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HANDBOOKS FOR

THE IDENTIFICATION

OF BRITISH INSECTS

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HANDBOOKS FOR THE IDENTIFICATION OF BRITISH INSECTS

DIPTERA BRACHYCERA

SECTION (*a*)

TABANOIDEA AND ASILOIDEA

By

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HANDBOOKS FOR THE IDENTIFICATION OF BRITISH INSECTS

The aim of this series of publications is to provide illustrated keys to the whole of the British Insects (in so far as this is possible), in ten volumes, as follows :

I. Part 1. General Introduction.
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„ 3. Protura.
„ 4. Collembola.
„ 5. Dermaptera and Orthoptera.
„ 6. Plecoptera.
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Part 9. Ephemeroptera.
„ 10. Odonata.
„ 11. Thysanoptera.
„ 12. Neuroptera.
„ 13. Mecoptera.
„ 14. Trichoptera.
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II. Hemiptera.
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IV. and V. Coleoptera.
VI. Hymenoptera : Symphyta and Aculeata.
VII. Hymenoptera : Ichneumonoidea.
VIII. Hymenoptera : Cynipoidea, Chalcidoidea, and Serphoidea.
IX. Diptera : Nematocera and Brachycera.
X. Diptera : Cyclorrhapha.

Volumes II to X will be divided into parts of convenient size, but it is not possible to specify in advance the taxonomic content of each part.

Conciseness and cheapness are main objectives in this series, and each part is the work of a specialist, or of a group of specialists. Although much of the work is based on existing published keys, suitably adapted, much new and original matter is also included.

Parts are issued, separately paged and priced, as they become available.

A second (revised) edition of *A Check List of British Insects*, by G. S. Kloet and W. D. Hincks, is being issued as an extra, eleventh, volume in this series.

The Society is indebted to the Royal Society for a grant towards the cost of initiating this series of *Handbooks*.

A list of parts now available appears on the back cover.

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DIPTERA BRACHYCERA

SECTION (*a*)

TABANOIDEA AND ASILOIDEA

By Harold Oldroyd

Introduction

The evolution of Diptera has clearly followed two main lines, one leading to Nematocera, and the other to all the rest, which are "Brachycera" in the broad sense (see Vol. IX (1) : 31). The second line of evolution led first to a sequence of more primitive families which have become stabilized, and (with few exceptions) are easy to separate from each other; and then to a complex of more advanced families (Cyclorrhapha) which appear to be much less stabilized, and which present many problems at the family level of classification.

We are concerned here with the first group, Brachycera in the narrow sense, and not with all of these. The families Empididae and Dolichopodidae, especially the latter, foreshadow the Cyclorrhapha to some extent, and this fact, together with their smaller size and greater abundance of species, makes it convenient to leave them for individual treatment by specialists.

The families dealt with in this part of the *Handbook* are those that were reviewed by Verrall in *British Flies, V* (1909), who dealt exhaustively with them, giving extremely detailed descriptions, as well as long discussions of synonymy and distribution. When the *Handbook* series was planned, therefore, it seemed unnecessary to cover these families until prior attention had been given to others, less well known. In the intervening 20 years, however, Verrall's book has become more difficult to obtain, while extensive work has gone on in some families, notably Tabanidae. The time now seems ripe for a *Handbook* on the "Verrall" families of Brachycera.

These comprise:—

TABANOIDEA Stratiomyidae, Xylomyidae, Xylophagidae, Rhagionidae, Tabanidae

ASILOIDEA Asilidae, Therevidae, Scenopinidae, Acroceridae, Bombyliidae

The segregation of families into two superfamilies is partly structural but mainly biological. The fission between Tabanoidea and Asiloidea is a fundamental one, which ought to receive more prominence than it does. In my book on *The Natural History of Flies* (1964) I stressed a dichotomy that runs through Diptera. Starting from an ancestor which probably lived in

moss, or in damp, rotting wood, flies seem to have segregated into those which moved into more fully aquatic habitats and those which became more terrestrial.

If we set aside Tipulidae as a basic group still showing great diversity of larval habitat, in materials of varying degrees of humidity, the rest of Nematocera fall into land midges which cluster round Bibionidae, Mycetophilidae, etc., and water midges and gnats which include Culicidae, Simuliidae, Ceratopogonidae and Psychodidae. The latter group primarily suck blood, in females only, by use of stylet-like mandibles and maxillae, though the habit has been lost in Chironomidae and Psychodidae (except for Phlebotominae). Coming now to Brachycera, we see that Tabanoidea invite comparison with the water midge group, though mandibles have again been lost in a few Tabanidae, the majority of Rhagionidae, and of course all Stratiomyidae. Many Rhagionidae are terrestrial (see p. 36).

Asiloidea, on the other hand, are a definitely terrestrial group. They have lost all trace of mandibulate mouthparts, and although both sexes of adult Asilidae suck the blood of insects, they have evolved an entirely different equipment consisting of the sharpened hypopharynx ensheathed in the labium. The further development of specialized structures on legs and head which enable the Asilid to catch prey, and defend itself against retaliation, show that there is a long evolutionary history behind the Asilidae. Related families have not adopted this predatory habit, and have evolved along totally different lines; Bombyliidae, for example, have adapted not only the proboscis but the whole body to flower-feeding, as will be seen by comparing their legs with those of any Asilid. Larvae of this group, though carnivorous, are terrestrial, either living in earth, or being scavengers in nests, or internal parasites. From this point on, Diptera as a whole are terrestrial, and the few groups that have evolved aquatic larvae (e.g. Syrphidae, Ephydridae) have clearly done so by secondary return to the water.

One or two anomalies occur. Acroceridae have a pulvilliform empodium (three-padded foot), and for this reason are often keyed out with Tabanoidea as "homeodactyla", while Asiloidea with two pulvilli and a bristle-like empodium are "heterodactyla". Biologically it seems much more reasonable to consider Acroceridae as being closely related to Bombyliidae, and therefore as Asiloidea which have retained the primitive pulvilliform empodium.

Scenopinidae are always placed next to Therevidae, because their larvae are astonishingly similar: elongate, wormlike, with secondary subdivision of the abdominal segments. Even the head structure of the larva is similar in the two families, with a peculiar internal process which is spatulate in Therevidae and simple in Scenopinidae. Yet the adults of the two families are totally different. Therevidae are close to being the stem-group of Asiloidea, and it is possible that Scenopinidae form a link between them and Stratiomyidae, but at the present time there is little that can usefully be said about this.

Finally, Stratiomyidae themselves are an enigmatic family. It is customary to place them at the beginning of the Brachycera, yet they are certainly not a primitive family. In head structure, wing venation, and larval habits they give evidence of having existed for a long time. It is my own view that Stratiomyidae are an ancient family, long past its prime,

possibly suffering from the competition of the more efficient Syrphidae. It is perhaps misleading to place Stratiomyidae in Tabanoidea, though they are linked with Rhagionidae through Xylomyidae/Xylophagidae, and possibly both groups might trace back to some ancestor living in decaying wood. It should be borne in mind, however, that Stratiomyidae stand apart from all the others.

Volume IX, Part 1: Introduction and Key to Families discussed the structure of Brachycera, and only a few points need be mentioned here.

SIZE.—One criticism of the *Introduction* in this series was that I did not give sufficient indication of the *size* of the flies mentioned. Size is an obvious characteristic of a species, but a deceptive one, and a measurement in millimetres gives an appearance of precision that is often not justified. Shape, surface structure and pilosity all produce an optical illusion of relative size and shape that may be difficult to substantiate by actual measurements. An example is *Tabanus autumnalis*, which in practice is distinctive because of its intermediate size, too big for the *bromius*-group, but not big enough for the *bovinus*-group; yet the range of variation in *autumnalis* spans the two.

In the present Part of the *Handbook*, size is mentioned only when it is a positive help in identification, e.g. *Sargus minimus*, and the smaller Bombyliidae.

GENITALIA.—One development in taxonomy since Verrall's time has been the use of genitalia, especially external genitalia of males, as a specific character. This is now such standard practice in all groups of insects that it may be thought surprising to mention it. Yet the use of genitalia as a specific—or even a generic—character is not as simple as it is often made to seem. The genital armature of male Brachycera is often bulbous, dark, and covered with hairs. It is difficult to draw *in situ*, and when dissected the separated parts cannot be mounted flat, nor accurately drawn in two dimensions.

For the most part the male genitalia of Tabanoidea are simple and show few taxonomic differences. In the case of Tabanidae themselves, the females are so much more in evidence that female genitalia have been studied extensively, but only occasionally is a really significant difference to be seen: e.g. *Hybomitra bimaculata*. Male genitalia are much more complex in Asiloidea, and are widely used in specific determination. Female external genitalia are also conspicuous, and varied. The structure is related to the method of egg-laying, and often provides a valuable clue to the possible location of eggs: among Asilidae, those with a crown of spines on the paired acanthophorites lay eggs in sand or loose soil; those with an ovipositor more or less elongate, flattened or cylindrical, often equipped with spines or bristles at the tip, insert the eggs into sand or harder ground or into the tissues of plants; while those with a simple opening and no elaboration of parts indicate that the eggs are simply dropped to the ground.

Figures 2–3 give the names of component parts of male and female genitalia. When interpreting the male structures allowance must be made for possible *rotation* of the genitalia round a longitudinal axis. This phenomenon is better known in higher Diptera such as Muscoidea, and much is made of it in textbooks, more than is justified. Rotation is related to copulation position, and in some Diptera has become stabilized in evolution so that the genitalia of fully hardened males are always rotated to the same

degree. Among other Diptera, including Asilidae, rotation (or *torsion*) may vary in different individuals, and may even change during and after copulation. More is said about this under Asilidae, below.

Distribution

It will probably never be possible to compile a Vice-County list of the species of Brachycera, and if it were it would be of little value. England, in particular, is a country of miniaturized landscape, where abrupt changes in vegetation and microclimate occur every few yards. Any detailed list of the names of places where a particular species has been collected needs to be amplified with geological and topographical data of the kind that has been so excellently demonstrated by Stubbs (1967) for *Symphoromyia immaculata*.

As Mr. Stubbs points out (p. 83): "A few simple observations on the habitat, such as gross features of vegetation and aspect, make all the difference between a useful and a meaningless record." I have quoted detailed localities for rarities—I note that Stubbs thinks that the precision of a grid reference would be unwise, in case collectors converged on it, but this is not a serious risk in most Diptera!—but as far as possible I have tried to summarize the known distribution in words.

The geographers' concept of *Highland Britain* and *Lowland Britain* (fig. 1) is fundamental to understanding most aspects of British life, including natural history. In spite of the fact that we have no real mountains, the hills of west and north form a physical and ecological system which contrasts sharply with the mixed landscape of midland, southern and eastern England. The direct effect of altitude may be slight, but the indirect differences in rainfall, cloudiness and windiness in the two areas are significant. The annual total rainfall is less important than the number of rain-days; and the total hours of sunshine gives a misleading comparison unless monthly totals are compared, because in winter the angle of the sun is very low, especially in Scotland. Moreover, Brachycera are flies of the summer, May to early October, and are not to be lured out by winter sunshine like *Trichocera*, *Coelopa* or small muscids and acalyptrates.

Professor O. W. Richards (1964) presented visitors to the XIIth International Congress of Entomology with an admirable survey of ecological conditions over Lowland Britain, and stressed more than once the adverse effect upon larvae and pupae of our ". . . wet winters with many sudden changes of temperature. The unpredictability of the weather at all times of the year is as troublesome to most insects as it is to field entomologists". This degree of unpredictability is greater in Lowland than in Highland Britain, where mild, damp winds blow throughout the year, and severely restrict the range of vegetation, thus affecting the insect fauna both directly and indirectly. The relative uniformity of conditions in Highland Britain tends to maintain a stable insect population, though in practice collecting—at any rate of aerial insects—is restricted by both insects and collectors having to struggle against fresh wind, wet vegetation, and lack of sunshine.

In Lowland Britain collecting conditions are more often favourable, but the insects themselves are subjected to more variable conditions. Occasionally—very occasionally—drought dries up possible breeding-sites; in other years these become waterlogged, or washed away in floods. The narrowness of the Straits of Dover means that in periods of persistent easterly winds

insects may be blown over here, and may become established for a few years, only to die out after a series of adverse summers, or some sudden catastrophe such as a flood (see the section below on Stephens' British records). Sometimes a species enters and spreads westwards, as the Syrphid *Volucella zonaria* appears to have done some 20–25 years ago, or like the Asilid *Laphria gilva*, which "reappeared" in 1938 in Windsor Forest. Species such as these, which were often included in British Lists of the last century, but had not been seen in living memory, may suddenly reappear, flourish for a few years,

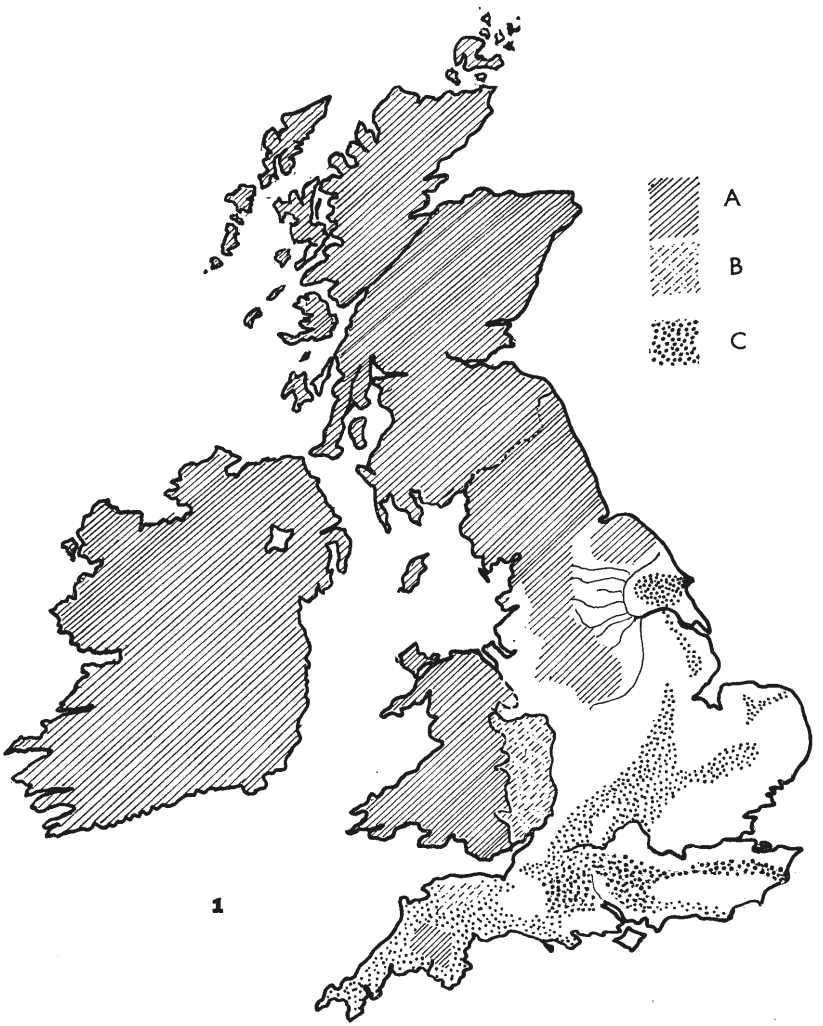
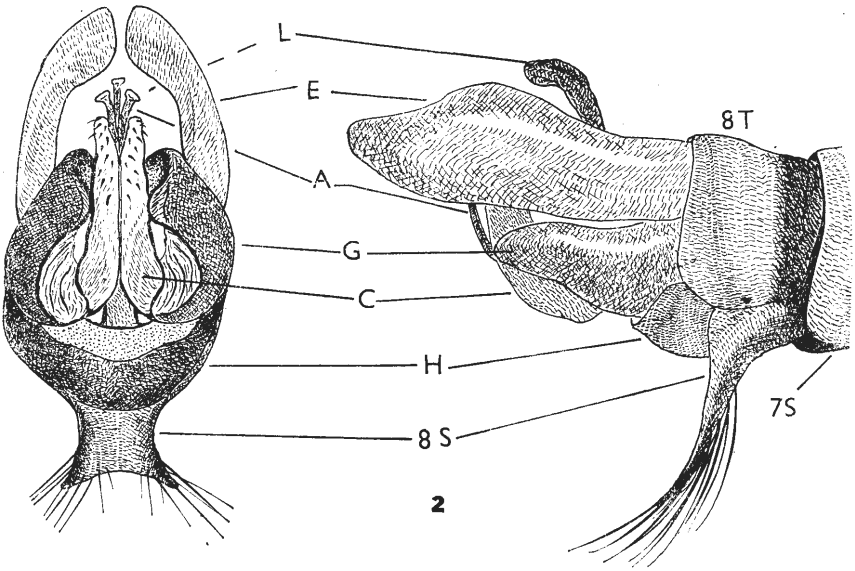
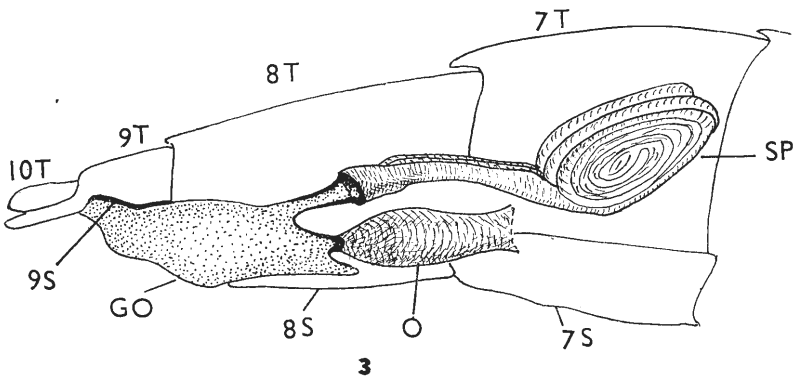


FIG. 1.—The British Isles, showing approximate extent of Highland Britain (A) and Lowland Britain (the rest). B = fringe areas, Welsh Marches and Exmoor; C = uplands of Lowland Britain.

and then vanish again. It is difficult to tell whether such species continue to survive in small colonies in very restricted habitats, or whether they die out completely and are reintroduced when favourable meteorological cycles come round again.

Man-made changes are another hazard to the insect fauna, though perhaps less so than is often supposed. There is almost nothing in the British Isles that is not man-made; even the hilltops of Highland Britain have been forested, cleared, grazed by sheep, re-afforested. Even a motorway or a big



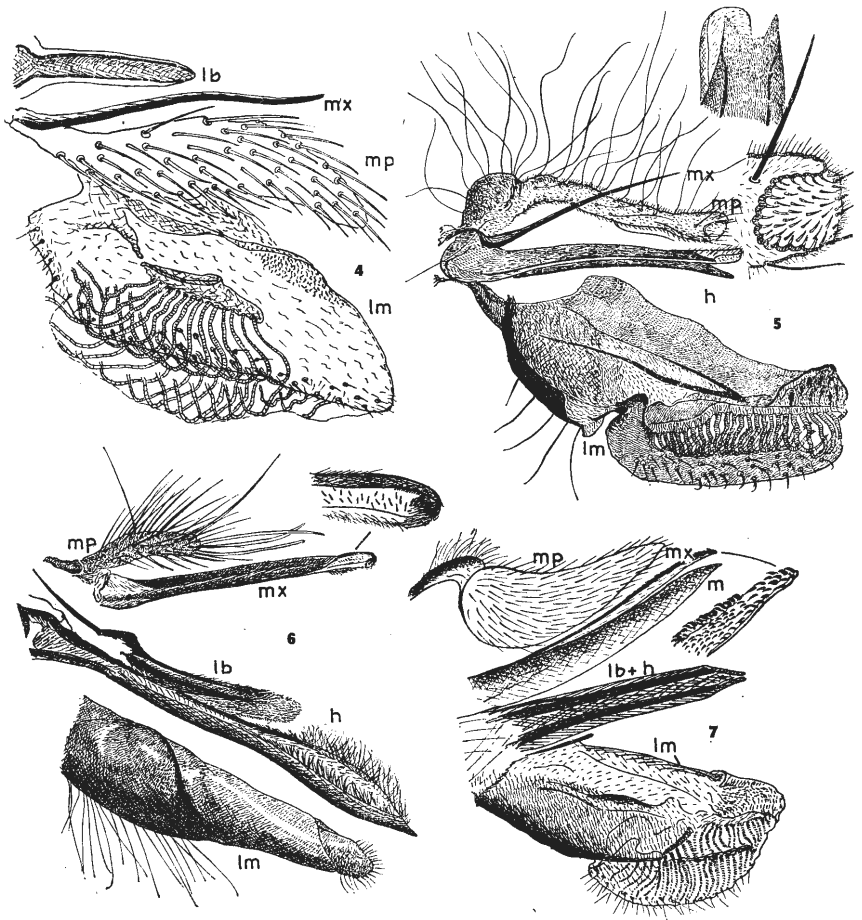


FIGS. 2, 3.—Genitalia of *Machimus atricapillus*, to show components of male (2) and female (3). L = dorsal lamellae; E = epandrium (9th tergite) here divided into a pair of upper forceps); A = aedeagus; G = gonopods; H = hypandrium (9th sternite); GO = genital opening of ♀; O = terminal section of oviduct; SP = spermatheca. Numbers refer to segment: T = tergite; S = sternite.

building development, though it eliminates some habitats, creates others. The distribution of Diptera, even of the relatively conservative Brachycera, which are not so readily adaptable as *Drosophila* and many acalypterates, is not static. Stubbs' example could be followed with other species of Brachycera, not only by collecting but also by observation and photography, to find out more about the relations between the species and its environment.

Notes on Stephens' "British Entomology"

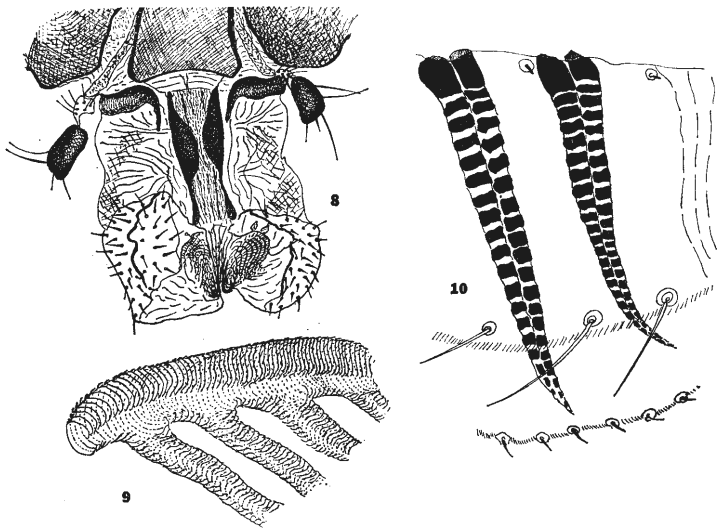
The Supplement (1846) to J. F. Stephens' *Illustrations of British Entomology* is correctly described on its title-page as being "embellished with



Figs. 4–7.—Mouthparts, cleared and dissected, of: (4) *Rhagio scolopaceus*; (5) *Thereva nobilitata*; (6) *Machimus atricapillus*; (7) *Tabanus* sp.; lb = labrum; mx = maxilla; mp = maxillary palp; h = hypopharynx; lm = labium, sometimes expanded into fleshy labella, with branching pseudotracheae. The small drawings show the tips of various components in greater detail.

coloured figures of the rarer and more interesting species". The coloured drawings were made by J. O. Westwood, and engraved by C. E. Wagstaff, and no one who looks at, say, *Dasypogon diadema* (pl. 45, fig. 1), or *Clitellaria ephippium* (pl. 46, fig. 1) can doubt that they were drawn from actual specimens of those particular species. The contrast between these and the stiff, unnatural figures that Macquart was publishing in his *Diptères exotiques* at the same period is remarkable.

The existence of these figures places Stephens' records in a different category from the many other reputed British species discussed in detail by Verrall (1909 : 756–66). They cannot be dismissed as misidentifications, nor as hearsay. In each case there must have been a specimen, and one in good condition, to have served as model for the drawing. Of course this specimen may not have been taken in Britain, but any doubt that is cast on Stephens' records must be confined to the labelling of the localities, and these, in their turn, are very precise: *Clitellaria ephippium*, for instance was said to be



FIGS. 8–10.—Mouthparts: (8) proboscis of *Stratiomys furcata*; (9) details of pseudotracheae in *Thereva nobilitata*; (10) pseudotracheae of *Dolichopus* (Dolichopodidae) for comparison, showing chitinous rings modified into crushing teeth.

"very rare: taken in June in Coombe wood, whence I possess a fine pair". This pair is now in the British Museum, and is certainly correctly identified.

A notable feature of all Stephens' named localities for Brachycera is that they are plausible for the species concerned, both in the nature of the locality and in the relative abundance of the species. To reject these records, as has sometimes been done, because a conspicuous species has not been seen in Britain in living memory, is to err on the side of over-caution. Certainly errors may have occurred, but the consensus of evidence inclines one to accept these records at their face value.

After all, *Laphria gilva* is dismissed in Verrall's *List* with the simple comment: "The old English authors . . . seem to have considered this species

to be British." It certainly became British again for about a decade from 1938 onwards, since when it seems to have faded into obscurity again. *Chrysopilus laetus* is not even mentioned by Verrall, yet it, too, appeared in 1938, and has recently been bred again from the same area, Windsor Forest. Several of Stephens' records are from Kent, including "Coombe Wood", which I assume to be the Coombe in the parish of Eastry, just west of Deal. This would be a likely place for introductions from the continent.

It seems, therefore, that the larger Brachycera compensate for their sparseness in the British fauna by occasionally producing a startling surprise. Collectors should be prepared for this.

The Families of Brachycera

In general, the families of Brachycera are the most distinctive of Diptera, and can be recognized at sight. The principal difficulty occurs at the beginning of the Suborder, where a number of primitive genera, in various regions of the world, cannot satisfactorily be allocated to any of the larger families. The simplest solution is to assemble all these genera into one family, Coenomyiidae, while recognizing that this is not necessarily a natural unit. Opinion has rather turned against this course, and the N. American Catalog (Stone, 1965 : 296–9) reverts to the practice of grouping the genera in some way that attempts to indicate their natural relationships.

Two British genera fall into this category: *Xylophagus* Meigen, 1803 and *Xylomyia* Rondani, 1861. It has been customary to classify *Xylophagus* into Rhagionidae and *Xylomyia* into Stratiomyidae, but the present work will follow the example of the N. American Catalog, and place each of these genera in a separate family.

Although the families of Brachycera were included in the key given in *Introduction and Key to Families* (Vol. IX.1), a key to the families discussed in the present Part may be useful.

Key to the Families of Tabanoidea and Asiloidea

1 Antennae composed of two basal segments, and a flagellum with numerous similar segments, usually clearly separated. Palpi with several segments, often drooping. Anal cell of wing open, almost never narrowed towards wing-margin ..... Suborder Nematocera

– Antennae composed of two basal segments, and a flagellum of closely compressed segments, often fused together into a compound "third segment" (figs. 33–37, 138–49). Palpi with 1–3 segments, the terminal segment enlarged and often porrect (held forwards). Anal cell narrowed towards wing-margin, or closed and stalked ..... Suborders Brachycera and Cyclorrhapha 2

2 Humpbacked flies, with tiny, spherical head, and large squamae (figs. 307, 338). Venation as in figs. 295–7 ..... Acroceridae (Cyrtidae) (p. 106)

– Not humpbacked, and if squamae are large, then head is at least as broad as thorax, and wings do not have this venation 3

3 Anal cell elongate, narrowed or closed; veins R_4 and R_5 forming a radial fork 4

– Anal cell abbreviated or absent; or if elongate, then R_{4+5} is not forked (Empidoidea + Cyclorrhapha)

4 Three tarsal pads, i.e. a pulvillus beneath each claw + a median pulvilliform empodium 5

– Only two tarsal pads, the pulvilli; empodium bristle-like 9

5 Discal cell of wing small, crowded towards anterior margin of wing (figs. 11–22) less so in *Pachygaster* (figs. 16–19) ..... Stratiomyidae (p. 10)

– Discal cell of wing not reduced in size, and not crowded towards anterior margin of wing .....

6 Squamae large. Wings broad, with radial fork widely spread, and straddling the wing-tip (fig. 209) ..... TABANIDAE (p. 46)
– Squamae small. Radial fork not straddling the wing-tip 7
7 Flagellar segments completely fused into a compound "third segment", which bears either an apical style or a dorsal arista (figs. 115–19). Vein R_1 curved forwards, enclosing stigma (figs. 102–10)..... RHAGIONIDAE (p. 34)
– Flagellum of antenna still clearly consisting of a series of separate segments (figs. 84–8). Vein R_1 not so curved except in *Xylophagus* 8
8 Thorax and abdomen elongate, rather like a wood-wasp. Fourth posterior cell open. Both branches of radial fork well forward of wing-tip (fig. 101). Fore tibiae with spurs..... XYLOPHAGIDAE (p. 33)
– Thorax and abdomen sturdily built, with distinct abdominal segmentations. Fourth posterior cell closed. Vein R_5 reaches wing-tip (figs. 99, 100). Fore tibiae without spurs ..... XYLOMYIIDAE (p. 31)
9 Five posterior cells (figs. 207, 208) 10
– Four posterior cells, or fewer (figs. 308–14)..... 11
10 Vertex sunk between eyes, leaving the ocellar tubercle prominent (figs. 195–7). Face convex, often strongly prominent, and with a "moustache" of hairs and bristles (figs. 218–20, 231–5). Both sexes dichoptic..... ASILIDAE (p. 69)
— Vertex not sunk between eyes (figs. 277–84). Face deeply excavated in centre, without "moustache". Males holoptic..... THEREVIDAE (p. 93)
11 Four posterior cells (figs. 308–14). Furry or scaly species, with very slender legs, and often a long proboscis. Head globular, very mobile..BOMBYLIIDAE (p. 110)
— Only three posterior cells (fig. 285). Venation as in figs. 285, 337. Very bare flies, of small size, neither furry nor covered with coloured scales. Proboscis very short. Head not globular, but rather transverse, with distinct postocular rim ..... SCENOPINIDAE (p. 104)

Family STRATIOMYIDAE

The "Soldier Flies" are strictly so-called because of the spines on the scutellum, and sometimes on the mesonotum: "mouche armée" was the term used by Geoffroy himself (1762). The name is equally appropriate to the appearance of many of the species, which are brightly coloured, shining metallic, or with a bold pattern of spots of crude colour. This appearance, reminiscent of toy soldiers, is the more obvious because Stratiomyidae spend much time sitting on vegetation, basking in the sun, and only occasionally dancing in spots of sunlight.

MORPHOLOGY

HEAD.—Males usually holoptic, though the eyes often meet only in one point, and in a few genera do not quite meet at all; eyes always closer together in males than in females of the same species. Hairy eyes are common, either in both sexes or in males only; males often have the upper facets larger than the lower. Ocelli invariably present and well developed, usually on a prominent tubercle. Face generally prominent to some extent (*cf.* Syrphidae), and developed into a snout in *Nemotelus* (figs. 23–30). Only the tip of the snout is formed from the face, which is not more prominent than in many other genera; most of the forward projection is a result of development of the area surrounding the antennae, which are borne well forward on the snout.

Antennae consist of scape, pedicel and flagellum. The first two are usually unremarkable, except in *Stratiomys*, where the scape is unusually long and cylindrical (fig. 75). The flagellum is the striking part of the antennae, and assumes a great variety of shapes throughout the family. What is apparently the most primitive condition (recalling that in *Xylomyia* and the genera of

the basic Brachyceran stock) is found in *Beris*, where the flagellum forms a simple awl-like structure of eight annuli, with clearly visible sutures. Rings of sense organs are visible on the outer face of the flagellum. An essentially similar condition persists in *Stratiomys*, though the number of annuli is reduced to six, and the sensory pits are much more numerous. Other genera have the flagellum modified into a styliform appendage (*Nemotelus*), or a well-formed, two-segmented arista resembling that found in muscoid flies (*Sargus*, *Chloromyia*).

Mouthparts are much simplified by reduction. Figure 8 shows those of *Stratiomys furcata*, after boiling in potash and clearing, which has the effect of expanding the labium into a somewhat shapeless mass. The labium is short and fleshy, about half of its length being occupied by soft labella with poorly developed pseudotracheae. Dorsal to this lies a labrum in the form of a scroll-like half-tube. There are no mandibles, and maxillae are reduced to mere vestiges. Maxillary palpi persist, but are very short and, apart from hairs show no evidence of prominent sense-organs. Modifications in other genera include the unexpectedly long palpi of *Chorisops tibialis*, and the long, thin, geniculate proboscis of *Nemotelus*. Perhaps the snout of *Nemotelus* is no more than a housing for this proboscis.

Posterior margin of head often forms a postocular flange, which is especially prominent in certain genera such as *Oxycera* (figs. 63, 64). Besides being conspicuous when it is bright yellow, this postocular flange clearly has some structural significance, since it is a notable feature in many exotic genera: e.g. *Cyphomyia* in the Neotropical Region.

THORAX.—The most remarkable feature of the thorax is the spinulation from which the family derives both its scientific and its vernacular name. Occasionally there are spines on the mesonotum, though the only British example of this is the single pair of lateral (supra-alar) spines of the reputed British species *Clitellaria ephippium* (fig. 83). Most genera have spines on the scutellum: these are most numerous in *Beris* and its allies, where a range of short spines is evidently a primitive condition. In other subfamilies the spines are reduced to two (often very large, as in *Clitellaria*), and in Sarginae they are lost altogether.

