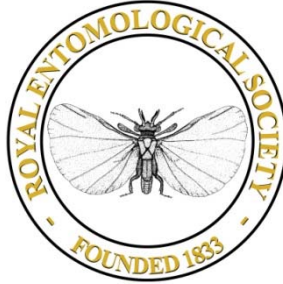


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Handbooks for the Identification of British Insects
Vol. 6, Part 4

SPIDER WASPS

HYMENOPTERA: POMPILIDAE

M. C. Day



ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

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Identification of British Insects

Vol. 6, Part 4

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SPIDER WASPS
HYMENOPTERA: POMPILIDAE

By

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1988

ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

The aim of the *Handbooks* is to provide illustrated identification keys to the insects of Britain, together with concise morphological, biological and distributional information. Each handbook should serve both as an introduction to a particular group of insects and as an identification manual. Details of handbooks currently available can be obtained from Publications Sales, British Museum (Natural History), Cromwell Road, London SW7 5BD.

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Introduction

The family Pompilidae is one of the best-characterised and most easily recognised of the aculeate families represented in the British fauna. Known as the 'spider-hunting robber wasps' or, more simply, as 'spider wasps', they are predominantly of tropical distribution, numbering between four and five thousand species; 41 species are included in the British List, with a further three occurring in the Channel Islands. Their characteristic long-legged adult habitus (fig. 1) is complemented by their inherently agitated activity; they are readily recognisable when seeking the spiders which are the provision made for the nourishment of their larvae. They run and make short flights amongst vegetation, usually only during periods of warm sunshine, their antennae and wings in ceaseless vibration. Thus they well deserve the facetious appellation 'Hymenoptera Neurotica' which has been applied to them together with some of the other ground-running solitary aculeates. They have developed their powers of running to such a degree that they might better be termed 'cursorial' rather than 'fossorial' Hymenoptera.

Family Pompilidae

Pompilii Latreille, 1805: 277. Type-genus: *Pompilus* Fabricius, 1798 (Pompilidae)
Psammocharidae Banks, 1910: 114. Type-genus: *Psammochores* Latreille, 1796. Suppressed by ICZN Opinion 166, 1945.

The family name has been the subject of much unfortunate controversy. In brief, the well-established name Pompilidae was rejected (Fox, 1901) because the generic name *Pompilus* was thought to be preoccupied in the Cephalopoda. Of several alternatives, Psammocharidae Banks, 1910 emerged as a valid and appropriate replacement and was used throughout the early decades of this century in nearly all substantial works on the group. However, the name was eventually rejected and Pompilidae adopted by decision of the International Commission on Zoological Nomenclature in 1945; I have previously summarised the details of this involved history (Day, 1981).

The Pompilidae have traditionally been regarded as a taxonomically difficult group. The British fauna is a partial representation of that of Europe, inevitably so with our short post-glacial history. Many of the difficulties of that larger fauna remain to be solved, but the British species are now quite well known. In particular, the few genera which contain multiple closely related species, though difficult to identify in the female sex, have males equipped with diagnostic genitalia. Thus it is possible to be confident about the actual composition of the British fauna. Most nomenclatural problems were dealt with in an earlier work (Day, 1979).

Diagnosis: Aculeata with 12 antennal segments in the female, 13 in the male; female antennae often curl characteristically in death; pronotum loosely hinged to mesothorax dorsally, reaching back to tegulae; mesopleuron traversed by a more or less straight posterior oblique sulcus (= median episternal groove); metapostnotum transverse or invaginated; metapleuron often with anterovenal metapleural pit; legs unusually long, longer hind tibial spur modified as a calcar; fore wing with 10 closed cells, hind wing with C+Sc+R+Rs fused basally, basal hamuli clustered, second abscissa of 1A lost; abdomen lacks any kind of constriction or articulation between first and second segments; first sternum overlies second totally, with no specialised posterior margin; female abdomen lacks cerci, with six visible segments; seventh tergum internal, centrally divided, sixth sternum envelopes sting sheath; male abdomen with cerci, sixth sternum with a pair of sclerotised hooks posteriorly, seventh sternum reduced, internal; genitalia with parapenial lobes and often with basal hooklets.

Functional morphology and terminology

The terminology employed herein largely follows that of Richards (1977). For easy comparison with other works, some features are labelled in illustrations though not otherwise discussed.

The head of Pompilidae is the source of many characters which are dependent on subtle appreciation of differences of shape which must be conveyed by illustrations or measurements. Illustrations are used in this handbook, but the relative proportions of the eyes, face, ocelli, malar space and temples have been used by various authors.

The head is orthognathous, with a pair of well developed compound eyes and three ocelli; the front is the area between the ocelli and the antennae. The mandibles are strong, usually with one or two subsidiary teeth on the inner margin in addition to the sharp apex and are said to be edentate if devoid of such teeth, uni- or bidentate otherwise. They are principally organs of manipulation despite their relative simplicity. Males have antennae of 13 segments, females 12: the antennae of females curl characteristically after death, with a predictability which has led to this feature frequently being cited as a principal recognition character of the family. However, modern collecting techniques frequently rely on the collection of material into alcohol; such material is physiologically fixed so that the antennae rarely adopt this configuration.

The clypeus is well developed, transverse, with the antennae inserted close to the upper margin; the extent to which the labrum protrudes from beneath is frequently of taxonomic significance. A maxillary palp of six segments and a labial palp of four is the rule. The mouthparts in some groups are elongated to take nectar from flowers; those of females of some genera bear groups of specialised erect hairs or bristles which assist in the manipulation of materials and play some part in nest construction or excavation (figs 26, 27).

The body often bears a uniform coat of fine hairs which, though erect, incline posteriorly at an angle. In most Pompilinae, these hairs have become closely adpressed to the surface of the body which thus superficially appears glabrous. Groups of more or less strong erect hairs or bristles occur variously and may have taxonomic significance. In some groups the head and thorax may be extensively punctate or microsculptured.

The 'thorax' of Hymenoptera Apocrita consists of the three true thoracic segments

with which the first abdominal segment (the propodeum) has been incorporated. The remaining abdominal segments articulate *via* the second segment, displaying a characteristic 'wasp waist'. The names applied to the thorax and abdomen in these circumstances have generated much debate and various solutions, but none of these has resolved the problem of defining absolutely and unambiguously a uniquely hymenopterous structure. I therefore employ thorax and abdomen for the readily recognised major divisions of the body; abdomen is thus a synonym for gaster or metasoma in the sense of those terms as applied to solitary aculeates. Labelled figures of the thorax are given (figs 2, 3).

The pronotum of Pompilidae is dorsally loosely articulated with the mesothorax. Specialised areas include the anteriorly projecting collar separated from the transverse, vertical face of the pronotum by a groove, the streptaulus. This terminology accords with most other groups save the Sphecidae, in which 'collar' is applied to the dorsal surface of the pronotum adjacent to the mesonotum! The ventrolateral portion overlies and is free of the mesopleura. Ventrally, the propleura are the main sclerites, the minute prosternum being overlain by the bases of the large fore coxae. The propleura project forwards from beneath the collar as a distinct neck. A large area of intersegmental membrane ventrally permits substantial movement between pro- and mesothorax. Well-developed posterolateral lobes cover the first thoracic spiracles which lie intersegmentally and connect with a substantial tracheal trunk. The lobes normally reach back virtually to the tegulae.

The mesothoracic notum consists of a large, dorsal sclerite transversely divided by a sulcus (the scuto-scutellar suture) which internally forms a strengthening flange. The sclerite anterior to the sulcus is the mesoscutum and bears notauli anteriorly, parapsidal sulci posterolaterally. The posterior sclerite is the scutellum; its median area is often called the disc. The fore wings articulate anterolaterally behind the tegulae. The mesopostnotum is entirely invaginated, and is thus unseen. The mesopleura are large sclerites, thought to be contiguous ventrally, the sternum being lost. The larger, anterior portion of the mesopleuron, the mesepisternum, is diagonally oriented to a marked degree; anteriorly it projects forwards beneath the pronotum. A well-defined sulcus, the posterior oblique sulcus, traverses it at mid-height to intercept the scrobe: this sulcus is a definitive recognition feature of the Pompilidae. The mesopleuron posterodorsally and posteriorly consists of the much reduced mesepimeron, bearing the fore wings dorsally and articulating with the metathorax posteriorly.

The metathorax is a smaller segment than the mesothorax. Dorsally the metanotum is a U-shaped, transverse, often elevated sclerite; the hind wing articulates at its antero-lateral edge. Posteriorly it is bordered by the postnotum (properly, metapostnotum), which may be a well-developed transverse sclerite, somewhat depressed relative to the metanotum, or may be very short or even invaginated so that only a transverse groove separates the metanotum from the propodeum. To be sure of the identity of these sclerites, note that the wings insert adjacent to the mesonotum and metanotum respectively; the scutellum and metapostnotum are the respective posterior sclerites of the wing-bearing segments. Laterally the metapleura are most obviously contiguous with the postnotum, even when it is greatly reduced. Dorsally, just anteroventral of the hind wing base, is the epimeral lobe which conceals the second thoracic spiracle. In contrast with the first, this connects with a very thin tracheal trunk. The spiracles appear to be intersegmental, which is why they are referred to as first and second thoracic; however, they probably derive from the meso- and metathorax. In the larva, the second thoracic spiracle is virtually lost, a character which links several solitary aculeate groups and correlates with the very limited development of this tracheal trunk in the adult.

Anteriorly, the metapleuron articulates relatively rigidly with the mesepimeron. Medially it is more or less constricted adjacent to a distinctive endophragmal pit. A distinct suture marking the propodeal boundary passes to it, and another runs forward and down to the meso-metapleural suture. In a variety of forms, this suture may be seen

to reach a pit, the anteroventral metapleural pit; in others, the pit may be seen but part of the suture is enveloped by the meso-metapleural suture; and in others, the pit also is enveloped. Examples only of the last condition were included in recent phylogenetic studies (Brothers, 1975).

The propodeum is a convex sclerite which has become immovably fused with the metathorax. The posterior surface may become more or less abruptly vertical, when it is said to be declivous: the vertical surface is then the declivity. The posterior margin usually has a laminate rim beneath which the abdomen articulates via two strong condyles. The uniquely apocritan dorsal muscle of the petiole, an external levator muscle of the abdomen, arises from a foramen in the rim and inserts on the first abdominal tergum anterocentrally. No propodeal sternum is discernible and the hind coxae and abdomen articulate within a common orifice. The propodeal spiracles are borne anterolaterally and connect with a very large tracheal trunk, similar to that associated with the first thoracic spiracle. Thus the muscles of locomotion and flight are ventilated from fore and aft, with only a small air 'balance pipe' between meso- and metathorax.

The wings of Pompilidae are of considerable value as a source of characters, both at specific and supraspecific level. However, the nomenclature employed in past treatments has often ignored contemporary opinion on the homologies of wing veins, and is thus considered in detail here.

Early descriptive systems for hymenopterous venation date from the time of Jurine (1807). Cresson (1887) developed Jurine's system in an interpretation which still has currency in the Pompilidae today (Wasbauer & Kimsey, 1986). Comstock & Needham (1899) and Comstock (1918) gave a system which emphasised structures homologous with those of other insects, whilst Rohwer & Gahan (1916) emphasised the needs of systematists at the expense of homology and gave an exhaustive compendium of terms and definitions applied up to that date. Haupt (1927) rejected Comstock and employed an eccentric system which he later modified (Haupt, 1930), based on a novel interpretation of a supposed proto-hymenopteran wing described by Tillyard (1927). All subsequent German works on Pompilidae have followed this peculiar system.

Ross (1936) derived a hypothetical hymenopterous prototype venation from the study of extant Symphyta, Megaloptera, Mecoptera and Trichoptera. He extrapolated from observations of the origins of veins in relation to the axillary sclerites in the wing base. This hypothetical apocritan fore wing venation is adjusted to coincide with a pompilid configuration in fig. 4. The most significant consequence of Ross's analysis, not disputed by subsequent workers, though ignored by some, is the identification of an unexpected relationship between the radial sector (then thought to be a major branch of the radius) and the media. Basally fused with the subcosta, the radial sector is free for a short distance, then is fused with the media. The next free segment, or abscissa, is parallel with the crossveins which link the distal segments of Rs with the media. It then resumes a path consistent with its identity as a longitudinal vein; this has consequences for the naming of most parts of the venation. This configuration is approached in the Cephidae, which is intermediate in structure between the Apocrita and the tenthredinid sawflies. Within the Tenthredinoidea R_s+M is modified by fusion with $Sc+R$ to generate a unique configuration.

Evans (1950) adopted the Jurine-Cresson system as summarised in a current textbook (Matheson, 1947) for his revision of the Nearctic Pompilinae. Lanham (1951) developed Ross's views in respect of the higher Hymenoptera but Townes (1957), in his revision of the Nearctic Pepsinae, opted to apply strictly the Rohwer & Gahan system. The model handbook for the Swiss Pompilidae (Wolf, 1972), is a recent example of Haupt's system. Eady (1974) made recommendations to simplify and standardise terminology whilst taking account of Ross's contribution to the study of vein homology. Brothers (1975) interpreted the recent work of Hamilton (1972), who developed Ross's views. He postulated a separate rather than a branching origin for the radial sector,

which he renamed 'sector', and he discussed the nature of the plical furrow (= vannal fold) and jugal fold. Richards (1977) summarised current usages throughout the Hymenoptera and suggested preferable terms. Wootton (1978) reviewed hypotheses of structure in relation to function and made recommendations which embraced both a nomenclatural conservatism and an enhanced consideration of homology.

Traditionally, veins and cells have been both named and referred to by index letters, convenient for labelling diagrams. Cells are simply the consequence of the presence or absence of particular veins, which are the actual structures responsible for the perceived configuration. However, the cell patterns are often stable, are more simply recognised and thus have been used relatively frequently. Therefore I have followed Eady in the naming of cells, which ensures a high degree of compatibility both with the diverse systems of previous authors on the Pompilidae and with current work on other groups. However, I have followed Wootton in the naming of veins and folds. For clarity, I have tabulated the similarities and differences of the various systems. Table 1 (pp. 55–58) is based on the pompilid wing configuration of figs 4–6, but with little modification is appropriate to all Apocrita. In order to make comparisons it proved necessary to list each individual segment, or abscissa, of each vein. Thus, where segments are fused with other veins, multiple entries result. The number of abscissae of a vein is variable, depending on the actual numbers of interceptions that occur; these can differ even between one wing and its counterpart.

As previously intimated, Ross identified an unexpected interrelationship between the radial sector and its adjacent veins. To reiterate, the radial sector is thought basally to be fused with the subcosta, is then free for a short distance, and is then fused with the media. The next free segment, or abscissa, is parallel with the crossveins which link the distal segments of Rs with the media. It then resumes a path consistent with its identity as a longitudinal vein; figure 4 is a diagrammatic modification of the fore wing of *Dipogon* (figs 7, 8), representing the maximum number of veins for any extant apocritan fore wing. It has 11 closed cells (10 is normally represented to be the primitive number because of the loss of crossvein 1r–rs). In addition, Rs and M are shown separately, to emphasise the effects of their fusion, Crossvein 1rs–m, present in some Xyelidae, is included to justify the numbering of the succeeding radio-medial crossveins; this crossvein has been obliterated by the fusion of Rs with M in the remote ancestors of the Apocrita. Each longitudinal vein is represented in the diagram by a different pattern; in addition, dotted lines represent the claval furrow (parallel to vein 1A) and radial fold. The fore and hind wings of *Dipogon* are further illustrated in figs 5 & 6, labelled appropriately for the nomenclature adopted in this handbook. Note that a high degree of compatibility of interpretation is obtained for both wings. Of particular interest is the implication that the fore wing radial fold system and its hind wing equivalent are homologous; and that these are probably specific hymenopteran derivatives of the median flexion line *sensu* Wootton, 1978. Further, the veins constituting the stigma of the fore wing appear to be homologous with those of the hind wing which bear the distal hamuli. However, the actual homologies of these last veins are the least certain of all.

A major inconsistency in modern works which have assigned a terminology to cells has been in the treatment of those adjacent to the stigma. These are the cell or cells usually referred to as 'submarginal' or 'cubital'; but if the conclusions reached by Ross are to be incorporated, the system must take account of the fact that submarginal 1 is anterior to Rs whilst the others are posterior to this vein. Further, in most sawflies and those Apocrita with 1r–rs present, there are two cells which occupy the position of 'submarginal 1'; these are 1R₁, 2R₁ whilst submarginal 2 = 1Rs and submarginal 3 = 2Rs. The inherent difficulties of the situation can be circumvented, if not resolved, by adapting Eady and using 'parastigmal 1' and '2' for 'submarginal 1' when it is divided by 1r–rs.

Most treatments of wing venation have ignored consideration of the various kinds of

wing fold, though illustrations may have included them. For fore wings, Richards (1977) discussed the radial and vannal folds and indicated the fundamental stability of the latter. Hamilton (1972) emphasised the functional importance of the vannal fold (as the plical furrow), as did Wootton (1978) who termed it the claval furrow. This last usage is followed here; however, as stated above, Wootton's conception of the so-called median flexion line in Hymenoptera is rejected pending further study. It may well be that the radial fold system in Hymenoptera is a unique development of the median flexion line. A flexion line which best fits Wootton's description is discernible in the fore wing of *Tiphia*: however, it does not transgress Rs or Sc + R + Rs in the manner of his illustration. These flexion lines and furrows are of significance in the mechanics of flight, whereas true fold lines are utilised during wing folding at rest. Frequently, fold lines are better observed when viewed from beneath the wing lamina.

Between the fore and hind wings a true homology can be discerned; the hind wing has a claval furrow as one of its most stable features. A major fold anterior to the claval furrow is the equivalent of the fore wing radial fold but probably functions principally as a fold line in repose. The jugal lobe in Aculeata is defined by a pronounced incision and by a remnant of the jugal fold. The application of various synonymic terms is summarised below, with the terms employed by three recent authors listed in columns.

Brothers, 1975	Richards, 1977	Wootton, 1978
Fore wing		
—	Radial fold	Median flexion line
Plical furrow	Vannal fold	Claval furrow
Hind wing		
—	Radial fold	—
Plical furrow	Vannal fold	Claval furrow
Jugal fold	Jugal fold	Jugal fold

Salman (1929) referred to the radial fold of the hind wing as the intermedian fold.

The jugal fold is normally detectable only basally; it is usually replaced by a substantial incision from the wing margin which generates the jugal lobe (= anal lobe).

The claval furrow runs to the so-called preaxillary incision in both fore and hind wings. When the incision is sufficiently marked, it may generate a lobe (plical lobe *sensu* Brothers, 1975), here called a claval lobe to maintain consistency of usage.

Day (1984b) proposed terms to differentiate between fully developed veins and the conditions exhibited during various stages of reduction. During the same period, Mason (1986) was developing a similar system with recommendations for conventions governing illustration of veins. These systems are complementary, not mutually exclusive; similarities and differences are summarised below. The terms are listed in columns below the authors, with a simple definition between.

Day, 1984b		Mason, 1986
Vein	(with definite edge)	Tubular vein
Relict (vein)	(pigmented)	Nebulous vein
intergrades with		
Relict (vein)	(unpigmented)	Spectral vein
Atrophied	(a reduced tubular vein)	—
Evanescent	(a tubular vein reduced almost to extinction)	—
Adventitious	(a <i>de novo</i> structure)	Adventitious

Pompilidae exhibit examples of most of these conditions, largely in the distal sections of the wing.

Pompilid venation is remarkably uniform by comparison with some other groups, but many minor characteristics are of taxonomic value within the family. Most species exhibit a fore wing with a complement of 10 closed cells; the most common reduction is loss of the second radio-medial crossvein (2rs-m). This may occur sporadically in one or other fore wing in many species; it is normal in *Evagetes dubius* and *Aporus unicolor*. The position of crossvein cu-a (nervulus) in relation to the separation of M and CuA is useful; if distal of the point of separation, cu-a is 'postfurcal'. The degree of angularity of 2rs-m is a useful character in some Pepsinae.

The fore wing of Pompilinae is normally recognised by the presence of a distinct 'pocket' or deflection of the course of CuA₁ (fig. 21) at its branching from CuA₂. In addition, many pompilines have a longitudinal fold line anterior to M + CuA which transgresses the second segment (abscissa) of M and 1m-cu to link with the radial fold distally (fig. 21). It is not always readily observed in set specimens of which the wings have been flattened but material killed in alcohol often dies with the wings folded longitudinally. It is not easy to observe Pompilidae at rest in the field, but it seems probable that, after the Vespidae, they are the largest group of wasps to exhibit such longitudinal folding.

The hind wing has several noteworthy features. Basally, the costa is composed of a single fused vein C + Sc + R + Rs, whereas in most other aculeates C + Sc and R + Rs are basally fused, but Sc separates from C distally before fusing with R + Rs. The costal cell is never entirely closed by a true vein, but usually has a pigmented relict (= nebulous) vein defining the anterior edge. The basal hamuli are clustered towards the base of the costa. In true pompilines (fig. 22) the cluster is strongly proximal to the separation of C from Sc + R + Rs, but in most other groups the cluster is at or distal to the separation (fig. 8). This character is of a consistency which gives it at least equal value with the fore wing 'pocket' in vein CuA₁. In all pompilids, the second segment (abscissa) of 1A is lost. Primitively, cu-a is a short crossvein more or less perpendicular to 1A, but it progressively adopts the form of a contiguous extension of 1A which extends distally to encounter CuA. If it encounters CuA distally to the separation of M from M + CuA it is said to be postfurcal.

The legs of Pompilidae are long; they are principally adapted for agile, fast running, and secondarily, in various species, for excavation of burrows. The coxae are large and powerful, those of the fore legs inserted relatively remotely from the other two pairs. The mid coxae are contiguous; the hind coxae lack any lamella. There is usually no trochantellus at the base of the femur; however, *Epipompilus* and *Dipogon* have a trochantellus at the base of the mid femur. Five tarsal segments is the rule. The fore leg bears a single tibial spur, the other legs a pair each; they differ from spines in that they articulate in intersegmental membrane rather than on the surface of the tibia. That on the fore leg, as in other Hymenoptera, is modified as a comb or calcar; those of the mid tibia are simple; and the larger of the hind pair is also modified as a calcar. The internal face of the hind tibia bears for its entire length a dense brush of short, erect hairs. Each tarsal segment bears a lamellate pad or plantula posteroventrally (fig. 25). Terminally the tarsi bear a pair of claws which may be bifid (fig. 19) or dentate (fig. 20) or, exceptionally, edentate. Between them is a sac-like structure, the arolium or pulvillus (fig. 25). This is partly covered by a plate, the orbicula or pulvillar pad, bearing setulae terminally which form the pulvillar comb. The fore claws of males of many genera are markedly asymmetrical (fig. 101), as may be the internal faces of the terminal tarsal segments (figs 99, 100). Spines which articulate on the surface of the segments of the legs fulfil various functions. When the second fore tarsal segment bears a spine midlaterally which is equal in length to that borne anterolaterally the tarsus is said to bear a tarsal comb (fig. 18). Such a comb is employed as a rake in the removal of spoil during digging. The fore tibia may also bear spines used in excavation. The kind and

distribution of spines on the legs (figs 15–17) are of importance in segregating the major groups of Pompilidae, as indicated in the keys and figures. Many Pepsinae bear serrate, scale-like teeth in a row on the dorsal surface of the hind tibia. These are formed directly from the integument rather than from modified spines (figs 12–14).

