upturned. Propodeal keels closest to mid line parallel to surface of first tergite (Fig. 57) . . . . . *Idris* (males)

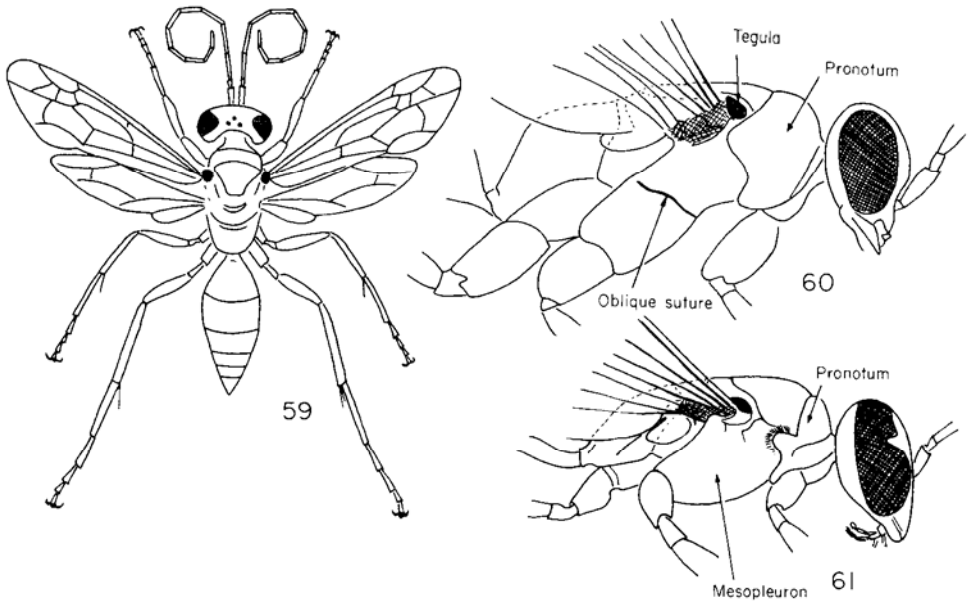
— Anterior half to one-third of first tergite of gaster raised into a low hump dorsally. Propodeal keels diverging ventrally (Fig. 58) . . . . . *Ceratobaeus* (males)
(Males of *Ceratobaeus* have not been collected in Europe. The



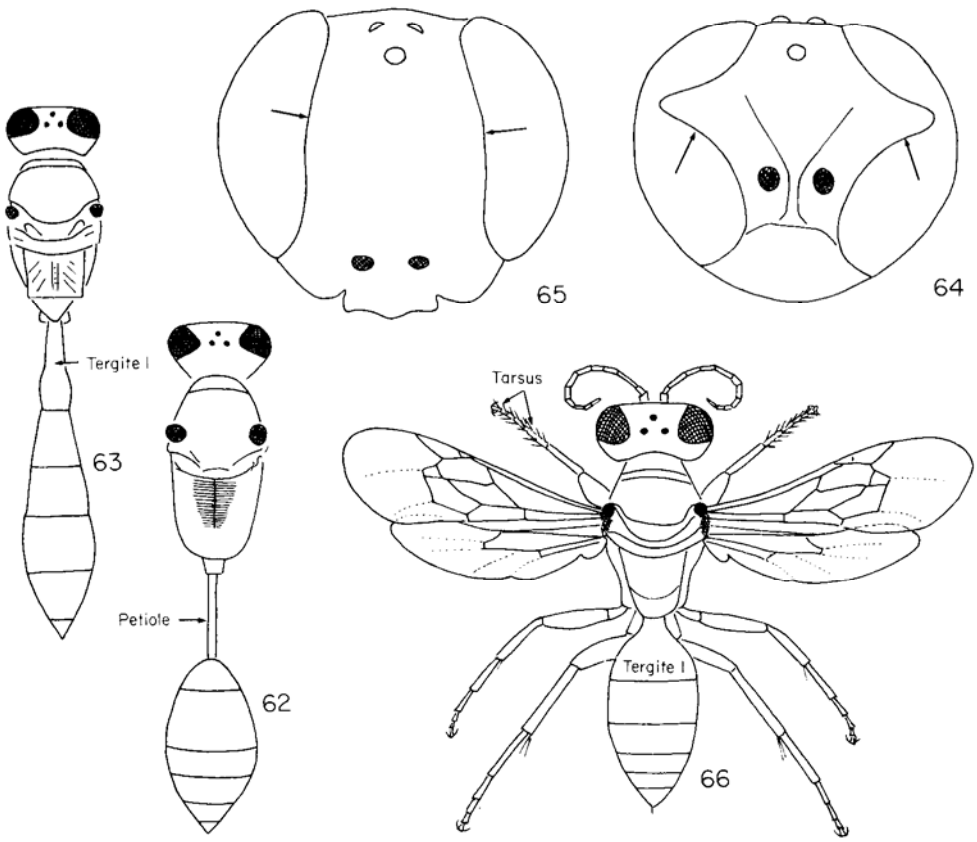
Figures 51–58. Fig. 51, dorsal view of female *Idris*. Fig. 52, lateral view of female *Idris* (wings not shown). Fig. 53, lateral view of female *Ceratobaeus* (wings not shown). Fig. 54, antenna of male *Idris* showing partly fused segments 11 and 12. Fig. 55, antenna of male *Baeus*. Fig. 56, dorsal view of male *Baeus* (wings not shown). Fig. 57, dorsolateral view of male *Idris*. Fig. 58, dorsolateral view of male *Ceratobaeus*.

above characters are based on non-European species.)

38 Posterodorsal corner of pronotum touching or almost touching tegula (at base of wings) or nearly so. Mesopleuron divided by an oblique suture (Fig. 60) . . . . . Family Pompilidae



Figures 59–61. Fig. 59, dorsal view of *Caliadurgus* (Pompilidae). Fig. 60, lateral view of *Pompilus*. Fig. 61, lateral view of *Trypoxylon*.



Figures 62–66. Fig. 62, dorsal view of *Sceliphron* (wings not shown). Fig. 63, dorsal view of *Trypoxylon*. Fig. 64, anterior view of head of *Trypoxylon* showing emarginate eyes (arrowed). Fig. 65, anterior view of head of *Miscophus* showing rounded inner border of eyes (arrowed). Fig. 66, dorsal view of *Miscophus*.

— Posterodorsal corner of pronotum clearly separated from tegula. Mesopleuron not divided by an oblique suture (Fig. 61). (Family Sphecidae) 39

39 First tergite of gaster forming a long, evenly thin petiole (Fig. 62) 40

– – First tergite of gaster short and very broad posteriorly (Fig. 66), or if elongate then widening posteriorly (Fig. 63) 41

40 Body black with yellow markings . . . . . *Sceliphron*

– – Body metallic dark blue . . . . . *Chalybion*

41 Eyes emarginate above antennal insertions (Fig. 64). First tergite of gaster very much longer than wide (Fig. 63). Fore tarsi without long spines . . . . . *Trypoxylon*

– Border of eyes evenly curved (Fig. 65). First tergite of gaster about as long as posterior width. Fore tarsi with long spines (Fig. 66) . . . . . *Miscophus*

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