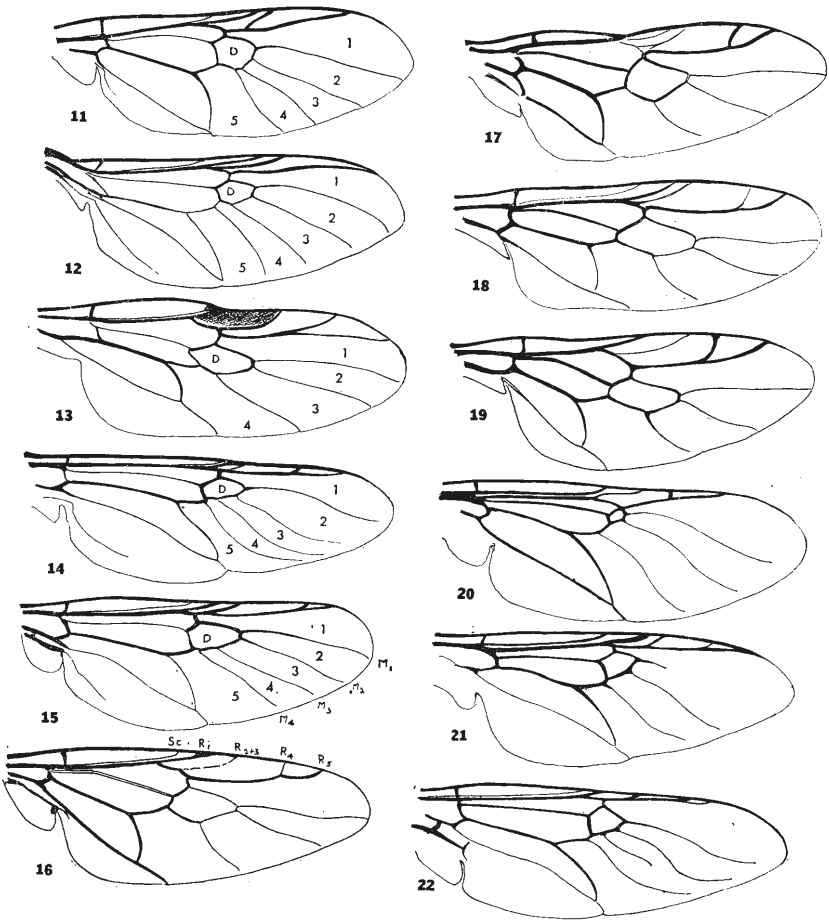
Pleura not remarkable, though in *Sargus* metapleuron and postscutellum are somewhat inflated.

ABDOMEN.—Varies in shape between near-cylindrical (*Sargus*) and ovoid (*Pachygaster*), but always dorso-ventrally flattened. Often decorated with pattern of spots, which occupy more than one-third of area of tergite, and may occasionally (but not often) be united into transverse bands. In *Beris* at least seven tergites can be counted, though it is difficult to be sure of the precise number because of the existence of transverse grooves, coupled with the varying extent to which the eighth tergite is concealed beneath the seventh. Other genera have fewer visible tergites, partly by concealment at tip of abdomen, and partly by reduction of basal segments. The pattern, also, easily leads to confusion about the number of segments: in fig. 62 (*Oxycera pulchella*) the first broad segment, without markings in this species, is numerically the second segment, and the first pair of spots occurs on the third tergite.

LEGS.—Unremarkable, without structural peculiarities. No macrochaetae, and no tibial spurs in any British species. Legs fairly well developed

for standing and walking, more substantial than the legs of Bombyliidae, but not robustly developed like those of Asilidae.

WINGS.—One of the most remarkable features of the wings of Stratiomyidae and a useful recognition feature, lies in the small discal cell. This is associated with a contraction of the radial veins towards the costa, so that R_5 reaches the wing-margin well before the tip of the wing. Discal cell biggest in *Pachygaster*, where it retains its central or "discal" position on the wing. The discal cell is also central in *Beris*, though somewhat reduced in size, but in other genera it is both reduced and moved forward towards the costal margin. The branches of the radial vein are thick and closely packed together, and in consequence some of the veins tend to become very short,



FIGS. 11–22.—Wings of Stratiomyidae. (11) *Oxycera formosa*; (12) *Chloromyia formosa*; (13) *Beris vallata*; (14) *Stratiomys potamida*; (15) *Clitellaria ephippium*; (16) *Pachygaster atra*; (17) *Pachygaster tarsalis*; (18) *Pachygaster leachii*; (19) *Pachygaster orbitalis*; (20) *Odontomyia viridula*; (21) *Odontomyia tigrina*; (22) *Odontomyia ornata*.

or to disappear altogether. Thus one must look carefully to see whether R_1, and R_{2+3} are both present, while species of the same genus may differ in whether R_{4+5} is forked or not.

Veins arising from, and posterior to, discal cell are always weaker, fading towards wing-margin; often they are so faint as to be little more than an indentation of the membrane. Nevertheless, much importance has been attached to details of venation in this region, and particularly to whether two, three or four veins (branches of M) arise from the discal cell itself. Sometimes the base of M_4 forms part of the posterior wall of the discal cell ("small cross-vein absent" of Verrall); sometimes M_4 arises before the boundary of the discal cell ("small cross-vein present" of Verrall). *Stigma* largest and most pronounced in *Beris*, rather indeterminate in more advanced genera.

Biology

Adult Stratiomyidae are associated with sunshine. They are most typically seen sitting on a broad leaf, basking in the sunshine. They do not pierce, or suck blood, vertebrate or invertebrate, nor the sap of plants. They do feed from flowers, and specimens preserved in collections often have grains of pollen clustered round the head.

The proboscis (fig. 8) seems less well adapted for sucking than is that of Syrphidae, in that there are no stylets, and the labrum is no more than a rudimentary half-tube. Nor are the pseudotracheae as elaborately developed as they are in Syrphidae. Syrphidae both suck nectar and swallow grains of pollen (see Müller, 1873 : 336). It seems evident that some Stratiomyidae, at least, swallow grains of pollen, but possibly they do not suck nectar. This is more probably true of those with a short, fleshy proboscis such as the *Odontomyia* figured (figs. 73, 74): the elongate proboscis of *Nemotelus*, with its more tapering labella, seems to be developed for penetrating deep into the Umbelliferae and Compositae on which this genus is found.

Although they spend so much time at rest, Stratiomyidae are competent fliers, and the males of many species hover, or dance, in the air. This is undoubtedly a mating device, and when a swarm of males is discovered, females are usually to be found by sweeping among nearby vegetation. Here the coloured spots of the abdomen are effective, and especially the silvery pile that is present on the abdomen of the males of some species. When Stratiomyidae come to rest the wings are folded one above the other on top of the abdomen, in which position they effectively cover most or all of the pattern. In this way a fly that has been most conspicuous when flying may suddenly disappear when it alights.

The *larval habits* of Stratiomyidae are varied within a limited range. It seems likely that the family arose from a primitive stock with larvae in decaying wood, a line from which *Xylomyia* and *Xylophagus* have survived (p. 3). *Pachygaster* represents a line that has preserved this habit, and developed it to the point at which "... at least some of the species are confined to certain (species of) trees" (Brindle, 1962 : 77). The trees apparently preferred by British *Pachygaster* are listed under the individual species concerned. The larvae live under the bark, but the exact nature of their food is uncertain; probably they eat anything available, whether animal or vegetable.

As discussed elsewhere (Oldroyd, 1964 : 19), there is evidence to suggest that the ancestral Diptera probably bred in wet moss, a habitat that is neither truly terrestrial nor truly aquatic, and that throughout the Order different groups have moved either towards a more "earthy" habitat or a more "watery" one. This has happened in Stratiomyidae. Beridinae and Sarginae are more terrestrial in habitat, breeding in "dung, grass-heaps or compost heaps, or other decaying vegetable material" (Brindle, 1965 : 208). In contrast, six out of the twelve British genera have become aquatic in the larval stages. "*Oxycera* larvae occur in mosses in hydropetricous habitats, i.e. in mosses growing in water flowing down rocks, or in semi-aquatic mosses growing in marshes, or amongst mud in marshy places" (Brindle, 1964 : 135). *Nemotelus*, placed in the same subfamily as *Oxycera*, lives in mud and shallow water, and larvae of *Stratiomys* and *Odontomyia* ". . . are aquatic, living in mud or silt which is covered with more or less static water, or occurring freely in ponds and marshes" (Brindle, 1964 : 92). They are water-living rather than truly aquatic, in the sense that they need to come to the surface for air, and can hang from the surface film by means of the hairs which surround the anal segment. Hinton (1953 : 220–5) describes and discusses the use of an air-bubble as a physical gill by larvae of *Oxycera*.

The remarkable feature of aquatic Stratiomyid larvae is the way in which they have adapted themselves to the perils of desiccation. This is achieved by the deposition of calcium carbonate, which gives the cuticle a shagreened appearance that is one of the recognition characters of the family. This carbonate can be dissolved in hydrochloric acid, with the release of carbon dioxide. Such larvae can be dried out for long periods, and become so brittle that they can be broken in pieces, yet, if undamaged, they will revive when returned to water.

A further peculiarity of the life-history is that the pupae of Stratiomyidae are enclosed within the last larval skin. Though this recalls—or more accurately foreshadows—the puparium of the Cyclorrhapha, it is doubtful whether the resemblance has any significance, other than convergence.

Classification

The Stratiomyidae of the world are divided among a number of subfamilies and tribes, into which the British genera fall as follows:

- *Beris*, *Chorisops* — BERIDINAE
- *Sargus*, *Chloromyia*, *Microchrysa* — SARGINAE
- *Stratiomys*, *Odontomyia* — STRATIOMYINAE
- *Pachygaster* — PACHYGASTERINAE
- *Nemotelus*, *Clitellaria*, *Oxycera*, *Vanoyia* — CLITELLARIINAE

The subfamilies are well established, and valuable when a wider fauna is being studied, but they have limited value in understanding the genera of the British fauna. It is more convenient, therefore, to take the key directly down to genera.

KEY TO GENERA

1 Scutellum without spines 2
– Scutellum with 2–6 spines on its margin 6
2 Face in both sexes conically produced (figs. 23, 26)... **Nemotelus** Geoffroy (p. 15)
– Face not conically produced 3
3 Wing with only four posterior cells (figs. 16–19)..... **Pachygaster** Meigen (p. 17)
– Wing with five posterior cells (figs. 11–15, 20–2) 4
4 Eyes densely hairy in both sexes, hairs longer in male (figs. 35, 36)
Chloromyia Duncan (p. 19)
– Eyes no more than microscopically hairy 5
5 Elongate and narrow species with distinct wing-veins. Eyes of males closer together than those of females, but not touching..... **Sargus** Fabricius (p. 18)
– Short, stout species, with very fine wing-veins issuing from discal cell; eyes of males touching ..... **Microchrysa** Loew (p. 19)
6 Scutellum with four, five or six spines; abdomen with seven obvious segments... 7
– Scutellum with only two spines; abdomen with fewer than seven segments..... 8
7 Scutellum usually with six spines. Eyes hairy, touching in the male
Beris Latreille (p. 21)
– Scutellum with only four spines. Eyes bare, separated in both sexes
Chorisops Rondani (p. 23)
8 Thorax with a pair of strong spines above wing-bases (fig. 83)
Clitellaria Meigen (p. 23)
– Thorax without any such spines 9
9 Fifth posterior cell having a common boundary with discal cell (fig. 11)..... 10
– Fifth posterior cell separated from discal cell by base of fourth posterior cell (figs. 14, 20–2) 11
10 Antennae as in fig. 63, flagellum terminating in a bristle-like appendage
Oxycera Meigen (p. 25)
— Antennae as in fig. 65, flagellum not bristle-like at tip.. **Vanoyia** Villeneuve (p. 26)
11 First antennal segment elongate (figs. 75, 76). Antennae normally sharply angled
Stratiomys Geoffroy (p. 27)
— First antennal segment as long as second; antennae not angled (figs. 73, 74)
Odontomyia Meigen (p. 29)

Genus **Nemotelus** Geoffroy

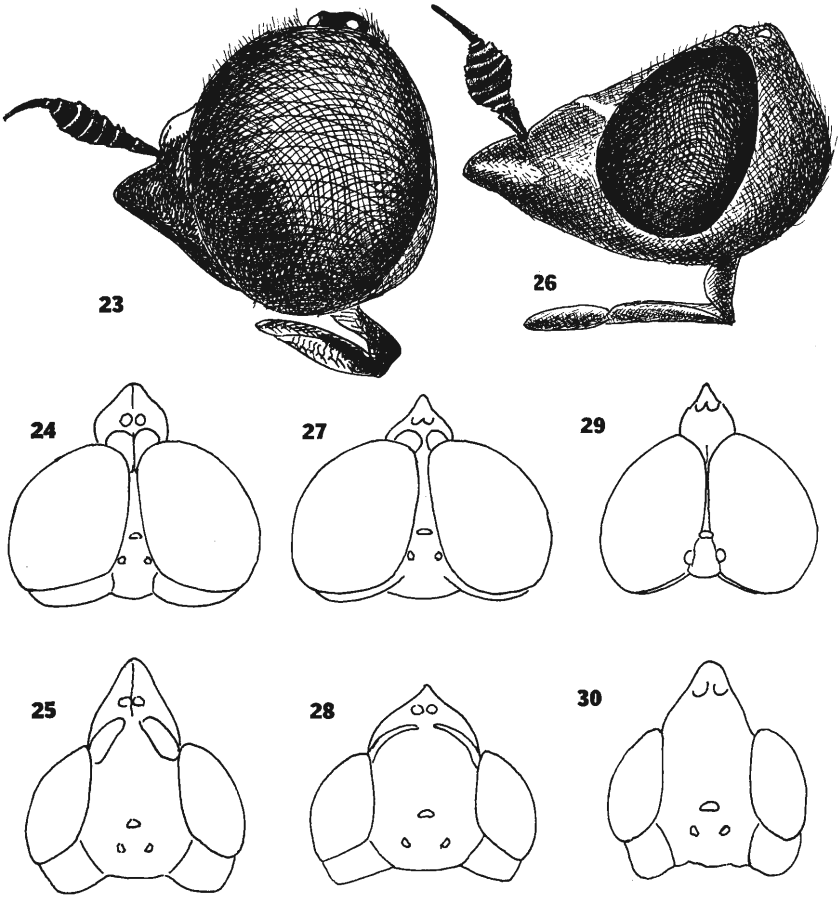
Nemotelus are among the smallest Stratiomyidae, and are readily distinguished in either sex by the conical snout (figs. 23–30). Not only is the facial lobe, below the antennae, conical and prominent, but the whole facial area is pushed forwards by an expansion of the parafacials, and of the frons immediately above the antennae. This has the effect of bringing the antennae well forward, so that they overhang the tip of the snout.

Frons not unusually developed. Eyes of the male almost meeting, and with bigger facets in upper area of eyes. Proboscis geniculate, folding away into a long cavity beneath the snout. Body-shape and wing-venation generally similar to that of *Oxycera* (fig. 62), except that R_{4+5} is generally forked, and R_{2+3} evanescent.

Out of a large number of exotic species of *Nemotelus*, only five occur in Britain.

KEY TO SPECIES

All British *Nemotelus* occur in marshy localities, and may be locally abundant anywhere in the British Isles: *fraternus* Loew has so far been recognized only in Norfolk—Horning Ferry (Collin); Wheatfen Marsh (Biggs)—and in Ireland, but probably occurs elsewhere.

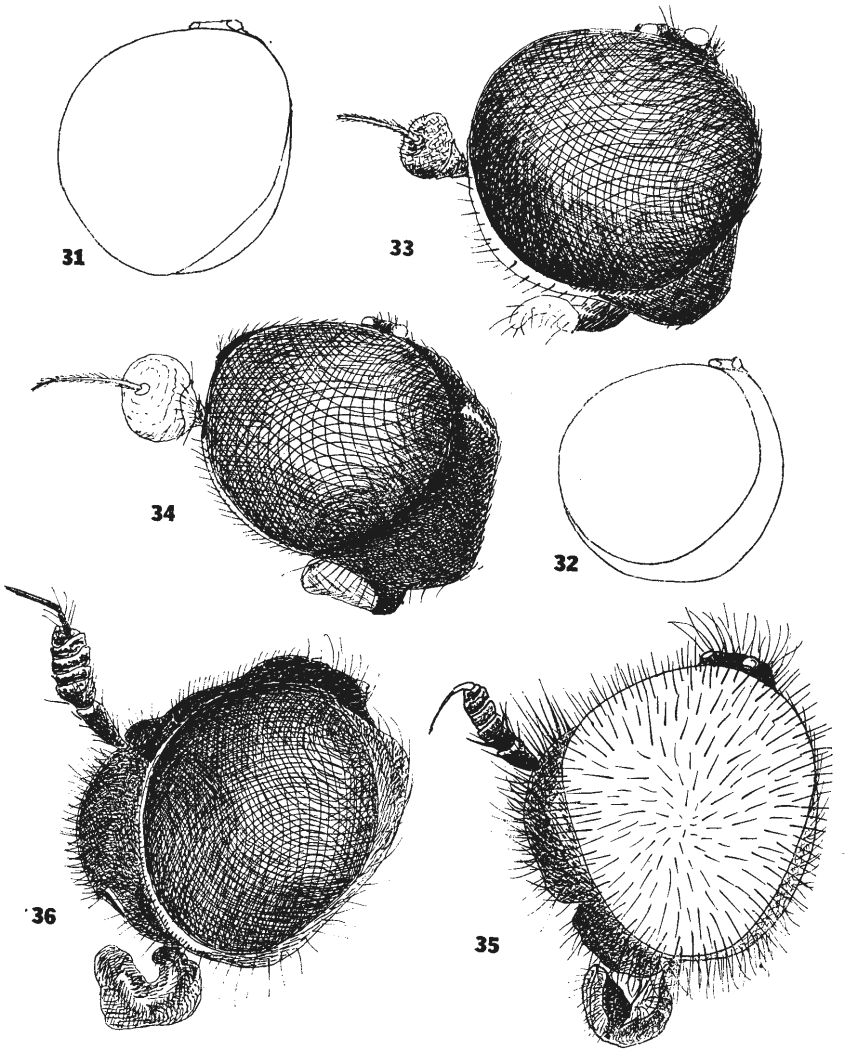


FIGS. 23–30.—Heads of *Nemotelus*. (23, 24) *uliginosus* ♂; (25, 26) *uliginosus* ♀; (27) *notatus* ♂; (28) *notatus* ♀; (29) *pantherinus* ♂; (30) *pantherinus* ♀.

1 R_{4+5} unforked. Body all black, without pale pattern.....**nigrinus** Fallén
– R_{4+5} forked. Body with some abdominal pale areas, extensive in males.....2
2 Snout short (figs. 27, 28).....3
– Snout long in both sexes (figs. 23–26, 29, 30).....4
3 Eyes of male almost touching at one point. Females without any pale markings immediately above antennae. Humeral yellow spot small, extended to wing-base as a mere line.....**fraternus** Loew
– Eyes of male distinctly separated by at least breadth of median ocellus. Females with yellow spots above antennae. Humeral yellow spot large, with distinct yellow band connecting back to wing-base.....**notatus** Zetterstedt
4 Female with two large white spots above antennae; spots smaller in male, which has eyes distinctly separated. Humeri with large yellowish spots extending back to wing-base.....**uliginosus** Linnaeus
– Female without any white spots above antennae; males with one large white spot occupying entire subantennal region. Humeral spot very small
pantherinus Linnaeus

Genus **Pachygaster** Meigen, 1803

The name *Pachygaster* describes the rotund appearance of the abdomen of this genus of small, black flies, which are otherwise recognized principally by the reduced venation, with only three faint veinlets issuing from the discal cell (i.e. four posterior cells; figs. 16–19). Note that an element of confusion occurs here in reading Verrall because he writes: "Wings with only *two* veinlets issuing from the discal cell *besides the upper branch of the postical vein*" (my italics).



FIGS. 31–36.—Heads of Stratiomyidae. (31) *Pachygaster tarsalis* ♂; (32) *P. tarsalis* ♀; (33) *P. atra* ♂; (34) *P. atra* ♀; (35) *Chloromyia formosa* ♂; (36) *C. formosa* ♀.

The eggs are laid in the burrows of wood-boring beetles, especially in rather crumbly wood. The larvae of the four British species are broadly associated with different genera of trees: thus *P. minutissima* with *Pinus*; *P. tarsalis* with *Fagus* and *Populus*; *P. atra* with *Ulmus*; *P. orbitalis* with *Ilex*; and *P. leachii* with *Quercus*.

KEY TO SPECIES

1 R_{4+5} not forked ..... **minutissima** Zetterstedt
Very rare in British Isles, though recorded from Somerset and again from Inverness-shire (Verrall), and from Wiltshire (C. H. Andrewes). Larvae under bark of birch or pine. vi–vii.
– R_{4+5} forked 2
2 Wings darkened in basal half 3
– Wings entirely hyaline 4
3 Fore margin of wing dilated, anterior cross-vein short, discal cell well forward, so that its upper margin is almost in line with stem of R_5 (fig. 17). Lower postorbital flange narrow in both sexes (figs. 31, 32) ..... **tarsalis** Zetterstedt
Rare, but widely distributed in British Isles. Hants (New Forest), Somerset (Portishead), Dorset (C. H. Andrewes) and Scotland (Inverness-shire). Larvae in beech, pine and poplar. v–vii.
– Fore margin of wing not dilated. Anterior cross-vein longer, discal cell less far forward, so that its upper margin is by no means in line with stem of R_5 (fig. 16) Lower postorbital flange broader in both sexes (figs. 33, 34) ..... **atra** Panzer
Locally numerous in England, Wales and Scotland. Larvae in burrows of beetles boring in elm. v–vii.
4 Femora black, except for extreme tip. Face with narrow silvery band on each side. Wing venation as in fig. 19 ..... **orbitalis** Wahlberg (*meromelas* Dufour)
Known as British only from Hants (New Forest), in burrows of beetles in holly, and Hereford, Moccas Park, larvae in horse chestnut (Skidmore). vi–vii.
– Femora yellow, hind pair with a subapical dark ring. Face without silvery band. Wing venation as in fig. 18 ..... **leachii** Curtis
Southern half of England and Wales, in beetle burrows in oak, rotten elm (Chandler), Angelica roots (K. G. V. Smith). vi–viii.

Genus **Sargus** Fabricius, 1798

One of the most distinctive genera of Stratiomyidae, with narrow, elongate abdomen, spherical head, and wings broad and paddle-like from a narrow base. The metallic green, blue or purple colours are specially well developed in *Sargus*.

The brilliant, conspicuous, adult flies are to be seen sunning themselves on leaves, or in the vicinity of dung or decaying vegetable material, on which they oviposit.

The name *Geosargus* Bezzi (1907) was proposed in the belief that *Sargus* was preoccupied, and has been widely current, especially since it was used by Lindner in *Die Fliegen der Palaearktischen Region* (1936, 4 (1) : 37). Latterly this substitute name has been rejected—as was anticipated by Verrall (1909 : 166)—and *Sargus* is again the accepted generic name.

KEY TO SPECIES

1 Legs orange 2
– Legs, especially femora, black 5
2 Males 3
– Females 4
3 Wings infuscated in middle. Abdomen metallic green ..... **albibarbus** Loew
Rare and doubtful species. 1 ♂ *Devon (Avon Valley) (see Verrall, 1909 : 172)* 1 ♀ *Glos. (Bristol), 27.ix.57 (Fonseca). vii–ix.*

– Wings not darkened in middle. Abdomen dorsally with a bronze tint, covered with yellow hair. Male genitalia as in fig. 38. Head fig. 37
bipunctatus Scopoli ♂

4 Abdomen bi-coloured: first two segments orange, with a small metallic spot; rest of abdomen, orange at extreme sides only.....**bipunctatus** Scopoli ♀
Sexually dimorphic species (see couplet 3). Widespread throughout Britain, including Ireland. Not uncommon. viii–x. Oviposits in cow-dung and rotting fruiting bodies of Polyporus squamosus *(Chandler).*

– Abdomen unicoloured, metallic bronze.....**splendens** Meigen ♀
[including *flavipes* Meigen, *rufipes* Wahlberg, *nitidus* Meigen, all as interpreted by Verrall, 1909]
A very variable species, which on present interpretation includes several forms which Verrall (1909) *doubtfully accepted as distinct. Widespread throughout British Isles, including Ireland. vii–late ix.*

5 Postocular ciliation, behind eyes, as long as tuft of hairs at vertex.....6

– Postocular ciliation distinctly shorter than tuft of hairs at vertex.....7

6 Wings clear, with a conspicuous brown cloud in middle. Knees and hind basitarsi distinctly pale .....*__cuprarius__ Linnaeus ♂, ♀
Throughout British Isles, but less common in north than the next species. vi–end ix.

– Wings more or less uniformly smoky, with no conspicuous cloud. Knees and hind basitarsi only very narrowly pale .....**iridatus** Scopoli ♂, ♀
Widespread throughout British Isles, including Ireland. A long season, v–viii. Oviposits on cow-dung (Chandler).

7 Female, tiny (5 mm.). A doubtful species in which, apart from the small size, the *female* has dark legs, whereas it is the *male* of the larger *splendens* that is the dark-legged sex .....**minimus** Zetterstedt ♀ (no British ♂ known)
Verrall records specimens from Dolgelly and Milford-on-Sea and Grimshaw from Ireland, Clare Is. In the B.M. is a female from the New Forest (Adams coll.). Fonseca has a specimen from Somerset. vi–ix.

– Males, larger (9–18 mm.) (see notes to couplet 4, above).....**splendens** Meigen ♂

Genus **Chloromyia** Duncan, 1837

A smaller version of *Sargus*, not so conspicuously elongate, and recognizable at once by the densely hairy eyes (figs. 35, 36).

ONE BRITISH SPECIES

Eyes of both sexes covered with dense, brown hairs, rather longer in male. Thorax brilliant metallic green, pitted with hair-sockets from which arise long, pale brown hairs (♂), or short whitish ones (♀). Abdomen of male a coppery green, with dense, semi-recumbent yellow hairs; female with dense brown hairs centrally, whitish ones laterally. Legs dark, with broad yellow tips to femora and bases to tibiae
formosa Scopoli

Widespread throughout British Isles, including Ireland. Common in gardens, sunning itself on leaves. v–vii.

Genus **Microchrysa** Loew, 1855

These small, brilliantly metallic flies are separated from *Sargus* by the short, broad abdomen, and from *Chloromyia* by the bare eyes, which in males almost touch for a considerable distance.

The three western Palaearctic species of *Microchrysa* all occur in Britain.

* *S. nubeculosus* Zetterstedt was listed as a synonym of *cuprarius* by Lundbeck and Lindner, though Verrall believed that it could be distinguished by the smaller and darker males.

KEY TO SPECIES

1 Antennae black. Males with eyes longer, and distinctly separated by about half the breadth of the median ocellus (fig. 40). Female with frons green **polita** Linnaeus

Widespread and common all over British Isles, including Ireland. Frequent in gardens, on leaves of shrubs. iii–ix. Oviposits in cow-dung, females folding their wings and entering crevices (Chandler). Bred from rotting grass by A. A. Allen.

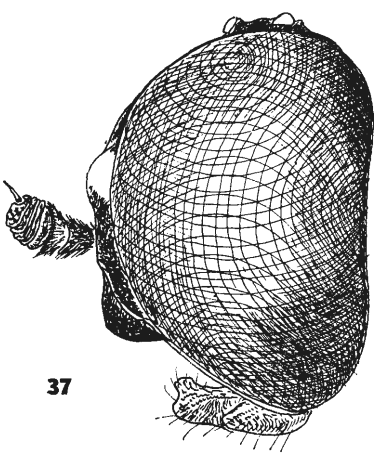
– At least first antennal segment yellow. Male with eyes shorter, their inner margins more strongly curved, and at one point virtually touching (figs. 41, 42) 2

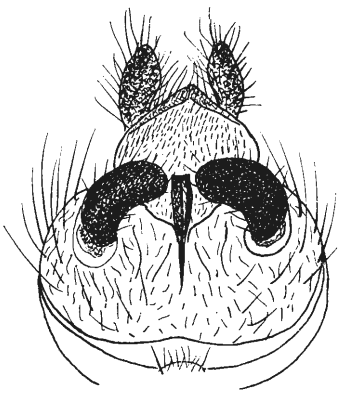
2 Frons of female, and abdomen of both sexes, blackish..**cyaneiventris** Zetterstedt

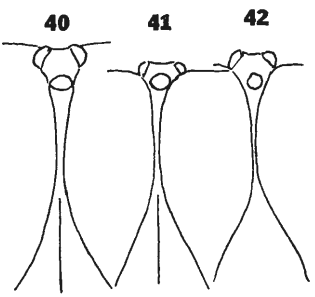
A northern Palaearctic species that occurs all over Britain including Ireland, though less commonly than the following species. Common in some Yorkshire localities (Chandler). vi–viii.

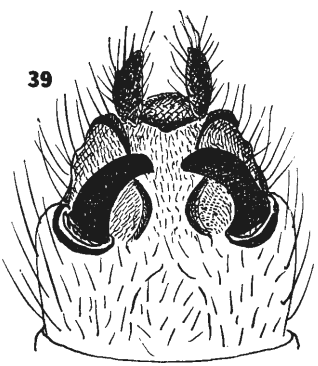
– Frons of female, and abdomen of both sexes, green.....**flavicornis** Meigen

Widespread throughout British Isles, including Ireland, and only less common than M. polita. *vi–viii.*





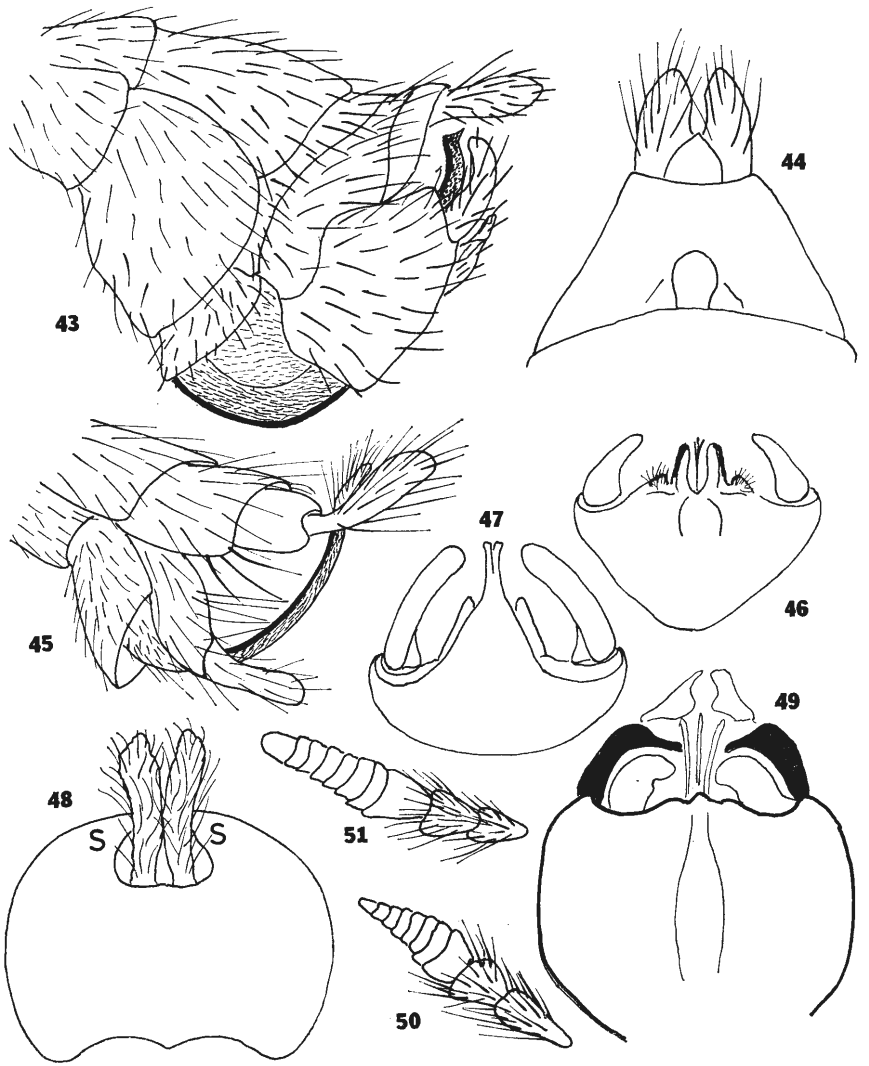




FIGS. 37–42.—Stratiomyidae. (37) *Sargus bipunctatus* ♂, head; (38) *S. bipunctatus* ♂, genitalia in ventral view; (39) *S. splendens* ♂, genitalia in ventral view; (40–42) separation of eyes in males of *Michrochrysa polita* (40), *M. flavicornis* (41) and *M. cyaneiventris* (42).