The abdomen of Pompilidae consists of six visible segments in the female and seven in the male; only the male has cerci (= pygostyles). As previously stated, the abdominal articulation is between the propodeum and the second true abdominal segment. The terga and sterna are simple and each segment telescopes within the preceding one. Spiracles are exposed on the first and second terga but those on terga 3 to 7 are often concealed by the preceding tergum. Thyridia (= gastrocoeli), specialised areas of the tergum of unknown significance, are known from the Ichneumonidae; they are present in Pompilidae (and many other Apocrita) but are concealed beneath the hind margin of the first or second tergum. Each tergum overlaps its corresponding sternum laterally without differentiation of a laterotergum save on the first segment, where a fine lateral rib or crease is visible in most groups. When the first visible segment is elongate and narrower immediately behind the articulation than its width at the articulation itself, then it is said to be petiolate. However, the abdomen has no constriction or articulation between the first and second segments: the first sternum is always simple and posteriorly overlaps the front edge of the succeeding sternum.

The female abdomen derives its considerable flexibility from this structure. It is probable that, when reflexed forwards to sting, the first tergum is pulled downwards between the hind coxae such that the faces of the lateroterga contact the internal faces of the hind coxae. Thus the first tergum forms, with the abdominal articulation as the anchor point, a stable platform from which the musculature acts. In contrast, the female abdomen of many other apocritan groups has developed particular articulations between specific segments. The second sternum, particularly in Pepsinae, exhibits an external transverse furrow (fig. 9) which does not itself provide an insertion for muscles internally. It probably enhances the three-dimensional structure of the sclerite, giving it greater rigidity under tension. Even when devoid of this furrow, the second sternum is usually the only abdominal sclerite to include some kind of concavity in its structure.

The sixth tergum forms a pygidium which is not especially differentiated but may bear developed bristles or small spines, or may be flattened and polished. It may be used as a hammer to compact the substrate during nest closure or as a trowel during cell construction. The sternum which it overlies is functionally a most significant sclerite; as in other Aculeata, it is specialised to envelope the sting, and thus control its deployment. It is probably as a consequence of this that in the Aculeata *s. str.* the seventh tergum (which would otherwise obstruct this development) is reduced to a small internal sclerite which survives mainly because it bears spiracles. The sternum forms a U-shaped trough with a pronounced carinate edge posteriorly; the sting apparatus protrudes at the base of the trough. Thin laterosterna overlap dorsally, thus enclosing the sting apparatus completely (figs 10, 11). The sting itself is normally downcurved, but in *Dipogon* and its allies a weak to very strong upcurve is characteristic. The sixth sternum in groups which have abandoned the nesting habit has no distinctive carina or U-shaped configuration but exhibits a pronounced lateral compression; in our fauna, *Ceropales* (fig. 11) is an example. It is noteworthy that *Epipompilus*, a genus with a marsupial kind of present-day distribution, is particularly distinguished from other Pompilidae by the form of the ventrally flattened sixth sternum.

The male abdomen reflects in a weaker form the female general structure. Terminally the seventh tergum is normally developed; in many genera it may be translucent white or yellow. Some genera develop complex mats or tufts of erect hairs on the sterna which are of value in species recognition. The sixth sternum bears a pair of strongly sclerotised sharp hooks posteriorly, a feature unique to the Pompilidae.

The male abdomen of a large proportion of species contains a peculiar exocrine

structure, hitherto unnoticed because it is usually overlain by the hind margin of a tergum or terga. Usually it is located in the intersegmental membrane between the second and third terga, but is occasionally found anteriorly in tergum 3, or infrequently (Ageniellini) both intersegmentally and in the tergal surface between multiple segments. A great diversity of form suggests an evaporative surface fed by micropores from gland cells which are expected to produce some kind of pheromone. This would be released in high concentration if exposed by elevation of the covering tergum. This structure has been called 'Day's organ' (Menke, 1982: 5); its presence in *Cryptocheilus* was briefly recorded (Day, 1984a: 92). Beneath the microscope it is often seen to be an extravagantly spectacular structure: preliminary investigation suggests that in some instances its form may be of generic value, but there are cases of closely related species in which the structure is present in one but absent in the other. However, some of those which appear to lack a specialised evaporative surface have nevertheless proved to possess gland cells and micropores so that the system may be almost universal in the Pompilidae. It is possible that the pheromone plays a role in species recognition during mating.

The terminal ventral sclerite appears to be the seventh sternum, that of the true eighth segment. However, the sternum of this segment is reduced to a small chevron-shaped transverse sclerite which is entirely withdrawn beneath the preceding sternum and overlaps the apodeme-like central process of the subgenital plate, the true ninth segment (fig. 23). The shape of this latter sclerite and the configuration of the erect hairs it bears, are often of great value in the recognition and diagnosis of species. The male genitalia are remarkable for another typically pompilid feature, the development of an additional pair of elongate 'appendages' from the basiparamere, the parapenial lobes (fig. 24). A further feature, more often absent, is the development of one or two pairs of sclerotised hooks on the lamina volsellaris, the basal hooklets. The structure of the genitalia is complex, and replete with minor specific characters in many genera.

Affinities

The Pompilidae have often been treated as a discrete superfamily and in recent years have been allied with the Rhopalosomatidae, a rare pantropical group of parasitoids of crickets. Taxonomic treatments of the latter group overlap historically with the Pompilidae because Arnold (1935), in his review of the African 'Psammocharidae', described brachypterous rhopalosomatids as pompilids. The subsequent identification of these taxa as rhopalosomatids has not provoked analysis of their true relationships other than in the broad context of reassessments of the Aculeata (e.g. Brothers, 1975).

The individual characters which have been used to support a relationship between Pompilidae and Rhopalosomatidae are:

(a) The larger hind tibial spur is developed as a calcar, by development of a basal tuft of bristles. This supposed similarity ignores the very different structure of the hind basitarsus and the great development of a shaped brush of bristles basally, very different from the simple bristles of the pompilid hind tarsus.

(b) Loss of the second abscissa of 1A in the hind wing; this supposed similarity ignores the strong development in rhopalosomatids of the preaxillary excision such that a marked claval (= plical, = vannal) lobe is present in addition to a well-marked jugal lobe. No pompilid has a claval lobe, indeed, the preaxillary excision is hardly ever developed at all.

(c) The hind wing C + Sc + R + Rs are fused to form a single vein basally, and bear clustered basal hamuli. However, the basal hamuli are large and more numerous than those of Pompilidae; in fact they are more like those of Xyelidae, indicating that the clustering of the basal hamuli is of little taxonomic value. The distal configuration of the hind wing leading edge is quite different, with C virtually eliminated.

I conclude that the Rhopalosomatidae have no special affinity with the Pompilidae. Several features, however, parallel those of the vespid (*s.str.*) branch of the Aculeata. In particular:

(a) The eyes are emarginate.

(b) A trochantellus is well developed in most rhopalosomatids as in many vespoids. However, a weak trochantellus at the base of the mid femur is present in Pompilidae such as *Dipogon* and *Epipompilus*.

(c) The pronotum is relatively strongly coadapted to the mesothorax and produced rather than rounded beneath.

(d) The propodeal to abdominal articulation is not reinforced by a thickened posterior rim as in Pompilidae, but is laterally strengthened and protected by vertical carinate flanges, as in Vespidae.

(e) The abdomen exhibits a pronounced articulation between segments 1 and 2 whether or not the abdomen is petiolate.

(f) The anterior surface of tergum 2, between the hind margin of tergum 1 and the spiracle, bears a well-marked, exposed thyridium, elongate in *Rhopalosoma* and *Paniscomima*, less so in *Liosphex*; this is evident also in many Eumenidae. This is really a consequence of the development of the preceding character.

A character of interest, probably synapomorphic in the Rhopalosomatidae, is the obliteration of the costal cell of the fore wing.

Thus, I have no doubt that the Rhopalosomatidae are more or less correctly placed as an early and distinctive divergence of the vespoid line in all recent classifications. The real problem is that of placing the Pompilidae. Current placements are the result of emphasising particular characters, just as earlier classifications resulted from different emphases, such as the postulated relationship with the Sphecidae implied by Haupt (1950). As modern analyses of the morphology of the Aculeata progress, so these emphases will continue to alter. However, from the characters listed in the diagnosis, the following can readily be stated:

(a) The Pompilidae form a highly homogeneous, distinct lineage with several highly consistent synapomorphies but with a relatively primitive groundplan.

(b) Nevertheless, the groundplan is unequivocally that of a member of the Aculeata *s.str.*, with female tergum 7 reduced and withdrawn; with 12 female antennal segments and 13 in the male.

It is not appropriate to attempt to juggle with the classification of the Aculeata using the characters of a single contained group. However, I expect that future studies, using more refined assessments of the character set, will place the Pompilidae as one of the earliest and most discrete branches of the Aculeata *s.str.* For the present, it is best to continue treating the family Pompilidae as an early offshoot of the vespoid stock.

Within the family, two generally discernible morphological trends, which are difficult to characterise absolutely, correspond to the separation of the traditional subfamilies Pepsinae and Pompilinae, whose major attributes are used in the key to genera. A profusion of additional specialised groups has variously been assigned status as subfamilies or as tribes; I have earlier listed these (Day, 1981). However, most have simply been based on genera of markedly atypical habitus rather than on a synthesis of significant characters. The pepsine morphology has generally been regarded as the more primitive and the pompiline as derived. Groups such as the Ceropalinae are an unassignable remnant of the taxa based on atypical genera. It may be that the Aculeata became excavators to discover prey rather than to inter them and have progressed to fossorial nesting *via* prey transport as an intermediate stage. In particular, the stereotype sand-nesting Pompilidae are largely pompiline and the most primitive habits may be those exhibited by genera such as *Epipompilus* and *Dipogon*. A more detailed understanding of pompilid biology may well give valuable insights into the evolutionary relationships of these taxa.

Biological evolution

Pompilidae exist at the expense of spiders, an ancient group of terrestrial invertebrate predators. It is thus probable that the ancestors of Pompilidae are amongst the earliest evolved segregates of the solitary Aculeata, though the fossil record is inadequate to confirm this. Certainly, assignable aculeate forms are recognisable from the Lower Cretaceous, though the earliest reliably pompilid fossils are inclusions in Baltic amber. Published opinion (Evans, 1962: 775) assigns these to *Epipompilus*, but I have re-examined this material, which consists largely of male specimens, and I am convinced that the bulk belongs to *Dipogon*. One female specimen can be seen to possess the tuft of bristles on each maxillary cardo which is characteristic of *Dipogon*. Both *Epipompilus* and *Dipogon* are extant genera whose habits are consistent with entrapment in resin.

The only reliable exception to the rule that spiders form the prey of Pompilidae is a single observation of a phalangid (also an arachnid) as prey (Evans, 1948). No other records of non-spider prey can be confirmed from specimens, and must be suspect. Similarly, records of spiders as prey must be regarded as suspect as to the identity of both pompilid and spider unless confirmable from specimens and I have thus, somewhat arbitrarily, ignored early records unless frequently repeated. The following summary also includes information gleaned from European records when the prey cited is a species which occurs in Britain. It is intended to give an overall view of the prey relations of the British Pompilidae but it must be emphasised that observations in Britain are infrequent and indeed are still completely lacking for several species. Richards & Hamm (1939) published a comprehensive review of the biology of the British fauna, as known at that time, but it is subject to the above constraints. Bristowe (1948) summarised his own observations of certain species; Grandi (1961) gave a summary of his experiences of the European fauna. Evans (1953) reviewed the biology of Pompilidae in the context of taxonomic implications; and later, developed this theme in relation to behaviour patterns (Evans & Yoshimoto, 1962). Gros (1982; 1983a; 1983b) has recently published observations on a diversity of species in France and the Mediterranean Basin. Fitton, Shaw & Austin (1987) review the hymenopterous groups associated with spiders.

The British spider fauna contains 30 families; of these, 13, representing 45% of the British species, contain species recorded as prey of Pompilidae. However, only about 60 species, less than 10% of the British fauna, have actually been reported. Record details are given under the treatments of the individual pompilid species. Members of the large family Linyphiidae (the money-spiders), with about 265 British species, are untouched by Pompilidae, but are often the prey of sphecid wasps such as *Trypoxylon* in Britain (and *Sceliphron* in Europe). There is a single European observation of the pompilid *Auplopus* feeding on a specimen of *Theridion* but not using it as provision.

Pompilidae universally use a single prey individual as provision for each larva. This contrasts with the sphecid spider-hunters which provision with multiple prey that they carry in flight rather than drag on the ground as pompilids invariably do; only *Miscophus* in the Sphecidae may perhaps drag prey. There is thus a clear division between the needs of Pompilidae and their sphecid competitors which may in part explain the limited pompilid prey spectrum. However, spiders as a prey group differ from holometabolous insects in that immature as well as full-grown individuals are available as prey. Thus, a pompilid species may have available a significant size range of prey and in consequence may produce progeny of similar size range. I have discussed (Day, 1981) the probability that fertilised eggs are laid on the larger host spiders and unfertilised eggs on the smaller, thus producing larger female progeny and smaller males, which is demonstrably the rule.

Spiders are fierce, well-armed predators, active in a variety of habitats and weather conditions. A pompilid, in order to vanquish its prey (which often may be of greater size than itself) must outmanoeuvre the prey to avoid its fangs (chelicerae) yet grapple

closely enough to administer its own paralysing sting. In most cases the wasp must then be able to drag off its prey. It seems that the evolution of morphology and behaviour in the Pompilidae, having early developed a successful combination of features, has since remained comparatively conservative. Long-legged agility at the expense of flight correlates with activity largely confined to periods of warm sunshine which will raise the respiratory rate and enhance activity. This contrasts with the attributes of spiders, which may be active on overcast days, often eschew sunlight and frequently depend on hunting strategies based on immobility and surprise, or on various kinds of snare.

The pompilid strategy depends on their ability to grapple with a spider at close quarters in order to gain a hold with the mandibles, usually at the base of one of the spider's coxae. Thence, however the spider reacts, the pompilid will be thrown about accordingly, but should be able to avoid the spider's chelicerae. Conversely, it is still well placed to reflex the abdomen towards the spider's venter. Thus, once the pompilid has secured its hold, it is virtually invincible and can easily sting the spider ventrally. In most instances the contest is almost instantaneously resolved. Some pompilid species have been observed to imbibe blood from the site of the wound.

The ecological niche in which spider prey are sought is the first variable determining the range of pompilid life histories. Species may be adapted to encounter a range of free-running spiders, or to seek and flush them from various kinds of refuges such as funnel webs or burrows closed by trap-doors, or from the typical orb spider's web. Within these limits the degree of prey specificity is determined. For example, in Britain web-spinning spiders are largely attacked only by *Caliadurgus fasciatellus* (Spinola) and *Episyron rufipes* (L.), representatives of distinct subfamilies which nest in different habitats in very different ways. Two British species of *Dipogon* take thomisid spiders, but the third, *Dipogon subintermedius* (Magretti), takes Segestriidae.

In evolutionary terms, a series of alternative strategies is presented once the prey has been overcome. The simplest, exemplified by *Aporus*, *Homonotus*, and the *Anoplochaes* group of *Arachnospila*, is to oviposit on the prey *in situ* and leave it to be consumed by the larva. In tropical regions this is a much more frequent strategy than has traditionally been supposed. The majority of our species, however, engage in some kind of transport of the prey. The manner of transport varies between species and genera; for example, *Pompilus cinereus* usually runs forwards, holding the prey in its mandibles, whereas most other Pompilinae run backwards, dragging the prey. *Auplopus* amputates the legs of its spider before transport and *Episyron* is more prone to fly for short distances with its prey. Transport may be to a place of temporary concealment, or to a predetermined nest site or cell (most Pepsinae) which may be a simple niche or crevice or an excavated cell, or a cell within a hollow stem or beetle boring (*Dipogon*) or a concealed but free-standing cell of mud globules, smoothed internally (*Auplopus*). In the Pompilinae, *Anoplochaes* and *Agenioideus* use simple crevices in a variety of substrates, and *Anoplius s.str.* uses multiple cells in stems or beneath stones, requiring minimum excavation. However, most other Pompilinae are equipped to tunnel in friable soils until a single cell is excavated terminally. The mandibles are used to break up the substrate, but a rake of spines on the fore tarsus, the tarsal comb, is used to eject spoil from the burrow. The site of the burrow is apparently not predetermined; after incarceration of the prey, the tunnel is back-filled and deserted. The tip of the abdomen is frequently used to tamp down the fill during closure; the surface may then be levelled to complete the process. The site of subsequent burrows bears no relation to earlier ones.

In contrast with the majority of genera which prey directly on spiders, *Evagetes* and *Ceropales* are cleptoparasites of other Pompilidae. *Evagetes* is a pompiline genus the species of which locate the provisioned cells of other pompilids, using the sensilla on their characteristically thickened antennae. *Evagetes* bears a distinct tarsal comb with which the female excavates down to the cell of the host pompilid, where she consumes the incumbent egg and substitutes her own. The burrow is then reclosed.

Ceropales is a member of a very distinctive group of Pompilidae of uncertain affinities, and operates quite differently. The female intercepts the female of another genus engaged in prey transport and, whether or not in the presence of the original captor, succeeds in introducing her egg into the lung-book of the spider. The *Ceropales* then leaves the scene, allowing the original captor to complete the process of nesting. However, the larva of *Ceropales* hatches first, seeks out the host egg and consumes it, thus taking possession of the provisioned spider.

Pompilid eggs are laid on the host in a species-specific position; individual pompilid females may be 'left-' or 'right-handed' in this respect. The spider may be more or less deeply paralysed; in the case of *Pompilus cinereus* (Day, 1981), the spider recovers much of its powers of movement and spins silk continuously whilst ambling about its cell, thus binding together and consolidating the sand grains which compose the walls. In three days the larva hatches and immediately punctures the host integument and begins sucking blood. As the larva grows the spider becomes weaker until it expires and is eventually almost entirely consumed.

The larva is a typical apodous mandibulate aculeate larva, with the second pair of thoracic spiracles very reduced, a character shared with the Tiphidae and Mutillidae. Evans (1959) has reviewed and, where possible, redescribed the larvae of the 20 or so species for which descriptions or material exist. A considerable lacuna in our knowledge is the larva of *Ceropales*: though it has been reared and observed, there is no published morphological description.

The pupal stage is passed within a characteristic, brown, silk cocoon which internally has a parchment-like quality. The pupa in all cases so far observed is noteworthy for a wealth of fleshy protuberances from the appendages and abdomen which serve presumably to position the pupa firmly within the cocoon. Most species overwinter as the mature larva, but *Anoplius viaticus* overwinters only as the adult female. Some species have only a single generation each year, but most are multivoltine. As with many predatory aculeates, it becomes impossible to specify the number of generations once they overlap.

The nature of pompilid life histories is such that some species can proliferate locally, in response to favourable microclimate, abundance of prey or suitability of nesting site. Thus species which are thought to be rare or which have not been seen for several years, may be relatively common when and where they are encountered. Other species may be widely distributed but not often taken in series. Thus two kinds of terms describing occurrence have been used in the species notes. A species may be frequent or infrequent, referring to the number of occasions on which it may be encountered; and it will be common, uncommon or rare referring to the numbers which occur when it is found. This may be further qualified e.g. locally common.

Males, usually the smaller sex, normally emerge in advance of females and seek them actively. However, copulations are very rarely observed and last only a few tens of seconds. Modern studies indicate that a full behavioural range of mating strategies (Day, 1984a) probably exists within the group, but little is known of this aspect of the British species. I have speculated above that the abdominal exocrine gland may play a role in species recognition during mating activity; this kind of information will only be acquired through life-history studies.

Records of natural enemies of Pompilidae are few in the literature; predators such as Cicindelidae and Asilidae may take pompilid adults. Hardly any parasitoid rearing records are available. Host species which nest in discrete cells are most suitable for such life history studies, thus records predominate for genera such as *Auplopus* and *Dipogon*. Ants are a frequent nuisance for nesting females, and parasitic Diptera such as miltogrammine Sarcophagidae are often observed shadowing pompilids which are transporting prey. Bombyliidae have been reared from tropical Pompilidae and Ichneumonidae and Chrysididae have been reared in Europe. Thus, some of the British Chrysididae must be expected to attack pompilids, as must mutillids such as *Myrmosa*

atra (Panzer). Chalcids such as *Melittobia acasta* which are general parasitoids of aculeate larvae are a further possibility. A chalcid, *Tetrastichus pompilicola* Graham, (Lindroth & Graham, 1960) has been reared from the Holarctic *Anoplius nigerrimus* in Newfoundland.

Pompilids themselves are frequent enemies, both intra- and interspecifically. During prey transport a preponderance of species deposit the prey temporarily in order to reconnoitre or to begin nest excavation. The prey may be hung above ground on the petiole of a leaf or on a branch of some low herb, or may be buried shallowly or simply hidden. Other females, conspecific or not, which encounter suitable, paralysed prey will immediately take advantage of the windfall. It has often been speculated that the cleptoparasitic habit evolved intraspecifically in some such manner. However, the cleptoparasitic genera such as *Ceropales* and *Evagetes* are not directly derivable from any extant non-cleptoparasitic species or genera. It seems more probable that *Ceropales* has evolved from an ancestral group already specialised as ectoparasitoids, which developed a behavioural preference for the prey of other genera, rather than from a group which itself transported prey. Likewise, *Evagetes* is behaviourally more easily derived from a group which sought and attacked subterranean prey *in situ*, located using the enhanced sensory capacities of the antennae. The prey would then have been exposed by excavation and overpowered in the usual way. The simple step of discriminating pompilid prey from active spiders would then give rise to the successful evolutionary line which *Evagetes* represents. Significantly, the capacity to paralyse prey is retained.