Genus **Beris** Latreille

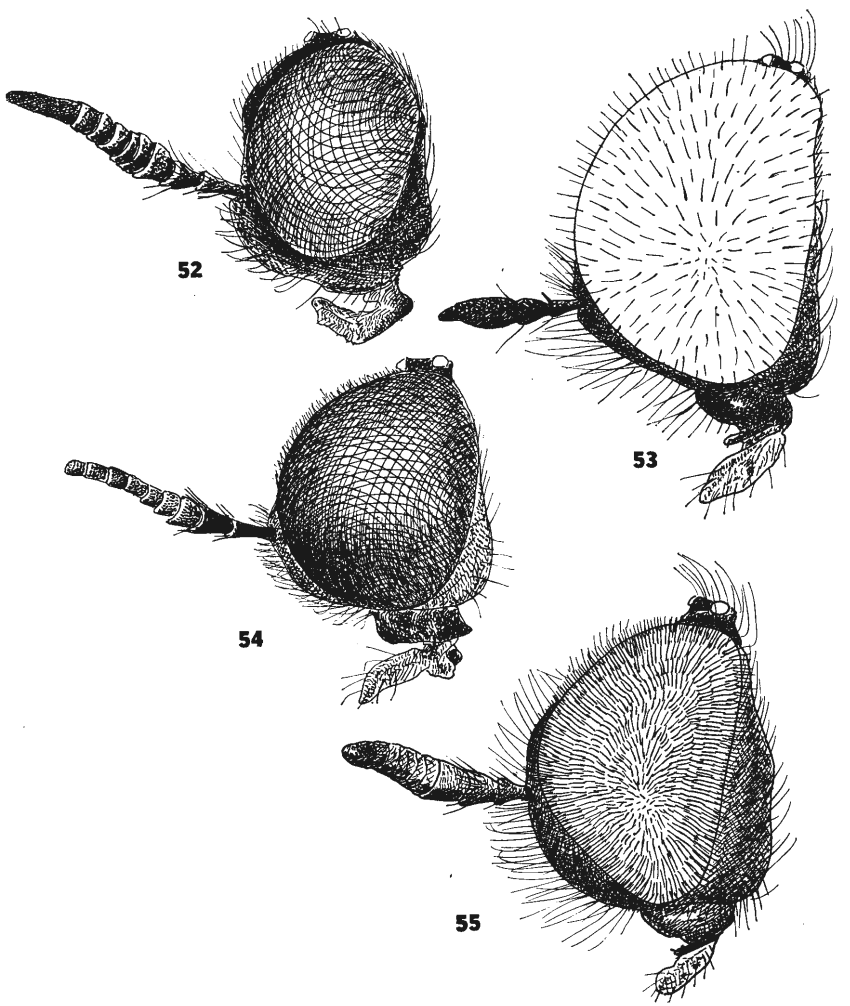
Together with the closely related *Chorisops*, this genus represents the subfamily Beridinae, which is evidently the most primitive subfamily of Stratiomyidae, and the one most closely related to Rhagionidae and certain other basic Brachyceran families. Beridinae are distinguished from other



FIGS. 43–51.—Stratiomyidae. Male genitalia of: (43) *Beris vallata*; (44) *B. chalybeata*, epandrium; (45) *B. clavipes*; (46) *B. chalybeata*, hypandrium; (47) *B. geniculata*, hypandrium; (48) *B. fuscipes*, epandrium; (49) *B. fuscipes*, hypandrium; (50, 51) antennae of *B. fuscipes* (50) and *B. chalybeata* (51).

Stratiomyidae by having at least seven distinct segments in the abdomen, and an awl-like flagellum of about eight annuli.

Among both Brachycera and Cyclorrhapha, evolution seems to have resulted in a reduction of the number of visible abdominal segments, and in a fusion of the flagellar segments of the antenna into a compound third segment. The wing-venation of *Microchrysa*, and especially the strongly curved R_{2+3}, which encloses a stigma, recalls some of the features of Rhagionidae, though the position of the radial fork in relation to the wing-tip is typically Stratiomyid.



FIGS. 52–55.—Heads of Stratiomyidae, in side view. (52) *Beris vallata* ♀; (53) *B. morrisii* ♂; (54) *B. vallata* ♂; (55) *B. geniculata* ♂.

Six species of *Beris* occur in the British Isles. Males sometimes hover or dance in swarms.

KEY TO SPECIES

1 Head and thorax black, abdomen orange, resembling a saw-fly (*Athalia*) 2
– Not bi-coloured in this way, though abdomen is duller and browner than thorax..3
2 Hind tibiae entirely yellow or only indistinctly dusky at tip. Abdomen orange, with narrow, blackish, preapical band on each segment (fig. 45) **clavipes** Linnaeus
Local in southern half of England and Wales, Northumberland (Tongue); Ireland (Co. Down). v–vi.
– Hind tibiae distinctly darkened on at least apical half. Abdomen entirely orange, without any narrow preapical bands, though segments sometimes dusky on extreme hind margins (figs. 43, 52, 54, 56).....**vallata** Forster
Common throughout the British Isles, including Ireland. vi–viii.
3 Antennae placed low on head; lower occiput less prominent than following species (fig. 53). Hairs of eyes sparse, light brown. Long hairs of thorax of male pale. Legs pale yellow. Hypandrium similar to that of *geniculata*, fig. 47. ♀ frons narrow, parallel-sided.....**morrisii** Dale
Local throughout Great Britain. vi–viii.
– Antennae placed higher on head; lower occiput more prominent in both sexes (fig. 55). Hairs of eyes dense, dark brown. Long hairs of thorax of male black. Legs darker, dull orange or dusky.....4
4 Third antennal segment less than twice as long as first two together (fig. 50). Epandrium with surstyli (figs. 48, 49).....**fuscipes** Meigen
Rare. Verrall gives Cornwall (Padstow), Oxford (Kingswear), Herts. (Ashridge); Wales (Anglesey) (C. H. Andrewes), Glamorgan (Porthcawl), Co. Kerry (Kenmare), and doubtful record from Aberlady. Eire: Stradbally in Andrewes' coll.; Wicklow, nr. Blessington (Chandler). No authentic specimens in the B.M. vi–ix.
– Third antennal segment more than twice as long as first two together (fig. 51). Epandrium without surstyli.....5
5 Male hypandrium as in fig. 47. Female frons as in fig. 58.....**geniculata** Curtis
Locally common throughout Great Britain, perhaps more abundant in north. vi–ix.
– Male hypandrium as in fig. 46. Female frons as in fig. 57....**chalybeata** Forster
Widely distributed, and locally common throughout Great Britain and Ireland. Earliest species of genus, mid-v–viii. Breeds in garden compost (Chandler).

Genus **Chorisops** Rondani, 1856

The name of this genus is sometimes misunderstood; it refers to the separated eyes of the male, and has no connection with *chloros*, green.

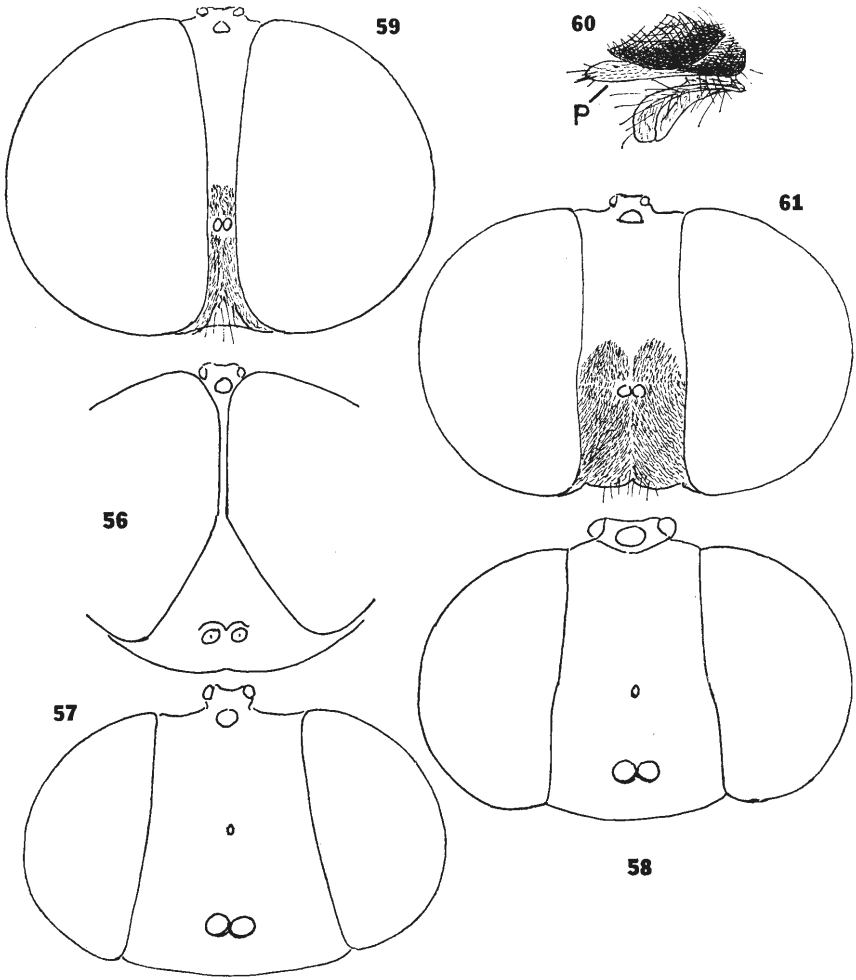
Chorisops is easily distinguished from *Beris* by the fact that the eyes of the male are distinctly separated (figs. 51, 59, 61), as well as by the elongate palpi (fig. 60), the latter an unusual feature in Stratiomyidae.

ONE BRITISH SPECIES

Thorax metallic green (♂), or greenish black (♀); scutellum metallic with four yellow spines, and humeri more or less distinctly yellow. Abdomen in both sexes more or less extensively yellow on discs of segment, blackish at sides and posteriorly. Legs of ♀ yellow with dark tarsi; hind legs of ♂ extensively black. Wings almost clear with large, distinct, dark brown stigma.....**tibialis** Meigen
England and Wales from Yorkshire southwards. Frequent. Males sometimes in rapidly moving swarms under trees. vii–ix.

Genus **Clitellaria** Meigen, 1803

This genus, though only reputed to occur in Britain, is included here as much for its striking appearance as for the remote possibility that more specimens may one day be found here.



FIGS. 56–61.—Heads of Stratiomyidae in front view. (56) *Beris vallata* ♂; (57) *B. chalybeata* ♀; (58) *B. geniculata* ♀; (59) *Chorisops tibialis* ♂; (60) *C. tibialis*, detail of proboscis and palp (P); (61) *C. tibialis* ♀.

It cannot be confused with any other British genus, because it is the only genus with a large, black spine on each side of the thorax, behind the transverse suture, and above the wing-base (fig. 83).

There are two Palaearctic species, one of which occurs only in the extreme east of the Region. The larvae are known to live in the nests of *Lasius fuliginosus* during the summer, overwintering in soil or debris.

ONE BRITISH SPECIES

Rather large and bulky, about 12 mm. long. Eyes hairy in both sexes, those of female with a broad postocular rim. General colour black, but mesonotum covered with

close-lying, rusty-red hairs, so that thorax contrasts strongly with black abdomen. Thoracic spines (fig. 83) strong, black. Legs entirely black. Wings heavily infuscated: R_{4+5} forked; four posterior cells; vein M_4 leaving discal cell at its extreme posterior angle ..... **ephippium** Fabricius

No authoritatively British specimens exist, but the B.M. has five, four from the Stephens' Collection, and one fine female labelled by F. W. Edwards: "Locality unknown, possibly Darenth Woods, about 1850. *Coll. by W. Marshall (see F. C. Adams' notebook)." Stephens gives a beautiful drawing (pl.* 46, *fig.* 1), *undoubtedly made directly from a specimen, and he writes about the species: "Very rare: taken in June in Coombe Wood (? near Deal) whence I possess a fine pair."*

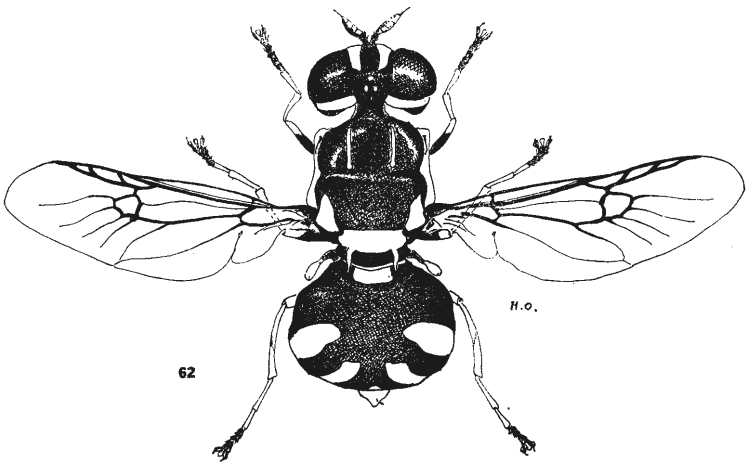


FIG. 62.—*Oxycera pulchella* ♀.

Genus **Oxycera** Meigen, 1803

Related to *Clitellaria*, of which it is almost a miniature version, but without the lateral thoracic spines. Females of *Oxycera* have the same broad postocular flange, which, together with the wing-venation, is characteristic of the subfamily Clitellariinae (figs. 62–64).

The various species of *Oxycera* differ in size over a wider range than any other British genus of Stratiomyidae.

Verrall (1909 : 88) begins his key to the species by separating those species with R_{4+5} simple from those in which R_{4+5} is forked. This is a decisive structural character, but one that is often difficult to see, since R_4 may be very faint. A mistake at the beginning of a key can lead to great confusion, so I have attempted to use other, more obvious colour characters at first, bringing in the condition of R_{4+5} at a later stage of the key.

The larvae of *Oxycera* occur in mosses covered with flowing water, or in mosses and mud in marshy areas. The adults of all species are to be found among vegetation, or on the margins of marshy areas.

KEY TO SPECIES

1 Notopleural area (sides of mesonotum anterior to transverse suture) black, with only a very narrow yellow border; pleura otherwise black; no longitudinal yellow stripes, except in females of *pardalina* 2

– Notopleural area with a large yellow spot 7

2 Abdomen black, with only tip yellow; no lateral yellow spots 3
– Abdomen with lateral yellow spots (fig. 62) 4
3 Wings heavily darkened in middle, around and anterior to discal cell. Vein R_{4+5} simple, unforked ..... **analis** Meigen
Uncommon. Southern and western England: Kent, Eynsford (Andrewes), Somerset, Shapwick (Cowley), Herefordshire, Cambs., Chippenham Fen (Hammond). vi–vii.
– Wings not darkened in middle. R_{4+5} forked (see also ♂ *Vanoyia tenuicornis*) **terminata** Meigen
Rare. Southern and western England: Dorset, Somerset, Welsh Border. Fonseca found it in great numbers on one occasion at Blaise Castle Woods, Bristol, where a stream had been diverted. vi–vii.
4 Scutellum almost entirely yellow 5
– Scutellum yellow only narrowly at tip, at base of spines; or else all black 6
5 R_{4+5} forked. Female with two yellow stripes on mesonotum (if no stripes, see ♀ *Vanoyia tenuicornis*) ..... **pardalina** Meigen
Rare. Southern and western England; Derby, Dovedale (Parmenter). ♂ hovering 20–30 feet up near trees by stream; ♀ swept from nearby vegetation (Fonseca). vii–viii.
– R_{4+5} simple. Both sexes with mesonotum black, unstriped ..... **pygmaea** Fallén
Locally common. Southern England; Scotland, E. Lothian (Fonseca); Ireland, Clare Is. (Grimshaw). vi–vii.
6 R_{4+5} forked. Hind femora yellow basally, black only on apical half **morrisii** Curtis
Widely distributed, but rare and local. England and N. Ireland. vii.
– R_{4+5} unforked. Hind femora entirely yellow ..... **nigripes** Verrall
Very rare. Scotland: Sutherland, Inchnadamph. vii.
7 Notopleural spot linked with postalar spot, to form a broad, continuous lateral margin; mesonotum in both sexes with two broad stripes ... **trilineata** Fabricius
Widely distributed in England and Wales, Scotland and Ireland. Frequent. vi–early ix.
– Notopleural spot always separated from postalar spot by a black patch. Mesonotum sometimes with stripes in females but never in males 8
8 R_{4+5} simple. Thorax very bare and shining in both sexes; in females, longitudinal stripes are joined anteriorly to large notopleural patches ..... **formosa** Meigen
Numerous, but very local. Southern England to Norfolk; Wales. vi–viii.
– R_{4+5} forked. Thorax more or less hairy, sometimes very pilose. Longitudinal stripes in females separated from notopleural patches 9
9 Notopleural spot large and long extending from humerus to suture, and down in front of wing 10
– Notopleural spot reduced to a triangle, situated on transverse suture. A large dark species, with black legs and head, and almost circular yellow abdominal spots ..... **dives** Loew
Very rare. Scotland: Perthshire. vi–vii.
10 Abdomen with three pairs of yellow spots, in addition to yellow base and tip **fallenii** Staeger
Rare. Ireland: Co. Wicklow, Bellevue (Stelfox). viii.
— Abdomen with only two pairs of yellow spots; second segment entirely dark (fig. 62) **pulchella** Meigen
Scattered distribution in southern England and Wales. "Frequents bramble leaves in sunny localities" (Fonseca). vi–viii.

Genus **Vanoyia** Villeneuve, 1908

Villeneuve (1908) described a new genus and species from France, *Vanoyia scutellata*, naming the genus in honour of Dr. van Oye. Enderlein (1914) altered the spelling to *Vanoyea*, and this was followed by Lindner and some other authors, but was not adopted in the *Check List of British Insects* (1945), nor in the present work.

The original specimens were three: a male and female from Lille, and a male from Mt. Canigou in the Pyrenees—a rather scattered distribution.

Verrall (1909 : 769) quickly pointed out that *Vanoyia scutellata* Villeneuve was clearly synonymous with *Oxycera tenuicornis* Meigen.

The genus is distinguished from *Oxycera* solely by the structure of the antenna, which lacks the spine-like tip to the flagellum that is characteristic of true *Oxycera*. Instead, the third segment retains five clearly marked annuli, terminated by a sixth annulus which is blunt and hairy (figs. 63–65).

One other species of *Vanoyia* has been described: *V. separata* Kertész (1920) from Morocco; but there is strong presumption that this, too, may be a synonym of *tenuicornis*.

One British Species

Strongly sexually dimorphic. Male with thorax and abdomen black, and no yellow pattern except on notopleural suture and postalar callus. Legs mostly black. Female with mesopleuron extensively yellow, and a yellow scutellum. Legs mainly orange. If specimens with broken antennae are run down in the key to *Oxycera*, the male will run to *terminata* and the female to couplet 5 ..... **tenuicornis** Macquart

Local in south-western England, and South Wales. Also Norfolk, Coltishall (Parmenter). "♂ in small, dense swarms, hovering close above bramble bushes at Berrow, Somerset, at back of salt-marsh" (Fonseca). vi–vii.

Genus **Stratiomys** Geoffroy, 1762

This, the nominate genus of the family, consists of handsome, strongly built flies, with large, geniculate antennae (figs. 75, 76), broad postocular rim, almost square thorax, and broadly ovate abdomen. They are usually boldly patterned in black and yellow.

Though individuals may sometimes be locally numerous, *Stratiomys* is not a common genus, particularly having regard to its conspicuous appearance. Perhaps the flight period is short. The larvae are aquatic, but very tough, and resistant to desiccation. The length of life of the carnivorous larva is much affected by the vicissitudes of food supply and drought, and it may be that the appearances of adults are sporadic for this reason.

Key to Species

1 Second abdominal segment with a large triangular yellow spot on each side. Females with a yellow postocular flange, but with median postvertex black. Both sexes with bare eyes 2

Second abdominal segment without a large yellow spot at each side; either a small, oval spot, or none at all. Females with a black postocular flange, but with a paired yellow spot on postvertex. Either males, or both sexes, with hairy eyes 3

2 Third abdominal segment with shallow spots (♂) (fig. 77) or a narrow transverse band (♀) (fig. 78). Female with postocular flange in profile shallower (fig. 81) **potamida** Meigen

Infrequent in marshy areas of southern England, as far north as Warwickshire, Northamptonshire and Huntingdonshire. vi–viii.

– Third abdominal segment with large paired spots (figs. 79, 80). Male with bare eyes; female with postocular flange broader (fig. 82)..... **chamaeleon** Linnaeus

Rather rare in southern England, as far north as Norfolk and Leicestershire. vii–ix.

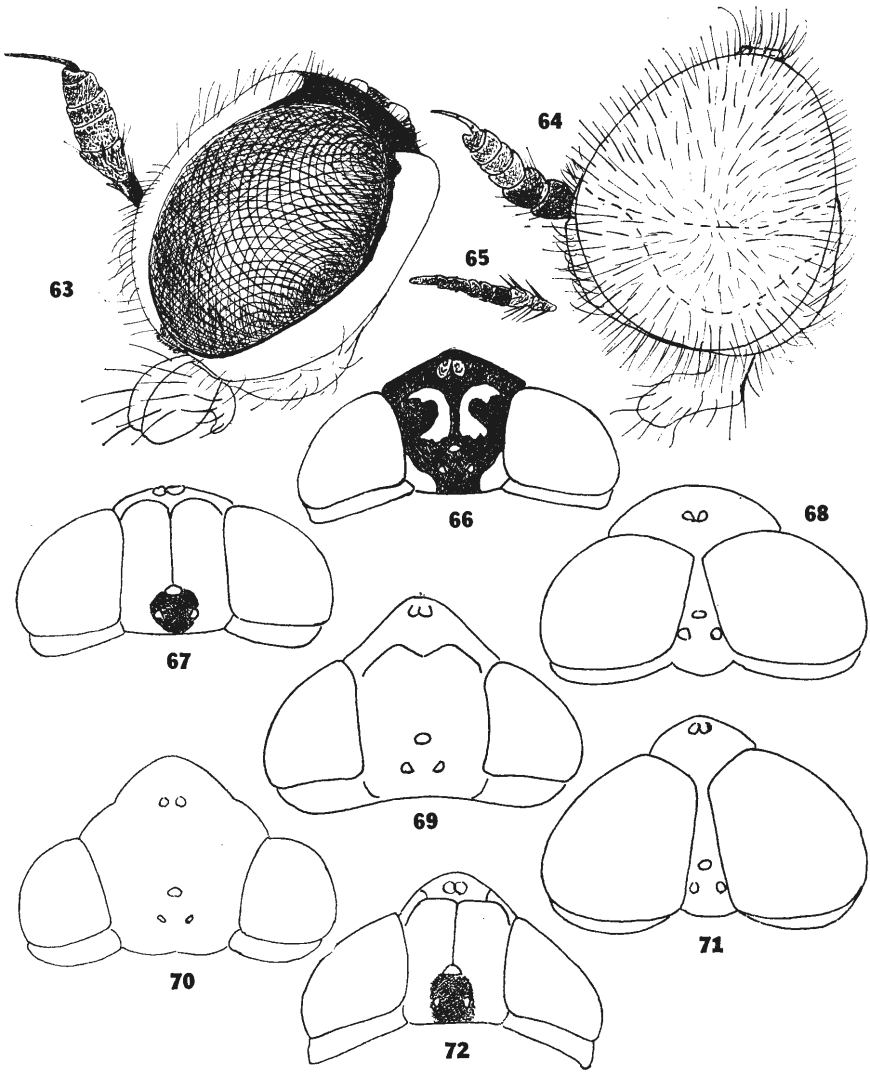
3 Densely hairy species, with tawny hairs mixed with grey. Yellow colour of scutellum practically confined to the two spines. Abdomen dorsally almost without trace of yellow spots, but with triangles of grey hairs laterally, especially on second segment. Both sexes have hairy eyes..... **longicornis** Scopoli

Local in England and Scotland, particularly on or near coast. London, Wood Green (Hammond). v–vii.

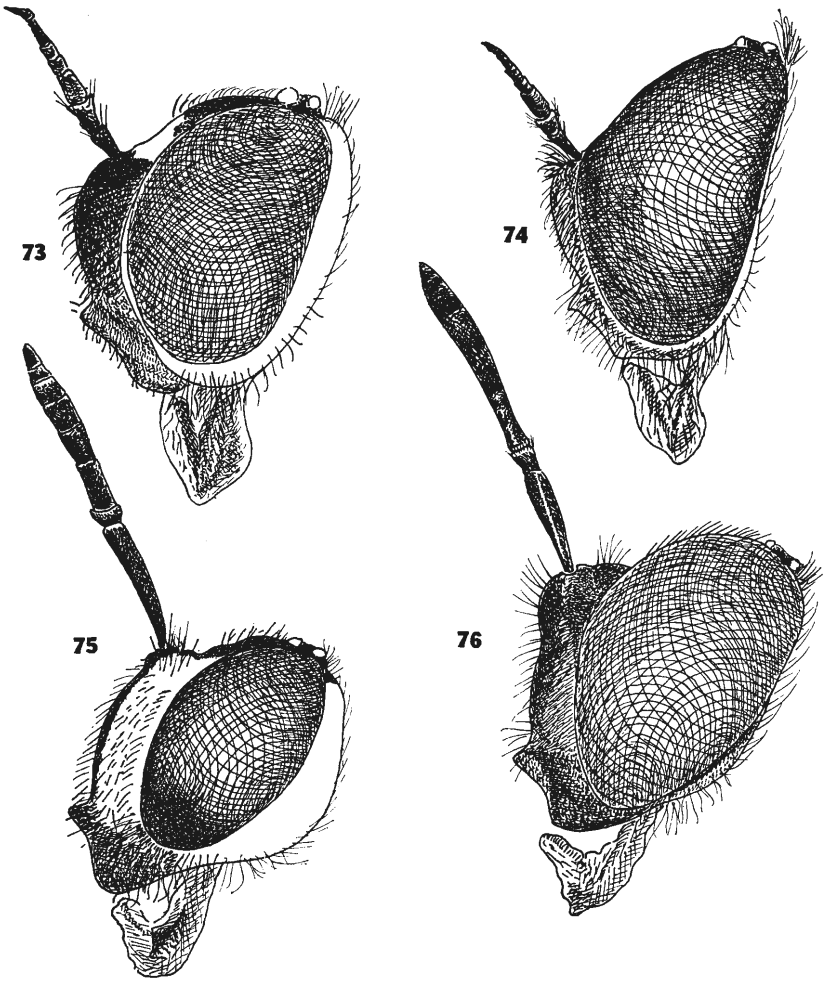
– Not conspicuously hairy, and without tawny hairs on thorax; yellow colour of scutellum not confined to spines. Abdomen dorsally with three pairs of distinct, though small, yellow spots. Male has hairy eyes, female eyes bare.

furcata Fabricius

Local; sometimes numerous in brackish or salt marshes in England, Scotland and Ireland. Generally a more northern species, but Essex, Benfleet (Stubbs) along with longicornis. *vii, viii.*



FIGS. 63–72.—Heads of Stratiomyidae. (63) *Oxycera pulchella* ♀; (64) *O. pulchella* ♂; (65) antenna of *Vanoyia tenuicornis* for comparison; (66) *Odontomyia ornata* ♀; (67) *O. angulata* ♀; (68) *O. argentata* ♂; (69) *O. tigrina* ♀; (70) *O. argentata* ♀; (71) *O. tigrina* ♂; (72) *O. hydroleon* ♀.

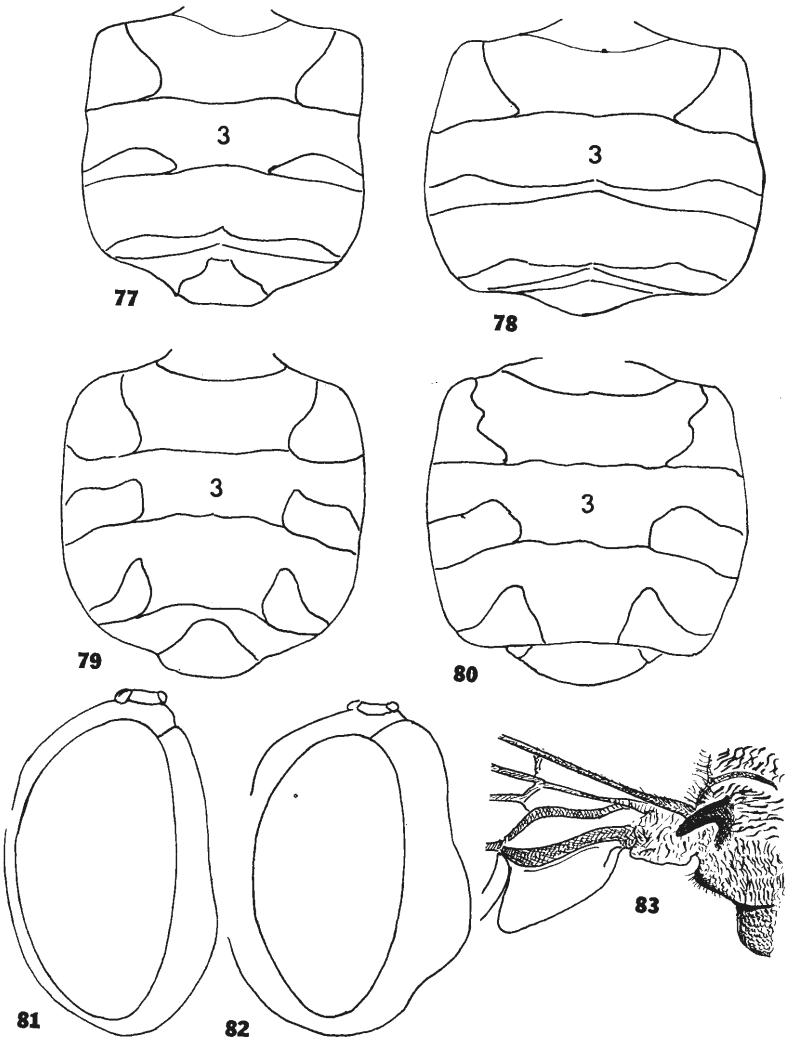


FIGS. 73–76.—Heads of Stratiomyidae in side view. (73) *Odontomyia ornata* ♀; (74) *O. ornata* ♂; (75) *Stratiomys potamida* ♀; (76) *S. potamida* ♂.

Genus **Odontomyia** Meigen, 1803

This is like a smaller and less spectacular version of *Stratiomys*, with shorter antennae which lack the conspicuous bend of *Stratiomys*. There is more variation in size in this genus, and some species are small and inconspicuous. Though patches of yellow colour, such as those of *Stratiomys*, are also a feature of *Odontomyia*, they are more variable in colour, and are frequently green, particularly in fresh specimens; they tend to become yellow or a rusty brown after death.

Of the six British species of *Odontomyia*, several species are distinctly rare, and only *viridula* is at all common. *O. ornata* may be locally numerous in the south-east corner of England, but is not often collected.



FIGS. 77–83.—Stratiomyidae. (77–80) *Stratiomys*, dorsal view of abdomen showing shape of spots in third segment of *S. potamida* ♂ (77), *S. potamida* ♀ (78), *S. chamaeleon* ♂ (79), and *S. chamaeleon* ♀ (80); (81, 82) heads of ♀ *Stratiomys* to show different breadth of postoccipital flange. *S. potamida* (81), and *S. chamaeleon* (82); (83) *Clitellaria ephippium* base of left wing to show strong thoracic spine.

KEY TO SPECIES

1 Discal cell conspicuously small, and vein R_{2+3} absent (fig. 20). Thorax black with bronze hairs. Abdomen with large, rectangular lateral spots merging into broad sidemargins, leaving only a notched black stripe in centre. Legs reddish yellow **viridula** Fabricius

Widespread throughout British Isles, including Ireland. Very common in southern England. vi–viii.

– Discal cell not conspicuously small; vein R_{2+3} present (figs. 21, 22).....2
2 Discal cell emits only 2 veins (M_3 absent) (fig. 21).....3
– Discal cell emits 3 veins (M_3 present) (fig. 22).....4
3 R_{4+5} forked. Abdomen dorsally entirely dark, without coloured spots. Head in both sexes narrower and more conical when seen in dorsal view (figs. 69, 71); eyes of male sparsely, but distinctly hairy.....**tigrina** Fabricius
Widespread in England and Scotland, sometimes not uncommon. v–vii.
– R_{4+5} not forked. Abdomen dorsally with three pairs of small, but distinct, lateral yellow spots, hoary pile especially obvious in males; females with pile sparser and more bronze. Head in both sexes broader, more transverse (figs. 68, 70); eyes of male only microscopically hairy.....**argentata** Fabricius
Rare. Southern England. Middx., Stanmore; Surrey, Bookham (Parmenter). Fonseca found males hovering singly 10–15 *feet over heathland; females swept from low vegetation nearby. An early species. v.*
4 A distinctly larger, more bulky species, like a small Stratiomys (14 mm.). Frons of female broader, more square, black, with yellow, hooked markings (fig. 66)
ornata Meigen
South-eastern England: Essex; Kent; Middlesex; Sussex; Surrey; also Somerset (Fonseca). Uncommon. v, vi.
– Distinctly smaller species, body not more than 10 mm. long. Frons narrower, rather swollen, predominantly yellow-brown with reddish-brown pattern.....5
5 In both sexes, face less prominent between eyes, and in dorsal view less snout-like (fig. 67). Lateral spots of abdomen filling length of each segment, so that black areas do not reach lateral margins.....**angulata** Panzer
Rare. East Anglia; Somerset (Fonseca). vi–vii.
– In both sexes face more prominent between eyes, and distinctly snout-like (fig. 72). Lateral spots of abdomen smaller, allowing black areas to reach lateral margin on each segment.....**hydroleon** Linnaeus
A doubtful British species. The female from Berkshire (J. C. Dale) mentioned by Verrall (1909 : 757) *is still in the B.M., and is the basis for the above diagnosis.*

Family XYLOMYIIDAE

The adult flies resemble sawflies and are seen, though rarely, in the vicinity of rotting logs or tree-stumps. The structure of both adults and larvae relates them most closely to Stratiomyidae, though they lack the distinctive venation of the family. The venation of *Xylomyia*, especially *X. maculata*, has features which resemble the venation of *Coenomyia*, a Tabanid-like genus which at one time was the nominate genus of a family Coenomyidae, set up to accommodate all these anomalous, primitive genera of Brachycera, which probably represent survivors from early branches of the brachyceran stock.

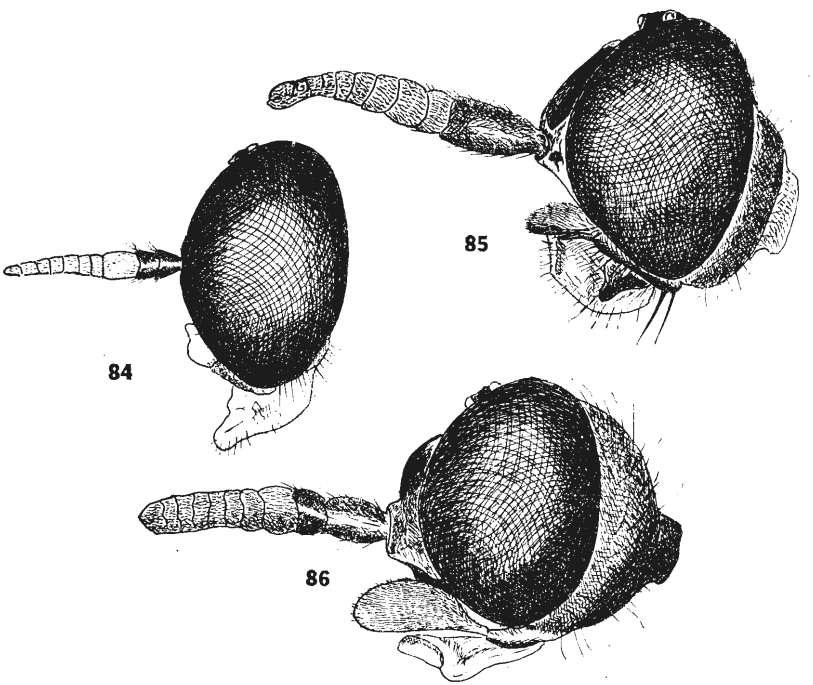
Essentially the family consists of the genus *Xylomyia*, which for a long time was included in the family Stratiomyidae. *Solva* Walker, 1859, founded upon the Oriental species *inamoena* Walker, is closely related, and as long as the two were regarded as synonymous, the name *Solva* had precedence. Current practice now separates them, so that *Xylomyia* is restored to use. There are about a dozen Palaearctic species, more than half of them Asiatic. An endemic species occurs in the Canary Islands, and the three species of western Europe all occur in Britain.

Morphology

Head.—Dichoptic in both sexes, but with eyes distinctly, though not conspicuously, closer together in males than in females. Face moderately hollowed, with a median facial tubercle. Proboscis short, fleshy, palpi large, porrect, two-segmented (figs. 84, 89–91). Antennae simple: first segment

triangular in profile, as long as, or slightly longer than, second segment; flagellum consisting of 8–9 compact segments, tapering gradually (figs. 87, 88).

THORAX.—Very different in mesonotum from that in the other two British species. In *maculata* the mesonotum is twice as long as broad, with humeri, transverse suture and postalar calli all strongly developed, as well as conspicuously marked with yellow; scutellum semicircular. In *marginata* and



FIGS. 84–86.—Heads in side view. (84) *Xylomyia maculata* ♀; (85) *Xylophagus ater* ♀ (86) *Xylophagus cinctus* ♀.

varia the mesonotum is much more square, with humeri and postalar calli weakly developed; scutellum transverse. In *maculata*, pleura are much more robust than in other two species, with coxae pushed back under abdomen.

ABDOMEN.—Seven to nine visible segments, depending on whether or not one includes the reduced first tergite and the terminal one or two that may be concealed. Male genitalia complex, visible; females with two small anal lamellae.

LEGS.—Tibial spurs 1 : 2 : 2. Legs simple, rather elongate in *maculata*; shorter and stouter, with hind femora armed ventrally (fig. 94) in *marginata* and *varia*.

WING.—Venation relatively simple, with fourth posterior cell closed.

Genus **Xylomyia** Rondani, 1861

KEY TO SPECIES

1 Venation as in fig. 99, M_1 strongly arched. Mesonotum black, with conspicuous yellow markings on and around humeri, on transverse suture, and on postalar calli. Scutellum yellow with black base. Pleura with extensive yellow areas especially a pair on postscutellum, in front of halteres. Palpi as in fig. 89 **maculata** Meigen

Old forests of southern England: New Forest; Berkshire, Silwood Pk. (Southwood). Middx., Finchley (Andrewes); Essex, Epping Forest (Parmenter). Larvae and pupae occasionally numerous in rotting wood. v–vi.

– Venation as in fig. 100, M_1 not strongly arched. Mesonotum entirely black. Scutellum entirely yellow 2

2 Coxae yellow. Palpi as in fig. 91. Flagellum of antenna elongate, little broader at base than at tip (fig. 87) ..... **varia** Meigen

Still known as British only from the two specimens in the British Museum, ex Stephens' Collection that were mentioned by Verrall (1909 : 229). *No data*

– Coxae black. Palpi as in fig. 90. Flagellum of antenna shorter, distinctly broadened basally (fig. 88). Hind femora swollen, with two rows of tiny black spines ventrally (fig. 94) ..... **marginata** Meigen

Very local in southern England: Cambs., Wicken Fen (Verrall, 1909 : 227); Hunts., Wood Walton (K. M. Harris); Suffolk, Thornton Fen and Woodbridge (C. Morley); London, Syon Park (A. Stubbs), Bushey Park (K. M. Harris). Kent, Bromley, Beckenham (Waller). Larvae in rotten oak, walnut, sycamore; locally numerous. v–viii.

Family XYLOPHAGIDAE

Whereas *Xylomyia* is a primitive genus allied to, if not a member of, the family Stratiomyidae, *Xylophagus* is an even more basic genus near to the stem of all Brachycera. The larva is again associated with rotting wood, and the adult fly has a deceptive resemblance to the tipulid genus *Ctenophora*. The antennae of *Xylophagus* are simple, but those of the allied genus *Rachicerus* have a large number of small segments, each with a ventral process, so that the flagellum is heavily pectinate like that of *Ctenophora*.

MORPHOLOGY

HEAD (figs. 85, 86).—Eyes relatively smaller than in related forms, especially in females, where frons is as broad as, or broader than, one eye, and projects forwards into an antennal tubercle. Antennae with strongly developed first segment, which may be rather bulky as in *cinctus* (fig. 86), or more elongate as in *ater* (fig. 85). Palpi strongly developed in the three British species (figs. 92, 93). Proboscis short and fleshy.

THORAX.—Twice as long as broad; scutellum rather small and sessile, but postscutellum robust; pleura inclined posteriorly, as in *Xylomyia maculata*.

ABDOMEN.—Simple. In males, with seven tergites, small half-concealed eighth segment, and globular genitalia; in females sixth and subsequent segments tapered into a telescopic ovipositor, ending in a pair of small lamellae.

LEGS.—Simple, rather elongate. Tibial spurs 0 : 2 : 2.

WINGS (fig. 101).—Venation simple, not concentrated anteriorly as in Stratiomyidae; in fact discal cell is placed rather far out on wing, with smaller posterior cells, as in Tipulidae. Clouds on forks and crossveins in British species.

Xylophagus is more closely related to Rhagionidae than to Stratiomyidae. There are four species in the western Palaearctic Region, three of which have been recorded from Britain. Collin (1962) discussed and keyed these, and it is convenient to adapt his key, including all four species for comparison. *X. junki* Szilády is known only in the female sex, whereas *X. kowarzi* Pleske is known only from males. Collin rejects the obvious inference that these might be two sexes of the same species.

KEY TO SPECIES
(after Collin, 1962 : 273)

1 First antennal segment cylindrical, three to four times as long as second segment (fig. 85) 2
– First antennal segment shorter, less cylindrical, not more than twice as long as second segment (fig. 86) 3

2 Metapleural lobes bare.* Frons of both sexes dull blackish grey, with a shining patch. Male thorax practically all shining; female thorax with three obvious grey stripes on a shining ground. Palpi as in fig. 92 ..... ♂ ♀ **ater** Meigen
Local throughout the British Isles. Larva in dead wood of deciduous trees: birch, oak, elder, beech and aspen (Brindle, 1961 : 144). "Several females on dead pine trunk, Thursley Common, Surrey" (Chandler). v–vii.
– Metapleural lobes hairy.* Frons of male almost entirely shining. Thorax of male with a broad grey median stripe, but shining at sides. Female not known. (♂ **kowarzi** Pleske)

3 Metapleural lobes hairy.* Thorax in both sexes entirely dulled by greyish dusting, which is rather more distinct in certain longitudinal stripes. Palpi as in fig. 93 ..... ♂♀ **cinctus** Degeer
Locally abundant in Scotland: Inverness-shire, Nethy Bridge and Loch Morlich, Abernethy, Rothiemurchus; Aberdeenshire, Braemar. Larva in dead wood of pine, along with beetle larvae. iv–vii.
– Metapleural lobes bare.* Thorax in female entirely shining. Male not known ♀ **junki** Szilády
*Very rare. Known only from a single female taken in Scotland: Aviemore, Glenmore Forest, vi.*1913 *(Collin).*

Family RHAGIONIDAE

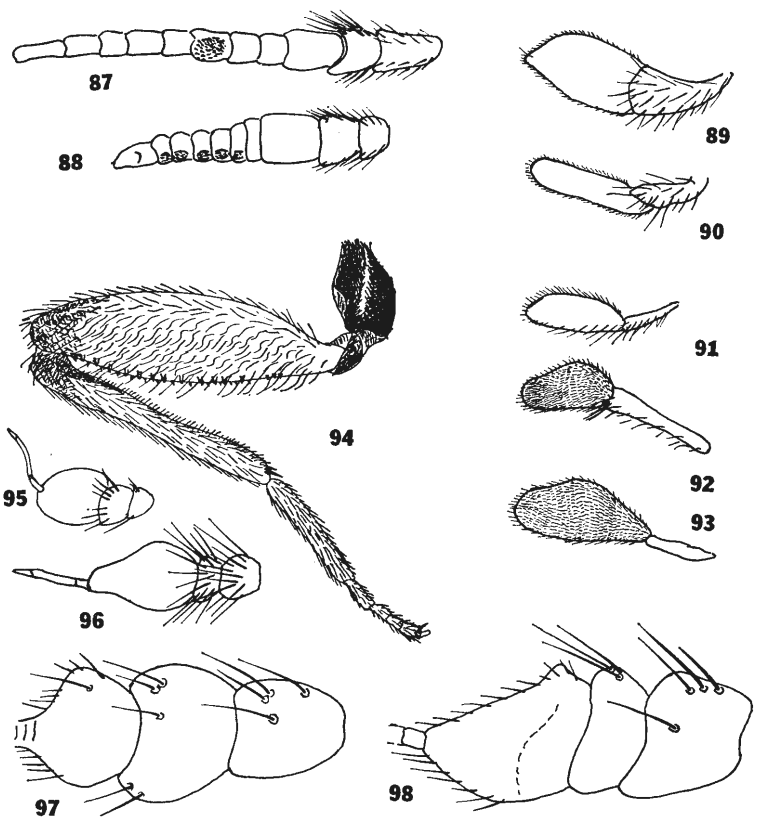
With the exclusion of *Xylophagus*, the other Rhagionidae are divisible into the tiny, black, Empid-like flies belonging to the genera *Ptiolina* and *Spania*, and the larger, fragile-looking flies that are typical of the family. These are little known to the non-specialist, and even to the regular collector they are seldom familiar, though sometimes one of them turns up in numbers on a single occasion. This seems to be a combination of two factors: certain species have a very short flight season, or at least a tendency to emerge in a batch in any one locality, so that they are to be found only for a few days each year. This seems to be the case with *Atrichops crassipes*, which may still be numerous in the water-meadows near Ticehurst Road Station (now renamed) in Sussex, if one happened to be there at the right moment. The second factor is the silent flight and furtive behaviour of most Rhagionidae, so that even *Chrysopilus*, one of the commonest and most widespread, is seldom seen until it is taken by sweeping.

* This "important character" (Collin, 1962 : 272) seems to me to have little value. Certainly the region immediately before the halteres is bare in *ater* and densely hairy in some male *cinctus*, but this cannot really be employed in practical determination. It is simpler to remember that all those with longer first antennal segment are *ater*; those with shorter first antennal segment are *cinctus*; any female with a shining thorax should be examined as a possible *junki*.

Rhagionidae are a family of particular interest to the dipterist, because they are in some ways the most generalized of the bigger families of Brachycera, and provide many pointers to the possible evolution of the existing Tabanoidea and Asiloidea.

Morphology

Head.—Males usually holoptic, sometimes with narrow frons (figs. 114, 122); upper eye-facets distinctly bigger than lower ones in *Spania*, *Ptiolina*, *Chrysopilus*, but not in *Rhagio* or *Atherix*—and in *Symphoromyia crassicornis*, but not in *S. immaculata*. Eyes of females separated by varying distances; rather close in *Rhagio*, very far apart in *Symphoromyia crassicornis*. Female



Figs. 87–98.—Xylomyidae and Rhagionidae. (87) *Xylomyia varia*, antenna, showing sense organs on fourth flagellar segment; (88) *Xylomyia marginata*, antenna, showing sense organs on five flagellar segments; (89–93) palpi of *Xylomyia maculata* (89), *Xylomyia marginata* (90), *Xylomyia varia* (91); *Xylophagus ater* (92), and *Xylophagus cinctus* (93); (94) *Xylomyia marginata*, right hind leg, showing swollen femur with tiny black spines ventrally; (95) *Ptiolina obscura*, antenna; (96) *Ptiolina atra*, antenna; (97) *Rhagio strigosus*; and (98) *Rhagio scolopaceus*, comparison of second antennal segment.

of *Rhagio scolopacea* has vertex distinctly excavated, with ocellar tubercle elevated, in a style reminiscent of Asilidae. Antennae usually set rather low on head; face sharply divided into a facial knob which is strongly convex, often hemispherical, and a pair of side-cheeks or parafacialia which may be conspicuously hairy or bare (*cf.* Therevidae). Antennae short in all British species, except that *Rhagio* and *Chrysopilus* have a more or less elongate terminal arista: first two segments small, third either conical with a terminal arista or kidney-shaped with a dorsal arista (figs. 115–19). Proboscis short, with large, fleshy labella. All genera have a well-developed labrum, and *Symphoromyia* possesses blade-like mandibles. Palpi generally well-developed, cylindrical, and provided with long hairs.

THORAX.—Unremarkable, except for the entire absence of strong bristles. Scutellum large and inflated, covered with hairs like mesonotum.

ABDOMEN.—Usually conical or tapered, more ovate in *Atherix ibis*. Females with seven visible tergites, the posterior ones narrowed and telescoped in some genera. Males with seven visible tergites, and male genitalia resembling those of Asilidae rather than those of male Tabanidae.

LEGS.—Simple, moderately elongate and slender. All genera have two spurs on the middle tibia and none on the fore: *Rhagio*, *Atherix* and *Atrichops* have two hind tibial spurs; *Chrysopilus*, *Symphoromyia*, *Ptiolina* and *Spania* have only one. The hind spurs may be small and difficult to see.

WINGS.—Broad and simple. Anal cell closed and stalked in some genera, open in others. Other peripheral cells open. A characteristic feature of Rhagionid venation is the short R_{2+3}, which meets the costa closer to the tip of R_1 than is usual in the other families. In *Chrysopilus*, R_{2+3} is strongly curved forwards round the ovoid stigma (figs. 102–10).

BIOLOGY

Rhagionidae have a very varied biology, in accordance with their primitive evolutionary position in the group. In some ways their status parallels that of Tipulidae in Nematocera, with some terrestrial and some aquatic members.

Rhagionidae are basically terrestrial, with larvae living in decaying wood (*cf.* Stratiomyidae, Xylophagidae and Xylomyidae), mosses (*Symphoromyia*), liverworts (*Spania*) and soil (*Rhagio*). Only *Atherix* and *Atrichops* have aquatic larvae, and it seems evident that this is a secondary evolution, with elaborate development of structures for crawling and underwater respiration.

The extreme of terrestrial life among Rhagionidae is realized by the subfamily Vermileoninae, of which, regrettably, none occur in Britain. The reason is fairly obvious: the larvae of Vermileoninae ("worm-lions") make pit-traps for ants in very dry dust! In less humid countries than this the ground underneath an overhanging stone, or in the crevices of a wall, dries to a powder in the summer, and by a most remarkable evolutionary convergence the larvae of ant-lions (Neuroptera, Myrmeleontidae) and worm-lions (Diptera, Rhagionidae) have formed exactly the same habit of excavating a conical pit and attacking ants and other insects that fall into it.

The question of diet of Rhagionidae is still unsettled. Adult Vermileoninae have a long proboscis, and feed from flowers, and their larvae are conspicuously carnivorous. Larvae of *Atherix* and *Atrichops* are predatory,

like most aquatic organisms, and feed not only on diatoms, but, given the opportunity, on nymphs of Ephemeroptera and aquatic larvae of tipulids (Nagatomi, 1962 : 124). Adult *Atherix* have been accused of biting man, without definite proof, but adult *Atrichops* (*Heterosuragina*) were definitely seen to draw blood from frogs (Nagatomi, 1962 : 107). *Symphoromyia* is a well authenticated biter of man in the United States, though in Europe records of biting man are dubious; related genera *Dasyomma* in S. America and *Spaniopsis* in Australia also bite.

It is still disputed whether *Rhagio* ever bites, but since there are no strong stylets in the mouthparts except the labrum it seems unlikely that blood-sucking can be a regular habit of this genus. The large labella, with loose pseudotracheae, suggest the possibility that it might capture small, soft-bodied insects in the manner of Dolichopodidae.

Classification

Lindner (1924 : 2) recognizes six subfamilies of Rhagionidae in the Palaearctic Region, but one of these—Bicalcarinae—has been shown to be based upon the examination of erroneous type-material. Two others, Erninninae (=Xylophaginae) and Coenomyinae are currently regarded as distinct families, leaving Rhagionidae *sensu stricto* to fall into three subfamilies as follows:

VERMILEONINAE	no British genera
RHAGIONINAE	*Rhagio; Atherix; Atrichops*
CHRYSOPILINAE	*Chrysopilus; Symphoromyia; Ptiolina; Spania*

The last two subfamilies are separated solely according to whether they have one or two hind tibial spurs, but this may well be an artificial distinction. Other characters, especially the head and the shape of the antennae, suggest that it would be more natural to combine *Rhagio* with *Chrysopilus*, and the rest, with kidney-shaped third antennal segment, into a second subfamily.

Key to British Genera

1 Antennae as in figs. 95, 96, 117, 118. Metapleura (immediately in front of halteres) bare. Tiny black flies 2

– Antennae as in figs. 115, 116, 119. Metapleura hairy. Usually larger, often brown or patterned 3

2 Antennae as in figs. 95, 96. Terminal style of antenna centrally placed **Ptiolina** Zetterstedt (p. 39)

– Antennae as in fig. 117. Without a true style, but ventral margin produced into a pseudostyle. Vein M_3 usually fails to reach wing-margin **Spania** Meigen (p. 39)

3 Third antennal segment kidney-shaped, pendulous with a dorsal arista (figs. 115, 116)..... 4

– Third antennal segment onion-shaped, with a terminal arista (fig. 119)..... 6

4 Anal cell open, or barely closed on wing-margin. Stigma inconspicuous or absent. Hind tibiae with only one spur. First antennal segment enlarged (fig. 116) **Symphoromyia** Frauenfeld (p. 40)

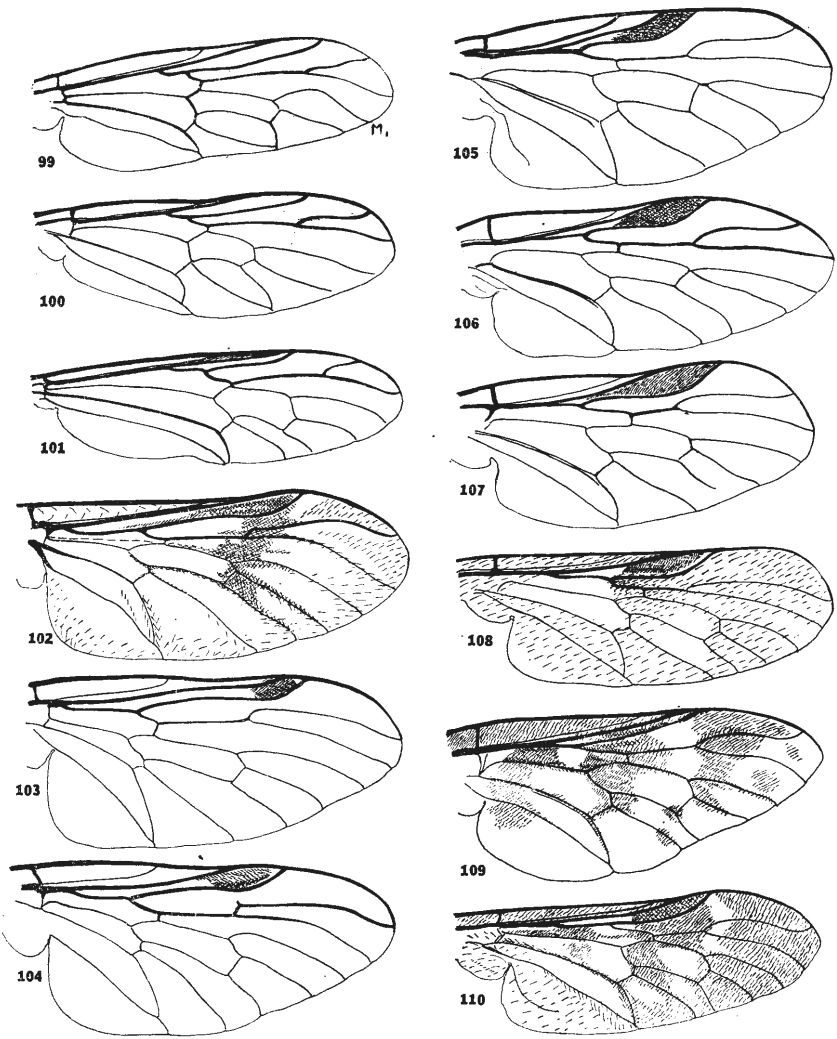
– Anal cell closed and stalked. Stigma conspicuous, or whole wing spotted. Hind tibiae with two spurs. First antennal segment not bigger than second (fig. 115) 5

5 Cheeks hairy. Wings heavily spotted with brown. Propleura without any lateral process ..... **Atherix** Meigen (p. 41)

– Cheeks bare. Wings smoky, but not distinctly spotted. Propleura with a small, pointed process above base of each anterior coxa.....**Atrichops** Verrall (p. 43)

6 Hind tibia with two spurs. Anal cell open. Vein $_{2+3}$ not sharply turned towards costa (fig. 333). Third antennal segment pointed (but *cf. R. strigosa*, fig. 119) **Rhagio** Linnaeus (p. 43)

– Hind tibiae with only one spur. Anal cell closed and stalked. Vein R_{2+3} turning sharply towards costa, almost meeting R_1 (figs. 102–4). Third antennal segment rounded .....**Chrysopilus** Macquart (p. 46)



FIGS. 99–110.—Wings of Xylomyidae, Xylophagidae and Rhagionidae. (99) *Xylomyia maculata*; (100) *Xylomyia marginata*; (101) *Xylophagus ater*; (102) *Chrysopilus laetus*; (103) *Chrysopilus aureus*; (104) *Chrysopilus cristatus*; (105) *Ptiolina atra*; (106) *Ptiolina obscura*; (107) *Spania nigra*; (108) *Atrichops crassipes*; (109) *Atherix ibis*; (110) *Atherix marginata*.

Genus **Ptiolina** Zetterstedt

Flies of this genus and the next are tiny and black, quite unlike the normal conception of Rhagionidae, and may easily be mistaken for small Empididae. They are relatively little known, and Verrall's comment is apt: "It appears possible that the species sometimes occur in considerable numbers for a very short period" (1909 : 309). This is a characteristic of many, perhaps most, Rhagionidae, and a similar comment is made by Nagatomi (1962 : 106). Roskošný & Spitzer can quote only four records of *Ptiolina* for the whole of Czechoslovakia.

Once *Ptiolina* has been recognized as a Rhagionid, it can be confused only with *Spania* or *Symphoromyia*. *Symphoromyia* is immediately distinguished by the kidney-shaped third antennal segment, or if this is broken off, by the hairs on the metapleuron. Separating *Ptiolina* from *Spania* is more difficult, but apart from the antennal difference quoted in the key and shown in figs. 95, 96, 117, 118, it is convenient that *Spania nigra*, the only British species, nearly always has the vein M_3 cut off before it reaches the margin of the wing.

Verrall (1909 : 309, 313) discussed at length the involved synonymy of the European species of *Ptiolina*, and we need not go into this here. Two species occur in Britain, in both of which the males are darker, more chocolate-coloured than the females. Nothing seems to be recorded about their biology, though Brauer (1883 : 60) described the larva of *Ptiolina nigripes* Zetterstedt.

Key to Species

1 First segment of antenna with conspicuous hairs, which in male are as long as third segment. Third antennal segment elongate-oval, pointed at tip (fig. 96). Wing broader, discal cell 3·5 times as long as broad (fig. 105).....**atra** Staeger
Rare and local. England; New Forest; Yorks., Austwick (Edwards). S. Wales, Porthcawl (Yerbury). Scotland: Aberlady (Waterston); Brodie (Yerbury); Bonhill (Malloch). v, vi.

– First segment of antenna bare, except for usual circlet of short hairs. Third antennal segment short-oval, rounded at tip (fig. 95). Discal cell 5·0 times as broad as long (fig. 106).....**obscura** Fallén
Uncommon, local, throughout England and Wales. Rozkosný & Spitzer (1965 : 265) suggest that this may be a montane species, but British records are scattered between Bettws-y-Coed and the New Forest and Devon (Fonseca). Also Scotland, Banffshire, Tomintoul (Andrewes). v–vii.

Genus **Spania** Meigen

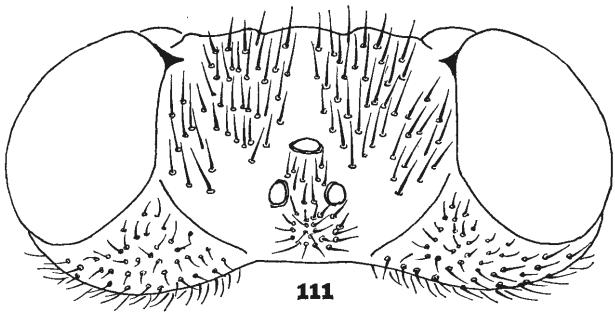
Very closely allied to *Ptiolina*, and often confused with it in the past (see Verrall, 1909 : 310). *Spania* can be recognized with confidence by the shape of the third antennal segment, as well as that of the wing venation (see figs. 105–7.

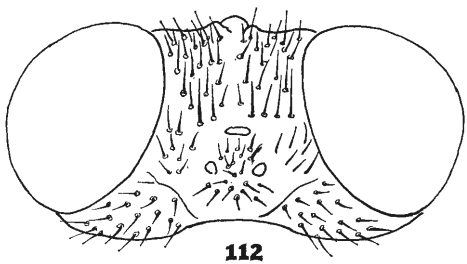
One British Species

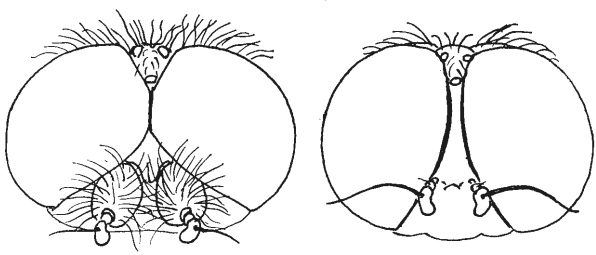
Even smaller than *Ptiolina*, about 1 mm. long, with a wing-span of over 2 mm., so that its shape is rather that of a Pipunculid. Distinguished by the key-characters already given. Males predominate in collections, suggesting that they are the more active sex, and possibly hover .....**nigra** Meigen
Uncommon and local. A scattered distribution throughout England, Wales and Scotland. F. W. Edwards found a number in the New Forest, Mark Ash. Also Oxon, Somerset, Hants. (Fonseca), Kent Sevenoaks, Knowle Park (Chandler). v–vi. Larvae mine the leaves of the liverwort Pellia neesiana, *along with certain Lestremiine Cecidomyiids.*

Genus **Symphoromyia** Frauenfeld

Small, or very small, grey flies, looking like Muscids. Although superficially they resemble *Ptiolina* and *Spania* to some extent, *Symphoromyia* can be easily distinguished from these genera by the kidney-shaped third antennal segment, and—if this is broken off—by the hairy metapleura, immediately before the halteres.







FIGS. 111–114.—Heads of *Symphoromyia*. (111) *crassicornis* ♀; (112) *immaculata* ♀; (113) *crassicornis* ♂; (114) *immaculata* ♂.

Symphoromyia is particularly interesting because of the bloodsucking habits of the females of some species. The significance of bloodsucking habits in Brachycera, both from a biological and a physiological point of view, is discussed elsewhere in this *Handbook* (p. 2). In North America *Symphoromyia* is sometimes a considerable nuisance. Pechuman (1967) lists many references, and summarizes their conclusions, though his statement that: "Unlike most species of *Chrysops* the circling flight of *Symphoromyia* is almost noiseless . . ." is at variance with the statement of Shemanchuk

& Weintraub (1961) that: ". . . their intense hum was characteristic of larger insects." The last two authors say that the female *Symphoromyia* gather in "following swarms" like Chironomid midges.

I know of no records of biting by *Symphoromyia* in this country, and only occasional rumours of it in Europe. As discussed on pp. 2, 37, it seems likely that we are seeing in Rhagionidae the dwindling of an animal-biting habit. In its vestigial state some species possess mandibles and some do not, and not all species possessing mandibles use them for sucking blood. This may account for some of the conflicting reports in the past about bloodsucking habits in this genus.

Any reports of the behaviour of British *Symphoromyia* including any attempts by the females to bite, are well worth recording.

Beling (1882) first bred *Symphoromyia crassicornis* from soil at the edge of a beech forest. Sommerman (1962) gives a detailed account of the biology and breeding of several species of *Symphoromyia* in Alaska, where the larvae were found in damp soil underneath certain "indicator plants". In Alaska these were *Veratrum escholtzii* Grey and *Heracleum lanatum* Mich., which provide shade, and encourage the growth of certain mosses. This author noted that the females of some species would bite humans, and others would not.

The two British species are easily distinguished, not only by a conspicuous difference in size, but also by several structural characters.

KEY TO SPECIES

1 Larger species, 8 mm. long, and robust. First antennal segment strongly swollen in both sexes, bigger than second and third segments together, and very hairy, especially in male (fig. 116). Palpi somewhat swollen. Eyes of males touching for a short distance (fig. 113), and upper facets greatly enlarged. Frons of female broader (fig. 111) ..... **crassicornis** Panzer

Locally numerous, chiefly in "Highland Britain": Scotland, Wales, and Northern England down to Lancs., Rivington, and Yorks., Wensleydale, and Aberford (in vale of York). Somerset (Fonseca): "damp meadows and marshy ground." vi–vii.

– Smaller species, 4 mm. long, lightly built. First antennal segment not swollen, bare except for usual row of fine bristles. Palpi slender. Eyes of males separated by at least breadth of median ocellus and with uniform facets (fig. 114). Frons of female narrower (fig. 112) ..... **immaculata** Fabricius

Locally numerous in "Lowland Britain", which includes the chalk downs from Yorkshire to Sussex. "Chiefly on chalk or magnesium limestone" (Stubbs, 1967). Hants., Wilts., Dorset, Kent: Surrey, Coulsdon (Parmenter) "among grass on chalk" (Fonseca). Somerset, Charterhouse in Mendip (Audcent). v–viii.

Genus **Atherix** Meigen

Rather like a small *Chrysops*, with pictured wings (figs. 109, 110), *Atherix* is recognized by the Rhagionid venation, with short R_{2+3}, the kidney-shaped third antennal segment (fig. 115), the closed anal cell, and the two hind-tibial spurs.

Atherix and *Atrichops* (see below) are the most aquatic of British Rhagionidae. The eggs are attached to leaves, rocks or artificial objects such as the supports underneath bridges over water, and the females of *A. ibis* may oviposit collectively and remain *in situ* over their eggs, so that a mass of dead flies builds up, looking like a small swarm of bees. According to Nagatomi (1962 : 125) the larvae fall into the water immediately after hatching, and hide in the sand and mud at the bottom of the stream. He gives the number of females in one cluster as "several hundred, to tens of thousands", and in

another place mentions "the mass of flies and eggs which was about the size of a grown-up person's head". During the period of egg-laying females came on successive days to join clusters already formed the previous day. Nagatomi notes that the flies may appear and yet not form a cluster, and they may form a cluster but not lay any eggs, particularly in bad (?cold) weather. He considered it possible that flies might oviposit singly elsewhere, even though he did not find any in the act of doing so.

These points are of particular significance in Britain because few people have actually found a cluster of *A. ibis*: Verrall himself had not seen one (1909 : 288). In view of the intensive use of our rivers and streams by fishermen, bird-watchers and naturalists, it would seem certain that clusters would be commonplace objects if they were the standard, and only way in which *A. ibis* could oviposit. Moreover, Walker (quoted by Verrall) agrees with Nagatomi that a cluster may contain "sometimes many thousands of dead flies, and continually receives accessions by newcomers settling upon it". It is true that insects may exist in nature in very large numbers without attracting attention until they congregate: an example of this was the remarkable spread inland of seaweed flies (*Coelopa frigida*) some years ago, when they were quite undetected until they assembled in large numbers under the attraction of certain chemicals. So it is not impossible that thousands of *A. ibis* may exist at certain times, but it does seem impossible that they could gather for oviposition without being seen more often. It is therefore a reasonable presumption that *A. ibis* may keep itself going by solitary oviposition, and that possibly the conspicuous clustering is a phase of behaviour that only comes into being when the numbers are great enough.