Collection and preparation

The Pompilidae is traditionally one of the aculeate families sought in dunes, sandpits and on sandy heaths. Several species are characteristic of these areas, but the real charm of open sand is that the collector has a better chance of seeing pompilids and a fair chance of catching them. Unlike other aculeates, a pompilid is not disposed to fly when a net is placed over it. Instead, it will run rapidly amongst vegetation or stones until it encounters a gap beneath the perimeter of the net through which it will instantly escape, perhaps unseen, leaving a puzzled entomologist to examine his net with fruitless care. It is for this reason that open sand is such a suitable habitat in which to collect, since the net ring may make complete contact with the ground. Even when a wasp is contained in the net-bag, care and dexterity are needed to transfer the specimen to a killing-jar for it will take immediate advantage of any opportunity for escape.

However, species of woodland and other vegetated situations offer greater promise to those who wish to study life histories rather than collect for its own sake. For example, none of the British *Priocnemis* has been observed nesting, but recent collecting suggests that, once a locality is found in which species are common, worthwhile results await a patient observer.

Pompilidae have universally been obtained by handnet, a technique which biases collections in favour of the numerous, the accessible and the attractive. British species such as *Priocnemis exaltata* or *Episyron rufipes*, which often visit flowers, can readily be taken in this fashion and can be despatched in a conventional killing bottle using ethyl acetate or cyanide. Specimens prepared directly after collection in this way give the most attractive results; otherwise they can be papered or stored in alcohol to await a more convenient time for preparation.

Some modern techniques developed for mass collecting are particularly suited to the collection of Pompilidae. The Malaise trap is especially good for taking series of males of species which otherwise are most frequently encountered as females. The catch is taken in a collecting pot which usually contains 95% alcohol, so a trap can be left in the field unattended for several days. Water traps or yellow pan traps are useful in taking

both sexes in vegetated situations, but material is collected into water containing a drop of detergent. They thus require daily servicing to replenish the water and to remove and store material in alcohol to forestall decomposition.

Both techniques thus impose the need to prepare material from alcohol. Specimens should be washed in clean water with a dash of detergent for a short period. They may be agitated or brushed with a fine paint brush to remove debris if necessary, then rinsed in clean water and returned to strong alcohol. Thence the specimens should be laid to dry on their sides on blotting paper, taking care to see that the wings are not crumpled. When dry externally, the specimens can be prepared conventionally, though they are less pliable than relaxed dry material due to fixation of the tissues.

Most specimens can be mounted directly using a continental pin. Because of the configuration of the thorax, the pin should be inserted through the right posterolateral part of the mesonotum, and should emerge through the venter of the mesepisternum in front of the right mid coxa. If the pin passes through the intersegmental membrane behind the fore coxae the specimen will be significantly weakened. When old and brittle, the prothorax will be prone to detach at the slightest vibration, taking head, fore legs and antennae with it. This may mean that the pin is not inserted perpendicular to the thorax but is directed more or less rearwards as compared with a pinned sphecid or bee. The long-term security of the specimen is, however, better ensured.

Small specimens (less than a few mm long) may be glued to the side of a pin with an alcohol-based adhesive such as Shellac. A small quantity of glue is applied to the pin at an appropriate height, nearer the head than the point. The pin is then laid with light pressure across the right side of the dry specimen against the thorax. Alternatively, specimens may be mounted on card points or micropinned. The latter is a more old-fashioned and time-consuming technique; if employed, it is best if the specimen is staged transversely on a very short piece of polyporus, with the right side of the specimen adjacent to the staging pin. Thus the abdomen will project clear of the stage, enabling the features of the male abdomen in particular to be examined more easily. Ideally, the subgenital plate and genitalia of males should be partially exerted before pinning, using a bent pin, manual dexterity, and practice. It is better if the legs and wings are not spread wide and set in traditional fashion. Specimens are more prone to breakage during microscopic examination if set, and also take up more space in the store box; thus the cost of storage is directly related to the attitude imposed. The wings are best disposed posterodorsally above the thorax, the legs close to the body with the femora more or less erect and the tibiae angled sharply downwards. If specimens are sufficiently relaxed, it is particularly useful for females to be set with at least one mandible open and the head tilted up so that the other mouthparts can be examined.

Checklist of British Species

The names listed as valid in the revised edition of Kloet and Hincks (Fitton *et al.*, 1978) are given in square brackets where they differ from those used here; Channel Island species not found in the British Isles are denoted by an asterisk (*).

References to original descriptions and subsequent taxonomic changes were given earlier (Day, 1979). Details of our spider fauna are culled from Bristowe (1971) and the checklists of Locket, Millidge & Merrett (1974) and Merrett, Locket & Millidge (1985).

POMPILIDAE

PEPSINAE

PEPSINI

CRYPTOCHEILUS Panzer, 1806

S. ADONTA Billberg, 1820
notatus (Rossius, 1792)
affinis (Vander Linden, 1827)

PRIOCNEMIS Schiødte, 1837
S. PRIOCNEMIS s.str.
agilis (Shuckard, 1837)
obtusiventris Schiødte, 1837
cordivalvata Haupt, 1927
exaltata (Fabricius, 1775)
fennica Haupt, 1927
gracilis Haupt, 1927
hyalinata (Fabricius, 1793)
femorals (Dahlbom, 1829)
parvula Dahlbom, 1845
propinqua (Lepeletier, 1845)
pusilla Schiødte, 1837
schioedtei Haupt, 1927
S. UMBRIPENNIS Junco, 1946
coriacea Dahlbom, 1843
periturbator (Harris, 1780)
susterai Haupt, 1927

CALIADURGUS Pate, 1946
fasciatellus (Spinola, 1808)

DIPOGON Fox, 1897
S. DEUTERAGENIA Suster, 1912
bifasciatus (Geoffroy in Fourcroy, 1785)
hircanus (Fabricius, 1798)
subintermedius (Magretti, 1886)
[*nitidus* (Haupt, 1927)]
variegatus (Linnaeus, 1758)

AGENIELLINI

AUPLOPUS Spinola, 1841
carbonarius (Scopoli, 1763)

POMPILINAE

AGENIOIDEUS Ashmead, 1902
cinctellus (Spinola, 1808)
sericeus (Vander Linden, 1827)*

POMPILUS Fabricius, 1798
cinereus (Fabricius, 1775)
plumbeus (Fabricius, 1787)

APORINELLUS Banks, 1911
sexmaculatus (Spinola, 1806)*

HOMONOTUS Dahlbom, 1843
sanguinolentus (Fabricius, 1793)

EPISYRON Schiødte, 1837
rufipes (Linnaeus, 1758)

ANOPLIUS Dufour, 1834
S. ANOPLIUS s.str.

caviventris (Aurivillius, 1907)
cardui (Perkins, 1917)
concinus (Dahlbom, 1845)
nigerrimus (Scopoli, 1763)
 S. ARACHNOPHROCTONUS Howard, 1901
infuscatus (Vander Linden, 1827)
viaticus (Linnaeus, 1758)
fuscus (Linnaeus, 1758)

ARACHNOSPILA Kincaid, 1900
 S. ARACHNOSPILA s.str.
rufa (Haupt, 1927)

S. AMMOSPHEX Wilcke, 1942
anceps (Wesmael, 1851)
consobrina (Dahlbom, 1843)
trivialis (Dahlbom, 1843)
wesmaeli (Thomson, 1870)

S. ANOPLACHARES Banks, 1939
minutula (Dahlbom, 1842)
spissa (Schjødte, 1837)

EVAGETES Lepeletier, 1845
crassicornis (Shuckard, 1837)
dubius (Vander Linden, 1827)
pectinipes (Linnaeus, 1758)
siculus (Lepeletier, 1845)*

APORUS Spinola, 1808
unicolor Spinola, 1808
femoralis (Vander Linden, 1827)

CEROPALINAE

CEROPALES Latreille, 1796
maculata (Fabricius, 1775)
variegata (Fabricius, 1798)

Keys to species

Keys are presented separately for females and for males, each for the entire fauna rather than as generic keys with separate keys to species. Notes on the species follow; these contain a summary of the variation in body length, which is quite variable in many species and thus undesirable as a key character. Where appropriate, comments are also given on difficulties which may be encountered in use of the keys.

- 1 Antennae of 12 segments; abdomen with six visible terga, often with visible sting **Females** (p. 19)
- Antennae of 13 segments; abdomen with seven visible terga, without sting **Males** (p. 24)

Females

- 1 Second sternum without a well-defined transverse groove; mid and hind femora almost always with dorsal preapical spines or bristles set in pits (figs 15, 16) 2
- Second sternum with a well-defined transverse groove (fig. 9); mid and hind femora without dorsal preapical spines or bristles set in pits [subfamily **Pepsinae**] 3

- 2 Spines at apex of hind tibia splayed outwards, irregularly spaced, of differing lengths (fig. 17); vein M of fore wing not reaching wing margin; eyes not close together beneath antennal sockets, labrum rarely strongly exerted; hind tarsal claws not rectangularly bent; sixth sternum not longitudinally carinate or folded ventrally, not terminally spout-like; vein CuA₁ deflected posteriorly forming a distinct 'pocket' (fig. 21) [subfamily **Pompilinae**] 7
- Spines at apex of hind tibia not splayed out, of regular length and spacing; vein M of forewing reaching wing margin; eyes much closer together opposite and below antennal insertions, labrum strongly exerted (fig. 149); sixth sternum longitudinally carinate or folded ventrally, terminally spout-like (fig. 11); vein CuA₁ deflected posteriorly but not forming a distinct 'pocket' [subfamily **Ceropalinae**] 43
- 3 Dorsal surface of hind tibia with a row of pronounced scale-like teeth (figs 12–15); without specialised groups of long, curved hairs on mentum or maxillary cardo; anterior terga almost invariably red 4
- Dorsal surface of hind tibia more or less smooth, without scale-like teeth; with specialised groups of long, curved hairs on mentum or maxilla; terga black 6
- 4 Thorax short, compact, pronotum short with abruptly vertical anterior face, propodeum strongly sloping posteriorly, smooth; fore tibia apically with a stout, curved spine opposite tibial spur (fig. 36); crossvein cu-a of fore wing not strongly postfurcal of vein M; fore wing bifasciate (fig. 35), face (fig. 34) **Caliadurgus fasciatellus** (Spinola) (p. 31)
- Thorax otherwise formed, with more rounded contours of pronotum and propodeum; latter usually with fine transverse striae, occasionally rugulose or smooth; fore tibia lacking a stout, curved spine apically; fore wing crossvein cu-a strongly postfurcal of vein M (e.g. figs 54, 57); wings variously infusate 5
- 5 Vein Rs distad of crossvein 3rs-m strongly curved towards wing margin (fig. 31); wings hyaline, with tips beyond closed cells infusate; propodeum strongly rugulose transversely; anterior terga red **Cryptocheilus notatus** (Rossius) (p. 28)
- Vein Rs distad of crossvein 3rs-m straight, meeting wing margin obliquely; wings more or less infusate, often with a whitish or hyaline spot beyond cells of fore wing; propodeum only rarely rugulose, usually striate, occasionally smooth; anterior terga almost invariably red [genus **Priocnemis** Schiodte] 16
- 6 Fore wing bifasciate; cardo of each maxilla bearing a group of forwardly directed, long, curved bristles (fig. 27); abdomen not narrowed just behind point of articulation with propodeum; sixth tergum with many strong, backwardly directed hairs densely grouped posteriorly; sting upcurved [genus **Dipogon** Fox, subgenus **Deuteragenia** Suster] 28
- Fore wing hyaline; mentum of labium bearing a group of forwardly directed, long bristles (fig. 26); abdomen distinctly narrowed just behind point of articulation with propodeum; sixth tergum posteriorly flattened, polished; sting curved downwards; fore wing hyaline or mildly infusate (fig. 45) **Auplopus carbonarius** (Scopoli) (p. 32)
- 7 Fore wing with two submarginal cells [crossvein 2rs-m is occasionally lost in individuals of many species of Pompilidae that normally have three submarginal cells, but only rarely from both fore wings simultaneously]; anterior terga red 8
- Fore wing with three submarginal cells; anterior terga red or black 9
- 8 Crossvein 2m-cu meeting vein M distally of, or occasionally interstitial with, the apparent crossvein 2rs-m; marginal cell twice as long as second submarginal cell (fig. 146); without a comb of spines on fore tarsus; antennae cylindrical in section; front swollen above antennal insertions; occipital carina lacking; pronotum elongate; fore femora swollen **Aporus unicolor** Spinola (p. 38)
- Crossvein 2m-cu meeting vein M proximally of the apparent crossvein 2rs-m; marginal cell of equal length to second submarginal cell (fig. 144); with a comb of spines on fore tarsus; antennae stout, ventrally flattened; front not swollen; occipital carina present; pronotum and fore femora normal **Evagetes dubius** (Vander Linden) (p. 37)
- 9 Vertex and temples sharply margined, antennae inserted beneath pronounced frontal swelling, clypeus elongate (fig. 147); crossvein cu-a of hind wing straight, perpendicular to vein 1A; black, thorax largely reddish; fore wing (fig. 148) **Homonotus sanguinolentus** (Fabricius) (p. 34)
- Head capsule not as above; crossvein cu-a of hind wing curved, not perpendicular to vein 1A; thorax never reddish 10
- * 10 Sixth tergum terminally bearing no setae which are distinctly more robust than the erect hairs of the sterna 11

20 * CAN BE AS LONG BUT THE THICKNESS IS IMPORTANT

- Sixth tergum bearing many backwardly directed long, thick setae most of which are distinctly more robust than the erect hairs of the sterna (figs 131–132); [genus *Anoplus* Dufour] 30
- 11 Tarsal claws bifid (fig. 19); pronotum, scutellum, postnotum, propodeum and first tergum with adpressed scale-like white hairs; postnotum distinctly shortened medially, expanded then contracted laterally (fig. 136); hind tibia red, abdomen yellow-maculate 30
 - Claws edentate or with a simple tooth; thorax and abdomen lacking scale-like hairs; postnotum more or less transverse; abdomen black, with or without anterior terga red 12
- 12 Abdomen black, with or without adpressed grey pubescence 13
- Abdomen with some red on anterior terga, usually the first three 15
- 13 Propodeum flattened, posterolaterally produced (fig. 30) as distinct conical projections; black, extensively grey-blue pubescent (*Channel Islands*) 33
 - Propodeum not flattened or posterolaterally produced; black, with or without grey-blue pubescence 14
- 14 Mandible with single subapical tooth behind apex; terminal tarsal segments with a longitudinal row of spines beneath, much smaller than those of the preceding segments (fig. 137); tergum 6 with closely packed, small globular spines, appearing densely punctured; face (fig. 138) 33
 - Mandible with two subapical teeth behind apex; terminal tarsal segments lacking spines beneath [genus *Agenioideus* Ashmead] 34
- 15 Pronotal hind margin distinctly angulate (fig. 29); antenna cylindrical, third flagellar segment at least three times as long as wide; mandible with two clearly defined teeth behind apex [genus *Arachnospila* Kincaid] 35
- Pronotal hind margin subangulate or arcuate (fig. 28); antenna stout, third flagellar segment less than three times as long as wide, ventral surface distinctly flattened (fig. 145); mandible with a single, clearly defined tooth behind apex [genus *Evagetes* Lepeletier] 41
- 16 Propodeum without erect hair; fore wing bifasciate, often with a whitish or hyaline spot in the wingtip beyond the closed cells (figs 51–56); [subgenus *Priocnemis* s. str.] 17
- Propodeum with erect hair; fore wing uniformly infusate (fig. 57); [subgenus *Umbripennis* Junco] 26
- 17 Anterior terga black; propodeum with markedly rugulose transverse sculpture 26
 - Anterior terga red; propodeum striate or smooth 18
- 18 Tooth of tarsal claw large, with proximal edge at a right angle to body of claw (fig. 63) 19
- 19 Tooth of tarsal claw small, with proximal edge sloping at the same angle as distal (fig. 20) 20
- 19 Postnotum equal to or not quite as long as metanotum (fig. 62); antennal segments shorter, thicker (third flagellar segment three times as long as thick, fig. 50); propodeum distinctly rounded to declivity; second submarginal cell (fig. 56) equal in width to third on vein Rs; a robust species 29
 - Postnotum at least as long as metanotum (fig. 61); antennal segments longer, thinner (third flagellar segment at least three and a half times as long as thick, fig. 49); propodeum sloping evenly to declivity; second submarginal cell (fig. 54) wider than third on vein Rs; a more slender species 29
- 20 Postnotum longer than metanotum (fig. 58); fore wing, fig. 55 29
 - Postnotum equal to or shorter than metanotum 21
- 21 Postnotum equal to or shorter than metanotum, sometimes little more than half as long; fore wing more or less uniformly infusate, with at most a limited hyaline area in wingtip beyond closed cells (most marked in Scottish specimens); propodeum appearing granular, with more or less weak striae posteriorly 29
 - Postnotum about half as long as metanotum, normally less; fore wing only very rarely without a definite hyaline or whitish area in wingtip 22
- 22 Margin of clypeus with a definite unpunctured, polished transverse area, at least equal to length of terminal segment of maxillary palp; crossvein 2rs-m sharply bent inwards adjacent to vein M, second submarginal cell much longer than third on vein Rs (fig. 51); legs variously red coloured, but hind femora and tibiae almost always so coloured 28
 - Margin of clypeus dull, if with a shining area then only centrally; crossvein 2rs-m less sharply 28

- bent adjacent to M, second submarginal cell usually subequal to third on vein Rs; legs normally black, occasionally diffusely red; when, rarely, hind legs are markedly red, then propodeum is granular or smooth and shining, lacking transverse striae 23
- 23 Propodeum lacks obvious striae, usually appearing granular or smooth and shining; postnotum about half as long as metanotum, sometimes less, its posterior margin more or less transverse 24
- Propodeum with obvious striae, at least on posterolateral and posterior surfaces; postnotum less than half as long as metanotum, posterior margin of postnotum reflexed forwards somewhat, not always transverse 25
- 24 Area of wingtip outside closed cells large, i.e. length of R between stigma and Rs subequal to distance between wingtip and confluence of R with Rs (fig. 53); hind legs often with some red colour **Priocnemis gracilis** Haupt (p. 29)
- Area of wingtip outside closed cells small, i.e. length of R between stigma and Rs greater than distance between wingtip and confluence of R with Rs (fig. 52); hind legs rarely red, often brownish **Priocnemis cordivalvata** Haupt (p. 29)
- 25 Propodeum markedly striate posteriorly, less so dorsally; postnotum almost half as long as metanotum; collar black anteriorly; marginal cell relatively narrow, cf. fig. 53 **Priocnemis pusilla** Schiødte (p. 30)
- Propodeum striate posteriorly, hardly or not so dorsally; postnotum very narrowly constricted medially; collar red anteriorly; marginal cell relatively broad, cf. fig. 56 **Priocnemis schiødtei** Haupt (p. 30)
- 26 Antennae relatively short and thick, first flagellar segment as long as scape, second and third two and a half times as long as thick; clypeal margin convex (fig. 46) **Priocnemis coriacea** Dahlbom (p. 30)
- Antennae relatively long and thin, first flagellar segment exceeding scape, second and third at least three times as long as thick; clypeal margin concave 27
- 27 Fore femur with erect hairs ventrally; mid femur with erect hairs more or less equally dense on both dorsal and ventral surfaces, viewed laterally; clypeal margin only weakly concave (fig. 47); postnotum interrupted medially by a triangular polished depression (fig. 59) **Priocnemis perturbator** (Harris) (p. 30)
- Fore femur with little erect hair when viewed laterally; mid femur with erect hairs dorsally; clypeal margin weakly concave but faintly protuberant medially (fig. 48); medial interruption of postnotum not distinctly triangular (fig. 60). **Priocnemis susterai** Haupt (p. 30)
- 28 First flagellar segment approximately equal in length to scape (fig. 44) **Dipogon subintermedius** (Magretti) (p. 31)
- First flagellar segment substantially longer than scape, at least equal to scape plus pedicel (fig. 43) 29
- 29 Propodeum with marked transverse rugulosity; vertex with strong, erect black hairs **Dipogon variegatus** (Linnaeus) (p. 31)
- Propodeum smooth but with some punctures; vertex not strongly hairy **Dipogon bifasciatus** (Geoffroy) (p. 31)
- 30 All terga black; fore tarsus without a tarsal comb, i.e. second tarsal segment externally lacking a second spine equal in length to that borne terminally (figs 133–135); [subgenus *Anoplius s. str.*] 31
- Anterior terga at least partly red; foretarsus with a tarsal comb, i.e. second tarsal segment externally with a second spine equal in length to that borne terminally [subgenus *Arachnoproctonus* Howard] 33
- 31 Outer surface of fore basitarsus with two vertical rows of three spines, including those terminally; those of superior row little more developed than short, stiff hairs, those of inferior row definitely spinose, but not as long as segment bearing them is thick (fig. 135); second submarginal cell twice as long on vein Rs as third (fig. 123); clypeus long (fig. 130); sixth sternum with long, thin, hair-like setae (fig. 131) **Anoplius caviventris** (Aurivillius) (p. 34)
- Outer surface of fore basitarsus with two vertical rows of three or four spines, including those terminally; at least one spine of inferior row longer than thickness of segment bearing it (figs 133, 134); second submarginal cell otherwise (figs 121, 122); clypeus shorter, broader; sixth sternum with setae shorter, thicker (fig. 132) 32
- 32 Third submarginal cell (fig. 121) almost triangular, triangular or petiolate; comb spines of inferior row on fore basitarsus longer than those of superior row (fig. 133); erect hairs of thorax fine, short, with a few fine hairs on propodeum; largely with dark pubescence

- Third submarginal cell (fig. 122) subequal to second on vein Rs; comb spines of inferior row on fore basitarsus approximately equal in length to those of superior row, at least as long as segment bearing them is thick (fig. 134); erect hairs of thorax long, propodeum with many long hairs; with extensive pattern of fine silvery pubescence **Anoplius nigerrimus** (Scopoli) (p. 35)
- 33 First three terga with red bands, colour not reaching hind margins and more or less interrupted medially with black; propodeum with distinct erect hairs **Anoplius concinnus** (Dahlbom) (p. 34)
- First two terga light red, third light red anteriorly, with no median black interruption; propodeum devoid of erect hairs **Anoplius viaticus** (Linnaeus) (p. 35)
- 34 Fore tarsus with comb of long spines; mandible with two subapical teeth immediately behind apex; abdomen uniformly black, otherwise black with silvery pubescence (*Channel Islands*) **Anoplius infuscatus** (Vander Linden) (p. 35)
- Fore tarsus without comb of spines; mandible with one subapical tooth immediately behind apex, and a second remote from it, often hidden by mandible; black, with mandible and maculae on head and pronotum yellow, legs red **Agenioideus cinctellus** (Spinola) (p. 32)
- 35 Fore tarsus with comb of spines; labrum clearly exerted 36
- Fore tarsus without comb of spines; labrum clearly exerted [subgenus *Anoplochares* Banks] 37
- 36 Vein R of marginal cell approximately its own length from tip of wing (fig. 88); with substantial erect hair on head, thorax, propodeum; fore basitarsus with four comb spines (fig. 109); [subgenus *Arachnospila s. str.*] **Arachnospila rufa** (Haupt) (p. 36)
- Vein R of marginal cell at least 1.25 times its own length from tip of wing; normally with little erect hair on thorax or propodeum; fore basitarsus with three comb spines [subgenus *Ammosphex* Wilcke] 38
- 37 Face broad, width clearly exceeding twice width of an eye (fig. 107); third submarginal cell longer than second on vein Rs (fig. 93); fore basitarsus with a pair of spines at midpoint (fig. 103) **Arachnospila spissa** (Schiødte) (p. 37)
- Face narrow, width approximately twice width of an eye (fig. 108); third submarginal cell much shorter than second on vein Rs (fig. 94); fore basitarsus with a single strong spine at midpoint (fig. 102) **Arachnospila minutula** (Dahlbom) (p. 37)
- 38 Head with substantial erect hair; comb spines of second tarsal segment three-quarters length of third tarsal segment (fig. 104); vein R of marginal cell approximately 1.25 times its own length from tip of wing (fig. 92) **Arachnospila consobrina** (Dahlbom) (p. 36)
- Head with little erect hair; comb spines of second tarsal segment rarely three-quarters as long as third tarsal segment; vein R of marginal cell at least 1.5 times its own length from tip of wing (figs 89–91) 39
- 39 Propodeum with a characteristic coarse, reticulate-coriaceous surface sculpture, appearing granular, with a few fine semierect hairs posterolaterally; postnotum at least 0.75 times length of metanotum (figs 97, 98), little constricted medially; face narrow, temples narrow (figs 109, 110); clypeus angularly concave **Arachnospila anceps** (Wesmael) (p. 36)
- Propodeum without coarse surface sculpture, or if so, then without erect hairs posterolaterally; postnotum less than 0.70 times length of metanotum, or constricted medially; face broader, more convex, temples broader, clypeus transverse or angularly concave; if the latter, then margin brownish (figs 111–113) 40
- 40 Vein R of marginal cell less than twice its own length from tip of wing (fig. 90); clypeus not markedly angularly concave, margin black, polished; head (figs 112, 113); propodeum long, shining; postnotum 0.5–0.6 times length of metanotum (figs 95, 96); third flagellar segment not more than three times as long as thick **Arachnospila trivialis** (Dahlbom) (p. 36)
- Vein R of marginal cell twice its own length from tip of wing (fig. 89); clypeus angularly concave, margin brownish, polished, head (fig. 111); propodeum short, reticulate-coriaceous, devoid of hairs; postnotum about 0.6 times length of metanotum, constricted medially; third flagellar segment at least three times as long as thick **Arachnospila wesmaeli** (Thomson) (p. 36)
- 41 With four comb spines on fore basitarsus, each spine much longer than second tarsal segment, proximal spine sometimes shorter than other three (fig. 142) **Evagetes pectinipes** (Linnaeus) (p. 38)
- With at most three comb spines on fore basitarsus 42

- 42 Tarsal comb spines hardly longer than thickness of tarsal segments; head, thorax, and particularly propodeum with substantial erect hair; propodeal declivity mildly concave [*Channel Islands*] **Evagetes siculus** (Lepelletier) (p. 38)
- At least the two distal basitarsal comb spines clearly longer than thickness of segment (fig. 143); head, thorax and particularly propodeum lacking substantial erect hairs; propodeum convex posteriorly **Evagetes crassicornis** (Shuckard) (p. 37)
- 43 Mesonotum closely punctate, additionally with a few large punctures; maculae on head, thorax and abdomen, terga black, some red on femora and tibiae; face (fig. 149) **Ceropales maculata** (Fabricius) (p. 39)
- Mesonotum closely punctate; black, with yellow maculae on head, thorax and abdomen; anterior terga and much of legs extensively ferruginous **Ceropales variegata** (Fabricius) (p. 39)

Males

(The male of *Priocnemis propinqua* is unknown)

- 1 Spines at apex of hind tibia short, regular in length and spacing, not splayed out; vein CuA₁ not deflected posteriorly to form a distinct 'pocket' (fig. 7); mid and hind femora usually lacking dorsal preapical spines set in pits 2
- Spines at apex of hind tibia long, irregularly spaced, splayed out (fig. 17); vein CuA₁ deflected posteriorly to form a distinct pocket (fig. 21); mid and hind femora with dorsal preapical spines set in pits (figs 16, 17) [subfamily **Pompilinae**] 7
- 2 Hind legs of normal proportions relative to fore and mid legs, hind tarsal claws usually toothed (rectangularly bent in *Auplopus*, fig. 25); distal antennal segments tapering normally, antenna not appearing 'clubbed'; eyes not close together beneath antennal sockets; labrum not strongly exerted; sometimes with trace of a transverse groove on second sternum [subfamily **Pepsinae**] 3
- Hind legs exceptionally long relative to fore and mid legs, hind tarsal claws rectangularly bent (fig. 150); distal antennal segments broad, antenna appearing clubbed; eyes much closer together opposite and below antennal insertions, labrum strongly exerted (fig. 149); with no trace of groove on second sternum [subfamily **Ceropalinae**] 42
- 3 Crossvein cu-a meeting vein CuA of fore wing at a point strongly postfurcal of vein M by at least 0.5 of length of cu-a (figs 54/57) 4
- Crossvein cu-a meeting vein CuA of fore wing at a point postfurcal of vein M by less than 0.25 of length of cu-a (figs 7, 24) 6
- 4 Hind tarsal claws rectangularly bent (fig. 25); with substantial erect white hair; subgenital plate raised medially, keel-like, lower face with large yellow maculae adjacent to eyes; black, wings hyaline **Auplopus carbonarius** (Scopoli) (p. 32)
- Hind tarsal claws toothed; either virtually devoid of erect hairs, or substantial erect hair dark; only rarely with any erect white hairs, in which case spurs white; subgenital plate flat, with various patterns of erect hairs on ventral surface; face black, rarely with narrow yellow maculae adjacent to eyes; black, usually with red on anterior terga, wings with various infusate patterns 5
- 5 Vein Rs distad of crossvein 3rs-m strongly curved towards wing margin, wings hyaline with infusate tips beyond closed cells (fig. 31); propodeum transversely rugulose; face with yellow maculae adjacent to eyes **Cryptocheilus notatus** (Rossius) (p. 28)
- Vein Rs distad of crossvein 3rs-m straight, meeting wing margin obliquely (figs 54, 57); propodeum striate or smooth; wings variously infusate; face black [genus *Priocnemis* Schjødt] 16
- 6 Tibial spurs white or stramineous; mandible with a single tooth behind apex, not strongly hairy; antenna not crenulate beneath; body black, clypeus often with yellow maculae laterally, hind femora at least with some red colour, fore wing lightly infusate **Caliadurgus fasciatellus** (Spinola) (p. 31)
- Tibial spurs brown or black; mandible bidentate behind apex, strongly hairy; antenna often crenulate beneath (figs 37, 39); body black, fore wing bifasciate, sometimes only faintly so [genus *Dipogon* Fox, subgenus *Deuteragenia* Suster] 27
- 7 Fore wing with two submarginal cells (figs 144, 146) [crossvein 2rs-m is occasionally lost in individuals of many species of Pompilidae that normally have three submarginal cells, but only rarely from both fore wings simultaneously] 8
- Fore wing with three submarginal cells 9

- 8 Marginal cell twice as long as second submarginal cell (fig. 146); crossvein 2m-cu meeting vein M distally of, or occasionally interstitial with, the apparent crossvein 2rs-m; mandible with two teeth behind apex; hind femora with some red colour at least ventrally
Aporus unicolor Spinola (p. 38)
- Marginal cell of length equal to second submarginal cell (fig. 144); crossvein 2m-cu meeting vein M proximally of the apparent crossvein 2rs-m; mandible with one tooth behind apex; legs black; subgenital plate (fig. 140) **Evagetes dubius** (Vander Linden) (p. 37)
- 9 Vertex and temples sharply margined, antennae inserted beneath pronounced frontal swelling, clypeus elongate (fig. 147); crossvein cu-a of hind wing straight, perpendicular to vein 1A. **Homonotus sanguinolentus** (Fabricius) (p. 34)
- Head capsule not as above; crossvein cu-a of hind wing curved, contiguous with, not perpendicular to, vein 1A 10
- 10 Tarsal claws bifid (fig. 19) 11
- Tarsal claws dentate (fig. 20) or lacking any tooth 12
- 11 With adpressed scale-like pubescence on prothorax, propodeum and first tergum; fore claws symmetrical; postnotum distinctly shortened medially, expanded then contracted laterally (fig. 136) **Episyrus rufipes** (Linnaeus) (p. 34)
- Without adpressed scale-like pubescence; foreclaws asymmetrical; postnotum not medially constricted [genus *Anoplius* Dufour] 29
- 12 Abdomen black, with or without adpressed prey pubescence 13
- Abdomen with some red on anterior terga, usually the first three 15
- 13 Propodeum flattened, posterolaterally produced (fig. 30) as distinct conical projections; black, extensively grey-blue pubescent (*Channel Islands*) **Aporinellus sexmaculatus** (Spinola) (p. 33)
- Propodeum not flattened or posterolaterally produced; black, with or without grey-blue pubescence 14
- 14 Tarsal claws usually lacking a tooth; terminal four antennal flagellar segments thicker than proximal seven; fore basitarsus with a distal and a median spine externally, each at least as long as the segment is thick; black, extensively grey or grey-blue pubescent; subgenital plate, genitalia (figs 23, 24) **Pompilus cinereus** (Fabricius) (p. 33)
- Tarsal claws toothed; terminal flagellar segments not thicker than proximal; without long spines on fore basitarsus; not grey pubescent, but black at least with some adpressed silver pubescence on propodeum, tergum 7 with a white spot [genus *Agenioideus* Ashmead] . 33
- 15 Posterior pronotal margin very strongly angulate (fig. 29); first antennal flagellar segment at least twice as long as thick [genus *Arachnospila* Kincaid] 34
- Posterior pronotal margin subangulate or arcuate (fig. 28); first antennal flagellar segment not more than twice as long as thick [genus *Evagetes* Lapeletier] 40
- 16 Face, temples and propodeum with little or no erect hair; crossvein cu-a meeting vein CuA of fore wing at a point postfurcal of vein M by less than 1.1 times the length of cu-a (fig. 55) [subgenus *Priocnemis s. str.*] 17
- Face, temples and propodeum with substantial erect brown hair; crossvein cu-a meeting vein CuA of fore wing at a point postfurcal of vein M by at least 1.1 times the length of cu-a (fig. 57) [subgenus *Umbripennis* Junco] 25
- 17 Subgenital plate not **clearly*** incised apically (figs 70, 79) 18
- Subgenital plate with an angularly incised posterior margin (figs 80-87) 22
- 18 Subgenital plate parallel-sided, narrow, tongue-like (figs 72-75) 19
- Subgenital plate broader, posteriorly tapering slightly (figs 70, 76-79) 20
- 19 Subgenital plate with a median row of long, erect hairs inserted on slight median longitudinal ridge (figs 74, 75) **Priocnemis agilis** (Shuckard) (p. 28)
- Subgenital plate with shorter erect hairs, scattered over whole surface save a small central area distally (figs 72, 73) **Priocnemis parvula** Dahlbom (p. 29)
- 20 Tarsal claws with small triangular tooth; at least first and second terga red; subgenital plate with straight erect hairs (figs 70, 71) **Priocnemis exaltata** (Fabricius) (p. 29)
- Tarsal claws with large triangular tooth, with proximal edge at a right angle to body of claw (fig. 63); terga black, at most with reddish band on second tergum; subgenital plate with hairs erect but abruptly bent posteriorly at tip (figs 76-79) 21
- 21 Sixth sternum with two groups of erect hairs posteriorly, not so long as those of subgenital plate (figs 78, 79); second submarginal cell subequal to third on vein Rs; postnotum approximately equal in length to metanotum; usually with red colour on hind femora, often with a red band on second tergum **Priocnemis byalinata** (Fabricius) (p. 29)

* SOME TIME V. REDUCE OR MISSH

* = deeply

- Sixth sternum with a group of erect hairs posteriorly, the central of which are marginally longer than those of the subgenital plate (figs 76, 77); second submarginal cell longer on vein Rs than is third; postnotum longer than metanotum; only very rarely with red on second tergum or hind femur **Priocnemis fennica** Haupt (p. 29)
- 22 Subgenital plate proximally with a fine transverse pattern of reticulate sculpture; with a few fine erect hairs disposed centrally, long erect hairs disposed in a single row bordering plate, projecting posteriorly at an angle, tips straight (figs 80, 81)
. **Priocnemis pusilla** Schiødte (p. 30)
- Subgenital plate lacking reticulate sculpture; tips of long lateral erect hairs variously bent 23
- 23 Central area of subgenital plate polished, with scattered short erect hairs arising from very small pits; long lateral erect hairs arising perpendicularly, variously bent at tip (figs 82, 83)
. **Priocnemis schiødteii** Haupt (p. 30)
- Central area of subgenital plate with large punctures; tips of long erect lateral hairs curved distally 24
- 24 Subgenital plate long, not broad, more or less flat, erect hairs irregularly bent at tip (figs 84, 85) **Priocnemis gracilis** Haupt (p. 29)
- Subgenital plate narrow proximally, much expanded distally, slightly concave, erect hairs smoothly tapered (figs 86, 87) **Priocnemis cordivalvata** Haupt (p. 29)
- 25 Clypeal margin convex; subgenital plate not angularly incised distally (figs 68, 69)
. **Priocnemis coriacea** Dalhborn (p. 30)
- Clypeal margin arcuately concave; subgenital plate angularly incised distally 26
- 26 Subgenital-plate with a proximal median swelling, with minute short erect hairs thereon; surface with a fine reticulate pattern; margin of apical incision not sharply angulate medially, pointed posterolaterally (figs 64, 65) **Priocnemis perturbator** (Harris) (p. 30)
- Subgenital plate more or less flat, without fine hairs in centre; surface with a coarse reticulate pattern; margin of apical incision sharply angulate medially, rounded posterolaterally (figs 66, 67) **Priocnemis susterai** Haupt (p. 30)
- 27 Antennal flagellar segments more or less tubular, not markedly crenulate ventrally (fig. 38); subgenital plate with no noticeable erect hairs on median keel (fig. 42)
. **Dipogon bifasciatus** (Geoffroy) (p. 31)
- Antennal flagellar segments markedly crenulate ventrally; subgenital plate with noticeable erect hairs on median keel (41) 28
- 28 Antennal segments with rounded ventral crenulations (fig. 37); subgenital plate with long, curved, erect hairs medially (fig. 41); propodeum transversely rugulose
. **Dipogon variegatus** (Linnaeus) (p. 31)
- Antennal segments with angular ventral crenulations (fig. 39); subgenital plate with short, straight, erect hairs medially, rectangularly bent at tip (fig. 40); propodeum with little sculpture, polished, with discrete punctures **Dipogon subintermedius** (Magretti) (p. 31)
- 29 All terga black, with more or less silver or grey pubescence [subgenus *Anoplius s. str.*] 30
- At least second tergum with a thin transverse band of red colour, more frequently whole of second tergum and part of first and third, red [subgenus *Arachnoproctonus* Howard] 32
- 30 Subgenital plate flat; sterna 4 and 5 with pairs of hair-mats composed of backwardly directed erect hairs (fig. 126) **Anoplius caviventris** (Aurivillius) (p. 34)
- Subgenital plate folded longitudinally; without hair-mats on sterna 31
- 31 Third submarginal cell triangular or petiolate; with very little erect hair on propodeum; subgenital plate boat-shaped, entire (figs 121, 124); largely dark pubescent.
. **Anoplius nigerrimus** (Scopoli) (p. 35)
- Third submarginal cell at least 0.5 times as long on vein Rs as is second submarginal cell; propodeum with noticeable erect hairs; subgenital plate large, strongly folded longitudinally, apically incised (figs 122, 125); with extensive patterns of fine silvery pubescence
. **Anoplius concinnus** (Dalhborn) (p. 34)
- 32 Hind margin of sternum 5 with a large, square incision (fig. 127); propodeum devoid of hairs; sometimes with red colour of terga much reduced; with mat of short, fine, erect hairs on sterna 4 and 5 **Anoplius infuscatus** (Vander Linden) (p. 35)
- Hind margin of sternum 5 not incised (fig. 128); propodeum with strong erect hairs; first three terga red; with mat of very fine hairs on sternum 4 **Anoplius viaticus** (Linnaeus) (p. 35)
- 33 Black except for white spot on tergum 7; subgenital plate flat (*Channel Islands*)
. **Agenioideus sericeus** (Vander Linden) (p. 33)

- Black, with small yellow spot on upper face adjacent to eye, hind tibia proximally with a yellow-white fleck above; tergum 7 white; subgenital plate longitudinally raised medially, carinate **Agenioideus cincitellus** (Spinola) (p. 32)
- 34 Vein R of marginal cell approximately its own length from tip of wing (fig. 88); head and thorax strongly hairy; subgenital plate with a strong longitudinal keel medially (fig. 114) [subgenus *Arachnospila s. str.*] **Arachnospila rufa** (Haupt) (p. 36)
- Vein R of marginal cell at least 1.3 times its own length from tip of wing; only rarely with substantial erect hair on thorax; subgenital plate otherwise [subgenera *Anoplochares* Banks, *Ammosphex* Wilcke. 35
- 35 Hind tibia distally with anterior face swollen (fig. 106); subgenital plate flat (fig. 120); terminal fore tarsal segment (fig. 99) **Arachnospila minutula** (Dahlbom) (p. 37)
- Hind tibia not dilated, subgenital plate otherwise 36
- 36 Third submarginal cell noticeably greater in area than second, longer on vein Rs than second (fig. 93); subgenital plate boat-like, slightly curved, with strong, short spines on posterior and lateral edges (fig. 119); terminal segment of fore tarsus as fig. 99 **Arachnospila spissa** (Schiodte) (p. 37)
- Third submarginal cell not of greater area than second; subgenital plate otherwise; terminal fore tarsal segment as fig. 100 [subgenus *Ammosphex* Wilcke] 37
- 37 Subgenital plate with group of long or short erect hairs centrally near tip, more or less perpendicular to surface. 38
- Subgenital plate without long or short perpendicular hairs near tip 39
- 38 Subgenital plate terminally with tuft of short hairs (fig. 117) **Arachnospila anceps** (Wesmael) (p. 36)
- Subgenital plate terminally with group of long, erect hairs, forming a 'hair pencil' (fig. 116) **Arachnospila wesmaeli** (Thomson) (p. 36)
- 39 Subgenital plate flat, with slight raised median longitudinal ridge, with numerous short, erect hairs generally distributed (fig. 118); without erect hairs on propodeum **Arachnospila trivialis** (Dahlbom) (p. 36)
- Subgenital plate a flattened boat-shape, lacking erect hairs (fig. 115); with long erect hairs on propodeum **Arachnospila consobrina** (Dahlbom) (p. 36)
- 40 Subgenital plate with strongly raised median keel; with strong, erect, dark hairs on propodeum [*Channel Islands*] **Evagetes siculus** (Lepeletier) (p. 38)
- Subgenital plate flat; propodeum without strong, erect, dark hairs 41
- 41 Subgenital plate, when fully exposed, with a pair of longitudinal carinae, one each side of median line (fig. 139); second antennal flagellar segment twice as long as thick **Evagetes crassicornis** (Shuckard) (p. 37)
- Subgenital plate, when fully exposed, with a pair of laterally disposed nipples (fig. 141); second antennal flagellar segment 1.5 times as long as thick **Evagetes pectinipes** (Linnaeus) (p. 38)
- 42 Mesonotum closely punctate, additionally with a few large punctures; black, with yellow maculae on head, thorax and abdomen, some red on femora and tibiae **Ceropales maculata** (Fabricius) (p. 39)
- Mesonotum closely punctate; black, with yellow maculae on head, thorax and abdomen; anterior terga and much of legs extensively ferruginous **Ceropales variegata** (Fabricius) (p. 39)

Notes on the species

Subfamily Pepsinae Tribe Pepsini Genus *Cryptocheilus* Panzer

This widespread genus is best represented in the warm Palaearctic, with species in the Nearctic, Africa and the Orient. So far as can be determined, species excavate

multicelled nests in pre-existing cavities; the cells are excavated in advance of hunting, each with its own short entrance burrow. The single British species is a member of the subgenus *Adonta* Billberg.

Cryptocheilus notatus (Rossius). Female 9–15 mm, male 7–11 mm. Infrequent, sometimes locally common; one of our larger pompilids and not easily confused with other British species. Cornwall and Glamorgan to Berks, Kent and Essex; Channel Islands; June to September; on sandy ground, heathland. The species was reported in Poland using small mammal burrows in which to excavate cells. Spiders particularly of the families Agelenidae (*Tegenaria*) and Dictynidae (*Ciniflo*) are recorded as prey, but Gnaphosidae (*Drassodes*) and Lycosidae have also been reported.

Genus *Priocnemis* Schiødte

Priocnemis s. l. is a large genus of worldwide distribution, with many and diverse groups of species in the tropics which are as yet poorly collected and little understood. So far as is known, species are fossorial nesters, largely in woodland and forest. It is probable that multilocular nests are excavated, the cells of which have very short entrance tunnels, usually taking advantage of natural cavities or abandoned aculeate burrows. The taxonomic complexity of the two Holarctic subgenera which are represented in Britain suggest that, even when well collected, the genus will still present considerable difficulty. Most British species frequent flowers such as *Daucus* and *Heracleum*, otherwise they would be even less well known.