The clustering habit is indeed the exception in the genus *Atherix*, being known only in *A. ibis* in the Palaearctic Region and *A. variegata* in North America. The South African *Atherix* are not known to cluster (Stuckenberg, 1960), though a similar habit occurs there in *Pachybates braunsi* (according to Nagatomi, 1962 : 112). In South Africa: "*Atherix* seems able to exist only in mountainous areas where there are clear, fairly fast-running streams" (Stuckenberg, 1960 : 300).

The two British species are easily distinguished from each other by their general appearance, by several structural characters, and by the fact that the second species, *A. marginata*, is always found singly.

Key to Species

1 Bee-like, rather squat, with broad wings. Submarginal and posterior cells largely clear. Head of female more transverse, with relatively broader frons; eyes of male closely approximated below ocelli (see figs. 120, 121). Male with black thorax and orange abdomen with black spots; female more brownish-grey, with grey-striped thorax and black abdominal spots on an ashy-grey ground. Legs dull orange ..... **ibis** Fabricius

Local throughout Great Britain, though clusters are rarely seen. "Mainly a south-western insect" (Chandler). v–vi.

– More elongate, not bee-like. Wings narrower with more uniform infuscation at wing-tip. Female head more vertical, frons relatively narrower; male eyes more widely separated, not approximated below ocelli (see figs. 122, 123). Thorax shining black with grey scutellum. Abdomen shining black with whitish hind margins, expanding into grey lateral patches. Legs black.

marginata Fabricius

Local, though perhaps more often collected than ibis. *On waterside vegetation from Devon to the Lake District, and in Ireland. vi–viii.*

Genus **Atrichops** Verrall

Verrall (1909 : 291) erected this genus, in his *British Flies*, for the single species *Atherix crassipes* Meigen, which differed from the other two British species of *Atherix* in having bare cheeks. Subsequent authors, including Lindner (1924 : 8), disregarded this apparently trivial character, and treated *Atrichops* as synonymous with *Atherix*. On the other hand some workers on the tropical Rhagionidae, including Oldroyd (1939 : 15), considered that *Atrichops* was closely related to, if not synonymous with, the tropical genus *Suragina*. When Nagatomi (1958 : 61) placed two Japanese species in a new subgenus *Heterosuragina*, the problem of *Atrichops* was revived, and both Collin and Stuckenberg suggested that perhaps the two were the same. Stuckenberg (1965 : 91) compared British and Japanese specimens directly, and wrote: "*Atrichops* is characterized in the adult by a protruding process on the lower margin of the sclerite above the front coxa, the closeness of the antennae to one another, the frons of the female diverging towards the vertex, and the face being narrower than the frons."

The synonymy of *Atrichops* Verrall (1909) and *Heterosuragina* Nagatomi is now well established, and so Nagatomi's discussion of the biology, and descriptions of the larvae, of his two Japanese species *fontinalis* and *morimotoi* should provide a guide for future investigation of the biology of our single—and elusive—native species, *Atrichops crassipes* Meigen. Perhaps one day a flourishing colony of this species will once again be found in Britain, and provide material for a parallel study of biology.

One British Species

Rather like *Anisopus*, or a small ichneumon, for which it could easily be mistaken in the field. Thorax shining black in male, more brownish with black stripes in female. Abdomen elongate-cylindrical, with yellow-brown and black bands, more yellowish towards base, especially in male. Legs elongate and slender, hind tarsi a little inflated in both sexes. Wing (fig. 108) with an elongate radial fork, a dark, prominent stigma, and indistinct clouds over most of membrane. Length 6 mm.

crassipes Meigen

Local in south-east England. Apparently not recorded from this country since Verrall (1909 : 294). *Between* 1900–4 *it was found in some numbers on alders in a water-meadow near Ticehurst Road Station, Sussex, and again near Milford-on-Sea, Hants., as well as in two or three localities in the New Forest. vi–vii.*

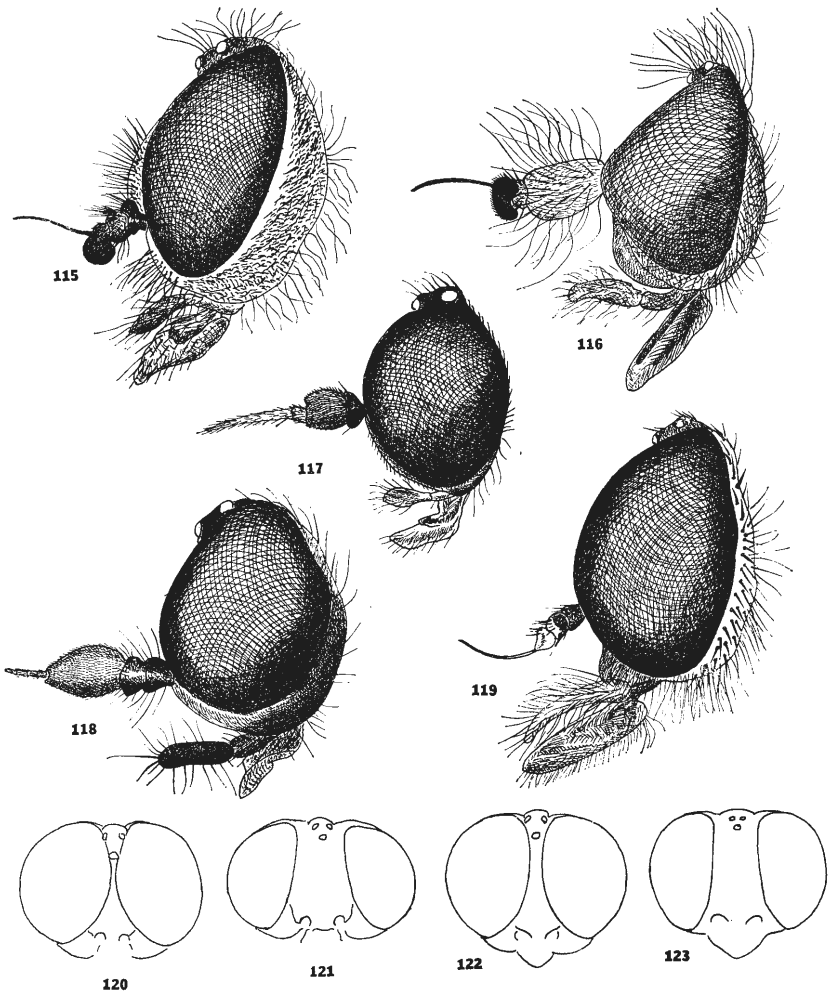
Genus **Rhagio** Fabricius, 1775

Fabricius himself (1805 : 70) changed the name of this genus to *Leptis*, because he considered *Rhagio* too similar to his own beetle genus *Rhagium*. The family was known as Leptidae until after Verrall's day, but *Rhagio* and *Rhagium* are not homonyms under the International Code, and since Lindner (1924) it has become current practice to call the genus *Rhagio* and the family *Rhagionidae*.

Except for the rather small *R. lineola*, species of *Rhagio* are the largest of British Rhagionidae, dart-shaped flies, with largish head and thorax, tapering abdomen, and broad wings. It is likely to be confused only with *Chrysopilus*, from which *Rhagio* may be distinguished by the larger size, two-spurred hind tibiae and open anal cell.

Rhagio scolopaceus is called the "down-looker fly" in books, though I have never met anyone who actually knows it under this name. It is

perhaps most familiar to fishermen, who may see it sitting on a post or tree-trunk, with its head downwards. Whether or not *Rhagio* bites has long been a matter of conjecture, but, as fig. 4 shows, the mouthparts are ill-equipped for piercing the skin. There are no mandibles, and the maxillae, though stylet-like, are not particularly strong. The maxillary palpi are well developed, and the large labella are provided with a rather unusual array of pseudotracheae, narrow tubules arising from a central block. There is no pseudotracheal trunk of the kind that is usual in many Diptera (*cf. Thereva*,



FIGS. 115–123.—Heads of Rhagionidae. Side views: (115) *Atherix ibis* ♂; (116) *Symphoromyia crassicornis* ♂; (117) *Spania nigra* ♂; (118) *Ptiolina atra* ♂; (119) *Rhagio tringarius* ♂. Front views: (120) *Atherix ibis* ♂; (121) *A. ibis* ♀; (122) *A. marginata* ♂; (123) *A. marginata* ♀.

fig. 5), but each tubule leads directly into the common space. It is possible that the sclerotized block is paired and functions as a pair of crushing jaws, for feeding upon small, soft-bodied insects. This would then be a parallel development to the labella of Dolichopodidae, which have dispensed with the normal use of pseudotracheae, and have modified these into a crushing apparatus (fig. 10). However, the detailed studies of Bletchly (1954) seem to make this unlikely.

Seven species of *Rhagio* occur in Britain, five of which are familiar to collectors. The other two, *annulatus* and *strigosus* both occur in Surrey, and probably elsewhere, but each has been confused with a common species: *annulatus* with *tringarius* and *strigosus* with *scolopaceus*. It is hoped that the appearance of this *Handbook* may stimulate collectors to look even more closely at any *Rhagio* they may capture, in order to find other colonies of the two rare species.

Key to Species

1 Wings distinctly patterned 2
– Wings more or less strongly tinted brown, but without definite pattern 3
2 Third antennal segment bigger than second, and longer than broad (fig. 98). Thorax almost entirely grey, with humeri completely yellow. Fore coxae yellow, others grey. Stigma usually linked to radial fork by a dark patch. A very variable species (fig. **333**) ..... **scolopaceus** Linnaeus
Widespread and more or less common throughout British Isles, including Ireland. v–viii.
– Third antennal segment smaller than second, and ovate or broader than long (fig. 97). Thorax yellow, with narrow brown stripes dorsally. Coxae all same yellow colour as pleura. Stigma quite isolated from radial fork **strigosus** Meigen
A reputed British species until Kidd (1955 : 137) *reinstated it from specimens collected by P. Skidmore at Box Hill, Surrey. L. Parmenter* (1955 : 332) *recorded it again, at the same locality. Probably local elsewhere in south-eastern England, but confused with* scolopacea *when seen on the wing. vii.*
3 Wing-stigma present 4
– Wing-stigma absent or inconspicuous 5
4 A small species (6 mm.). Legs mainly yellowish, with broad brown band on fore and hind femora, though some Irish specimens have this pattern almost obscured by dark colour (var. *monticola* Verrall). Body with short, yellowish hairs. Scutellum yellow, grey at base ..... **lineola** Fabricius
Common all over British Isles, including Ireland, though less conspicuous than scolopacea *or* tringaria. *Often on leaves of undergrowth in woodland. Has a long flight season, from vi or earlier until ix.*
– A larger species (10–12 mm.). Body with abundant black hairs, especially strong on mesonotum and scutellum. Legs almost entirely black. Scutellum entirely grey ..... **notatus** Meigen
Highland Britain, including Scotland, north-western England, and Wales. Also Surrey, near Godalming (Stubbs). Locally common. v–vii.
5 Fore coxae grey, with thick, white hairs. Pubescence of thorax and abdomen pale ..... **annulatus** Degeer
Very rare, though possibly overlooked through confusion with tringaria. 1 *female Herefordshire, The Dowards (J. H. Wood),* 3.vi.1903 *(see Verrall,* 1909 : 280*);* 1 *male Surrey, Netley Heath (H. Oldroyd),* 12.v.1937. *v–vi.*
– Fore coxae yellow, pubescence of thorax and abdomen black 6
6 Venter of first four or five segments yellow ..... **tringarius** Linnaeus
Common throughout the British Isles, including Ireland. Among shrubs on damp ground. v–ix.
– Venter of abdomen dark, tergites with yellowish hind margins .. **nigriventris** Loew
Occurs along with tringaria *during middle months of the summer. vi–viii. Doubtfully distinct.*

Genus **Chrysopilus** Macquart, 1826

The name *Chrysopilus* refers to the golden hairs and scales with which the thorax, and sometimes the abdomen, are adorned, and will provide a ready means of identification of good specimens. The pointed third antennal segment, with terminal arista, separates *Chrysopilus* from any other British genus except *Rhagio*, and its identity may be further confirmed by the single hind tibial spur, the closed and stalked anal cell, and the characteristic curve of the tip of the vein R_{2+3}, enclosing the stigma.

Larvae of *Chrysopilus* occur in rotting wood and mould, and the adults flit about in damp places such as water-meadows. The genus is widespread throughout the world, and shows remarkable uniformity in all regions. Out of nearly thirty Palaearctic species, only three occur in Britain.

Key to Species

1 Wings clear, except for stigma. Body mainly grey, with golden hairs and scales..2

– Wings with a distinct, if interrupted, dark band extending from stigma across radial fork and tip of discal cell; a second spot near apex of Cu_1 (fig. 102). Body mainly yellow. First two antennal segments orange (wrongly recorded by Oldroyd, 1939, as *nubecula* Fallén) ..... **laetus** Zetterstedt

Rare. First recorded as British by me in 1939 *from a single female bred from a pupa found in mud in Windsor Great Park by H. St. J. K. Donisthorpe. Mr. A. E. Stubbs has bred three other females from the same area in* 1968, *but no male has yet been taken in Britain. Reared iv–vi.*

2 Smaller species (6 mm.), with yellow legs. Base of radial fork opposite base of stigma (fig. 103) ..... **aureus** Meigen

Widespread; less common in collections than cristatus, *but possibly because it is less conspicuous in the field. vi–viii.*

– Larger species (8–9 mm.) with black femora. Base of radial fork opposite middle of stigma (fig. 104) ..... **cristatus** Fabricius

Widespread in damp, marshy localities throughout the British Isles, including Ireland. vi–viii.

Family TABANIDAE

Horseflies and clegs are familiar to most collectors, even to those who are not dipterists, and so it will not usually be difficult to recognize a female of this family, alighting in search of a blood-meal. Males too, coming to drink at pools and streams, sitting on tree-trunks, fence-posts or on damp ground, or feeding from flowers, are sufficiently like the females to be recognized as Tabanidae.

The diagnostic characters of the family are the three-padded tarsi, the large squamae, and in particular the wing-venation (fig. 124), with the radial fork opening wide and straddling the wing-tip. The marginal cell and all five posterior cells are open in British genera.

Morphology

Head (figs. 127–30, 162–76).—Male Tabanidae are usually holoptic, though the eyes are slightly separated in a few non-British species of *Chrysops*, and more widely so in a very few other genera. Often, but not invariably, the facets in the upper part of the eye of the male are bigger than the others. In females the eyes are separated by the frons, which may be an elongate, narrow band tapering towards the antennae, or may be much broader, as in

Haematopota or *Chrysops* (figs. 127, 128). The frons bears *frontal calli*, slightly raised areas of the surface which are bare of tomentum and therefore show as shining patches which may be one of the best ways of separating species. Structurally, the callus is the raised area itself, but taxonomically the term is usually applied to the bare area, which may vary in extent according to the amount of abrasion that has occurred. The callus is of relatively little taxonomic value in British *Chrysops* and *Haematopota* (but compare *facial* calli, figs. 127–30). In *Tabanus* the lower part of the callus may fill the breadth of the frons, with the upper callus either detached, or joined to the lower as a median prolongation. In *Atylotus* and *Hybomitra*, the structure of the calli is an indication of the genus. *Atylotus* has the two calli separated and rounded (figs. 167–74), sometimes vestigial or absent. *Hybomitra* has a well-developed lower callus, and a linear extension, and in addition the *ocellar tubercle* is distinct, though no ocelli are present (figs. 150–3).

The face consists of a median facial lobe and a pair of parafacialia, the latter forming the eye-margins below the antennae. In *Chrysops* the median facial lobe is often produced and somewhat snoutlike, with well-marked bare areas (*facial calli*, figs. 127–30): in *Haematopota*, *Tabanus*, *Atylotus* and *Hybomitra* it is normally inconspicuous. The antennal sockets unite to form a sclerite interposed between frons and face, and known as the *subcallus*. This is inconspicuous in *Chrysops*, and in *Haematopota* is greyish except for the velvety black or orange mark above and between the two sockets. In *Tabanus*, however, the subcallus is much bigger, and forms a triangular area above the antennae which is usually dull and tomented, but may be swollen, bare and shining in some species or species-groups: e.g. in *T. glaucopis* (figs. 175, 176). It may also be called the *frontal triangle*.

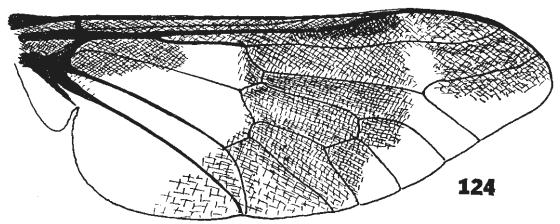
The antennae of Tabanidae consist of *scape*, *pedicel* and *flagellum* and, in accordance with the primitive status of Tabanidae among Brachycera, the flagellum retains distinct traces of its multisegmented origin. Pangoniinae (none British) have seven or eight flagellar segments, and, although this number is reduced in Chrysopinae and Tabaninae to five, the first of these shows traces of its composite nature. In *Tabanus* the first of the flagellar segments is often broadened and triangular in profile, whereas in *Haematopota* it is the first antennal segment that shows interspecific variation (figs. 141–9).

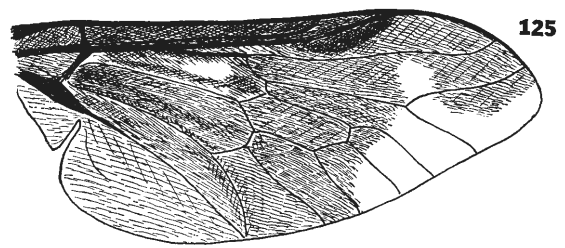
The proboscis of Tabanidae is developed for piercing and sucking blood, in a manner homologous with that of mosquitoes and bloodsucking Nematocera generally: i.e. piercing is carried out by *stylets* consisting of blade-like *mandibles* and *maxillae*, *labrum* and *hypopharynx*. The bundle of stylets is sheathed in a groove on the dorsal face of the labium, which itself ends in a pair of *labella*, with branching *pseudotracheae* forming a sponge-like mopping organ (fig. 7).

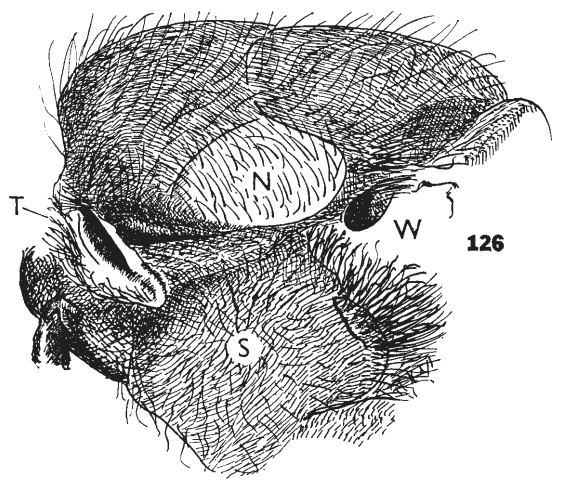
As is the rule among Nematocera, and in contrast to the independently evolved bloodsucking equipment of Asilidae, Empididae, and higher Diptera, mandibles have been lost in all males, as well as in the females of a few exotic genera. Only females ever suck blood. In many Pangoniinae the labium is drawn out, sometimes to extreme length, and is used to extract nectar from deep-blossomed flowers. The few British Tabanidae have no significant variations in proboscis, nor in the *palpi* alongside it.

The THORAX and ABDOMEN have no special structural features, but on the

other hand their colour and pattern still provide the only convenient way of recognizing many species. The basic pattern of the thorax is striped, while that of the abdomen consists of three rows of more or less triangular spots, with the hind margin of each segment also paler. The base of the abdomen is often red or orange at the sides. The number of permutations and combinations of these features, in varying degrees of development, is obviously very large, and hence Tabanidae throughout the world present a bewildering complex of differently patterned species. Even in Britain a number of difficult problems of identification occur.







FIGS. 124, 125.—Right wing of *Chrysops caecutiens*. (124) female; (125) male.
FIG. 126.—*Hybomitra distinguenda*. Left side of thorax, to show location of notopleural callus (N). S = sternopleuron; T = prothoracic spiracle; W = wing-base.

The LEGS have no very striking structural peculiarities. The middle tibiae always bear two apical spurs. The hind tibiae have spurs in all subfamilies except Tabaninae, and this is generally a good starting-point for the identification of a strange Tabanid, though rare exceptions do occur.

The WINGS of Tabanidae are characteristic (figs. 124, 125). The venation is almost the most complete of any Diptera (only a few Nematocera have five branches to the radius), and is often taken as a standard from which to discuss venation in other families. Apart from the closed, or nearly closed anal cell, all the other peripheral cells are wide open in British Tabanidae, though closures occur in some exotic genera. The few British genera are readily separated by wing-pattern, into *Chrysops* with transverse bands (figs. 124, 125), *Haematopota* with "rosettes" (fig. 334) and the rest with nothing more than perhaps an indefinite pale brownish colour.

In size British Tabanidae range from about 6 mm. (small male *Chrysops*) to 24 mm. (a big *Tabanus*). They are always rather squat in shape, and relatively uniform in appearance compared with, say, Asilidae: Tabanidae have nothing to compare with the contrast between *Leptogaster* and *Laphria*. Exotic Tabanidae, however, include some of more varied appearance, including some of wasp-like shape.

BIOLOGY

The larvae of Tabanidae live in wet places, either in damp soil or sand, or in mud that is covered by shallow water. Yet they are not fully aquatic, and depend on being able to breathe atmospheric air through anterior and posterior spiracles, at least at intervals. Cutaneous respiration allows them to lie in mud, especially if they remain inactive.

Cameron (1934) gives a very complete description and discussion of the larvae of *Haematopota pluvialis*, which has a pair of minute anterior spiracles, and a single posterior spiracle at the tip of its siphon, to which both tracheal trunks connect. He quotes: "In addition to tracheal respiration Stammer (1924) holds that there is also a generalized cutaneous respiration, and he assigns to the pair of swollen anal tubercles a special respiratory function."

Tabanid larvae may be recognized by their tough, striated integument, and by the circlets of swellings on each of the abdominal segments. These function as pseudopods when the larva is crawling in mud, or on the bottom under shallow water. The larva has powerful, curved mandibles and maxillae, which move in a vertical plane, and the larvae of *Tabanus* and *Haematopota* are fiercely carnivorous, even cannibalistic. When collected alive for rearing, these larvae must be kept alone and fed on earthworms, otherwise they will eat each other. Larvae of *Chrysops* feed on vegetable debris in the mud, and can easily be reared by gathering a bowlful of mud from the habitat and allowing it to stand under a gauze cover. The emergent flies should be given plenty of room, and killed as soon as they have developed their full colour, because they quickly break the tips of their wings by battering them against any obstruction.

CLASSIFICATION

The Tabanidae of the present day present a difficult problem to the taxonomist because of their lack of balance between primitive and advanced elements. The biting horseflies and deerflies that are familiar all over the

world are evidently of comparatively recent evolution, having perhaps radiated during Miocene or Pliocene times, in association with the great days of ungulate mammals, on which they fed. Even today, in suitable surroundings such as the game areas of Africa, enormous populations exist, and evolution is clearly still going on in habits and biology, if not in appearance. Museum taxonomy from dead specimens reaches a limit in such groups as the *Tabanus taeniola* complex, and can be further resolved only by population studies in the field. The multiplicity of "forms" proposed by Goffe for the British Tabanidae shows that this problem exists even in diminutive faunas such as our own.

In contrast to these, there are more primitive Tabanidae which seem to survive from an earlier period, as well as some peculiar lines such as the Rhinomyzini which are correctly described as "bizarre" in appearance, and which have either saprophagous or carnivorous larvae living in rot-holes in trees. Biogeographically there is clear evidence that the primitive elements of the family spread from the southern hemisphere, perhaps in Gondwanaland times, whereas the "modern" genera *Tabanus*, *Chrysops* and *Haematopota* have spread into the Old World tropics from the northern hemisphere. The two sections of the family may have had a common origin in South America.

Mackerras (1954) thoroughly reorganized the classification of Tabanidae, on a basis of genital differences between subfamilies and tribes, as the following table shows: unfortunately genitalia in Tabanidae have proved of rather limited use at generic and specific level.

CLASSIFICATION OF TABANIDAE

from Mackerras, 1954

Subfamily	Tribes	British genera
PANGONIINAE	PANGONIINI	—
	SCIONIINI	—
	PHILOLICHINI	—
SCEPSIDINAE	SCEPSIDINI	—
CHRYSOPINAE	BOUVIEROMYINI	—
	RHINOMYZINI	—
	CHRYSOPINI	*Chrysops*
TABANINAE	DIACHLORINI	—
	HAEMATOPOTINI	*Haematopota*
	TABANINI	*Atylotus*
		Hybomitra
		Tabanus

KEY TO BRITISH GENERA

1 Wings with a definite pattern of spots or bands.....2
– Wings without definite pattern, sometimes indistinctly brown towards fore-border.....3
2 Wings grey with pattern of white rosettes (fig. 135), giving a mottled appearance. Head and frons broad, with transverse callus, and either two or three velvety black spots above it (fig. 334). Eyes in life with zig-zag, coloured bands. Abdomen grey with indefinite white markings....**Haematopota** Meigen (p. 54)

– Wings with heavy black markings in form of a transverse band and more or less distinct apical patch (figs. 124, 125). Head and frons more upright, face forming a short snout. Eyes in life shining golden, with purple spots and patches. Abdomen sometimes all black, but usually with bold and distinctive pattern (figs. 131–4).....**Chrysops** Meigen (p. 51)

3 Eyes conspicuously hairy. Vertex ♀ with a well-formed ocellar tubercle, though functional ocelli are not present (figs. 150–3).....**Hybomitra** Enderlein (p. 57)

– Eyes inconspicuously hairy, or bare. Vertex sometimes with darker tomentum or hairs, but never with an ocellar tubercle in females though present in males..4

4 Head, seen from above, almost hemispherical, and its posterior margin straight. Frontal calli separate, and often reduced to mere irregular traces (fig. 174). Eyes with scattered, short hairs.....**Atylotus** Osten-Sacken (p. 63)

– Head, seen from above, more transverse, and posterior border hollowed out. If frontal calli are separated they are much larger (figs. 175–7), but usually upper callus is elongate, and joined to lower callus (figs. 178, 179)
Tabanus Linnaeus (p. 64)

Genus **Chrysops** Meigen, 1803

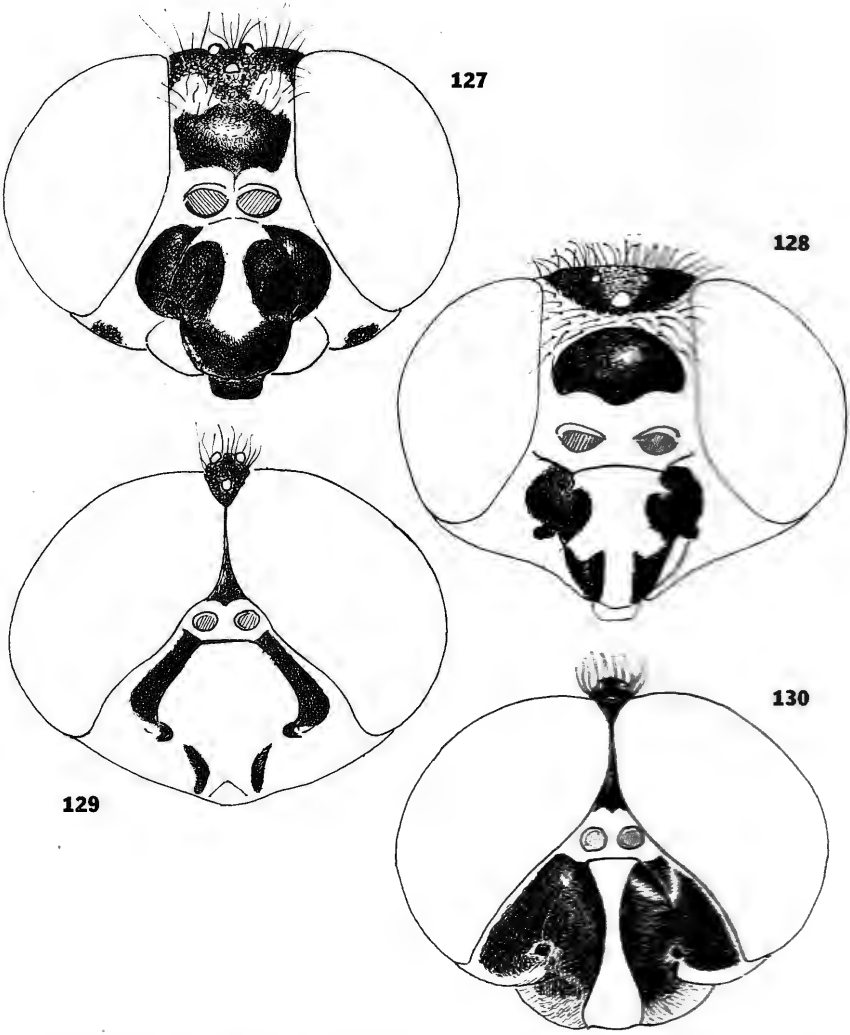
When a female *Chrysops* comes to bite it is unmistakable, with its banded wings, long antennae, and brilliantly glowing eyes, green with purple spots. Species of *Chrysops* are particularly abundant in North America, where they are known as "deerflies", and this name exactly expresses the type of country in which *Chrysops* is most likely to appear: wooded heathland, and rides and clearings in open woodland, never far from water.

Bites from *Chrysops* occur most often on the head and neck, and the specific name *caecutiens* ("blinding") undoubtedly refers to the effects of bites on the eyebrows and upper eyelids, which can cause swellings that effectively close the eyes. Jones (1920 : 7) records this experience.

The world distribution of *Chrysops* differs from that of *Haematopota* in having more species in the New World and fewer in the Old. Neither genus penetrates far into Australia, but *Chrysops*, besides being abundant in North America (in contrast to *Haematopota*), also has about 70 Neotropical species. Only four of the 64 Palaearctic species occur in Britain, and Verrall (1909) does not list any reputed British species; although Goffe (1930 : 60) mentions three others that might possibly occur here, he does not do so with any great conviction.

On the other hand Goffe (1930 : 51–58) recognized no fewer than 20 colour-forms of three of our species (*caecutiens*, *quadratus* and *relictus*) only *sepulcralis* being left without subdivision. It is important to be aware of the wide range of variation in the abdominal pattern of these species, and not to interpret the patterns shown in figures too strictly. All three typical markings of the second abdominal segment may vary both in size and intensity. It is not helpful, however, to give names to particular variants, as Goffe tried to do.

The wing-pattern of *Chrysops* is also striking, and in countries where there are many more species it is possible to distinguish certain species-groups or subgenera by the general pattern of the wing. Among the four British species the only notable specific difference is that the middle band has a *concave* outer margin in both sexes of *sepulcralis*, and a *convex* margin in the other three species. This is difficult to decide without previous experience, and this character has not been used in the key to species. There is a fairly constant difference between the sexes in wing-pattern, as illustrated in figs. 124, 125; the male has much more darkening of the basal and anal cells.



FIGS. 127–130.—Heads of *Chrysops* in front view. (127) ***pictus* (*quadratus*)** ♀; (128) *relictus* ♀; (129) *relictus* ♂; (130) ***caecutiens*** ♂.

KEY TO SPECIES

FEMALES

1 Middle tibiae black 2
– Middle tibiae reddish-yellow 3
2 Abdomen black, dorsally and ventrally, without conspicuous yellow pattern. Frons and face almost entirely bare, shining brown ..... **sepulcralis** Fabricius
Very local, chiefly found near ponds and boggy areas on heaths and moors (*compare* relictus). *vii–ix.*

– First two abdominal tergites yellow, with a black marking usually in the form of two crossed straps (fig. 131); sometimes reduced to a mere vestige; ventrally first two segments with black median stripe. Frons and face with sharply defined pattern of bare-shining areas (fig. 130)..... **caecutiens** Linnaeus

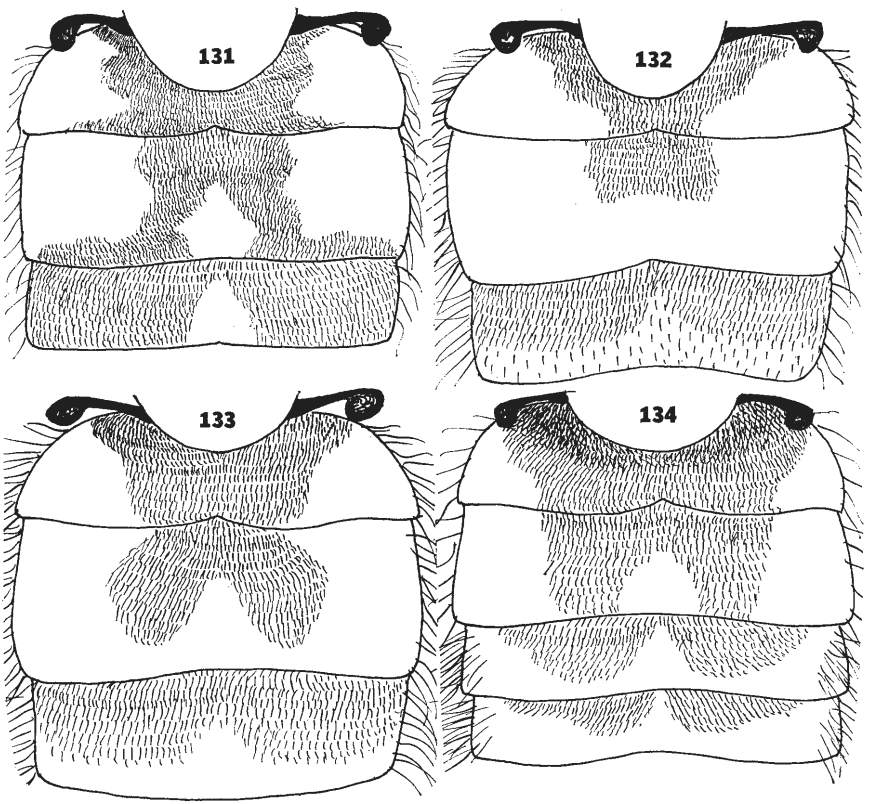
Occurs throughout Great Britain, and in south is commonest species of genus. v–ix.