Subgenus *Priocnemis* Schiødte

The ten British species of this subgenus include some of those most difficult to identify. Provided the males are adequately prepared, the subgenital plates are conveniently diagnostic. The females of the group itself are readily recognised since most have bifasciate wings with a characteristic whitish spot in the wingtip and the abdomen red anteriorly. Those of *P. agilis*, *P. parvula*, *P. pusilla*, *P. cordivalvata*, *P. gracilis* and *P. schiødtei* can adequately be identified using the key only when the individuals conform well to the characters employed. Some individuals of these species can be difficult or impossible, and the key reflects this. To present the indefinite alternatives which could be used might lead to confident positive identifications being made which might nevertheless be erroneous. In the key's present form identifications made confidently will most probably be correct, but a larger percentage of specimens will be impossible to place. The proportion of such specimens can be reduced only by experience of the group and access to adequate material for comparison. In particular, individuals of *P. parvula* with a short postnotum and translucent spot in the wingtip will most often be confused with *P. pusilla* or *P. gracilis*; individuals of *P. gracilis* with dark legs and reduced translucent spot will be confused most often with *P. parvula*; and occasional specimens with rudimentary striae on the propodeum posteriorly will suggest *P. pusilla*. Spooner (1932) was the first to confront these problems in identification of the British species.

Apart from reports of prey and records of flowers visited, there is a dearth of real information about the habits of the entire genus, a consequence of the vegetated habitats preferred by the species masking their activities. The identities of the pompilids cited in some old records are doubtful, and these are best ignored.

Priocnemis agilis (Shuckard). Female 6–10 mm 6–8 mm. Infrequent, sometimes locally common; east Kent to Dorset, Somerset, Glamorgan, north to Cheshire and

Lincolnshire; Channel Islands; June to September, frequenting dry grassy banks and open grassy areas on clay soils. Comes to *Daucus*; no reliable prey records. This is the best characterised of the 'difficult' species, particularly because of the strongly angled vein 2rs-m.

Priocnemis cordivalvata Haupt. Female 5–8 mm, male 4–7 mm. Infrequent, occasionally locally common; a species of sunny glades in mature woodland on clay soils; Kent to Devon, Essex, Bedford, Lincolnshire; July and August. A female was taken in Sussex: Hastings, 9.viii.1983, (*G. Dicker*) with an immature spider (Gnaphosidae). One of the 'difficult' species, but with a reliable character in the shape of the marginal and submarginal cells.

Priocnemis exaltata (Fabricius). Female 5–12 mm, male 5–9 mm. The largest species of the subgenus and one of the commonest British Pompilidae. England, Wales, Scotland and Ireland; Channel Islands; May to September. A wide variety of prey is recorded, all wandering spiders of the families Lycosidae, Salticidae and Pisauridae. The prey is grasped at the base of a leg whilst the wasp walks backwards. The species has been observed nesting on the continent, where it was found to stock multiple cells at the bottom of a single burrow.

Priocnemis fennica Haupt. Female 5–10 mm, male 5–7 mm. This species has only recently been discriminated in the British fauna (Day, 1979). It proves to be the more widely distributed component of the '*P. femoralis*' of earlier authors; England, Wales, Scotland (Aberfoyle), Ireland; Channel Islands; June to September. Sometimes locally common; published prey records of Lycosidae and Salticidae are all attributed to '*P. femoralis*'; many may therefore apply to *P. hyalinata*, the other component of the species-pair. The latter is predominantly a continental species restricted to southern England; *P. fennica* is dominant on the Atlantic seaboard and rare in the continental hinterland. A record of *Pardosa pullata* (Clerck) (as *Lycosa*) as prey in Ireland is thus certainly of *P. fennica*. Possibly a species with an affinity for watersides.

Priocnemis gracilis Haupt. Female 5–9 mm, male 4.5–9 mm. Infrequent, sometimes locally common; Kent to Dorset, north to the Humber; southern Ireland; June to September. A species of woodland, on stiff clay soils, and on more open broken ground with clay, particularly at coastal sites in the east and south. Gros (1982) recorded the species taking a spider (Salticidae) at Roffey in France. A specimen recently taken in Kent: Newington, 29.viii.1984 (*G. Dicker*) was transporting an immature *Clubiona* (Clubionidae). This is one of the difficult species; most easily confused with *P. parvula* and *P. pusilla* (see above). Traditionally, it has been thought most frequently to be confusable with *P. cordivalvata*, but the wing venation character illustrated (figs 52, 53) should suffice to separate these two species. Both species were believed to be rare, but recent collecting has yielded notable series from a few localities. The species occur together regularly on the Massif of Sart-Tilman in Belgium, and have been found to do so in Britain recently (Firestone Copse, Isle of Wight, and localities in Sussex).

Priocnemis hyalinata (Fabricius). Female 7–10 mm, male 6–8 mm. Infrequent; England south of Lincolnshire, south Wales; a continental species (see *P. fennica*, with which this species has in the past been confused); June to September. A female was taken in Sussex: Mountfield, 1.ix.1984 (*G. Dicker*) with a prey spider (Lycosidae).

Priocnemis parvula Dahlbom. Female 6–8 mm, male 5–7 mm. Frequent, often common; England, Kent to Cornwall, Wales, north to Scotland; Inverness, Sutherland; Channel Islands; no records from Ireland; June to September. The definitive *Priocnemis* of sandy soils and heathland. The female is usually distinctive; for the hyaline

spot in the wingtip is minimally developed. If in doubt, habitat is often a helpful pointer. Prey recorded are predominantly Lycosidae, also Thomisidae and Salticidae.

Priocnemis propinqua Lepeletier. Female 7–10 mm, male unknown. Known only from two females taken at the end of the last century at Lyndhurst, Hants; August; the specimens are still extant, and are certainly of this species; no other British species has a black abdomen or so strongly rugulose a propodeum. However, it has not been taken since and probably no longer occurs in Britain. The male is undescribed even from the continent; previous accounts are now believed to be of males of other species.

Priocnemis pusilla Schiødte. Female 6–10 mm, male 4–7 mm. Frequent, rarely locally common; southern England, Wales, north to Cumbria (Grange-over-Sands); Channel Islands; absent from Scotland, Ireland; June to September. The most frequently encountered of the 'difficult' *Priocnemis*, usually on lighter soils and the species most likely to be taken with *P. parvula*; the propodeum is usually sufficiently striate to permit identification according to the key, but it seems to be the most variable of the four; doubtful specimens of this group are best placed here. Early prey records will often be for this species but need confirmation; reliable records include Clubionidae and Salticidae; Gros (1982) reported the species in France using an abandoned burrow at the bottom of which a cell was excavated.

Priocnemis schioedtei Haupt. Female 5–11 mm, male 5.5–7.5 mm. Infrequent and uncommon but widely distributed; England and Wales: Kent to south Devon, Caernarvon, Leicestershire, Yorkshire, Cumbria; Scotland: Arran and Perthshire (Aberfoyle); July to early October; a species of woodlands. It has been reported taking prey at Hereford (Clubionidae). The red collar and constricted postnotum are the most reliable characters.

Subgenus *Umbripennis* Junco

In the British fauna the species of this Holarctic subgenus are vernal. All three species were said to overwinter as the adult female, and to emerge as soon as conditions were suitable. Males are infrequent in collections and were assumed to be the progeny of these emergent females; they were thought not to overwinter. There appears to be no justification for this view; both sexes seem to emerge together in the spring, probably having passed the winter as adults within the cocoon. The group includes some of our largest pompilids and has a characteristically hirsute habitus. Two of the species need care in determination; however, the key should suffice.

Priocnemis coriacea Dahlbom. Female 8–13 mm, male 8–11 mm. Infrequent, uncommon; southern England and Wales, Kent to Cornwall, north to Radnor and Lincolnshire; April to early June; on drier soils, often together with *P. perturbator*. An easily recognised species, for which no biological data are available.

Priocnemis perturbator (Harris). Female 9–17 mm, male 8.5–12 mm. Frequent but not particularly common; England, Wales, Scotland and Ireland; Channel Islands; April to early July; on drier soils. Most early prey records (of Lycosidae and Gnaphosidae) are unreliable since they could relate to several recently discriminated *perturbator*-group species, only two of which occur in Britain; collectively they were known as '*P. fuscus* (L.)' (see *P. susterai*, below).

Priocnemis susterai Haupt. Female 8–15 mm, male 9–11 mm. Infrequent, rarely common; southern England, Wales; April to June with the odd record in August.

The species occurs generally south of a line from East Anglia, Herts, Bucks, Gloucestershire, Hereford to N. Wales; perhaps commoner in the south-west, including Cornwall. Some early prey records for *P. perturbator* are perhaps for this species (see *P. perturbator*, above).

Genus *Caliadurgus* Pate

A well-defined genus with most species in the Neotropics, but some Oriental. The single British species has a Holarctic distribution.

Caliadurgus fasciatellus (Spinola). Female 5.5–9 mm, male 5–7 mm. Not readily confused with other species. Uncommon; southern England and Wales, north to Yorkshire (M. E. Archer, *in litt.*); June to early October, frequenting exposures of dry, sandy, or sandy-clay soils, in which a short, vertical burrow is excavated. The prey consists entirely of Araneidae (*Meta*, *Araneus*) which are sought on the web. The wasp employs forwards prey carriage, holding the spider between thorax and abdomen. The paralysed prey is interred in a vertical position in a smooth-walled ellipsoidal cell.

Genus *Dipogon* Fox

Dipogon is a distinctive genus of worldwide occurrence. The species nest in pre-existing cavities such as deserted insect borings in timber or hollow stems, or between the blocks of walls. Successive cells are provisioned; partitions are constructed from various materials, which are carried to the nest with the aid of the characteristic pair of bristle-tufts borne on the maxillae for which the genus is named. Undoubted specimens of *Dipogon* occur in Baltic amber. Three species occur in Britain, all members of the Holarctic subgenus *Deuteragenia* Susterka: They are black; the females have characteristically bifasciate wings; the males have a compact habitus with a short abdomen compared with those of other genera. The species may confidently be recognised by the characters given in the keys. The genus is not yet recorded from the Channel Islands.

Dipogon bifasciatus (Geoffroy *in* Fourcroy). Female 5–10 mm, male 4–6 mm. The least common *Dipogon* in Britain, restricted to southern England: Dorset, Hants, Wilts, Surrey, Gloucestershire, Bedfordshire, Suffolk; June to September. The species is said to overwinter as the adult female. It has been recorded nesting in rotten wood, insect borings, and walls; partitions are constructed of wood particles. The prey are spiders of the family Thomisidae, usually *Xysticus*.

Dipogon subintermedius (Magretti). Female 5–8 mm, male 4–5 mm. Locally common; a species of mature hedgerows and dead timber, a habitat in decline. Kent to Devon, north to Scotland (Aviemore); not recorded from Wales or Ireland; June to September. It will nest in walls, bramble stems and insect borings. *Segestria senoculata* (Linnaeus) (Segestriidae) is the prey; the paralysed spider is carried by the spinnerets, the wasp walking forwards. The recent edition of Kloet & Hincks's *Checklist* (Fitton *et al.*, 1978) recorded this species as *Dipogon nitidus* (Haupt); Wahis (1982) established the validity of the name here employed.

Dipogon variegatus (Linnaeus). Female 5–9 mm, male 4–6 mm. Not common, but widely distributed throughout England, Wales, Scotland and Ireland; June to September. It will nest in almost any cavity, including borings in timber, walls and snail shells. It has been observed to excavate a burrow rapidly in soft mortar using the robust mandibles. Spiders of the family Thomisidae are the prey, in Britain *Xysticus cristatus*

(Clerck). After provisioning, the cell is partitioned with detritus such as sand grains, earth particles and fragments of plant material, said to be bound together with spider's web. The species may be encountered in suburban gardens.

Tribe Ageniellini **Genus *Auplopus* Spinola**

Auplopus and its related genera constitute a worldwide assemblage, predominantly in the wet tropics, of rather homogeneous behaviour. The majority construct cells of mud prior to hunting, and store therein spiders from which some or all of the legs are amputated. After oviposition and closure of the cell, a further cell is constructed and provisioned, and so on. Within this broad framework, there is considerable diversity of architecture and location. Several species have evolved to a level at which a group of cells may be utilised jointly by a mother and several daughter wasps, though the constraint of hunting for and provisioning with single spiders inhibits true cooperation. The single British species is solitary.

Auplopus carbonarius (Scopoli). Female 7–10 mm, male 6–9 mm. A distinctive component of our fauna. Rare; Kent to south Devon, north to Merioneth and Lincolnshire; Channel Islands; June to August; females frequent banks of sandy clay by puddles or streamsides in order to collect nesting materials; males fly amongst vegetation, frequently settling on leaves. The species constructs small, barrel-shaped cells laid on their sides in sheltered situations such as beneath stones or in hollow trunks. Pellets of mud are held between the mandibles and the group of specialised hairs on the mentum during transport. The exterior appearance of the cells reflects their construction from individual mud pellets, each of which may be of different colour and texture, depending on its origin. The interior of each cell is trowelled smooth with the tip of the abdomen; after provisioning, the cell is closed. Subsequent cells are constructed in contact with the preceding so that a nest eventually may consist of a single block of cells, perhaps ten or more, somewhat irregularly oriented. The species hunts a wide range of free-living spiders amongst vegetation; Clubionidae (most frequently), Gnaphosidae, Salticidae, Agelenidae, Thomisidae, Lycosidae, Segestriidae and Anyphaenidae have all been recorded as prey. The wasp may fly with small prey individuals. As with many cell-building aculeates, the species may be found in outbuildings and houses; it is recently adventive in the eastern United States.

Subfamily Pompilinae **Genus *Agenioideus* Ashmead**

A worldwide genus, currently believed to include some of the more primitive Pompilinae. It is morphologically diverse, and subgeneric names have proliferated in attempts to analyse this diversity, with little success. I have thus omitted them in treating the two British species, only one of which occurs on the mainland.

Agenioideus cinctellus (Spinola). Female 5–7 mm, male 4–5 mm. Not easily confused. Infrequent, locally common; England north to Nottingham; Worcester, Suffolk, south Wales; Channel Islands; June to August. The species is typical of drier situations and sandy places; also dilapidated walls. It nests in a wide variety of natural cavities, also deserted aculeate burrows and empty mud cells; snail shells. Cells are closed with detritus; spiders principally of the family Salticidae are stored, sometimes Thomisidae.

Agenioideus sericeus (Vander Linden). Female 6–7 mm, male 4–6 mm. Channel Islands only; June to August. A species with a tarsal comb which excavates burrows in sandy slopes and loose stone walls. Spiders interred include Salticidae, Pisauridae, and Thomisidae.

Genus **Pompilus** Fabricius

The type-genus of the family is currently restricted to a few species widely distributed in the Old World, where they are dominant in habitats of open sand, particularly adjacent to water and subject to occasional inundation. The species are black with a vestiture of extensive adpressed grey pubescence which gives a characteristic habitus. The biology of the single British species has been the subject of many studies (Day, 1981).

Pompilus cinereus (Fabricius). Female 6–10 mm, male 4–6 mm. Readily recognised. Frequent, common; England, Wales, Scotland and Ireland; Channel Islands; May to September; in habitats featuring exposures of open sand. The species can become especially common in sheltered parts of coastal dunes; less so inland in sandpits and on heathland with sand exposures. Females hunt errant spiders, particularly Lycosidae (*Arctosa perita* (L.), *Xerolycosa*) and sometimes Clubionidae, Thomisidae and Pisauridae. The wasp is a rapid digger in loose sand, using the tarsal comb to rake back the sand grains; in damp sand, the particles are first loosened with the mandibles. After capture, the prey is temporarily buried whilst a suitable site for a nest burrow is sought. After partial excavation, the prey is carried in and the burrow extended. The spider recovers partially from paralysis after interment and wanders continually in the confines of the terminal cell. It is finally killed by the larva feeding on its abdomen, by which time it has laid a continuous filament of silk which binds together the sand grains of the cell wall and forms a complete protective envelope.

Genus **Aporinellus** Banks

A widely distributed genus with species on all continents except Australia. The characteristic posterolateral projections of the propodeum identify it easily in Europe. The vestiture is like that of *Pompilus*, a related genus. A single species, not recorded from the British mainland.

Aporinellus sexmaculatus (Spinola). Female 6–7 mm, male 5–6 mm. Channel Islands only; records only for June, but certainly active also in July and August. In France, Gros (1983a) observed the prey, a Salticid, temporarily hung above ground on vegetation whilst the female excavated a short burrow in sand.

Genus **Homonotus** Dahlbom

Homonotus is a non-fossorial genus widely distributed in the Old World. The very distinctive habitus is shared with other, unrelated genera, and has prompted some workers to accord subfamily status to this group. The appendages and body are so formed that they fit together and present a streamlined, bullet-like structure with no projections. This permits the females to squeeze through the material composing the nests of the host spiders, which are attacked *in situ*. Once the egg is laid, the spider is left to live normally until it succumbs to larval feeding.

Homonotus sanguinolentus (Fabricius). Female 7–10 mm, male 7–9 mm. Readily recognised. Rare, recorded from sandy heaths of Surrey, Hants (New Forest) and Dorset. July and August. Attacks *Cheiracanthium* (Clubionidae) in the nest.

Genus **Episyron** Schiødte

A distinctive worldwide genus, the species of which fly actively. *Episyron* and its relatives are specialist hunters of web-spinning spiders, and are fossorial in nesting habits. The British species is a dominant component of the aculeate fauna of open sand habitats in the Palaearctic.

Episyron rufipes (Linnaeus). Female 5.5–14 mm, male 5–10 mm. Well distributed on sandy soils, locally common on open sand, particularly coastal dunes; southern England to Lancashire and Yorkshire, Wales and south Ireland; Channel Islands; May to early September. Easily identified, but in Britain very variable in colour between populations; some males can be completely black. Both sexes frequent flowers. Araneidae (*Meta*, *Araneus*) are the usual prey, with a few records of Lycosidae. The prey is temporarily stored above ground on some convenient plant whilst the burrow is excavated in loose sand, employing the well-developed tarsal comb. Small prey individuals may be carried forwards by the wasp, using short, hopping flights.

Genus **Anoplius** Dufour

One of the better known pompilid genera, well represented in most regions of the world. Species of two of the principal subgenera occur in Britain.

Subgenus **Anoplius** Dufour

Most species of *Anoplius s. str.* are entirely black, sometimes with silver or other coloured pubescence. The group is of worldwide occurrence and is specialised towards exploitation of wet habitats. Some exotic species are capable of hunting over water, and one at least can follow *Dolomedes* spiders below the surface. Nesting habits tend towards the use of pre-existing cavities. Three species are found in Britain.

Anoplius caviventris (Aurivillius). Female 6–9 mm, male 5–7 mm. Infrequent, uncommon; southern England: Surrey to south Devon, north to the Forest of Dean and Northamptonshire; May to August; adequately characterised by the features given in the key. This is a species of bushy, vegetated places, particularly riversides and reed marsh. It stores spiders in serial cells in hollow plant stems (*Carduus* and *Phragmites*) and deserted aculeate burrows. Clubionidae are recorded as prey. Cell partitions are constructed of vegetable detritus; a nest was reported as terminally closed with pieces of grass.

Anoplius concinnus (Dahlbom). Female 7–12 mm, male 6–8 mm. Infrequent, rarely common; England, Wales, Scotland, Ireland; June to September; well characterised. This is a species particularly of stony or gravelly places; behind coastal shingle beaches or stony riversides. The females will run on wet stones exposed in streambeds, and fly between them and the banks. Multiple cells are excavated beneath stones and stocked with Lycosidae. The species appears not to have been taken in the south-east of England until the recent capture of a female at Dartford, Kent.

Anoplius nigerrimus (Scopoli). Female 6–8 mm, male 5–8 mm. Frequent, common; a Holarctic species; England, Wales, Scotland, Ireland; Channel Islands; May to September; well characterised. A widespread and versatile species, less strongly associated with wet habitats and nesting in a variety of situations; under stones, hollow plant stems, deserted aculeate burrows or snail shells, for example. Lycosidae, Gnaphosidae and Pisauridae have been reported as prey; however, care should be taken with old records since diverse species have been confused under the name *Pompilus niger*, once employed for this species.

Subgenus *Arachnoproctonus* Howard

This subgenus is particularly strongly represented in the New World and the Ethiopian region, where it is taxonomically very difficult. It is absent from Australia, but has several Palaearctic and Oriental species. Most species exhibit some red colour on the anterior terga. They are fossorial species largely associated with sandy soils or pure sand. The two British species are widespread in the Palaearctic.

Anoplius infuscatus (Vander Linden). Female 6.5–10 mm, male 5–8 mm. Frequent, common. A species of moist sand, especially of coastal England and Wales; Kent to Cornwall; Gower to Anglesey; Lancashire and Yorkshire; Channel Islands; June to September. Both sexes are usually easily recognised, although the female may be confused with some of the *Arachnospila* species with which it often occurs. Care should be taken to assess the terminal bristles of the sixth tergum in cases of doubt; even when broken, their insertions should be apparent. The female stores mostly Lycosidae, also Agelenidae and Thomisidae in short burrows in sand; the spiders are hung on low plants during nest excavation.

Anoplius viaticus (Linnaeus). Female 8.5–14 mm, male 7.5–12.5 mm. Infrequent, locally common; one of the larger Pompilinae; the tergal colour pattern of the female is diagnostic; sandy soils in England and Wales, north to Yorkshire, but inexplicably absent from many inland areas which appear suitable. Like the *perturbator* group of *Priocnemis*, the species is vernal; it overwinters as the adult female but unlike *Priocnemis* can be found throughout the summer. At the end of the season, females excavate burrows in sand to considerable depth, in which the winter is passed. Females are found from late March to September, males from late June to August. Prey consists primarily of Lycosidae with some Gnaphosidae and Agelenidae, sometimes also Thomisidae and Salticidae. This species is the subject of many biological accounts; after hunting, the prey is secreted amongst vegetation whilst the wasp excavates a short burrow in open sand.

Genus *Arachnospila* Kincaid

A predominantly temperate Holarctic genus, with a substantial boreal and montane element; limited Neotropical and African representation is montane. Several comparatively distinct groups are accorded subgeneric rank; examples of the three major groups occur in Britain.

Subgenus *Arachnospila* Kincaid

A Holarctic and Neotropical subgenus containing some of the larger, hirsute, fossorial species.

Arachnospila rufa (Haupt). Female 10–15 mm, male 8–11 mm. Taken on heathland in Dorset only twice (Spooner, 1937): Gore Heath, N. of Wareham, ♂, ♀, 15.vi.1934; Sherford Bridge, Gore Heath, ♂, 15.ix.1938 (*G. M. Spooner*); Channel Islands; June to September. The species is a common component of the north European fauna on sandy heaths, and well studied biologically. Readily recognised, it could not easily be overlooked in Britain unless it survives in unworked localities. Its catholic prey preferences include Gnaphosidae, Lycosidae, Clubionidae and Salticidae.

Subgenus *Ammosphex* Wilcke

This subgenus includes most of the smaller fossorial forms; it has the same distribution as the genus. The females in Europe are amongst the most difficult taxonomically in the family. Fortunately the British fauna contains only four relatively well-defined species, which nevertheless need care in identification. Spooner (1941) first demonstrated unequivocally the correct association of sexes in this group, shortly before Wilcke (1943) in Holland. Identification of males is fairly straightforward if the subgenital plates are well displayed. All four species may be found together in certain localities; one is widespread, the other three are of more restricted occurrence.

Arachnospila anceps (Wesmael). Female 6–10 mm, male 5–8 mm. Frequent, common; England, Wales, Scotland and Ireland; Channel Islands; May to September. One of the species most often encountered, on sandy and other soils, but rarely particularly numerous. The nesting behaviour is typical; prey spiders are hidden on a plant whilst a short burrow is excavated. Early prey records are unreliable because the identities of the pompilids are doubtful. However, recent captures indicate that a wide range of spiders is stored; Lycosidae, Clubionidae and Thomisidae certainly; perhaps also Gnaphosidae and Agelenidae.

Arachnospila consobrina (Dahlbom). Female 6–9 mm, male 5–7 mm. Rare; coastal sand and dunes of England and Wales; from Hayling Island east to Deal; Suffolk, Norfolk; south Wales: Porthcawl, Gower; north to Cheshire; July and August. This somewhat hirsute species is virtually unknown biologically, although it is distributed to the Canary Islands, Mt Kenya and Tadzhikistan. It is recorded taking a *Segestria* (Segestriidae) in Turkey.

Arachnospila trivialis (Dahlbom). Female 5.5–9 mm, male 5–7 mm. Infrequent, locally common. England and Wales north at least to Lancashire; Channel Islands; May to August; a species of open sand, most numerous in coastal dune habitats, but also occurring inland on heaths and in sandpits. It certainly preys on *Xysticus* (Thomisidae), perhaps also Lycosidae.

Arachnospila wesmaeli (Thomson). Female 5–8 mm, male 5–7.5 mm. Rare; England and Wales; coastal sand dunes and inland sandy heaths; Kent, Essex, Surrey, Berks, Hants, Dorset, Gower, Porthcawl, Aberdovey, Llanfairfechan, Cheshire and Lancashire; June to September. Less frequent than *A. trivialis* but more so than *A. consobrina*. In Europe, it is recorded taking Lycosidae, Gnaphosidae and Salticidae.

Subgenus *Anoplochares* Banks

A Holarctic subgenus of very uniform habitus. The female lacks a tarsal comb and the group is thus, exceptionally within the genus, non-fossorial. It is usual to separate *Anoplochares* males from those of *Ammosphex* on the form of the inner surface of the

terminal fore tarsal segment (figs 99, 100); however, the two species are much more easily recognised in the British fauna by the characters used in this key.

Arachnospila minutula (Dahlbom). Female 6–11 mm, male 6–9 mm. Infrequent, not common but surprisingly widely distributed. Southern England; Cornwall to Norfolk and Cheshire, with one record from Northumberland; recently, a male was taken in Scotland: Perthshire, Killiekrankie Pass; Channel Islands; June to September. No behavioural records had been made until Gros (1983a) found the species attacking a *Pardosa* (Lycosidae) beneath a stone, in France. He placed pompilid and spider in a glass tube, where he observed paralysis of the prey which was then pulled about the tube for a few seconds; oviposition ensued immediately. The spider recovered normal activity within the hour and survived, apparently normally, until killed by the well-grown pompilid larva. Thus *A. minutula* is probably an ectoparasitic species leaving the prey *in situ*.

Arachnospila spissa (Schjødte). Female 6–11 mm, male 6–9 mm. Frequent, fairly common; Great Britain and eastern Ireland; Channel Islands; May to August; on various soils, in woodland and other vegetated habitats. In Europe, the species has been observed attacking Lycosidae such as *Tarentula pulverulenta* (Clerck) in its nest burrow when the spider is guarding its eggs. The entrance was first blocked with vegetable detritus, after which the pompilid entered and paralysed the spider, which recovered soon after oviposition. Whilst the pompilid larva fed upon the spider, the spider consumed its own eggs. Thus the biology is very similar to that suggested for *A. minutula*.

Genus *Evagetes* Lepelletier

This behaviourally interesting genus is represented on all continents except Australia. It is extremely difficult to diagnose in the classic sense, yet the species present a typical stocky, robust habitus to the experienced eye. The female antennae are relatively short and thick for Pompilidae, with the ventral surface flattened and covered entirely with a well-developed sensory area. So far as can be determined, all the species are clepto-parasitic on other Pompilidae. The females bear a tarsal comb with which a route to the provisioned cells of pompilids of other genera is excavated. The egg of the original provider is consumed by the *Evagetes* female and her own is substituted, after which the cell is reclosed. It thus seems probable that fossorial species are the principal victims. There are three species in Britain and a fourth in the Channel Islands. Studies of the biology of these species are urgently needed.

Evagetes crassicornis (Shuckard). Female 6–9 mm, male 5–7·5 mm. Frequent, rarely common; a Holarctic species; England, Wales, Scotland and Ireland; Channel Islands; May to September; very widely distributed, even having been taken on a window in the Entomology Department of the British Museum (Natural History). However, it is most often encountered in sandy habitats where potential host species are plentiful. There is a dearth of reliable information because the host is rarely identifiable and most continental records cannot even be ascribed reliably to this species of *Evagetes*. The distribution of the species suggests at least that *Arachnospila anceps* and possibly *Anoplius nigerrimus* are hosts, and some of the fossorial species of sandy habitats. A record of *Arachnospila trivialis* as host in Sweden is probably reliable.

Evagetes dubius (Vander Linden). Female 4–9 mm, male 4–7·5 mm. Infrequent, sometimes locally common; south-east England, Dorset, Norfolk; June to September; principally on sandy heathland. This species remains an enigma; reports of it hunting spiders and nesting fossorially are current in the literature, yet most are repeats of early

observations which must be regarded as suspect. Reports that the species attacks the non-fossorial species of *Arachnospila* (*minutula*, *spissa*) are equally suspect. The morphology suggests that the species is cleptoparasitic; as it is the type-species of the genus, positive observations are urgently needed in order to clarify currently accepted biological extrapolations.

Evagetes pectinipes (Linnaeus). Female 9–11 mm, male 5.5–6 mm. Rare; probably recently adventive; sandhills at Deal, Kent; July and August. The female is readily recognised; the male needs more careful examination and can be confirmed only if the subgenital plate is extended. Almost certainly cleptoparasitic on *Epsyrion rufipes*, from which it is recorded on the continent and which occurs at Deal; perhaps other species as well.

Evagetes siculus (Lepelletier). Female 8–9 mm, male 8 mm. Channel Islands only; July and August. This is the most hirsute of the north-west Palaearctic *Evagetes* and thus fairly easy to recognise. There are no biological records.

Genus *Aporus* Spinola

Species of this predominantly Holarctic genus are enemies of trapdoor and other burrowing spiders, to attack which they have developed several specialised features. The head and thorax are variously elongated; the head is thin and somewhat flattened, the prothorax is elongate and accommodates powerfully developed fore femora; the fore legs are used to rip off the trapdoor to gain access to the host spider. The British species is one of the least modified of the genus.

Aporus unicolor Spinola. Female 6.5–11 mm, male 5–8 mm. Readily recognised. Local and irregular, rarely locally common in England south of the Thames; Channel Islands; July and August; often taken at wild carrot. The species has recently been shown (Else, 1975) to attack *Atypus affinis*, the purse-web spider. This, the only British mygalomorph spider, lives in a short, vertical burrow from which protrudes a closed sac of silk which lies upon the surface of the ground. Insects attracted to the sac are bitten through the silk by the spider which then cuts a hole through which the prey is drawn into the sac. *A. unicolor* must evade attack by the spider and gain access to the interior of the sac in order to paralyse its host. Development of the larva is at the bottom of the spider's burrow. The adult is morphologically one of the least specialised species of the genus presumably because it cuts rather than forces its way into the host cell. The known range of *Atypus affinis* is somewhat greater than that of *Aporus unicolor*, including S. Wales, Herts, Cambridge and Essex, so the pompilid may prove to be somewhat more widely distributed.

Subfamily Ceropalinae Genus *Ceropales* Latreille

This worldwide genus has adopted a uniquely specialised behaviour by which provision is made for the larva. The female *Ceropales* locates and intercepts a female pompilid of some other genus, engaged in the act of transporting a paralysed spider. The transporter is driven off, and *Ceropales* uses her highly modified abdomen to insert her egg into a lung-book of the inert spider, in which she then takes no further interest. The original captor normally then returns, to resume and complete the interrupted business of provisioning. The *Ceropales* larva hatches first, seeks out the egg of the host pompilid and consumes it. Development then proceeds normally. The morphological

specialisation of *Ceropales* is so pronounced that some authors have been disposed to grant the group status as a separate family.

Ceropales maculata (Fabricius). Female 6–9 mm, male 5–7.5 mm. Readily recognised. Generally distributed throughout the British Isles, including the Scilly Isles and the Isle of Man, but rarely locally common; Channel Islands; June to September. *Priocnemis exaltata*, *Pompilus cinereus*, *Agenioideus cinctellus*, *Arachnospila rufa*, *A. anceps*, *Anoplius nigerrimus*, *A. viaticus*, *A. infuscatus*, *Episyron rufipes* and *Auplopus carbonarius* have all been reported as victims of *C. maculata* either in Britain or Europe. Potentially, any species of pompilid which transports its spider prey is vulnerable. It is even possible that other hunters of spiders may be so (see under *C. variegata* below).

Ceropales variegata (Fabricius). Female 6–9 mm, male 5–7 mm. Readily recognised. A rare insect in Britain, on sandy heaths, Suffolk, Surrey, Hants, Dorset; Channel Islands; July and August. Maneval (1929) suggested that the species may attack spiders being transported by *Miscophus* species (Sphecidae).

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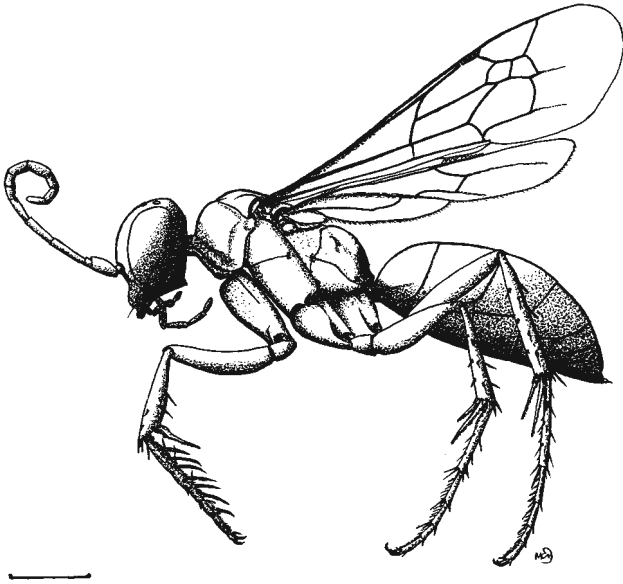


Fig. 1. *Pompilus cinereus* (F.) ♀, whole insect, general habitus, left lateral view; scale = 1.0 mm.

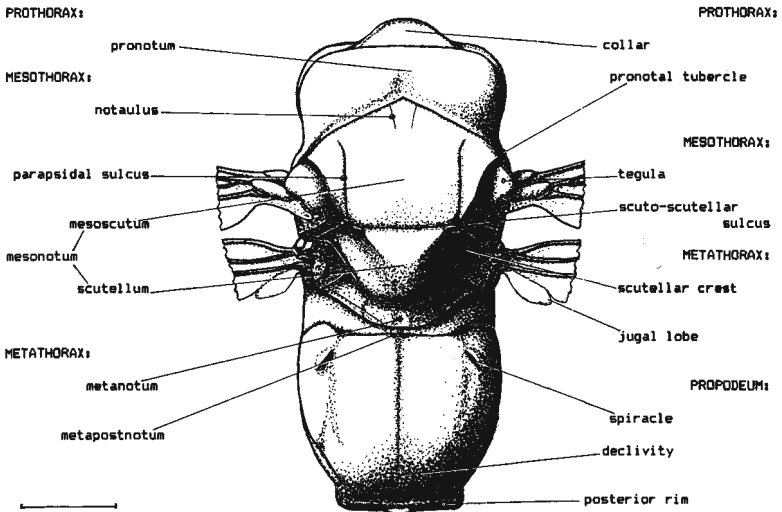


Fig. 2. *Pompilus cinereus* (F.) ♀, thorax, dorsal view, to illustrate terminology; scale = 0.5 mm.

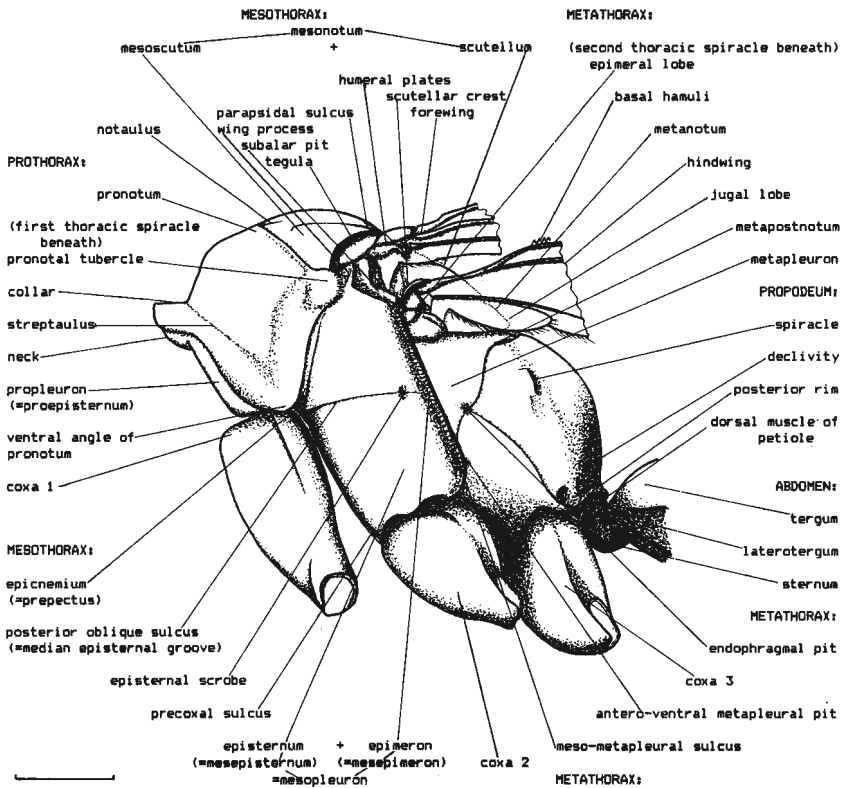
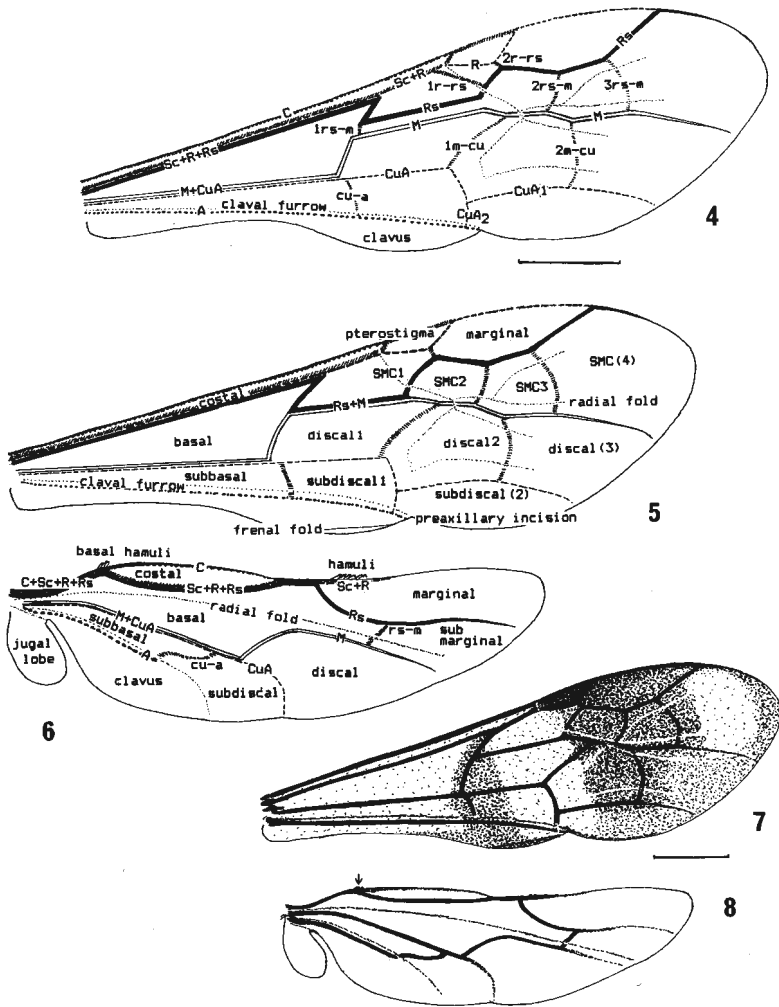
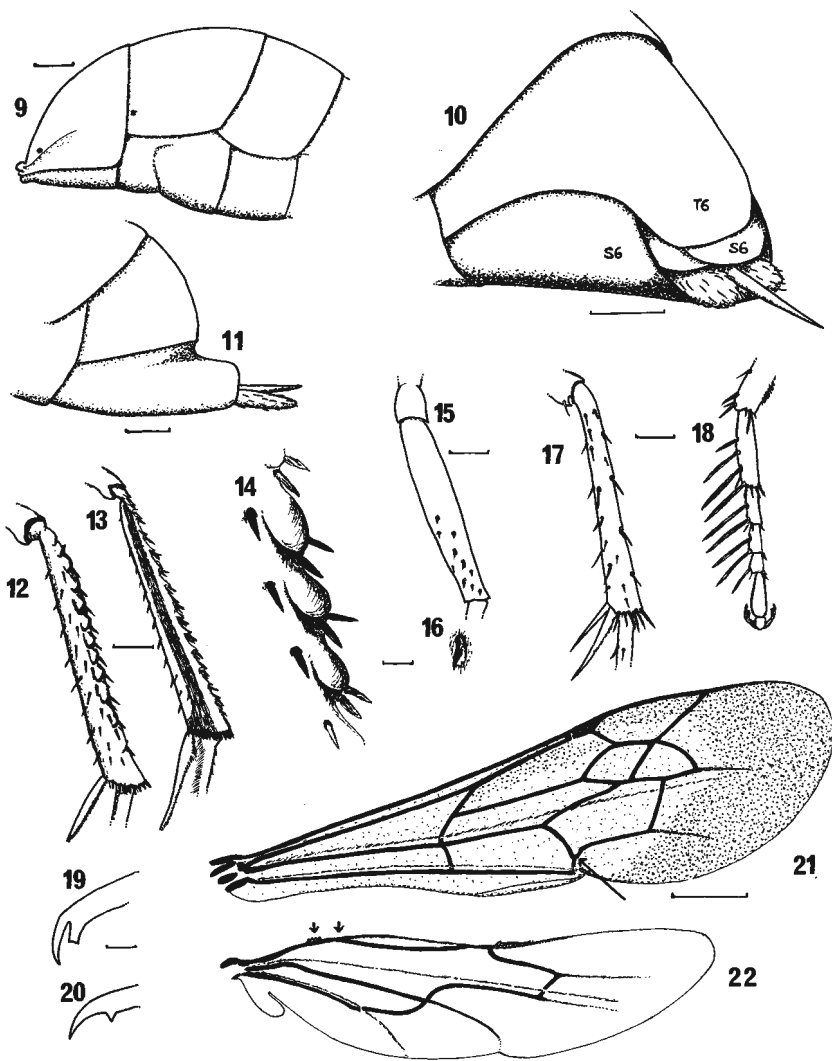


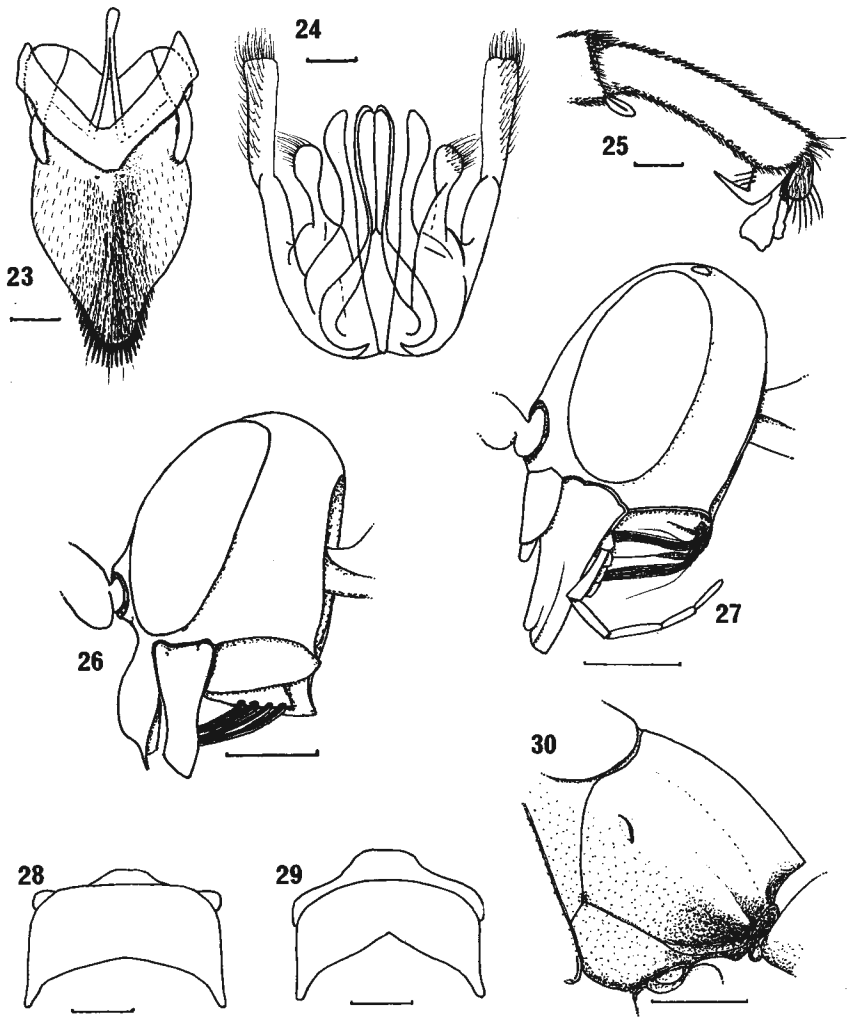
Fig. 3. *Pomilus cinereus* (F.) ♀, thorax, left lateral view, to illustrate terminology; scale = 0.5 mm.