3 Second abdominal segment with a single quadrate spot (fig. 132) which may vary considerably in size, from a large one that reaches to second segment, to a mere trace; occasionally entirely absent. Frons narrower (fig. 127) with quadrate callus; facial bare spots large, and closely approximated (better known as *quadratus* Meigen) **pictus** Meigen

Locally numerous in south of England (e.g. in parts of New Forest). Rare in Scotland. vi–ix.

– Second abdominal segment with a pair of diverging black lobes, united at base (fig. 133). Frons broader (fig. 128), with semi-lunar callus; facial spots smaller, widely separated..... **relictus** Meigen

Generally distributed throughout British Isles, including Ireland. Uncommon in most areas, but sometimes locally abundant, especially on water-plants in ponds or boggy areas in heathland and moorland; perhaps after a mass emergence (compare sepulcralis). *v–ix.*



FIGS. 131–134.—*Chrysops*, abdominal pattern. (131) *caecutiens* ♀; (132) *pictus* (*quadratus*) ♀; (133) *relictus* ♀; (134) *relictus* ♂.

MALES

1 Body and legs entirely black, without any reddish areas or yellowish hairs **sepulcralis** Fabricius ♂
– Body with some reddish-yellow areas, and with conspicuous yellow hairs on pleura, notopleura and base of abdomen, especially ventrally 2
2 Face with large bare spots almost meeting in middle line (fig. 130). Second abdominal segment with a more or less quadrate spot 3
– Face with smaller bare spots (fig. 129). Second abdominal segment with a pair of diverging lobes (fig. 134) ..... **relictus** Meigen
3 Middle tibiae distinctly yellow-brown. Second abdominal segment yellow with a well-defined quadrate black spot ..... **pictus** Meigen
– Middle tibiae all black. Second abdominal tergite black, only narrowly yellow at each side ..... **caecutiens** Linnaeus

Genus **Haematopota** Meigen, 1803

Clegs of the genus *Haematopota* are even more familiar to non-dipterists than the bigger horseflies, because they approach so quietly, and bite so painfully. Not content to bite only out of doors, and in sunny weather, they are even more active on warm, overcast days, and will come into outbuildings such as sheds and garages to do so.

Haematopota is a large and rather uniform genus, recognized by its speckled wings (figs. 135, 334) and the shape of head and frons. In the great majority of species the thorax has two grey longitudinal stripes, each of which ends in a triangular spot; the abdomen has a more or less interrupted median stripe and paired lateral spots on at least the posterior segments; and the middle and hind tibiae normally have two pale bands. Some or all of these features may be different in a minority of exotic species.

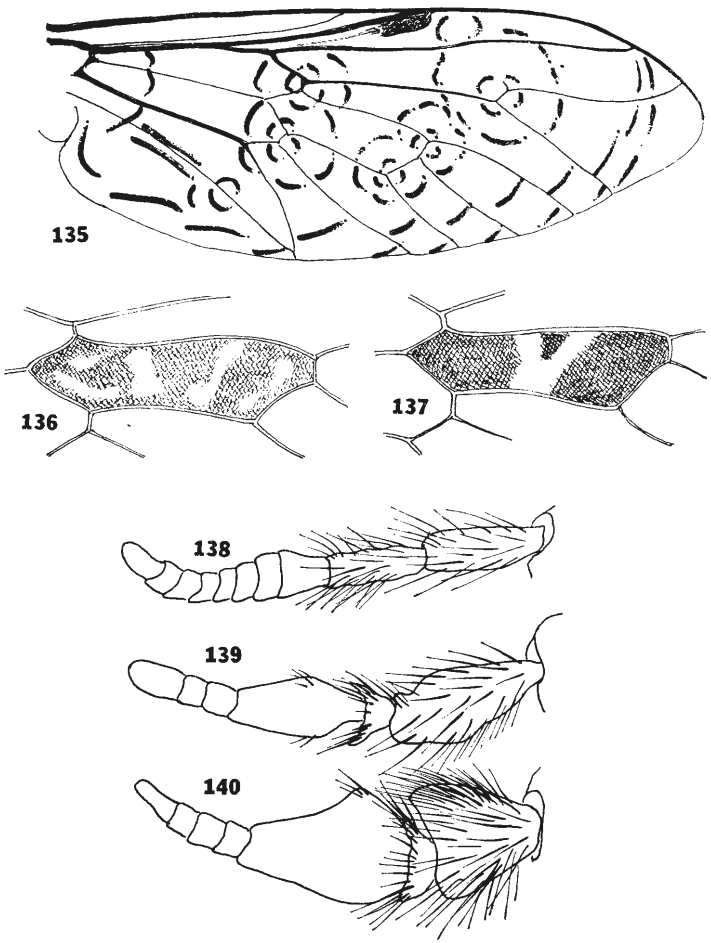
Species are most abundant in Africa (now over 200), in the Orient, and in the Palaearctic Region; in sharp contrast to this there are only five species in North America, none in South America, and only one which penetrates into north-eastern Australia. Various segregates—subgenera or even genera—have been proposed from time to time, but none of these need concern us in Britain, where we have only four, or possibly five, species.

Goffe (1930) uses the generic name *Chrysozona* Meigen, 1800, which at that time was held to be valid. This is one of the "Meigen 1800" names which were a bone of contention among dipterists from 1908—when Hendel resurrected them—to 1963 when they were invalidated by an Opinion (678) of the International Commission for Zoological Nomenclature.

Larvae of *Haematopota* live in damp earth rather than in water, and this is probably a factor in the wide dispersal of the adults. Sometimes they are numerous enough to be a local pest in wet, boggy, or badly drained areas of farmland, but single females of *pluvialis* or *crassicornis* may appear in search of a blood-meal almost anywhere in the country. The other two species, *italica* and *bigoti*, are more restricted to southern and eastern coastal areas. A colony of *Haematopota* discovered near Southport by Entwistle (1952) is either a form of *bigoti* or a closely allied species; its status and possible name cannot be decided without a detailed comparison with the *bigoti* of the south coasts of France, Spain and Portugal. It may be a relict of a Lusitanian distribution.

The characteristic speckled *wing-pattern* of *Haematopota* is an elusive character to use in the recognition of species, since no two specimens are exactly alike. Some order can be detected if the markings are looked upon

as "rosettes" based upon the principal forks and cross-veins as shown diagrammatically in fig. 135. Differences which seem complicated can often be interpreted as a spreading or shrinkage of the whole rosette-pattern, with the streaks in the cells along the hind-margin advancing towards the perimeter, or retreating into the middle of the cells. In this way the very useful difference in the pattern within the discal cell, which serves to distinguish *pluvialis* from *crassicornis* (figs. 136, 137), can be seen as the merging of fragments of two ring-systems.



FIGS. 135–137.—Wing-markings of *Haematopota*. (135) general diagram of pattern of rosettes (which are actually pale on a black ground); (136, 137) comparison of markings in discal cell of *H. pluvialis* (136) and *H. crassicornis* (137).

FIGS. 138–140.—Antennae of Tabanidae. (138) *Chrysops*; first four flagellar segments partly fused; (139) *Haematopota*; (140) *Tabanus*.

KEY TO SPECIES

FEMALES

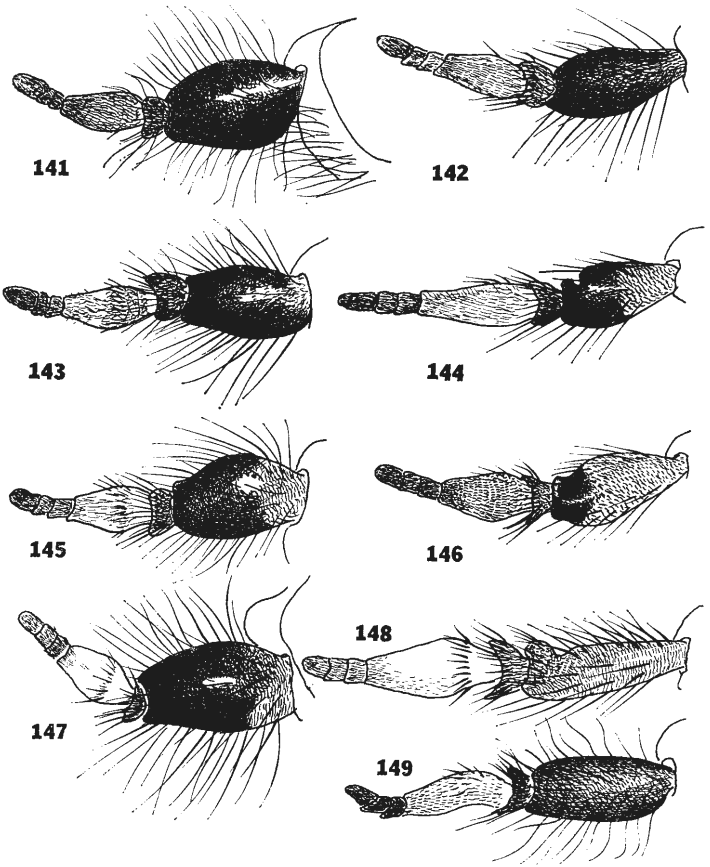
1 Antennae elongate, especially first segment, which is entirely covered with grey tomentum, and has a prominent subapical notch (fig. 148). Lateral abdominal spots usually prominent on all segments except first ..... **italica** Meigen

Southern counties from Suffolk to Cornwall. Wales, Cardiganshire, Borth Bay. Uncommon, principally coastal, or only a short way inland. vii–ix. Recent European work indicates that the British specimens—at least those from the East Anglian coast—are really grandis *Meigen, which may be a large subspecies of* italica.

– First antennal segment broader in lateral view (figs. 142, 144, 146) 2

2 Middle and hind femora reddish-yellow, with blackish tips. First antennal segment mostly covered with ashy grey tomentum, only a little of the bulbous tip bare and shining (fig. 146). Abdomen with very distinct lateral spots, including even first segment ..... **bigoti** Gobert

Coasts from Norfolk to Somerset. Local. Entwistle (1952) *recorded a colony on the Lancashire coast near Southport which have the first antennal segment and fore femora darker than typical* bigoti (*see also males*). *They may be a subspecies similar to* bigoti-monspellensis *Vill. vii–viii.*



FIGS. 141–149.—Antennae of *Haematopota*. (141) *crassicornis* ♂; (142) *crassicornis* ♀; (143) *pluvialis* ♂; (144) *pluvialis* ♀; (145) *bigoti* ♂ (Lancashire form); (146) *bigoti* ♀; (147) *bigoti* ♂ (typical form); (148) *italica* ♀; (149) *italica* ♂.

– Middle and hind femora all ashy grey. First antennal segment more extensively bare and shining (figs. 142, 144). First and second abdominal segments without distinct lateral spots 3

3 First antennal segment with grey tomentum basally, bare and shining apically, and with a well-marked subapical notch (fig. 144); third segment distinctly reddish basally. Discal cell of wing with four transverse markings (fig. 136) **pluvialis** Linnaeus

"The Cleg." Widespread and common throughout the British Isles. v–ix, sometimes into x.

– First antennal segment (in side view) with little grey tomentum and no subapical notch, more obviously swollen and shining black than in *pluvialis* (fig. 142); third segment blackish, indistinctly reddish only at extreme base. Discal cell of wing with only two transverse markings, which usually combine into the shape of V or Y (fig. 137) ..... **crassicornis** Wahlberg

Widespread, but less generally common than pluvialis, *though it predominates in some areas: Brindle* (1963 : 53) *suggests* crassicornis *dominant on higher ground in N.E. Lancashire, and this may be so in Scotland. Also Ireland. vi–viii.*

MALES

1 Vertex of head with a conspicuous tuft of silky yellowish hairs, which arise from a patch of pale tomentum 2

– Vertex of head with the long hairs either black, or mixed black and yellowish, arising from grey tomentum like rest of occiput 3

2 First antennal segment sausage-shaped (fig. 149) ..... **italica** Meigen

– First antennal segment shorter and inflated (figs. 145, 147) ..... **bigoti** Gobert

3 Antenna as in fig. 143; third segment partly reddish. Discal cell as in fig. 136 **pluvialis** Linnaeus

– Antennas as in fig. 141; third segment entirely blackish. Discal cell as in fig. 137 **crassicornis** Wahlberg

Genus **Hybomitra** Enderlein, 1922

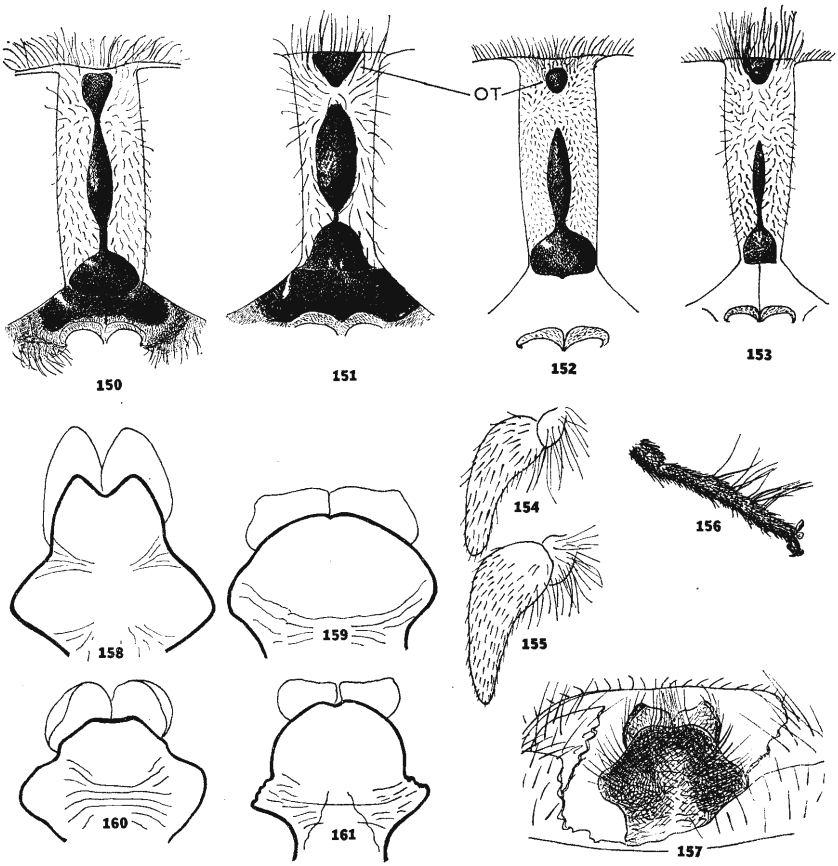
This is the *Tabanus* subgenus *Therioplectes* of Verrall (1909 : 350). The hairy-eyed species of "Tabanus" have always given trouble, the first problem being to decide when the eyes are hairy and when they are not. A great many Tabanidae have sparse hairs, which become visible under even moderate magnification, and so one has to fall back on the unsatisfactory practice of saying that the hairs must be "obvious". Even "obviously" hairy eyes are not, in themselves, a sufficient reason for classifying all such species together. Among African "Tabanus" I found that the nine species with hairy eyes belonged to six different genera and subgenera.

In the British fauna the problem is simplified by the small number of species involved. The British *Atylotus* have inconspicuous or microscopic hairs on the eyes, but these species can be segregated without difficulty from the structure of the frons (figs. 167–70). All British Tabanidae with densely hairy eyes belong to the genus *Hybomitra*, and have in common the characteristic frons (figs. 50–153) which bears an actual ocellar tubercle (O.T.), though no functional ocelli. Some species of *Tabanus* may have a dark spot in this position, but no tubercle.

The name of this taxon has been changed several times. Older authors, including Verrall, called it the subgenus *Therioplectes*, but in current usage this name is restricted to a distinctive genus of large, very hairy-eyed species from S.E. Europe and Asia Minor. Goffe (1930 : 88) suggested *Sziladynus* Enderlein, 1925, but earlier names were available in Enderlein's work of 1922. During the second world war a conflicting usage grew up between *Tylostypia* Enderlein, 1922, adopted in the Fauna of the U.S.S.R. by

Olsoufiev (1937 : 123) and *Hybomitra* Enderlein, 1922, proposed by Philip (1941 : 8). Only recently has this been resolved by mutual agreement among the specialists in this family, and *Hybomitra* is now the accepted name, with the status of a genus.

Hybomitra extends all round the Holarctic Region, and separation of species is one of the most difficult problems in the taxonomy of Tabanidae. A courageous effort, based on study of the existing British collections as well as on continental material, was made by Lyneborg (1959), who corrected long standing misidentifications of older names, and gave new names to some of the concepts that Verrall and others had suggested (e.g. the "Worcester" specimen mentioned by Verrall, 1909 : 359 became *Hybomitra*



FIGS. 150–161.—*Hybomitra*. (150–153) frons of female: (150) *micans*; (151) *lurida*; (152) *montana*; (153) *bimaculata*. OT = ocellar tubercle. (154, 155) palpi of females: *montana* (154), *bimaculata* (155). (156) fore tarsus of *micans* ♂, showing dorsal long hairs. (157) ventral view of tip of abdomen of *montana* ♀, showing eighth sternite and dorsal lamellae as they appear *in situ*, when seventh and sixth sternites are chipped away. (158–161) eighth sternite and dorsal lamellae of females: *mühlfeldi* (158), *bimaculata* (159), *distinguenda* (160), *schineri* (161).

TABLE I.—COMPARISON OF THE VIEWS OF SEVERAL AUTHORS ON CERTAIN SPECIES OF *Hybomitra*.

VERRALL, 1909	COLLIN, 1932 also [OLDROYD, 1939; COLLIN, 1940]	LYNEBORG, 1959	*Genitalia Type*	LECLERCQ, 1966	PRESENT HANDBOOK
tropicus Meigen (p. 355)	*tropicus* L. (p. 38) Glamorgan, Norfolk	*mühlfeldi* Brauer (pp. 119, 124)	3	*mühlfeldi* Brauer (p. 114)	*mühlfeldi* Brauer
	Worcester	*collini*, sp. n. (*tropica* Panzer, nec. L.) (p. 94)		*tropica tropica* Panzer (p. 121)	*bimaculata collini* Lyneborg
	bisignatus J., light form (p. 38)	*bimaculata* Meigen (p. 101)		*tropica bimaculata* Meigen (p. 122)	*bimaculata bimaculata* Meigen
tropicus Meigen (var. *bisignatus* J.) (p. 358)	*bisignatus* J., dark form (p. 39)	*bisignata* J. (p. 104)	> 1	*tropica bisignata* J. (p. 122)	*bimaculata bisignata* J.
solstitialis Meigen (p. 377)	*solstitialis* Meigen (p. 39)	*solstitialis* Meigen (p. 106)		*solstitialis* Meigen (p. 119)	*solstitialis* Meigen
		schineri, sp. n. (*solstitialis* Schiner, nec. Meigen) (p. 109)		*schineri* Lyneborg (p. 115)	*schineri* Lyneborg
distinguendus, sp. n. (p. 371)	*distinguendus* Verrall (p. 39)	*distinguenda* Verrall (p. 115)	2	*distinguenda* Verrall	*distinguenda* Verrall

collini, sp. n.). Collin (1940) had already pointed out that three species, then known in Britain as *tropicus* L., *solstitialis* Meigen and *distinguendus* Verrall, could be readily separated by the shape of the eighth sternite and dorsal lamella of the female. Lyneborg generalized these three forms into "type 1", "type 2" and "type 3", but it is not yet clear whether, in fact, the female terminalia of *Hybomitra* do fall into three groups, as Lyneborg implies. Within the limited compass of the *bimaculata* group of species "type 2" contains only *distinguenda*, "type 3" only *mühlfeldi* Brauer (= *tropicus* L. of Collin, 1940), and all the others have eighth sternite of "type 1".*

Genital differences as shown by Collin are therefore valuable for picking out *distinguenda* and *mühlfeldi* but we are left with a confusing group of species (and names!) centering round the familiar British species (or colour-form) known to every collector as *bisignata* Jaennicke. In Table I I have tried to show graphically how the names used by various authors compare with one another, both before and after Lyneborg's paper. Subsequently Lyneborg (1961 : 98) gave an account of the type material of *Tabanus tropicus* L., from the collections of the Linnaean Society in London, and chose a lectotype which made *tropicus* L. an older name for *tuxeni* Lyneborg, 1959. This is a species closely related to, if not identical with, *montana* Meigen; the "Tabanus tropicus" of Verrall and all other British authors was a mixture of at least two species (see Table I), and the "tropicus" of Collin (1940) should now be called *mühlfeldi* Brauer.

Later authors, Kauri, Trojan, and Leclercq have been more conservative than Lyneborg, and incline to merge some of his species. In particular there is general agreement at the present time that *bimaculata*, *bisignata* and *collini* are all variants of one species, which was the *tropicus* of Panzer but not of Linnaeus. The oldest valid name for this species is *bimaculata* Meigen, 1826.

This is not the place to argue in detail about either the nomenclature or the variability of these difficult species. Trojan (1962) has shown how variable are the structural and colour characters upon which the taxonomy of Tabanidae is normally based (fig. 166), and even the genitalic characters are by no means constant. The following key is no more than an interim one, which it is hoped will stimulate collectors to assemble more material of this genus.

Key to Species

Females

1 Subcallus (swelling immediately above antennae) at least partly bare and shining (figs. 150, 151) 2

– Subcallus entirely dull, covered with grey tomentum 3

2 Legs, thorax and abdomen all black in ground colour, with pattern of whitish hairs **micans** Meigen

Scattered, but sometimes locally numerous, throughout Great Britain. Early summer species. v, vi.

– Legs and sides of second abdominal tergite more or less reddish yellow. **lurida** Fallén

Mainly Scottish, but occurs infrequently in England. Shropshire, Widdop Moss. v–vii.

* Fig. 157 shows these structures as they are exposed in the dried specimen when it is turned over, and the seventh and sixth sternites are carefully chipped away with a pin. Fig. 180 shows them as they are extruded for egg-laying.

3 Palpi slender (fig. 154). Frons relatively broad, gently tapered at lower end; lower callus often broader than high. Subcallus (above antennae) relatively high (fig. 152).....**montana** Meigen

A characteristic species of Highland Britain, but also found locally in most lowland counties except the extreme south-east. v–vii.

– Palpi more swollen basally (fig. 155). Frons narrower and more obviously tapered towards lower end; lower callus higher than broad. Subcallus lower, more transverse (fig. 153).....4

4 Abdomen with orange colour extending well on to fourth tergite.....5

– Orange colour on three tergites, or scarcely extending on to fourth.....6

5 Eighth sternite as in fig. 160, broad, shamrock-shaped (Lyneborg's type 2). First and second antennal segments greyish black. Second tergite of abdomen with orange hairs over most of the orange area.....**distinguenda** Verrall

Widespread and sometimes very numerous. vi–ix. Care should be taken to distinguish it from the following species.

– Eighth sternite as in fig. 161 more mushroom-shaped, without a distinct median notch (Lyneborg's type 1). First and second antennal segments reddish brown. Second tergite of abdomen with distinct area of black hairs above orange ground **schineri** Lyneborg

Very rare in Britain, though "rather common" in Denmark (Lyneborg, 1959). Essex, Brentwood (P. Freeman). viii.

6 Eighth sternite shamrock-shaped as in fig. 160. A miniature form of *distinguenda* defined by Goffe, 1930 : 94 .....**distinguenda-parva** Goffe

Very rare in New Forest and Wyre Forest. viii.

– Eighth sternite not of this shape.....7

7 Notopleural calli (fig. 126) brown. Eighth sternite and lamellae as in fig. 158, all elongate and pointed.....**mühlfeldi** Brauer

This is the tropicus *of Collin* (1940 : 178), *and is known definitely from Glamorgan, Crymlyn Bog (now part of Swansea); Leech Pool, near Chepstow (J. H. Wood), and from various localities in the Norfolk Broads (Collin, Freeman; Biggs; Buxton, Wainwright and Fonseca all collected it there). vi–viii.*

– Notopleural calli (fig. 126) usually black, except in *bimaculata* (couplet 9). Eighth sternite low, dome-shaped, with almost no trace of a median notch (Lyneborg's type 1) (fig. 159).....8

8 "Thorax, especially the pleura, with pale greyish pubescence. Middle stripe of abdomen rather narrow, about one-fifth of the width of the third tergite. Brown sidemargins on upper side very light, without greyish shadows" **solstitialis** Meigen

This couplet is quoted verbatim from Lyneborg (1959 : 88). *Authentic British specimens of* solstitialis *are few. The British Museum has two from the New Forest, Aldridge Heath (Wainwright). viii.*

– Thorax with dark grey and black pubescence. Middle stripe broader, one-quarter to one-third as wide as third tergite. Brown sidemarkings on upper side with grey shadows .....forms of **bimaculata** Meigen.....9

9 Abdomen black with pattern of grey hairs, and little or no trace of reddish lateral spots .....**bimaculata** form **bisignata** Jaennicke

The most clearly defined form of the bimaculata *complex, and a familiar horsefly of the woodlands of southern England in early summer. Warwickshire southwards. v–viii.*

– Abdomen black with distinct reddish lateral spots near base.....10

10 Lateral reddish or yellow spots of abdomen stop short on second segment. Notopleural callus (fig. 126) often brownish...**bimaculata** form **bimaculata** Meigen

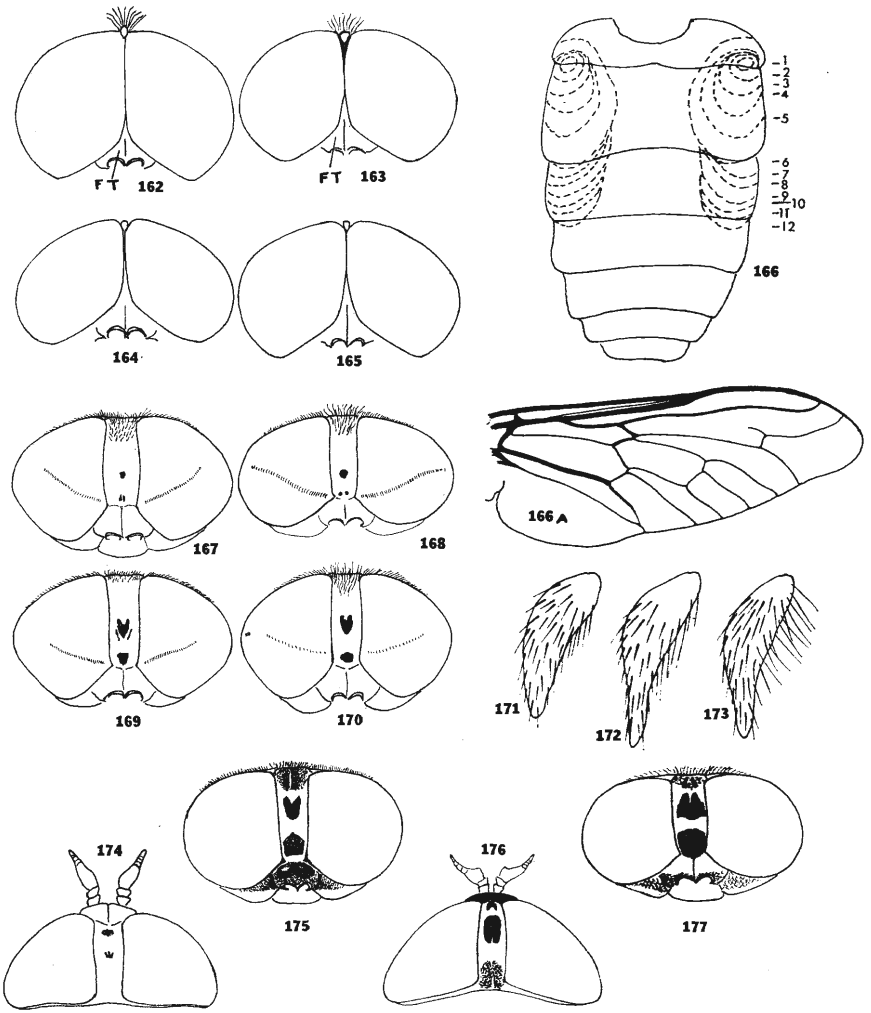
Most of Verrall's tropicus *belong here. Like* bisignatus, *this form occurs south of Shropshire and Huntingdon, frequently in woodland. mid v–vii.*

— Lateral reddish spots of abdomen reach to third segment. Notopleural callus black. **bimaculata** form **collini** Lyneborg (*tropica* Panzer, not Linnaeus)

Rare in Britain. Worcester (Verrall, 1909 : 359); *Shropshire, Wyre Forest (Wainwright); Shrewsbury, Longmer Hall (R. F. L. Burton). Lancs., Holker Moss (J. D. Ward); Kent, Ham Street Woods (Wainwright). mid v–vii.*

MALES

1 Body and legs entirely black. Fore tarsi with very long touch hairs dorsally (fig. 156). Subcallus abruptly prominent and partly bare and shining black **micans** Meigen



FIGS. 162–177.—Tabanidae. (162–165) heads of male *Hybomitra* from in front, to show length of contact of eyes: *mühlfeldi* (162); *bimaculata* (163); *lurida* (164); *distinguenda* (165). FT = frontal triangle. (166) dorsum of abdomen of *H. bimaculata*, showing 12 variants of the extent of the reddish yellow basal spots (after Trojan); (166A) wing of *Atylotus fulvus*; (167–170) heads of female *Atylotus* from in front: *fulvus* (167); *plebeius* (168); *rusticus* (169); *nigrifacies* (170). (171–173) palpi of female *Atylotus*: *plebeius* (171); *rusticus* (172); *nigrifacies* (173). (174–176) heads of females showing frontal calli: *A. fulvus* (174); *Tabanus glaucopis* (175, 176); *T. cordiger* (177).

– At least tibiae, and usually sides of first two or three abdominal tergites reddish yellow 2
2 Hairs of eyes short and whitish ..... **montana** Meigen
– Hairs of eyes brown, sometimes short, usually long and velvety 3
3 Abdomen with reddish yellow sidemargins on four tergites 4
– Abdomen with reddish yellow sidemargins on not more than three tergites 5
4 First antennal segment greyish-black. Eyes with upper facets larger than lower, but not sharply segregated. Abdomen with a narrow black stripe, tapering to third tergite; lateral reddish areas extensively covered with black hairs (*cf.* ♀), leaving only spots of yellow hairs ..... **distinguenda** Verrall
– First antennal segment reddish-brown. Eyes with upper facets bigger than lower, and sharply segregated. Middle stripe of abdomen more brownish, less strongly defined, sometimes interrupted ..... **schineri** Lyneborg
5 In front view, eyes flattened dorsoventrally, not quite meeting, leaving a distinct gap (fig. 164). No tuft of longer hairs on vertex ..... **lurida** Meigen
– Eyes higher and less transverse, actually meeting for a longer or shorter distance (figs. 162, 163). Vertex with distinct tuft of long, black hairs 6
6 Notopleural callus (fig. 126) brown. Frontal triangle small, eyes touching in a long, straight line, with tiny ocellar triangle (fig. 162) ..... **mühlfeldi** Brauer
– Notopleural callus black (fig. 126). Frontal triangle bigger, extending further up between eyes (fig. 163) ..... **bimaculata** Meigen

Lyneborg (1959 : 88, 102, *fig.* 9) *gives a number of characters for separating the males of the three forms of* bimaculata (bimaculata *s. str.*, bisignata *and* collini), *and figures the pattern of the underside of the abdomen. I have not found satisfactory differences in the limited material that I have seen.*

Genus **Atylotus** Osten-Sacken, 1876

(*Ochrops* Szilády, 1915)

This is another name that has been changed, and then changed back again for nomenclatorial reasons which we need not go into in this *Handbook*. For a time *Ochrops* was widely used in Europe, but recent authors have reverted to *Atylotus* in the same sense as the name was used by Verrall, but with the status of a full genus.

Species of *Atylotus* are easily recognized by the head-structure. The head is more strongly spherical than in *Tabanus* (figs. 174, 176), and the eyes in preserved specimens are usually light brown, often with a faint trace of a thin purple line as indicated in figs. 167–70. This line is almost a diagnostic feature of exotic species of *Atylotus*—a very widespread genus—but, as pointed out by Verrall (1909 : 380–1) it is not always discernible in dried specimens of *fulvus*. Traces can be revived in Goffe's solution (p. 65).

The frontal calli of *Atylotus* are characteristic. The two calli are small, widely separated, and very low in profile. Hence the visible bare, black spots are extremely variable in size and shape, and the figures should not be interpreted literally, nor used in an attempt to separate one species from another. Separate calli also occur in *Tabanus glaucopis* and *T. cordiger* (figs. 175–7) and care should be taken not to confuse these with *Atylotus*.

Key to Species

1 Both sexes covered with golden yellow hairs, which are particularly vivid and colourful in life. Abdomen reddish at sides, basally, but no distinct abdominal pattern is visible unless the covering of mingled black and yellow hairs is rubbed away. Calli small and sometimes absent ..... **fulvus** Meigen

Southern England, Wales and Ireland, especially on heaths and moors with some open water. Local. vi, vii.