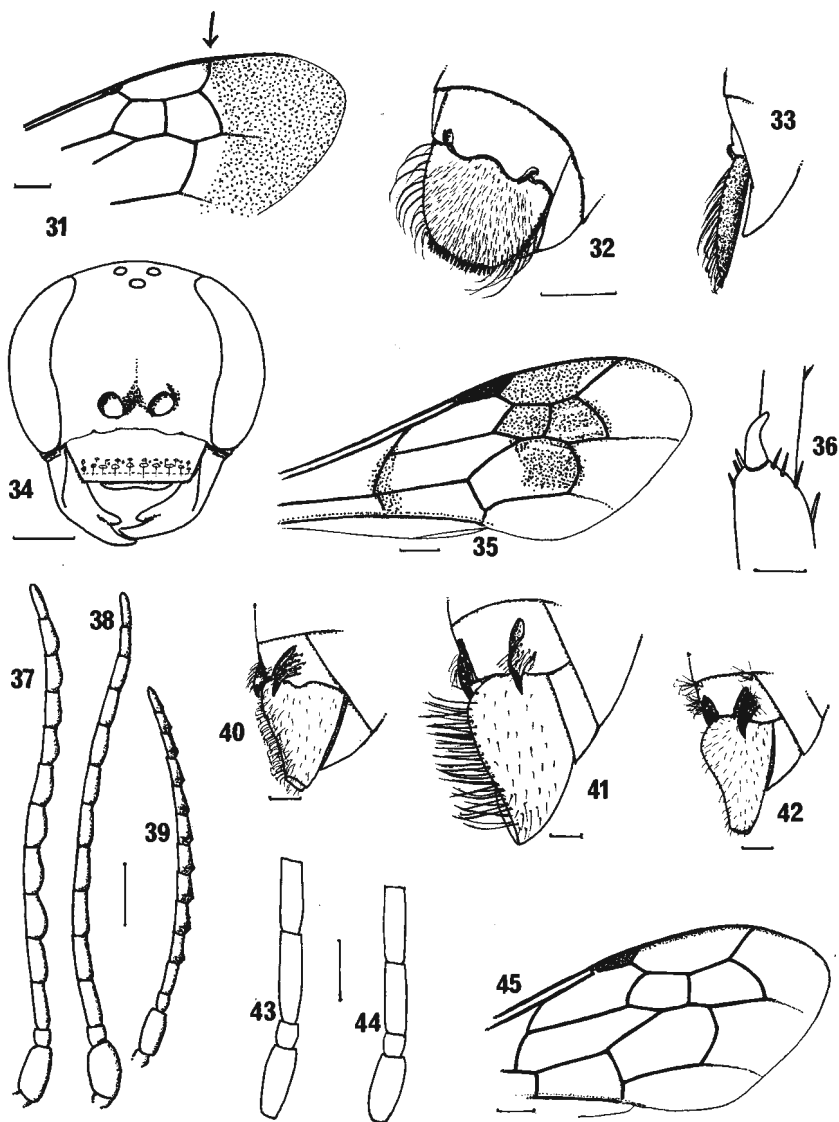
Figs 4-8. 4, hypothetical fore wing, labelled to illustrate vein terminology. 5, fore wing. 6, hind wing (diagrammatic), based on *Dipogon variegatus* (L.) ♀, to illustrate cell terminology. 7, 8, *Dipogon variegatus* (L.) ♀: 7, fore wing; 8, hind wing; scale = 1.0 mm.



Figs 9–22. 9, *Priocnemis exaltata* (F.) ♀, anterior abdomen, left lateral view showing sternal groove; scale = 0.5 mm. 10, *Episyron rufipes* (L.) ♀, abdomen, left posterolateral view; scale = 0.25 mm. 11, *Ceropales maculata* (F.) ♀, abdomen, left lateral view; scale = 0.25 mm. 12–14, *Priocnemis exaltata* (F.) ♀, hind tibia: 12, left tibia; 13, right tibia; both left posterolateral view; scale = 0.5 mm. 14, detail of tibial scale-like teeth; scale = 0.1 mm. 15–17, *Arachnospila rufa* (Haupt) ♀: 15, left mid femur, dorsal view, femoral spine-pits; scale = 0.5 mm. 16, detail of same; scale = 0.1 mm. 17, right hind tibia, left posterolateral view; scale = 0.5 mm. 18, *Evagetes pectinipes* (L.) ♀, right fore tarsus, tarsal comb; scale = 0.5 mm. 19, *Episyron rufipes* (L.) ♀, bifid tarsal claw. 20, *Priocnemis exaltata* (F.) ♀, dentate tarsal claw; scale = 0.1 mm. 21, 22 *Anoplius viaticus*, right fore and hind wings; scale = 1.0 mm.

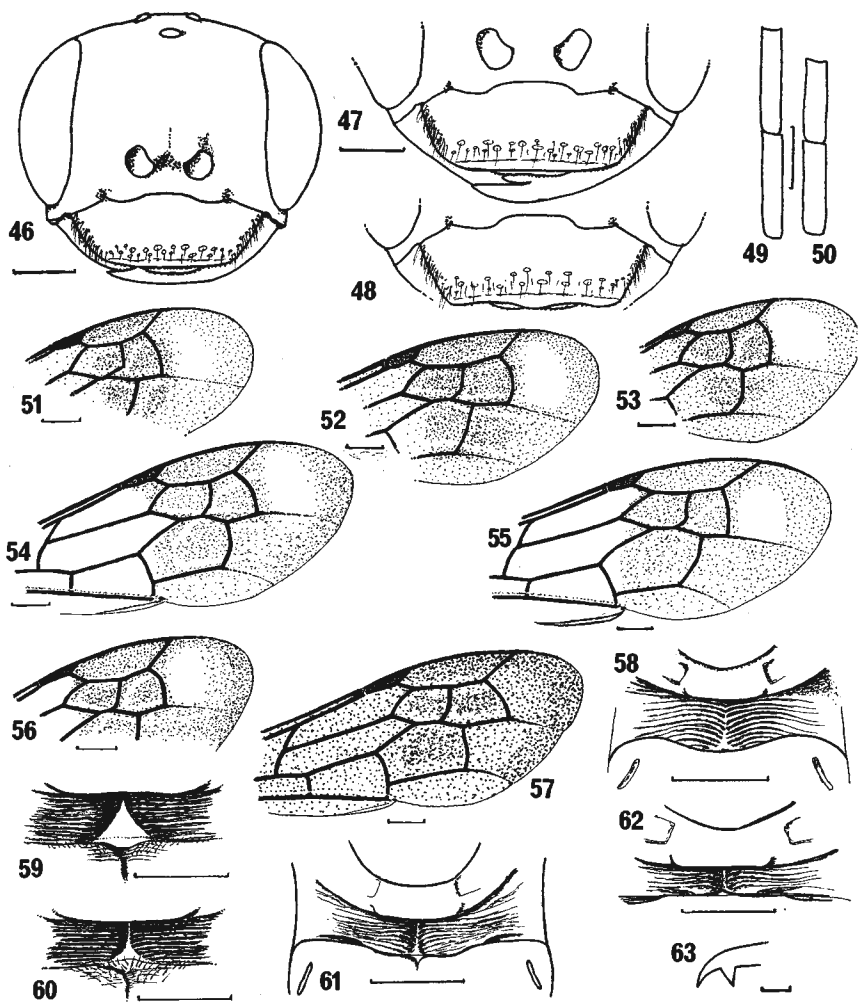


Figs 23–30. 23–24, *Pompilus cinereus* (F.) ♂, genitalia: 23, subgenital plate (SGP), ventral view; 24, genitalia, ventral view; by convention, SGP illustrated with anterior to top of page, genitalia inverted. 25, *Auplopus carbonarius* (Scopoli) ♂, right hind tarsus, posterolateral view. (23–25, scale = 0.1 mm.) 26, *Auplopus carbonarius* ♀, head, left ventrolateral view, palpi omitted. 27, *Dipogon variegatus* (L.) ♀, head, left ventrolateral view. 28, *Evagetes dubius* (Lepelletier) ♀, pronotum, dorsal view. 29, *Arachnospila anceps* (Wesmael) ♀, pronotum, dorsal view. 30, *Aporimellus sexmaculatus* (Spinola), propodeum, left lateral view. (26–30, scale = 0.5 mm).

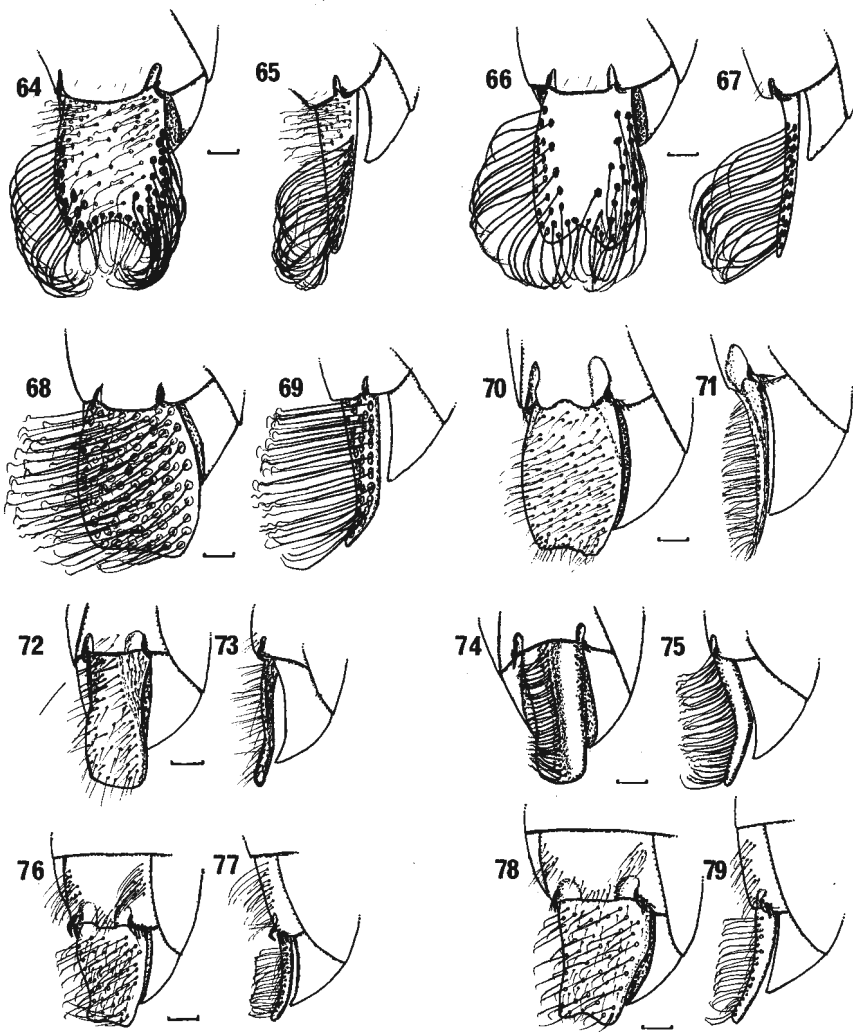


Figs 31-45. 31-33, *Cryptocheilus notatus* (Rossius): 31, ♀, right fore wing; scale=0.5 mm. 32, 33, ♂ subgenital plate: 32, left ventrolateral view; 33, left lateral view; scale=0.25 mm. 34-36, *Caliadurgus fasciatellus* (Spinola) ♀: 34, face; 35, right fore wing; scale=0.5 mm. 36, right fore tibial spine; scale=0.1 mm. 37-44, *Dipogon* Fox; 37-39, ♂ antennae: 37, *D. variegatus* (L.); 38, *D. bifasciatus* (Geoffroy); 39, *D. subintermedius* (Magretti); scale=0.5 mm. 40-42, ♂ subgenital plate, left lateral view: 40, *D. bifasciatus* (Geoffroy); 41, *D. variegatus* (L.); 42, *D. subintermedius* (Magretti); scale=0.1 mm. 43, 44, ♀ antenna: 43, *D. variegatus* (L.); 44, *D. subintermedius* (Magretti); scale=0.5 mm. 45, *Auplopus carbonarius* (Spinola) ♀, right forewing; scale=0.5 mm.

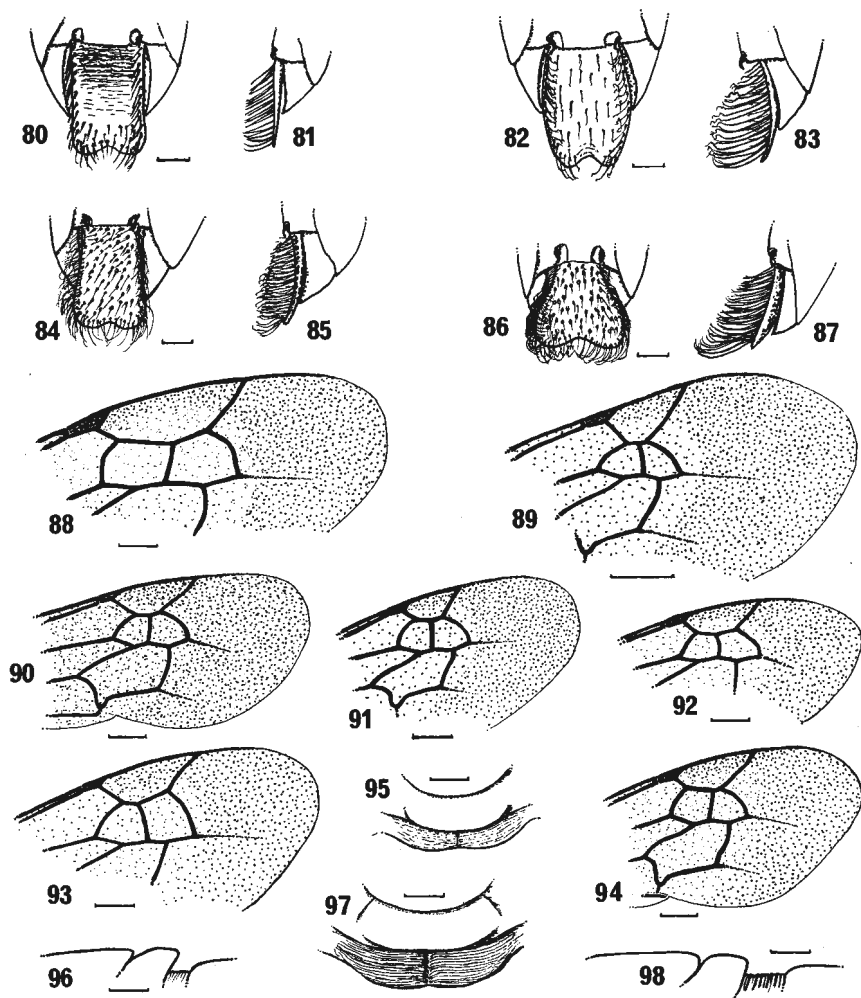
42 = bifasciatus
40 = subintermedius



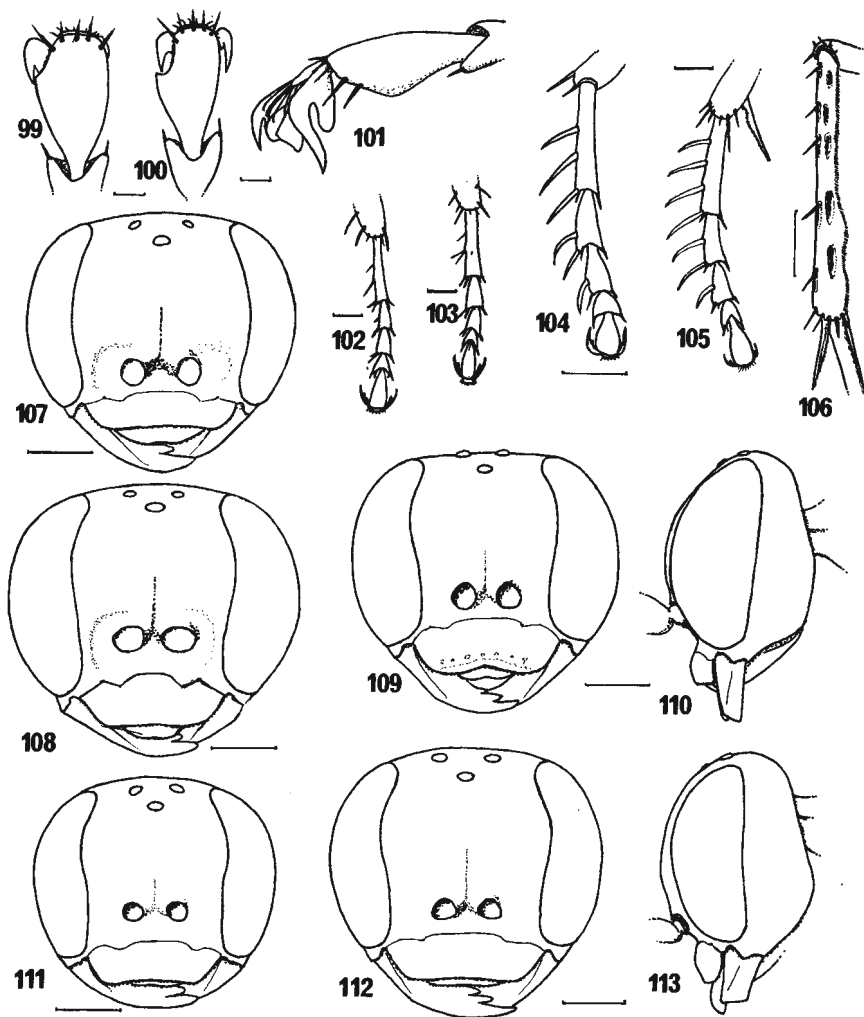
Figs 46–63. *Priocnemis* species, ♀. 46, *P. coriacea* Dahlbom, face. 47, 48, clypeus; 47, *P. perturbator* (Harris); 48, *P. susterai* Haupt. 49, 50, antennae: 49, *P. fennica* Haupt; 50, *P. hyalinata* (F.). 51–57, fore wings: 51, *P. agilis* (Shuckard); 52, *P. cordivalvata* Haupt; 53, *P. gracilis* Haupt; 54, *P. fennica* Haupt; 55, *P. exaltata* (F.); 56, *P. hyalinata* (F.); 57, *P. perturbator* (Harris). 58–62, metapostnotum, dorsal view: 58, *P. exaltata* (F.); 59, *P. perturbator* (Harris); 60, *P. susterai* Haupt; 61, *P. fennica* Haupt; 62, *P. hyalinata* (F.); scale = 0.5 mm. 63, *P. fennica* Haupt, claw; scale = 0.1 mm.



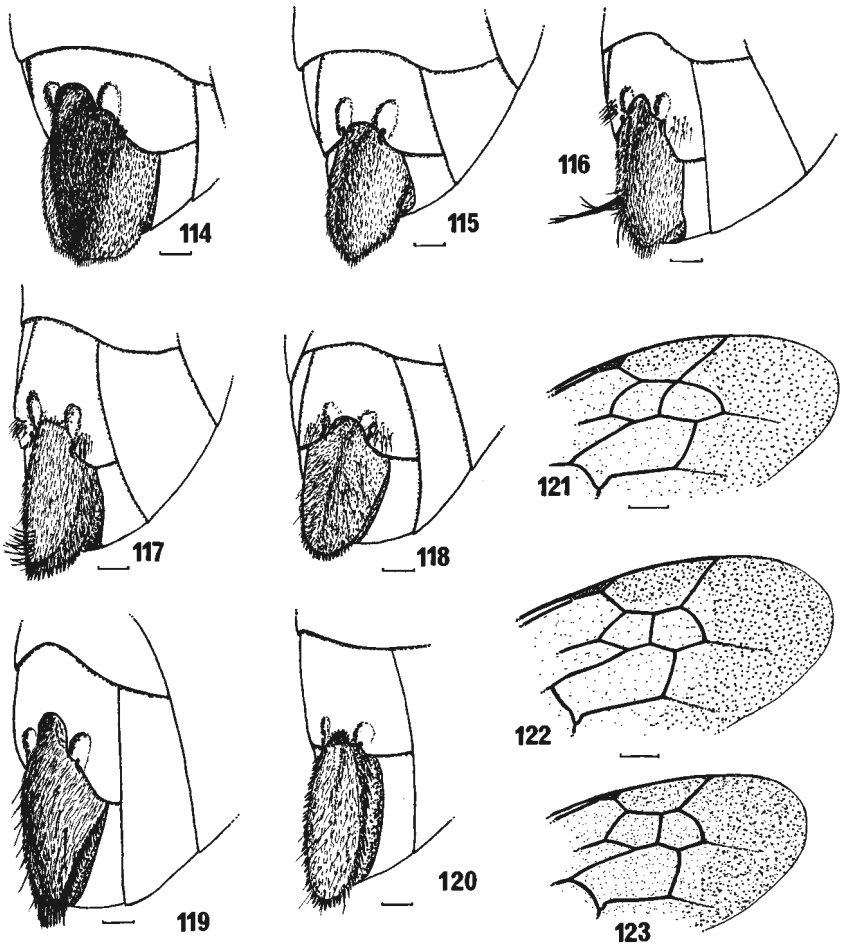
Figs 64-79. *Priocnemis* species. ♂ subgenital plates, oblique ventral and left lateral views: 64, 65, *P. perturbator* (Harris); 66, 67, *P. susterai* Haupt; 68, 69, *P. coriacea* Dahlbom; 70, 71, *P. exaltata* (F.); 72, 73, *P. parvula* Dahlbom; 74, 75 *P. agilis* (Shuckard); 76, 77, *P. fennica* Haupt; 78, 79, *P. hyalinata* (F.); scale = 0.1 mm.



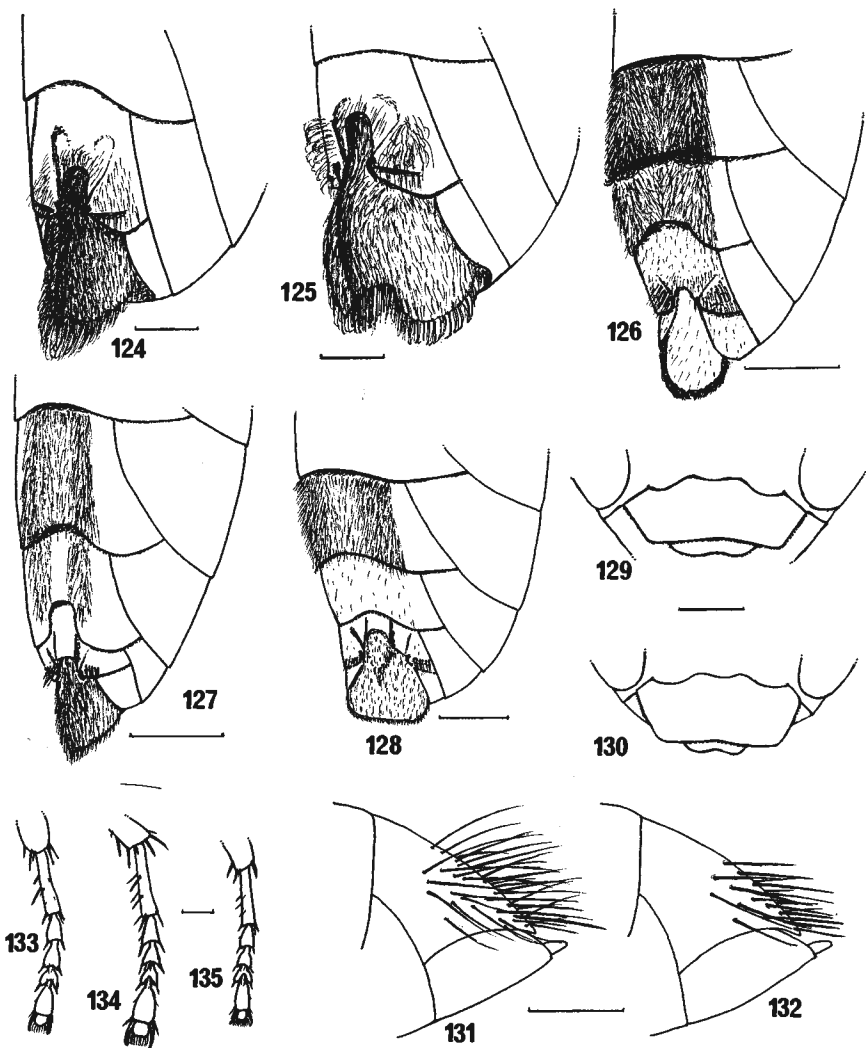
Figs 80–98. 80–87, *Priocnemis* species, ♂ subgenital plates, oblique ventral and left lateral views: 80, 81, *P. pusilla* Schiødte; 82, 83, *P. schioedtei* Haupt; 84, 85, *P. gracilis* Haupt; 86, 87, *P. cordivalvata* Haupt; scale = 0.1 mm. 88–98, *Arachnospila* species, ♀. 88–94, right fore wings: 88, *A. rufa* Haupt; 89, *A. wesmaeli* (Thomson); 90, *A. trivialis* (Dahlbom); 91, *A. anceps* (Wesmael); 92, *A. consobrina* (Dahlbom); 93, *A. spissa* (Schiødte); 94, *A. minutula* (Dahlbom); scale = 0.5 mm. 95–98, metapostnotum, dorsal and left lateral views: 95, 96, *A. trivialis* (Dahlbom); 97, 98, *A. anceps* (Wesmael); scale = 0.2 mm.



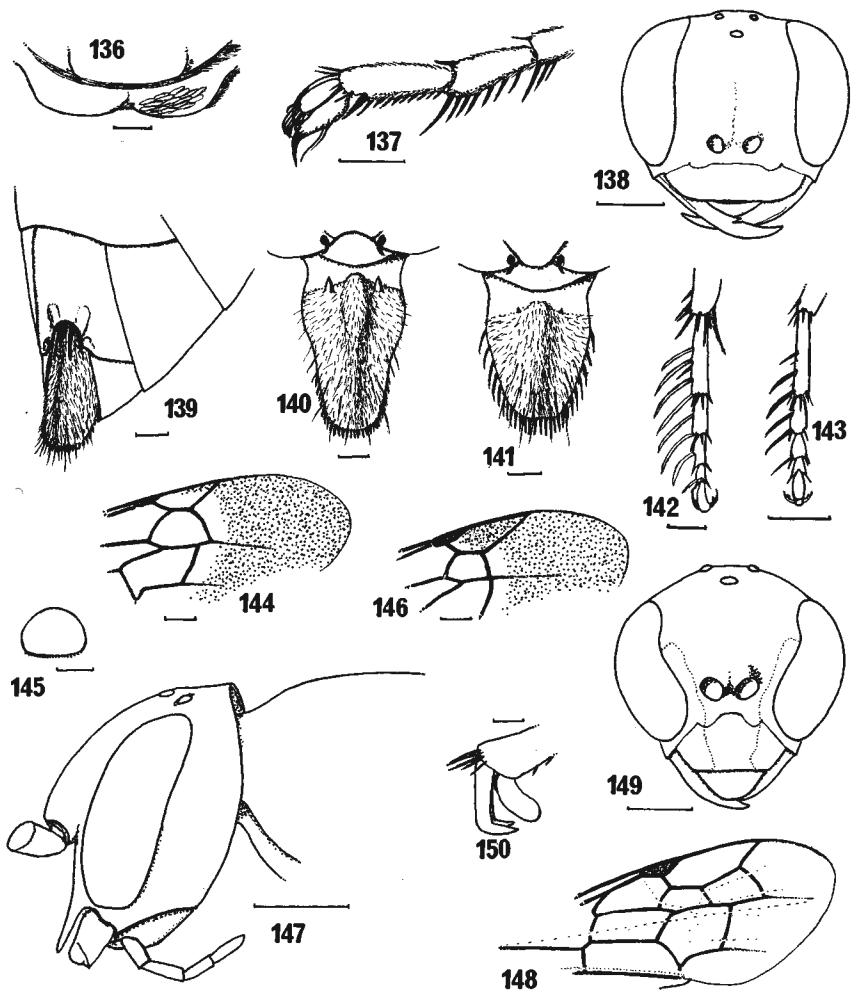
Figs 99–113. *Arachnospila* species. 99–101, ♂ terminal left fore tarsal segment: 99, *A. spissa* (Schiødte); 100, *A. anceps* (Wesmael); 101, *A. rufa* Haupt; scale = 0.1 mm. 102–105, ♀ right fore tarsus: 102, *A. minutula* (Dahlbom); 103, *A. spissa* (Schiødte); 104, *A. consobrina* (Dahlbom); 105, *A. rufa* (Haupt); scale = 0.5. 106, *A. minutula* (Dahlbom), ♂ left hind tibia, dorsal view; scale = 0.5 mm. 107–113, ♀ head, facial and lateral views: 107, *A. spissa* (Schiødte); 108, *A. minutula* (Dahlbom); 109, 110, *A. anceps* (Wesmael); 111, *A. wesmaeli* (Thomson); 112, 113, *A. trivialis* (Dahlbom); scale = 0.5 mm.



Figs 114–123. 114–120, *Arachnospila* species, ♂ subgenital plate, left anterolateral view: 114, *A. rufa* (Haupt); 115, *A. consobrina* (Dahlbom); 116, *A. wesmaeli* (Thomson); 117, *A. anceps* (Wesmael); 118, *A. trivialis* (Dahlbom); 119, *A. spissa* (Schjødt); 120, *A. minutula* (Dahlbom); scale = 0.1 mm. 121–123, *Anoplius* species, ♀ right fore wing: 121, *A. nigerrimus* (Scopoli); 122, *A. concinnus* (Dahlbom); 123, *A. caviventris* (Aurivillius); scale = 0.5 mm.



Figs 124–135. *Anoplius* species. 124–128, ♂ subgenital plate and abdominal venter, left ventro-lateral view: 124, *A. nigerrimus* (Scopoli); 125, *A. concinnus* (Dahlbom); scale = 0.2 mm. 126, *A. caviventris* (Aurivillius); 127, *A. infuscatus* (Vander Linden); 128, *A. viaticus* (L.); scale = 0.5 mm. 129–135, ♀. 129, 130, clypeus: 129, *A. nigerrimus* (Scopoli); 130, *A. caviventris* (Aurivillius). 131, 132, abdominal terminal spines, left lateral view: 131, *A. caviventris* (Aurivillius); 132, *A. nigerrimus* (Scopoli); scale = 0.5 mm. 133–135, ♀ right fore tarsus: 133, *A. nigerrimus* (Scopoli); 134, *A. concinnus* (Dahlbom); 135, *A. caviventris* (Aurivillius); scale = 0.5 mm.



Figs 136–150. 136, *Episyrus rufipes* (L.) ♀, metapostnotum with scale-like hairs, dorsal view; scale = 0.2 mm. 137, 138, *Pompilus cinereus* (F.) ♀: 137, terminal hind tarsal segments; scale = 0.1 mm. 138, face; scale = 0.5 mm. 139–145, *Evagetes* species. 139, 141, ♂ subgenital plate: 139, *E. crassicornis* (Shuckard), a little exerted; 140, *E. dubius* (Lepeletier), strongly exerted; 141, *E. pectinipes* (L.), strongly exerted; scale = 0.1 mm. 142, 143, ♀ right fore tarsus: 142, *E. pectinipes* (L.); 143, *E. crassicornis* (Shuckard); scale = 0.5 mm. 144, *E. dubius* (Lepeletier), ♀ right fore wing. 145, *E. crassicornis* (Shuckard), ♀ antenna, transverse section, diagrammatic; scale = 0.05 mm. 146, *Aporus unicolor* (Spinola), ♀ fore wing; scale = 0.5 mm. 147, 148, *Homonotus sanguinolentus* (F.) ♀: 147, head and thorax, left lateral view; 148, right fore wing; scale = 0.5 mm. 149, 150, *Ceropales maculata* (F.): 149, ♀ face; scale = 0.5 mm. 150, ♂, right hind tarsal claw; scale = 0.1 mm.

Table 1: Comparison of systems for naming veins and cells

Evans, 1950 (Matheson, 1947)	Lanham, 1951 (Ross, 1936)	Townes, 1957 (Rohwer/Gahan, 1916)	Wolf, 1972 (Haupt, 1930)	Eady, 1974	Brothers, 1975 (Hamilton, 1972)	Richards, 1977	Wootton, 1978
Primary longitudinal veins of fore wing							
COSTA: C: 1 abscissa							
1 costa	C: costa	costa	Costalader	C: costa	C	C: costa	C: costa
SUBCOSTA: Sc: 3 abscissae							
2 subcosta	Sc + R subcostal	subcostal	Subcostalader	Sc + R	Sc + R + S: sector	Sc + R	Sc + R + Rs
3 subcosta	Sc + R	subcostal	Subcostalader	Sc + R: parastigma	Sc + R	R ₁	Sc + R
4 stigma	Sc: stigma	stigma	Pterostigma	Sc: stigma	C	Sc	Sc
RADIUS: R: 5 abscissae							
5 subcosta	Sc + R	subcostal	Subcostalader	Sc + R	Sc + R + S	Sc + R	Sc + Rs + Rs
6 subcosta	Sc + R	subcostal	Subcostalader	Sc + R: parastigma	Sc + R	R ₁	Sc + R
7 stigma	R: stigma	stigma	Pterostigma	R	R	R ₁	R
8 stigma	R	stigma	Pterostigma	R	R	R ₁	R
9 —	R	metacarpus	Costalader	R ₁	C	R ₁	R
RADIAL SECTOR: Rs: 8 abscissae							
10 —	—	—	—	—	Sc + R + S	—	Sc + R + Rs
11 basal	Rs ¹ : parastigma	basal	Medialader	Rs: radial sector	S: sector	Rs	Rs
12 cubital	Rs + M	cubitus	Medialader	Rs + M	S + M	Rs + M	Rs + M
13 tranv cubital 1	Rs ² : radial sector	intercubitus 1	Radialquerader	Rs	S	Rs	Rs
14 radial	Rs ³	radius	Radialader	Rs	S	Rs	Rs
15 radial	Rs ⁴	radius	Radialader	Rs	S	Rs	Rs
16 radial	Rs ⁵	radius	Radialader	Rs	S	Rs	Rs
17 radial	Rs ⁶	radius	Radialader	Rs	S	Rs	Rs
MEDIAN: M: 8 abscissae							
18 median	M + Cu	medius	Cubitalader	M + Cu ₁	M + Cu	M + Cu ₁	M + CuA
19 basal	M ¹ : basal	basal	Medialquerader	M	M	M	M
20 cubital	Rs + M: submarginal	cubitus	Medialader	M	M	M	M
21 cubital	M ²	cubitus	Medialader	M	M	M	M
22 cubital	M ³	cubitus	Medialader	M	M	M	M
23 cubital	M ⁴	cubitus	Medialader	M	M	M	M
24 cubital	M ⁵	cubitus	Medialader	M	M	M	M
25 cubital	M ⁶	cubitus	Medialader	M	M	M	M

Table 1: (Continued)

Evans, 1950 (Matheson, 1947)	Lanham, 1951 (Ross, 1936)	Townes, 1957 (Rohwer/Gahan, 1916)	Wolf, 1972 (Haupt, 1930)	Eady, 1974	Brothers, 1975 (Hamilton, 1972)	Richards, 1977	Wootton, 1978
CUBITUS ANTERIOR: CuA: 7 abscissae							
26 median	M + Cu	medius	Cubitalader	M + Cu ₁	M + Cu	M + Cu ₁	M + CuA
27 discoidal	Cu ¹ : discoidal	discoideus	Cubitalader	Cu ₁	Cu	Cu ₁	CuA
28 discoidal	Cu ²	discoideus	Cubitalader	Cu ₁	Cu	Cu ₁	CuA
29 discoidal	Cu ³	discoideus	Cubitalader	Cu ₁	Cu	Cu ₁	CuA
30 subdiscoidal	Cu ₁	subdiscoideus	Cubitalader	Cu _{1a}	Cu ₁	Cu _{1a}	CuA ₁
31 subdiscoidal	Cu ₁	subdiscoideus	Cubitalader	Cu _{1a}	Cu ₁	Cu _{1a}	CuA ₁
32 discoidal	Cu ₂	discoideus	Cubitalquerader	Cu _{1b}	Cu ₂	Cu _{1b}	CuA ₂
ANAL: 1A: 2 abscissae							
33 anal	vannal/anal	anal	Analader	1A	E (empusal)	1A	1A
34 anal	vannal/anal	anal	Analader	1A	E	1A	1A
Crossveins of fore wing							
35 —	—	—	—	1r	—	1r	—(1r-rs)
36 radial	radial/marginal	radius	Radialader	2r	r-s	2r	—(2r-rs)
37 —	—	—	—	1r-m	—	1rm	—(1rs-m)
38 tranv cubital 2	intercub 2: 1r-m	intercubitus 2	Radialquerader 2	r-m	1s-m	2rm	—(2rs-m)
39 tranv cubital 3	intercub 3: 2r-m	intercubitus 2	Radialquerader 3	r-m	2s-m	3rm	—(3rs-m)
40 recurrent 1	1m-cu	recurrent 1	Medialquerader 2	1m-cu	1m-cu	1mcu	—(1m-cu)
41 recurrent 2	2m-cu	recurrent 2	Medialquerader 3	2m-cu	2m-cu	2mcu	—(2m-cu)
42 tranv median	cu-v: nervulus	nervulus	Cubitalquerader	cu-a	cu-e	cua	—(cu-a)
Primary longitudinal veins of hind wing							
COSTAL: C: 2 abscissae							
1 costa C + Sc	costal	costella	Costalader	C + Sc + R	C + Sc + R + S	C + Sc + R	C + Sc + R + Rs
2 costa C	costal C	costella	Costalader	C	C	C	C
SUBCOSTAL: Sc: 4 abscissae							
3 costa C + Sc	costa C + Sc	costella	Costalader	C + Sc + R	C + Sc + R + S	C + Sc + R	C + Sc + R + Rs
4 subcosta Sc	subcosta Sc + R	subcostella	Costalader	Sc + R	Sc + R + S	Sc + R	Sc + R + Rs
5 —	R ₁	metacarpella	Costalader	Sc + R	C + Sc + R + S	Sc + R	Sc + R + Rs
6 —	R ₁	metacarpella	Costalader	R ₁	C + Sc + R	R ₁	R

Table 1: (Continued)

Evans, 1950 (Matheson, 1947)	Lanham, 1951 (Ross, 1936)	Townes, 1957 (Rohwer/Gahan, 1916)	Wolf, 1972 (Haupt, 1930)	Eady, 1974	Brothers, 1975 (Hamilton, 1972)	Richards, 1977	Wootton, 1978
RADIUS: R: 4 abscissae							
7 costa	costa	costella	Costalader	C+Sc+R	C+Sc+R+S	C+Sc+R	C+Sc+R+Rs
8 subcosta	subcosta	subcostella	Costalader	Sc+R	Sc+R+S	Sc+R	Sc+R+Rs
9 —	R ₁	metacarpella	Costalader	Sc+R	C+Sc+R+S	Sc+R	Sc+R+Rs
10 —	R ₁	metacarpella	Costalader	R ₁	C+Sc+R	R ₁	R
RADIAL SECTOR: Rs: 5 abscissae							
11 costa	costa	costella	Costalader	C+Sc+R	C+Sc+R+S	C+Sc+R	C+Sc+R+Rs
12 subcosta	subcosta	subcostella	Costalader	Sc+R	Sc+R+S	Sc+R	Sc+R+Rs
13 —	R ₁	metacarpella	Costalader	Sc+R	Sc+R+S	Sc+R	Sc+R+Rs
14 radial	marginal/radial	radiella	Radialader	Rs	S	Rs	Rs
15 radial	marginal/radial	radiella	Radialader	Rs	S	Rs	Rs
MEDIAN: M: 4 abscissae							
16 median	media M+Cu	mediella	Cubitalader	M+Cu	M+Cu	M+Cu ₁	M+CuA
17 median	media	mediella	Cubitalader	M+Cu	M+Cu	M+Cu ₁	M+CuA
18 cubital	submarginal M	cubitella	Medialader	M	M	M	M
19 cubital	submarginal	cubitella	Medialader	M	M	M	M
CUBITUS ANTERIOR: CuA: 3 abscissae							
20 median	media M+Cu	mediella	Cubitalader	M+Cu	M+Cu	M+Cu ₁	M+CuA
21 median	media M+Cu	mediella	Cubitalader	M+Cu	M+Cu	M+Cu ₁	M+CuA
22 discoidal	discoidal Cu	discoidella	Cubitalader	m-cu+Cu ₁	Cu	Cu ₁	CuA
ANAL: 1A: 1 abscissa							
23 anal	anal/vannal V	submediella	Analader	1A	E (empusal)	1A	1A
Crossveins of hind wing							
24 tranv cubital	r-m (trv cubit)	intercubitella	Radialquerader	r-m	s-m	1rm	—(rs-m)
25 tranv median	cubitovannal/cu-v	nervellus	Cubitalquerader	cu-a	cu-e	cu-a	—(cu-a)
Cells of fore wing (names of open cells enclosed in brackets)							
A costal	costal	costal	Costalzelle	costal	C	costal	C
B stigma	stigma	stigma	Pterostigma	stigma	stigma	stigma	stigma

Table 1: (Continued)

	Evans, 1950 (Matheson, 1947)	Lanham, 1951 (Ross, 1936)	Townes, 1957 (Rohwer/Gahan, 1916)	Wolf, 1972 (Haupt, 1930)	Eady, 1974	Brothers, 1975 (Hamilton, 1972)	Richards, 1977	Wootton, 1978
C	marginal	marginal/radial	radial	Subcostalzelle	marginal	R	marginal/radial	R
D	submarginal 1	submarginal 1	cubital 1	Radialzelle 1	submarginal 1	Sc + R	submarginal 1/ cubital 1: 1R1	Sc + R
E	submarginal 2	submarginal 2	cubital 2	Radialzelle 2	parastigmal submarginal 2	1S (sector)	submarginal 2/ cubital 2: 1Rs	1Rs
F	submarginal 3	submarginal 3	cubital 3	Radialzelle 3	submarginal 3	2S	submarginal 3/ cubital 3: 2Rs	2Rs
G	(submarginal 4)	(submarginal 4)	(cubital 4)	(Radialzelle 4)	(submarginal 4)	(3S)	(submarginal 4)	(3Rs)
H	median	medial	median	Medialzelle 1	basal	Sc + R + S	medial/basal	Sc + R + Rs
I	discoidal 1	discoidal 1	discoidal 1	Medialzelle 2	discal 1	S + M	discoidal 1	Rs + M
J	discoidal 3	discoidal 3	discoidal 2	Medialzelle 3	discal 2	1M	discoidal 2	1M
K	(apical 2)	(apical 2)	(discoidal 3)	(Medialzelle 4)	(discal 3)	(2M)	(discoidal 3)	(2M)
L	submedial	submedial	submedian	Cubitalzelle 1	subbasal	M + Cu	submedial 1/ subbasal	M + CuA
M	discoidal 2	discoidal 2	brachial 1	Cubitalzelle 2	subdiscal 1	1Cu	submedial 2/ brachial	1CuA
N	(apical 1)	(apical 1)	(brachial 2)	(Cubitalzelle 3)	(subdiscal 2)	(2Cu)	(apical 2)	(2CuA)
O	(anal)	(vannal)	(anal)	(Analzelle)	(anal)	(E) (empusal)	(anal)	(clavus)
Cells of hind wing (names of open cells enclosed in brackets)								
P	costal	costal	costellan	Costalzelle	costal	C	costal	C
Q	median	median	mediellan	Medialzelle	basal	Sc + R + S	medial/basal	Sc + R + Rs
R	—	(marginal/radial)	(radiellan)	—	(marginal)	R	(radial)	R
S	submedian	submedian	submediellan	Cubitalzelle	subbasal	M + Cu	submedial/ subbasal	M + CuA
T	—	(submarginal)	(cubitellan)	—	(submarginal)	S	(cubital)	Rs
U	—	(discoidal)	(discoidelan)	—	(discal)	M	(discoidal 1)	M
V	—	(subdiscoidal)	(anellan)	—	(subdiscal)	Cu	(discoidal 2)	CuA
W	(anal)	(vannal)	(anellan)	—	(anal)	(plical lobe)	(vannal)	(clavus)
X	(anal lobe)	(jugal lobe)	(anal lobe)	(Anallappen)	(anal lobe)	(jugal lobe)	(anal/jugal lobe)	(jugum)

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