– Both sexes drab grey, with pale yellowish hairs in place of golden ones, and these not at all conspicuous on thorax. On abdomen the black and pale hairs form triangles, more or less combined into longitudinal stripes.....2

2 ♀ Palpi short and feeble, without an acute tip (fig. 171). A small species, (11 mm. or less), with relatively narrow frons (fig. 168). Abdomen ashy grey, without any reddish spots basally, and with pale hairs arranged in definite triangles, especially in median row; sometimes more uniformly pale (? distinct species)
plebeius Fallén

Rare. Known only from Cheshire, Abbots Moss and Delamare Forest. vii (see Collin, 1945 : 89).

– ♀ Palpi longer, and more acutely tipped (figs. 172, 173). Larger species (13 mm. or more), with relatively broader frons and usually bigger calli (figs. 167, 169, 170). Abdomen with distinct reddish-yellow spots at sides basally, and with light and dark hairs forming stripes.....3

3 Femora black, only extreme tips yellow. Notopleural calli black (fig. 126). Hairs of vertex not longer than postocular fringe (♀). Abdomen only indistinctly reddish-yellow, mainly on second segment.....**rusticus** Linnaeus

Rare. Sussex, near Lewes. Huntingdonshire, Monks Wood. vii–ix.

– Femora reddish-yellow, black only basally. Notopleural calli (fig. 126) reddish-brown. Hairs of vertex black, much longer than pale hairs of postocular fringe. Abdomen very densely reddish-yellow at sides of first two segments
(*latistriatus* Verrall, nec Brauer) **nigrifacies** Gobert

Local in East Anglia; numerous at Scolt Head. v–viii.

Genus **Tabanus**

Tabanus is a large and ill-defined genus, into which a large majority of species of the family are still dumped. Workers on Tabanidae continually try to reduce the size of the genus *Tabanus* by splitting off segregates, but with indifferent success. The present *Handbook* follows the current trend in admitting *Hybomitra* and *Atylotus* as distinct genera, and thereby restricts the genus *Tabanus* to those that have the eyes completely bare, and no raised ocellar tubercle (though they may have a patch of darker tomentum or hairs in that position).

In a larger fauna, the many species of *Tabanus* would be arranged in species-groups, and it may be helpful if our nine British species are thought of as falling into four groups as follows:

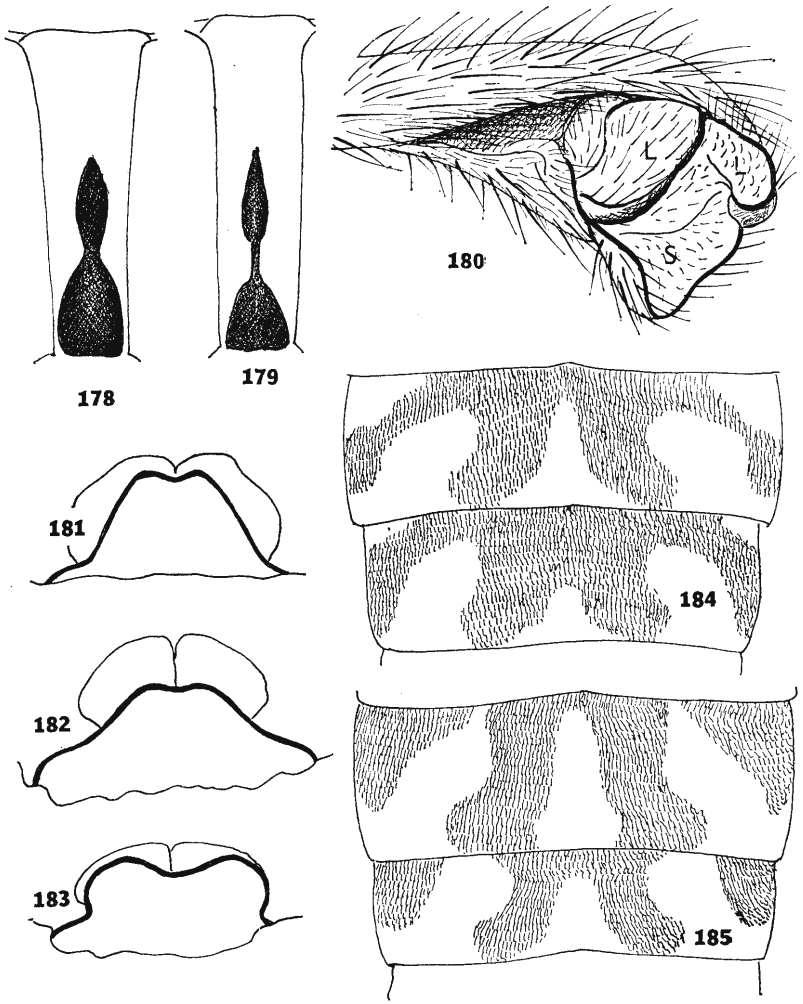
1. *cordiger*-group	*cordiger; glaucopis*
2. *bovinus*-group	*bovinus; verralli; sudeticus*
3. *autumnalis*-group	*autumnalis*
4. *bromius*-group	*bromius; maculicornis; miki*

Eye-bands in British Tabanus

Tabanidae in general are conspicuous for the brilliant colour of the eyes in life, and in many species the colour includes one or more bands or spots. The actual colour shifts according to the intensity and direction of illumination, but the pattern is an integral part of the structure of the eye, so that it remains constant for each individual, and—within limits—is characteristic for each species. Unfortunately the colours are produced by interference in the superficial layers of the ommatidia, and they fade when the eye shrinks after death. Often more or less distinct traces can be seen, even in dried museum specimens, and then the pattern of the living eye is known, though not its true colouring.

Relaxing the specimen causes the eye to swell again, and may restore the bands. Indeed Leclercq (1966 : 230) recommends this as standard

practice. Goffe (1932 : 15) stressed the danger of permanently damaging the superficial tomentum, dusting, or pollen which gives species of *Tabanus* their characteristic appearance, and is the chief means by which species are identified. Goffe recommended instead that either the whole specimen or just the head should be immersed in a solution made up as follows: glacial acetic acid 1 part; glycerine 1 part; solution of perchloride of mercury, B.P. strength, 1 part; rectified spirit 47 parts.



FIGS. 178–185.—Tabanidae. (178, 179) frons of female: *Tabanus bromius* (178) and *T. miki* (179). (180) a female of *Tabanus*, showing eighth sternite and dorsal lamellae in extended position, as for egg-laying. (181–183) eighth sternite of female: *T. bromius* (181); *T. miki* (182); *H. micans* (183). (184, 185) dorsal abdominal pattern of second and third segments of females: *T. bromius* (185); *T. miki* (185).

I have found that a good way of using Goffe's solution is to detach the head of the specimen over a dish of the fluid, so that it falls in, usually already with the eyes downwards. In this position the head is left until the eye-colours reappear, which may be a few minutes, or about a day. When the eye has become translucent, with shifting colours as it is turned, it is safe to conclude that an absence of bands indicates an unbanded eye in life. After drying the head can be stuck back on the body.

The eyes of *Haematopota* have zig-zag bands, and those of *Chrysops* the appearance of spots and whorls, though these can be related to a general pattern. In both genera the eye-pattern is too complex, and specific differences too intangible, for eye-pattern to have been used to any significant extent in taxonomy. The eyes of *Tabanus* are much simpler, and those of the females may have three bands, or one, or none at all. Those of males of all British species except *bovinus* have a big area of enlarged facets in the upper part of the eye. The lower area is coloured and banded exactly as in the female, but the upper area is normally quite different, of a different colour, and sometimes darker in the middle. *Tabanus miki* Brauer and *T. cordiger* Meigen are unusual in having no band in the female, but one in the male, along the line of demarcation of the two kinds of facets.

Since the eye-pattern can best be seen in the field, when the specimen is first taken, or alights to bite, the following summary may be helpful:

3 bands	*glaucopis*
1 band	*bromius; maculicornis; cordiger* (male only)*; miki* (male only)
no bands	*cordiger* (female only)*; miki* (female only)*; autumnalis; bovinus; verralli; sudeticus.*

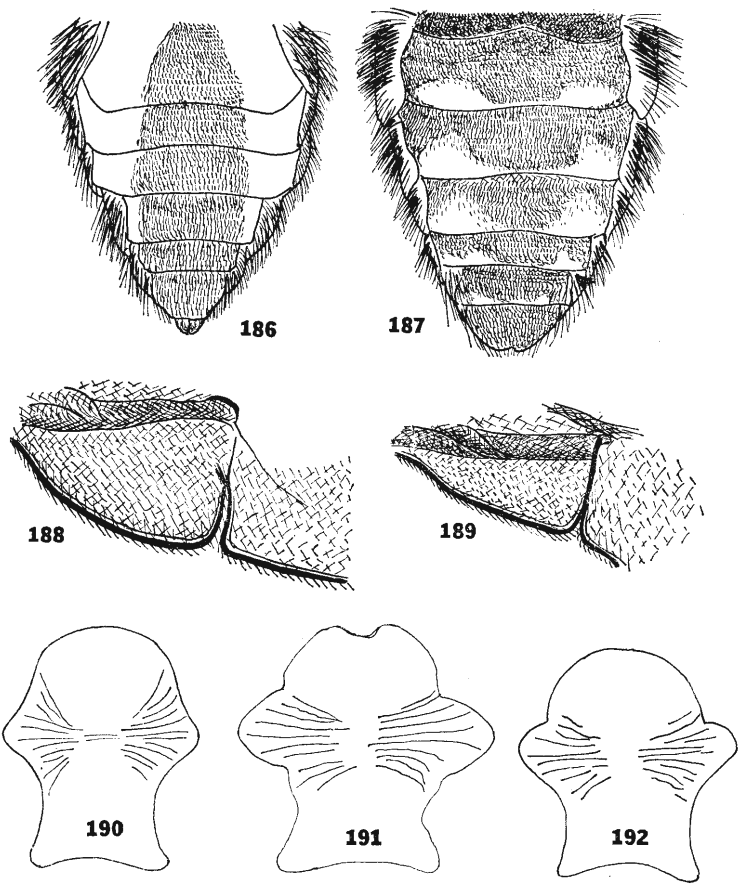
Key to Species

Females

1 Upper and lower frontal calli quite separate (figs. 175–7) (*cordiger*-group) 2
– Upper and lower frontal calli united, with upper forming a linear or lens-shaped extension of lower (figs. 178, 179).....3
2 Frons as in figs. 175, 176; narrow, upper and lower calli rather elongate, subcallus partly bare and shining black-brown; band of brown tomentum covers all this area and parts of parafacials. Antennae red. Abdominal spots large, ovoid and yellow; venter mainly reddish yellow.....**glaucopis** Meigen
Southern England, on chalk downs above about 200 feet. Wiltshire, Farley; Berkshire, Streatley; Sussex, Goodwood; Surrey, Box Hill; Kent, Eynesford. Locally abundant. vii–ix.
– Frons as in fig. 177; broader, upper and lower calli more transverse, upper callus roughly heart-shaped (hence specific name); subcallus entirely tomented and pale, with a band of brown tomentum running through bases of antennae. Antennae black. Abdominal spots small, more angular, and whitish; venter grey
cordiger Meigen
Throughout Great Britain, but rather local; perhaps overlooked. v–vii.
3 Very large species, 19–24 mm., with one median row of very distinct triangles, and indefinite lateral pale spots (*bovinus*-group).....4
– Smaller species; if approaching 18 mm. in length, then with three rows of very distinct grey triangles.....5
4 Abdomen, dorsally and ventrally, predominantly black, with small, equilateral, median pale triangles.....**sudeticus** Verrall
Goffe (1930 : 74–78) *divided* sudeticus *into five forms, only one of which is sufficiently distinct to be acceptable* (verralli, *below*). *The others show the range of* sudeticus *to extend throughout the British Isles, mainly in Highland Britain (Scotland, Lake District, Wales, Ireland), and along the extreme south of England, from Cornwall to the New Forest. Locally numerous.* ***vii–viii.***

– Abdomen distinctly reddish at sides, and median triangles usually longer and less distinct . . . **bovinus** Linnaeus; **verralli** Oldroyd (*perplexus* Verrall, nec Walker)
According to Goffe (1930 : 71–72) *true* bovinus *predominates in the northernmost part of the New Forest, and* verralli *in the more open forest to the south. No really good distinction can be given between these, and it is impossible to assign records with certainty to one or the other. It seems likely that most of them, from S. Ireland, S. Wales, and all along the southern strip of England, will apply to* verralli. *vi–viii.*

5 A distinctive species of medium size (length 16–19 mm.), with a conspicuous abdominal pattern of three rows of clear-cut grey triangles. Abdomen usually more yellowish at sides of base, especially in males, but sometimes also in females (var. *brunnescens* Szilády) (*autumnalis*-group) . . . . . **autumnalis** Linnaeus
Southern England and S. Wales, as far north as Huntingdonshire, Wood Walton Fen, and Merioneth, Barmouth, but chiefly south of the Thames. vi–viii.



FIGS. 186–192.—*Tabanus*. (186, 187) pattern of underside of abdomen of male: *autumnalis* (186); *sudeticus* (187). (188, 189) comparison of relative size of alula of wing: *bromius* (188); *maculicornis* (189). (190–192) eighth sternite of female: *verralli* (190); *sudeticus* (191); *bovinus* (192).

– Smaller species, in the range of 13–16 mm., with abdominal spots less sharply defined, more brownish and rounded (*bromius*-group) 6

6 Alula of wing narrow, distinctly smaller than axillary lobe (fig. 189). Postocular rim of head noticeably broader than usual. A small patch of black hairs beside base of each antenna. Eyes in life with a single band.
maculicornis Zetterstedt

Widespread in England (? except Cornwall), and in Scotland as far north as Perthshire. Less common in south than bromius, *with which it often flies, but sometimes locally abundant. vi–vii.*

– Alula of wing broader (fig. 188), not much narrower than axillary lobe. Postocular rim of head narrow, sometimes almost non-existent. No black hairs alongside base of each antenna. Eyes in life with either one band or none 7

7 Eyes in life unbanded. Abdomen considerably reddish at sides towards base. Frons narrower (fig. 179), and callus more flask-shaped, not touching eyes. Eighth sternite more flattened (fig. 182)
miki Brauer (*glaucus* Verrall, nec Meigen)

Probably widespread in southern England, and possibly midlands, but easily mistaken for bromius. *Records chiefly from the New Forest. vii–viii.*

– Eyes in life normally with one band, though occasionally this may be scarcely visible. Abdomen little reddish basally; some difference in shapes of dark markings can be seen in a series. Frons broader and more divergent towards vertex, with callus more square, and reaching nearer to eyes (fig. 178). Eighth sternite more acute (fig. 181) ..... **bromius** Linnaeus

Common throughout southern England, rare in northern England, unknown in Scotland. Variable in general appearance, from a yellow form resembling glaucopis *to a blackish form difficult to distinguish from* maculicornis. *vi–viii.*

MALES

1 Upper facets of eyes not strikingly larger than lower facets, and not sharply delineated from them. Large fly, 18 mm. or more long, with orange and brown abdomen, and long median pale triangles ..... **bovinus** Linnaeus

– Upper facets of eyes distinctly larger than lower facets, and sharply delineated from them. Size ranging from large to medium 2

2 Upper part of subcallus (tubercle immediately above antennae) bare and shining black ..... **glaucopis** Meigen

– Subcallus entirely dull and tomented, even though it may have brown areas 3

3 Larger flies (16–23 mm.), with conspicuous median triangles, and sides of abdomen extensively reddish 4

– Smaller flies (10–16 mm.), grey, with little lateral reddish colour, and with small, oblique lateral spots more conspicuous than the median triangles 6

4 Venter of abdomen with a black, longitudinal stripe, flanked by reddish side-stripes (fig. 186). Middle-sized species, 14–16 mm. ..... **autumnalis** Linnaeus

– Venter of abdomen with each segment black basally, and in a rounded median extension (fig. 187) 5

5 Black species, with yellow abdominal triangles, but little or no lateral reddish colour. Parafacials with abundant black hairs ..... **sudeticus** Zeller

– Sides of abdomen extensively orange. Parafacials with few or no black hairs
verralli Oldroyd

6 Scutellum with black hairs, especially on margin. A tiny grey species, with widely separated, small, lateral white spots on abdomen ..... **cordiger** Linnaeus

– Scutellum with pale hairs, at least on margin. Lateral spots larger and blurred, and with some reddish colour near base 7

7 Postocular rim narrow; ocellar tubercle bigger than space between eyes
bromius Linnaeus

– Postocular rim broader, ocellar tubercle smaller 8

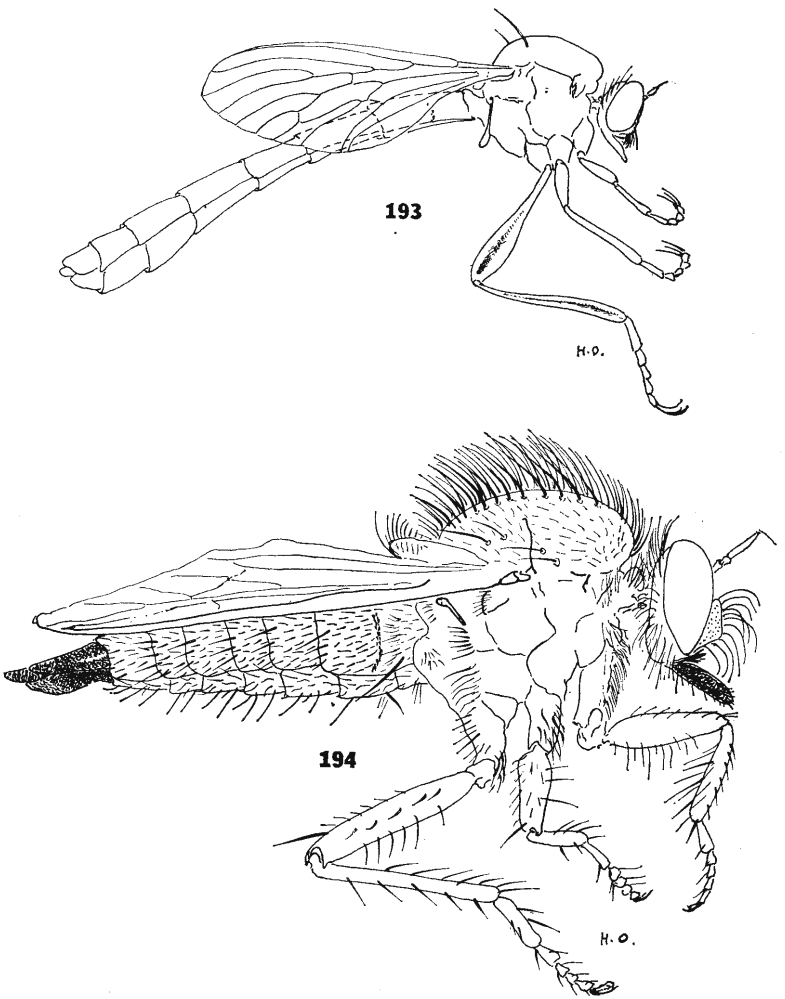
8 Vertex with a fringe of long, yellow hairs. Third antennal segment bright orange, more elongate, and narrower than first segment **maculicornis** Zetterstedt

– Vertex with a fringe of long, black hairs. Third antennal segment mostly black, reddish near base, less elongate, broader than first segment ..... **miki** Brauer

Family ASILIDAE

Asilidae are predatory flies, both sexes of which pursue other insects—usually in the air—seize them, and suck them dry. The morphology of the adult fly is highly adapted to this mode of feeding, and most external structures can be related to it.

The two sexes can be distinguished by the genitalia, which are usually easily visible, though sometimes concealed beneath the tip of the abdomen (figs. 210–17). Apart from the genitalia there is little obvious difference between males and females; occasionally there is a noticeable difference in



FIGS. 193, 194.—Asilidae. Comparison of body-shape and degree of bristliness: *Leptogaster cylindrica* (193); *Dysmachus trigonus* (194).

colour, and rarely the male develops marked secondary sexual characters (e.g. *Leptarthrus brevirostris* fig. 203).

Asilidae are most readily distinguished from other families by the way in which the vertex of the head is hollowed between the eyes, which appear to protrude dorsally (figs. 195–7). A few exotic genera, in which the vertex is not noticeably hollowed, can be recognized as Asilidae by the profile of the face, which is not hollowed as in most related families, but is filled in, if not inflated into a tubercle, and is protected by a bristly moustache, or face-beard, which is sometimes reduced to one or two bristles, but usually forms a prominent recognition feature.

The legs are stronger than is strictly necessary for walking (*cf.* Therevidae and Bombyliidae), and are equipped with strong bristles, which convert the legs into an efficient basket for trapping prey. The wings, also well developed for effective flight, have a full complement of veins and cells (fig. 208).

The two families in the British fauna with which the Asilidae might be confused are Therevidae and Empididae. Therevidae have no excavation at the vertex; have the face hollowed below the antennae, forming a cavity into which proboscis and palpi can be recessed; and have a more dusty, less bristly appearance. Empididae are predatory flies which resemble Asilidae to some extent, but which are more fragile in appearance, with the legs and body less powerfully bristly. The wing-venation of Empididae is reduced, particularly towards the anal area, and the eyes are often close together in males, sometimes in females too.

Morphology

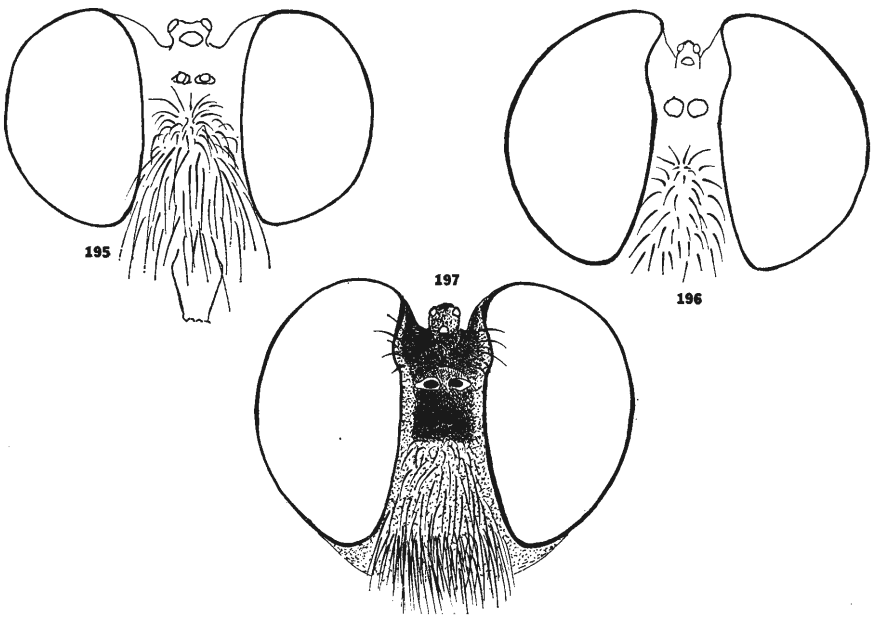
Bristles.—Although bristles are so well developed in Asilidae, chaetotaxy has not yet been applied to their taxonomy on the scale to which it has attained in the muscoid flies. The principal setae to be noticed are as follows: those of the moustache; the postoccipital row, extending more than halfway down the eye on each side; the transverse row on the pronotum; the dorsocentrals; the scutellars, marginal and discal; bristles occasionally present on the mesopleuron; and what are called the "discal" bristles of the abdomen, really the extreme ends of a row running transversely just before the posterior margin of each segment (fig. 206). Individual leg-bristles or spurs are sometimes significant, but a general chaetotaxy of the legs does not yet exist.

Head.—Eyes prominent, sometimes hemispherical, but usually more or less flattened antero-posteriorly, so that a large, relatively flat area faces forwards; often this forward-facing area has noticeably bigger facets than the rest. The eyes are usually bare and unicolorous, though in life the whole eye often has a blue or purple colour. In front view the inter-ocular space (vertex + frons + face) has a shape very characteristic of the genus. Among British genera the eyes are closest together in *Leptogaster*, and furthest apart in *Laphria* especially *flava*. The separation is the same in both sexes, and no Asilidae have holoptic males. *Lasiopogon* (fig. 195) shows the excessive widening of the vertex characteristic of the tribe Stichopogonini.

In profile the face shows a swelling, or *facial tubercle*, which bears the hairs and bristles of the moustache. The profile of the facial tubercle, and the extent, density and composition of the moustache are highly characteristic

of the genus. At the vertex the ocelli are prominent on their ocellar tubercle. The occiput also varies in shape, but is usually obscured by dense hairs enclosing the row of postoccipital bristles already mentioned.

The *antennae* (figs. 198–202) consist of two basal segments and a compound third segment, modified from the flagellum of the Nematocera. There is a large element, which may include more than one flagellar segment, and which is usually referred to as just "the third segment", followed by a variable number of smaller segments which are described as a "style" or an "arista" according to their shape and relative size; Hull (1962) calls them "microsegments". Aristiform microsegments are characteristic of the tribe



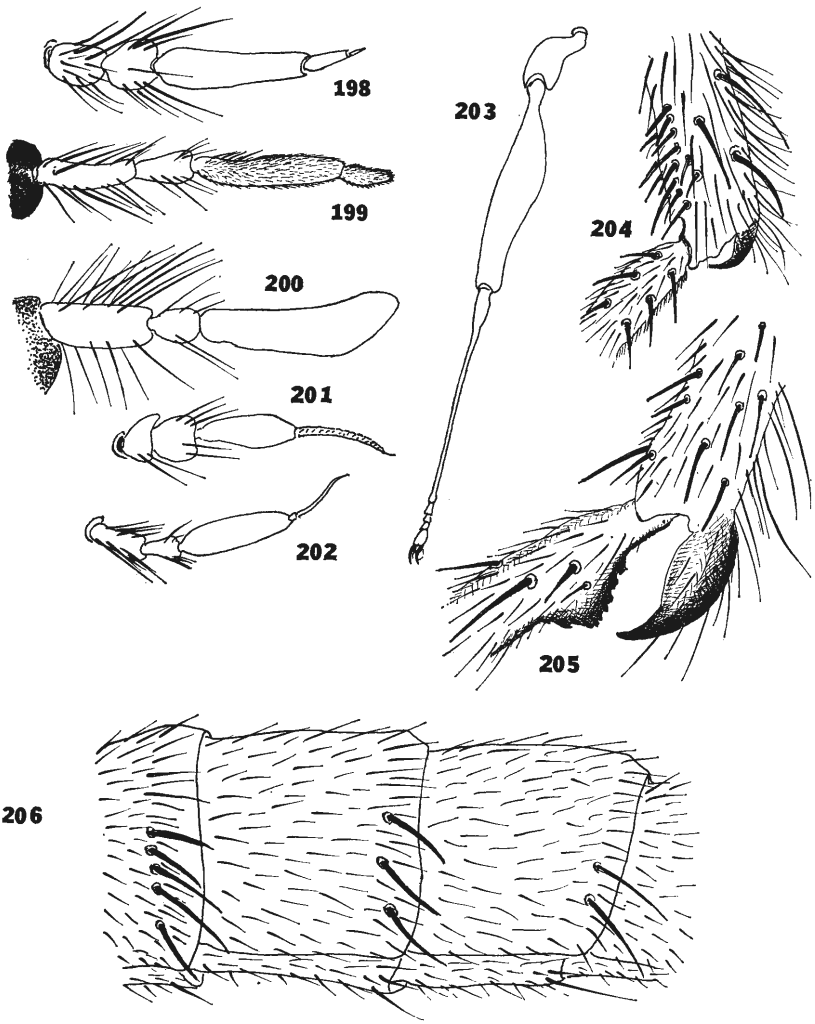
FIGS. 195–197.—Asilidae, heads from in front, to show shape of frons and face. (195) *Lasiopogon cinctus*; (196) *Machimus atricapillus*; (197) *Rhadiurgus variabilis*.

Asilini, and to a lesser extent of Leptogasterini. The other genera found in Britain have the microsegments in the form of a style. The two basal segments generally have long hairs or bristles; the third is generally bare.

The proboscis of Asilidae (fig. 6) is the centre-piece of their predatory way of life, and is modified into a device for piercing the integument of other insects, including such tough ones as beetles, bees and wasps. Mandibles have been lost, so that a tubular piercing fascicle of the type used by Tabanidae (fig. 7) as well as by bloodsucking Nematocera, is not possible in Asilidae. Piercing is carried out by the hypopharynx, which has a hard, sharp tip and a fringed dorsal groove which, together with the elongate maxillae, forms a salivary duct and a food-channel. These stylets are sheathed in a dorsal groove of the labium, with the tip of the hypopharynx often visible in dried specimens.

The proboscis is rigid, and is held horizontally or obliquely forwards, only rarely vertically downwards. In some exotic genera it assumes peculiar shapes, perhaps in association with a special kind of prey. Among British genera the only distinctive proboscis is that of *Laphria*, which is laterally flattened, with a sharp edge dorsally and ventrally, like a paper-knife held on edge.

The *palpi* are more or less porrect, and consist of 1–3 segments. Some



FIGS. 198–206.—Asilidae. (198–202) antennae: *Lasiopogon* (198); *Dioctria* (199); *Laphria* (200); *Leptogaster* (201); *Asilus* (202). (203) hind leg of male of *Leptarthrus brevirostris*. (204, 205) spurs on fore tibiae: *Leptarthrus brevirostris* (204); *Dasypogon diadema* (205). (206) *Philonicus albiceps*, abdominal segments showing "discal" bristles.

keys to tribes start off with the number of palpal segments, but these are often obscured by hairs, and difficult to distinguish in dried specimens. What is meant by "the palpi" in descriptions is usually the terminal segment, which is rather uniform in British genera, and distinguished mainly by the colour of the hairs.

THORAX (figs. 193, 194).—Pronotum well developed, often with a crown of strong bristles. Mesonotum smoothly convex, with well-developed humeri and postalar calli, and a clearly marked transverse suture on each side, just before wing-base. In *Leptarthrus brevirostris* the mesonotum is strongly convex, shining black, and obscured by long, dense, silky yellow hairs with no distinguishable strong bristles. Most Asilidae, however, have the mesonotum entirely covered with dense tomentum, which is greyish towards the sides and posteriorly, and bears a fairly standard pattern of dark colour, in varying degrees of distinctness: a median stripe, broader anteriorly, where it is split longitudinally into two, tapering to a point posteriorly; and on each side of this are three dark areas, one before the transverse suture and two behind this. In *Dioctria* the mesonotum is often partly bare and shining.

The normal complement of strong bristles on the mesonotum is 2–3 notopleurals, a variable number of supra-alars, 1–3 postalars, and a range of dorsocentrals. The dorsocentrals are usually confined to the posterior half of the mesonotum, behind the transverse suture, but sometimes (e.g. in *Dysmachus*) they extend forwards like a "mane". The scutellum is lunate or almost semi-circular, usually inflated, and mostly with a groove running just in front of its posterior margin. Usually fine, erect hairs are present on the disc, and from 2–8 strong marginal bristles; but sometimes the disc is bare, or has short, spiny bristles, and the marginals may be absent.

Pleura (figs. 193, 194) not of significance in classification, though sometimes useful in distinguishing species. Laphriini have a few strong bristles in a vertical line down the posterior margin of the mesopleuron. A few Asilini (notably the Mediterranean genus *Acanthopleura*) have strong bristles along the dorsal margin of the mesopleuron.

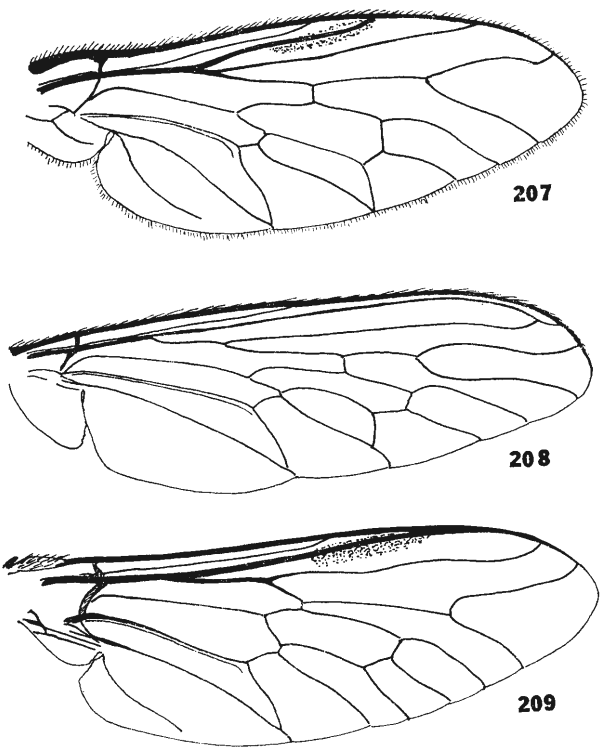
ABDOMEN.—Normally with seven pregenital segments, though in *Neoitamus* and *Leptarthrus* the sixth and seventh segments have become more or less incorporated into the genitalia, or into the ovipositor. The abdomen sometimes bears a recognizable pattern (e.g. *Leptogaster cylindrica*), but the chief detail of taxonomic importance is whether or not the segments have "discal" bristles, already discussed in the first paragraph above (p. 70). It is sometimes difficult to decide whether these are bristles or hairs, but this character has been used in several different complexes of genera, notably in Asilini, to distinguish the genera related to *Asilus* from those related to *Machimus*.

The *shape* of the abdomen contributes greatly to the characteristic appearance of Asilid genera. Most Asilini have the abdomen more or less cylindrical, tapering slightly posteriorly, and the very large number of flies in this tribe have a rather uniform, and sometimes drab appearance. Leptogasterini carry this cylindrical shape to extreme (fig. 193), whereas members of other tribes have very varied abdominal shapes. Laphriini tend to have the abdomen flattened, rounded in outline, and either furry like a bee, or covered with recumbent pile. The tribes of the old subfamily Dasypogoninae generally have a stout abdomen, varying in shape from ovate to

pedunculate like a wasp, and many genera are immediately recognizable by their general appearance.

The GENITALIA of Asilidae are often clearly visible, and they offer useful taxonomic characters in both sexes, at both specific and generic levels. The genitalia are given a separate section later.

LEGS.—There are the usual five components: coxa, trochanter, femur, tibia and five-segmented tarsus, the last ending in a pair of claws, two pulvilli, and a median bristle-like empodium. Pulvilli are always absent in Leptogasterini, and occasionally reduced or absent in other genera, or even in isolated species (though not in any of the British species).



FIGS. 207–209.—Wings typical of three families of Brachycera. (207) *Thereva nobilitata* (Therevidae); (208) *Philonicus albiceps* (Asilidae: Asilini); (209) *Tabanus maculicornis* (Tabanidae).

The coxae call for little comment. Between the fore coxae lies the prosternum, which may be an isolated sclerite in a membranous area, as in *Dioctria*, or strongly "bridged" to the pronotum as in *Lasiopogon*. Trochanters are well developed, especially the hind pair, and are clearly important in the mechanical operation of the legs which Asilidae use so much.

Among the Asilidae of the world there are many variations and elaborations of the structure of femora, tibiae and tarsi, but among the few British

species the most notable variations are the anterior tibial spur of *Leptarthrus* and *Dasypogon*, and the peculiar hind tarsus of *Leptarthrus* (figs. 203–5).

WINGS.—Wing-venation is of major importance in the taxonomy of Asilidae, and there is a very complete set of veins and cells: Sc, R_{1-5}, M_{1-4}, Cu, A; marginal, 2–3 submarginal, five posterior, discal, 2 basal, anal and axillary cells. Loss of even one vein is rare in Asilidae, and does not occur in any British species.

Important venational characters are based upon whether veins run independently to the wing-margin, or whether two veins meet and form a common stem. Undoubtedly the primitive condition is to have all the veins running independently to the wing-margin, and thus all the marginal and posterior cells open, as in *Leptogaster* (fig. 193) and most dasypogonine genera. The tribes Laphriini and Asilini are characterized, among other things, by having R_{2+3} curved forward at the tip to meet R_1 instead of the wing-margin; in consequence the marginal cell is closed, with a short stalk. This apparently trivial venational character is exceptionally stable in Asilidae. All Asilini, and all Laphriini in the strict sense, have the marginal cell closed. There is a group of genera, none of which occur in Britain, which are laphriine in general appearance, but have the marginal cell open, or just closed in a peculiar way; they are grouped round the genus *Laphystia*, and are often placed in a separate tribe Laphystiini.

Closure of the fourth posterior cell by meetings of veins M_3 and M_4 is very common, even in genera with the marginal cell open, and is normal when the marginal cell is closed (fig. 208). The first posterior cell is sometimes closed, though less frequently.

Apart from being convenient taxonomic characters, easy to see, these closures of cells in the wing probably have a marked effect in stiffening the wing-membrane, and must affect its characteristics during flight. Open cells round the wing-margin seem generally to be associated with a broad wing of rather irregular outline, which does not look very efficient. Asilidae in which the marginal, or the fourth posterior, or both are closed tend to have narrower, more streamlined wings, and to be powerful fliers. An extreme example of this is in a whole range of genera of Asilini centred round *Promachus*, in which the fore-margin and tip of the wing are further stiffened by an additional cross-vein from R_{2+3} to the fork of R_{4+5} (making three submarginal cells) and another group of genera related to *Proctacanthus* and the Nearctic *Nerax* in which the tips of R_4 and R_5 bend forward to support the wing-tip. Unfortunately none of these interesting genera occur in Britain.

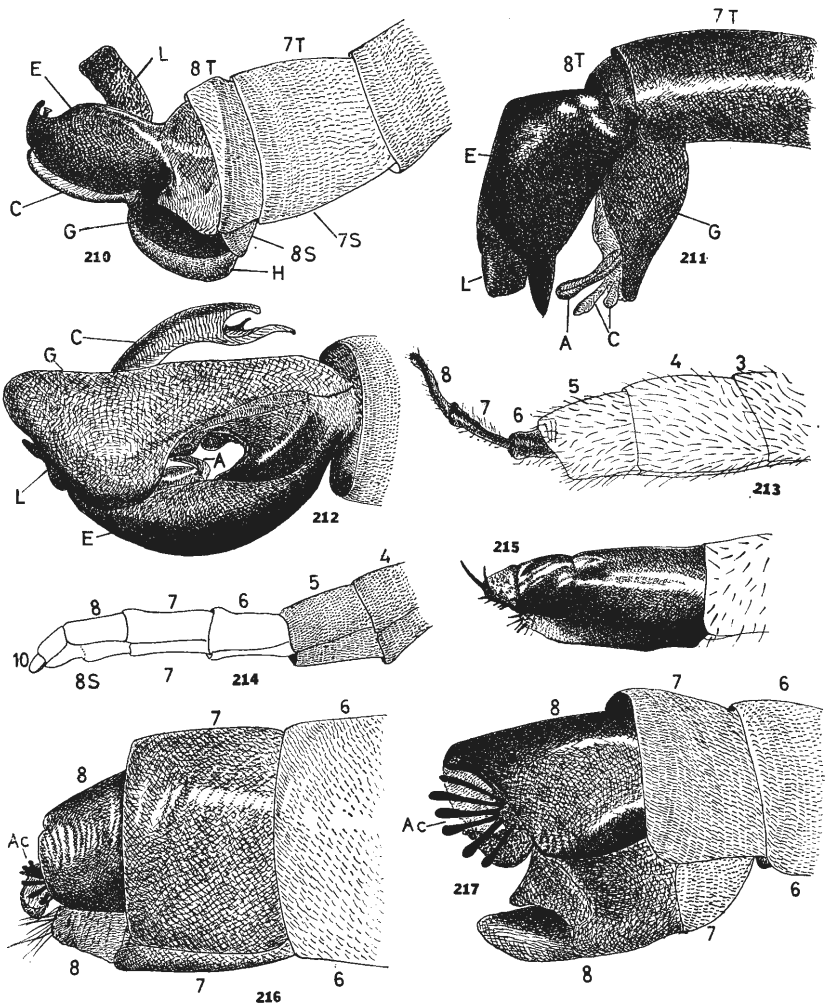
The wings of Asilidae are not generally brightly coloured. The membrane is sometimes stained brown, either along the veins, as in *Dioctria oelandica*, or in the centres of cells, as in *Asilus crabroniformis*. The chief indications of a pattern on the wings, however, come from the distribution of *microtrichiae*, tiny hairs which are present on both upper and lower surfaces, where they point in different directions. Superimposed, the two layers of microtrichiae produce grey patches in the centre of some or all of the cells.

Alar squamae are narrow and fringed, and thoracic squamae wanting (*cf.* Tabanidae and Acroceridae). Halteres are well developed, but unremarkable.

GENITALIA: MALE.—The external male genitalia consist of a trifid aedeagus flanked by a set of clasping organs developed from the tergite and sternite

of the ninth abdominal segment. Fig. 2 shows these structures as they are in *Machimus atricapillus*.

The ninth tergite, called the *epandrium*, is here split into a pair of large lobes, strongly convex externally and hollow inside, and known as the *upper*



FIGS. 210–217.—Genitalia of Asilidae. (210–212) males: *Leptogaster cylindrica* (210), *Dioctria oelandica* (211), and *Laphria flava* (212). (213–217) female: *Leptarthrus brevirostris* (213), *Neoitamus cyanurus* (214), *Philonicus albiceps* (215), *Dasypogon diadema* (216), and *Lasiopogon cinctus* (217). L = dorsal lamellae; E = epandrium (ninth tergite, sometimes divided into upper forceps); C = claspers; G = gonopod; H = hypandrium (ninth sternite); A = aedeagus; AC = acanthophorites with a crown of spines. Numbers indicate number of segment. T = tergite, S = sternite. Note that the male genitalia of *Laphria flava* show *inversion* (torsion), which makes the epandrium appear to be ventral. The spines of *Philonicus albiceps* are not acanthophorites.

forceps. The ninth sternite, or *hypandrium* is present as a complete arch of chitin. Arising from the inside of this is a smaller pair of convex lobes, the *lower forceps*, which Hull (1962 : 13) prefers to call the *gonopod*. Both upper and lower forceps are sclerites of "external" type, that is they are usually dark and either bare and shining or covered with dusting or hairs. Hinged to the inner surface of each of the lower forceps is a broad, blade-like appendage, the *clasper*, which lies alongside the aedeagus as a sheath.

Between the upper forceps, and usually protruding above them, is the *proctiger* of the tenth segment, generally divided into a pair of *anal lamellae*. The prolongation of the *eighth sternite* that is so conspicuous in fig. 2 is a peculiarity of some (not all) species of *Machimus*, and the forked tip is specific to *M. atricapillus*. The seventh and eighth segments are normally part of the preabdomen, and are dusted and patterned like the first six, but in male *Neoitamus* they are bare and shining and form part of the genitalia.

Most male Asilidae have these same lobes of the ninth segments more or less prominently displayed, though the relative size and shape—particularly the length, breadth and convexity of the upper forceps—show a wide range of diversity (figs. 210–12). The ninth tergite may remain undivided as a single epandrium, and in the tribe Laphriini the genitalia are inverted so that the undivided epandrium forms a boat-shaped sclerite that is apparently ventral in position. The lower forceps and claspers then appear to be dorsal (fig. 212). The twist occurs between the seventh tergite, which is upright, and the ninth, which is inverted, and the reduced eighth tergite and sternite can be traced in the connecting membrane.

Torsion of this kind occurs in all tribes of Asilidae except Leptogasterini and Asilini, and is associated with the relative positions of male and female during pairing. The torsion is not always permanent as it is in Laphriini. In many dasypogonine genera the male genitalia of dried specimens are twisted to varying angles, depending on their state at the time of death. Much has been written about torsion in other Diptera besides Asilidae but, apart from the risk of confusion to the morphologist, it is not of great practical importance.

GENITALIA: FEMALE.—Whereas the male genitalia are appendages of the ninth segment, the female genitalia, with their dual function of copulation and egg-laying, are concentrated between the eighth and ninth sternites (fig. 3).

As Melin (1923 : 218–42) showed, the shape of the ovipositor is closely linked with the method of egg-laying. Those genera which merely drop the eggs to the ground have no ovipositor in any real sense, and the eggs emerge between relatively undeveloped eighth and ninth sternites. At the opposite extreme, genera such as *Dysmachus*, *Eutolmus* and *Neoitamus* go to great trouble to insert the eggs into crevices in foliage, not perhaps so much to conceal them from predators as to ensure that they do not dry up. In *Dysmachus* (fig. 222) the anal lamellae are embedded in the preceding ninth tergite, together with which they form a pointed and laterally compressed probe which is used to push a way for the eggs into the heads of grasses. *Eutolmus* (fig. 223) has carried this further, with the lamellas even more deeply embedded, and with the postero-ventral edge of the eighth sternite formed into a knife-edge which can cut into the tissue of a leaf-sheath.

In contrast *Machimus*, which deposits its eggs more superficially, has the anal lamellae free (fig. 221), and the eighth sternite is softer and more flexible

at its tip. *Neoitamus* forms an even more complete contrast, having incorporated the sixth and seventh segments into the ovipositor, which has the form of an elongate, telescopic tube flattened from side to side. Melin (1923 : 238–9) discovered that this was used to probe deeply into the terminal buds of trees.

Philonicus albiceps (fig. 215) shows a very different modification. Here the eggs are laid in sand, which is afterwards brushed over to cover them. The anal lamellae and the tip of the eighth sternite are hardened and toughened, with short spines, and two long, upturned bristles form an effective brush which is used with a sweeping motion.

In its choice of oviposition site *Philonicus* is not unique. Other genera of Asilini such as *Proctacanthus*, *Apoclea*, *Alcimus* have hard and spiny ovipositors of a similar structure and use them in sand or loose soil. Among the other tribes those genera which oviposit in sand or loose soil often make use of *acanthophorites*, spine-bearing plates which lie anterior to the anal lamellae, and which may be part of the ninth tergite. Acanthophorites are not confined to the family Asilidae, but also occur in related families, notably Therevidae and Bombyliidae (see figs. 255–8, 324). There is some evidence, therefore, that acanthophorites may have been present in the common ancestor of the Asiloidea, but it appears that they persist only in genera which actively use them. Hence the presence or absence of acanthophorites is an indication of egg-laying habits rather than a simple primitive character.

Two British genera have acanthophorites. In *Lasiopogon* (fig. 217) the eighth sternite is developed into a scoop-like shape which is one of the reasons for placing this genus in the tribe Stichopogonini, in spite of its having somewhat different appearance and habits from the rest of that tribe.

In *Dasypogon diadema* the acanthophorites are present, but the eighth sternite is simpler (fig. 216).

Prey of Asilidae

Observers in various parts of the world have published records of the prey taken by particular species of Asilidae, and these give a clear impression that Asilidae will feed upon any insect that they can seize and kill. Oldroyd (1964 : 124) listed the following as prey of about 50 specimens of the African species *Promachus negligens*: "Five moths, five ants, an ichneumon, four wasps, two bees, five beetles, a dragonfly, an ant-lion, a termite, one large and one small horse fly, and several smaller flies, including a smaller species of Asilidae."

Hobby's (1931) comprehensive list for the British Asilidae supports this view, after taking into account the generally small stature of the British species. It should be realized that not only do very small robber flies find it impossible to overcome very big prey—though they are surprisingly bold in what they attack—but also very big robber flies may be unable to catch and hold very tiny prey.

Different species of Asilidae have marked differences in their hunting habits, perching in different places—on the ground, on stones, on fallen logs, at the tip of branches, on grasses—as well as in the relative length of time that they spend waiting passively, or actively patrolling in the air. They also prefer quite different ecological complexes; e.g. *Leptarthrus*

brevirostris on chalk downland, and *Philonicus albiceps* and *Dysmachus trigonus* among sand dunes. If they find a particular kind of prey ready to hand they may appear to "prefer it", as *Dioctria* seems to show a marked preference for Hymenoptera, and as in some countries "bee-killing robber flies" can be a pest. They are not particular, however, and will take anything they can get.

Classification

The Asilidae that occur in the British Isles consist of 27 species, which fall into 15 genera: *Leptogaster* (2); *Leptarthrus* (*Isopogon*) (1); *Dasypogon* (*Selidopogon*) (1); *Lasiopogon* (1); *Dioctria* (6); *Laphria* (3); *Rhadiurgus* (1); *Pamponerus* (1); *Philonicus* (1); *Asilus* (1); *Neoitamus* (2); *Dysmachus* (1); *Eutolmus* (1); *Machimus* (2); *Epitriptus* (3).

If we take out the six species of *Dioctria*, the remaining 21 species are distributed among 13 genera, showing clearly that the British Asilidae are a random selection. We have nothing that is endemic to the British fauna: even *Epitriptus cowini* Hobby, the only species to be described from British material, is known to occur in Hungary from old specimens in Kowarz' collection. Evidently the British Asilidae are simply one or two species such as *Laphria flava* which are at home in the conditions obtaining in at least part of the British Isles, plus a number of other species that exist here at the extreme end of their range, perhaps even breed here only intermittently. According to Hull (1962), the world total of Asilidae is nearly 5000 species, with almost one-fifth of them in the Palaearctic Region. The British list of 27 species is scarcely more than one-fortieth of the Palaearctic fauna.

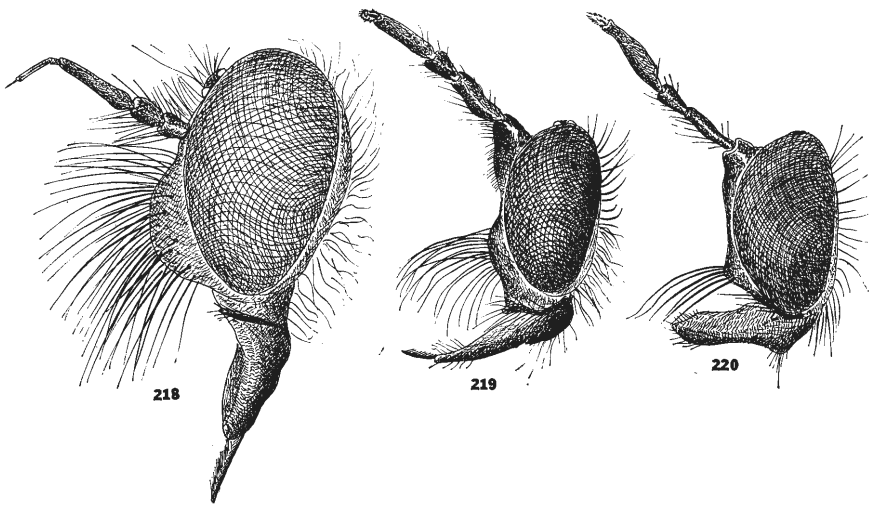
Loew (1848) divided the Asilidae into three subfamilies: Asilinae with the marginal cell closed and an aristiform antenna; Laphriinae with the marginal cell closed and a blunt antenna; and the rest with the marginal cell open were all Dasypogoninae. Later authors segregated *Leptogaster* and its allies, with open marginal cell, no pulvilli and a characteristically slim body-line (fig. 193) into a fourth subfamily Leptogasterinae. Three of these subfamilies raised few problems, but Dasypogoninae were clearly a "dump" or residual group which included a wide diversity of genera.

About 60 years ago Hermann began a series of papers that were unfortunately brought to an end by his premature death in 1924. He divided the Dasypogoninae into Acanthocneminae (with spur on the fore tibia, as in *Leptarthrus* and *Dasypogon*, figs. 204, 205); Eremocneminae (without this spur); and Prytaninae (transitional to Laphriinae). These names were not valid under the International Code, because they were not based upon the name of an included genus, but they were used by Engel (1929–38) in Lindner's *Die Fliegen der Palaearktischen Region*, and are therefore in active use at the present day.

G. H. Hardy (1934–35), revising the Asilidae of Australia, pioneered the division of Asilidae into tribes, each based upon a well-marked genus. Unfortunately the Australian fauna is not the best choice for this purpose, because it contains a confusing mixture of endemic and introduced elements, archaic and modern. It would be sounder to base a classification, as Hermann did, on circumtropical material, especially in Asilidae which are certainly more diversified in warm countries than they are in cold countries such as Britain. There is some indication that Asilidae, like Tabanidae (Oldroyd,

1957 : 52) and perhaps Brachycera in general may have originated in tropical South America. The valuable studies of Neotropical Asilidae by Carrera, who pursued Hardy's tribal system further, are particularly relevant.

Finally, Hull (1962) published a comprehensive monograph on the tribes and genera of Asilidae throughout the world. This work is based upon a detailed study of the type-species of each genus, followed in each case by a list of recorded species, grouped into zoo-geographical regions. There is a complete atlas of drawings of antennae, two views of the head, male and



FIGS. 218–220.—Heads of Asilidae in side view: (218) *Lasiopogon cinctus*; (219) *Dioctria rufipes*; (220) *D. atricapilla.*

female genitalia. All this greatly facilitates comparison of different genera, but there is no indication of variation within one genus. We have a British example of this in the comparison of the head of *Dioctria cothurnata* with other species of *Dioctria* (figs. 219, 220).

Hull employs an elaborate classification into tribes, which is a useful basis for consideration, but this is not the last word on the subject by any means. An example from the British fauna is the relationships of *Leptarthrus brevirostris*. Hermann's "Acanthocneminae" places this species along with *Dasypogon diadema* because both have a spur on the fore tibia, though the structures of these are quite different, as shown by figs. 204, 205. Hull removes *Leptarthrus* from his tribe Dasypogonini and puts it into a new tribe Dioctrini. Even in our limited fauna the disparity between *Dioctria* and *Leptarthrus* is obvious.

This *Handbook* is not a suitable place to enter into a controversy about tribal classification of Asilidae, but it is desirable to indicate to some extent the relationships of the genera that happen to occur in the British Isles. Hardy introduced into the classification of Asilidae the form of the prosternum, whether it was separate from the pronotum or bridged to it. A paper by Clements (1951) examined the status of the prosternum in a wide range of

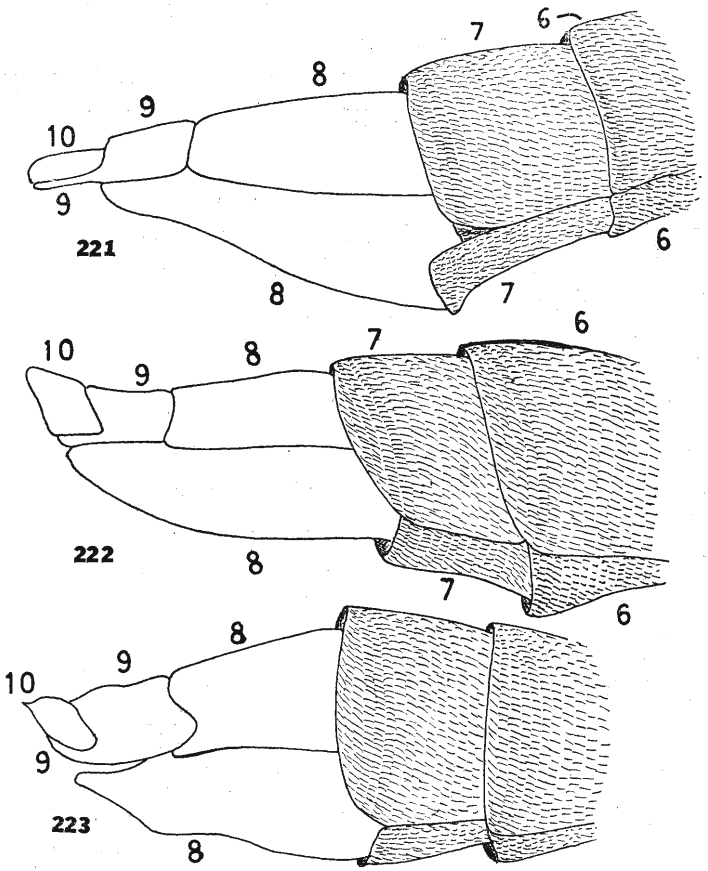
Asilidae, and drew attention to its variability among certain genera, or even between species in some genera. Clements certainly showed that great care is needed in making use of this character, but it is an oversimplification to conclude that therefore it is of no value. I think that it can be used to separate Stichopogonini (prosternum bridged, even if the bridge is slightly emarginated) from Saropogonini (all genera with prosternum completely isolated by membrane from the pronotum). Further subdivision of the last into Dioctrini, Stenopogonini, etc., is full of problems; even the apparently simple character of the fore tibial spur leads to difficulties. I therefore suggest that the genera recorded from Britain might be grouped as follows:

Tribe	Genera
LEPTOGASTERINI	*Leptogaster*
STICHOPOGONINI	*Lasiopogon*
SAROPOGONINI	*Leptarthrus; Dasypogon; Dioctria*
LAPHRIINI	*Laphria*
ASILINI	*Rhadiurgus; Pamponerus; Asilus; Neoitamus; Philonicus; Dysmachus; Eutolmus; Machimus; Epitriptus*

KEY TO BRITISH GENERA

1 Marginal cell open; veins R_1 and R_{2+3} reach the wing-margin independently (figs. 193, 230) 2
– Marginal cell closed; veins R_1 and R_{2+3} meet, and proceed as one stalk to the wing-margin (fig. 208) 6
2 Pulvilli absent. Elongate, slender flies (fig. 193) ..... **Leptogaster** Meigen (p. 83)
– Pulvilli present. Body not of this shape 3
3 Fore tibia with a curved spine at its tip (figs. 204, 205) 4
– Fore tibia without any curved spine 5
4 Fourth posterior cell open (*cf.* fig. 230). Female with telescopic ovipositor (fig. 213) ..... **Leptarthrus** Stephens (p. 83)
– Fourth posterior cell closed (*cf.* fig. 208). Female with concealed ovipositor which bears a circlet of spines (fig. 216) ..... **Dasypogon** Meigen (p. 83)
5 Hairy flies, with strong facial tubercle, short antennae, and characteristic ovipositor (figs. 217, 218) ..... **Lasiopogon** Loew (p. 84)
– Bare flies, with small facial tubercle, long antennae, and simple ovipositor (figs. 219, 220) ..... **Dioctria** Meigen (p. 85)
6 Third antennal segment blunt at tip. Mesopleuron with bristles on its posterior margin. Male genitalia inverted and boat-shaped (figs. 200, 212) **Laphria** Meigen (p. 86)
– Third antennal segment drawn out into an arista. Mesopleuron without bristles. Male genitalia not boat-shaped, but with paired forceps (figs. 2, 202) 7
7 Postoccipital bristles sharply bent forwards (proclinate) (figs. 231, 234) 8
– Postoccipital bristles not proclinate 9
8 Male with a characteristic milk-white colour to basal half of wings. Female with a short, conical ovipositor ..... **Pamponerus** Loew (p. 87)
– Male without any milky-white area of wing. Female with telescopic ovipositor (fig. 214) ..... **Neoitamus** Osten-Sacken (p. 89)
9 No discal bristles before the posterior margins of the abdominal segments (except the first) (fig. 206) 10
– Abdomen with discal bristles on other segments besides first (fig. 206) 11
10 Facial lobe bare and shining. Small, grey species ..... **Rhadiurgus** Loew (p. 87)
— Facial lobe not bare and shining. Large, yellow species ... **Asilus** Linnaeus (p. 89)

11 Tubercle occupying only lower half of face. Male upper forceps strongly convex, especially when seen from above. Ovipositor with a bunch of upturned bristles at tip (fig. 215) ..... **Philonicus** Loew (p. 90)
— Tubercle occupying more than half of face. Male upper forceps closely applied to each other. Ovipositor without upturned terminal bristles 12
12 Dorsum of thorax high, strongly convex (fig. 194) and covered with dense hairs and bristles from front to rear. Abdomen and legs abnormally bristly, with very long, stiff bristles. Ovipositor as in fig. 222, with anal lamella embedded in ninth tergite ..... **Dysmachus** Loew (p. 90)
— Dorsum of thorax lower, less convex, much less bristly anterior to transverse suture than posteriorly. Abdomen and legs with rather sparse, strong bristles 13
13 Ovipositor as in fig. 223. At least three notopleural bristles **Eutolmus** Loew (p. 92)
— Ovipositor with anal lamellae free. Not more than two strong notopleural bristles 14
14 Facial tubercle strongly developed (fig. 235). Males with eighth sternite produced into a backwardly pointing lobe (fig. 2) ..... **Machimus** Loew (p. 92)
— Facial tubercle small (fig. 233). Males with eighth sternite not produced **Epitriptus** Loew (p. 91)



FIGS. 221–223.—Ovipositors of female Asilini. (221) *Machimus atricapillus*; (222) *Dysmachus trigonus*; (223) *Eutolmus rufibarbis*.

Genus **Leptogaster** Meigen, 1803

Slender, elongate little flies, with cylindrical abdomen (fig. 193). In the British fauna they can be confused only with some species of *Dioctria* from which they are easily distinguished by the aristiform third antennal segment (figs. 199, 201). *Leptogaster* is the only British genus in which the tarsi are entirely without pulvilli.

The two British species of *Leptogaster* feed mostly in grass, where they cling to the stem by encircling it with the hind tarsus.

Leptogaster and one or two related tropical genera form a very distinctive subfamily *Leptogasterinae*. Some authors have suggested that they should be segregated into a distinct family, with the implication that their structure and habits resemble those of other Asilidae by convergence. There seems little justification, either morphologically or biologically, for this view, which is discussed by Oldroyd (1969).

Key to Species

1 Hind femur yellow, with a longitudinal black stripe. Abdomen with a distinct longitudinal dark stripe. Fourth posterior cell usually stalked at base (fig. 193) **cylindrica** Degeer
Southern and Central England, to mid-Lancs and Yorks. vi–viii.

– Hind femur reddish, with a longitudinal stripe basally, but with a dark ring on the swollen apical half. Abdomen with indistinct segmental dark bands. Fourth posterior cell not usually stalked at base..... **guttiventris** Zetterstedt
England and Scotland. Local. Wider range than cylindrica, *but less frequent. vi, vii.*

Genus **Leptarthrus** Stephens, 1829

(*Isopogon* Loew, 1847)

A single species, medium-sized, rather hump-backed, shining black in ground colour, densely hairy, but without strong bristles except on legs. The peculiar shape of the hind tibia and tarsus of the male, and of the female ovipositor (figs. 203, 213) are easily recognized.

The head-structure suggests relationship with the widespread Holarctic genus *Cyrtopogon* Loew, which however has no spur on the fore tibia. The habits of the two genera are similar, the flies being mostly found in the alpine meadow type of habitat, with grassy slopes and low bushes.

One British Species

Head with long, silky hairs and no strong bristles; facial tubercle smoothly rounded, reaching almost up to bases of antennae. Third antennal segment elongate, with style consisting of a short segment, a longer one, and an apical bristle. Male genitalia concealed. Male hind leg with tibia distorted, basitarsus elongate and compressed into a knife-blade, other tarsomeres very small. Female with legs normal. Ovipositor telescopic, much narrower than preabdomen.... **brevirostris** (Meigen, 1804)
England, Wales, Scotland. Very local in lowland areas, commoner in Highland Britain: "possibly restricted to chalk downland in the south" (Stubbs, 1968 : 22). *Ovipositing in cocksfoot, Banstead, Surrey (Stubbs, personal communication). v–viii.*

Genus **Dasypogon** Meigen, 1803

(*Selidopogon* Bezzi, 1902)

A robust black and red fly, with dusky wings, well known in S. Europe and the Mediterranean as *Selidopogon diadema* (Fabricius), and which has been a reputed British species for well over a century. The recent change of

generic name from *Selidopogon* to *Dasypogon* is an unfortunate nomenclatorial vagary.

This fine fly is common in scrubby areas, from the Landes district of France eastwards to Asia Minor, while related species occur in North Africa and Asia. At long intervals such a fly has been reported as having been seen on sand dunes along the Bristol Channel and the coast of Wales, and three specimens in the British Museum, from Stephens' collection, are believed to be those upon which he based the entries in his *Illustrations of British Entomology*. The *Supplement* to this work (1846) has very fine coloured plates of selected British flies, and pl. 45, fig. 1 is an accurate and convincing picture of *Dasypogon diadema*. Not only the coloration, but details of venation, and even the long hairs at the tip of the abdomen, make it certain that the artist had a male of this species before him at the time. This is no proof, of course, that it was captured in Britain, but the description on p. 25 states categorically: "Found, but very rarely, in June, near Swansea, in Glamorganshire." Corroborative detail, notably the remark that the second joint of the (black) antennae, and the base of the third are ochreous, and the correct description of the abdominal colour of the female "(of which sex I have not seen a British example)", all combine to make this record a most convincing one. Moreover, no evidence exists to suggest that the British locality for these specimens might be erroneous.

The only reason for hesitating to accept *D. diadema* as British is the fact that it is so conspicuous an insect, which would surely have been taken by collectors if it still occurred here. One possibility is that it was introduced from ships trading between Bordeaux and S. Wales, flourished for a while, and then died out. It is always possible that it may recur on any of these dunes of the Welsh coast, from Morfa Harlech and Newburgh Warren down to the Gower and the Bristol Channel.

Middle-sized (17 mm.), robust, with tapering abdomen not narrowed at base. Colour black or deep red, rather bare of tomentum or short hairs, but with strong bristles. Fore tibial spine much longer and stronger than in *Leptarthrus brevirostris* (figs. 204, 205). Ovipositor with acanthophorites, bearing a crown of spines, but eighth sternite not specially developed as in *Lasiopogon* (figs. 216, 217). Strongly sexually dimorphic: male is more uniformly black, with heavily tinted wings; female has wings only lightly smoky, and has marked tendency to red coloration on legs and abdomen, with segments 6–9 shining black ..... **diadema** Fabricius

Reputed British localities: Barmouth; nr. Swansea; nr. Bristol. Possibly sand-dunes and scrubby areas in Wales and west of England. vi.

Genus **Lasiopogon** Loew, 1847

Small, dark, hairy and bristly flies, with strong facial tubercle and dense moustache (fig. 218), and divergent frons (fig. 195). Male genitalia bulbous and rotated; ovipositor highly characteristic, with acanthophorites surmounting a keel-like eighth sternite (fig. 217).

Lasiopogon is a Holarctic genus of rather isolated taxonomic position. The divergent frons, and particularly the structure of the ovipositor, relate it to the tribe Stichopogonini, into which *Lasiopogon* is usually placed. All other Stichopogonini, however, are bare, dusty flies, which sit about on stones and sand, on beaches or in water-courses, in full sunlight, where the cryptic coloration of their bodies makes them invisible in the glare until they make short capture-flights. *Lasiopogon* diverges widely from the others in

its hairy appearance and its rather different habitat, living on sandy heaths and in open woodland.

ONE BRITISH SPECIES

Head and antenna as in fig. 218. Thorax patterned in ashy grey and brown, with long, erect, fine black hairs; abdomen rather shiny black-brown, each segment dusty grey posteriorly and laterally. Male genitalia prominent, bulbous, rotated. Ovipositor as in fig. 217, with prominent acanthophorites dorsally, and with eighth sternite produced into a pair of plates which form a ventral keel. Legs black-brown, with abundant hairs and bristles ..... **cinctus** (Fabricius)

Wales and Southern England, north to Lancs., and E. Riding of Yorks. Spring, mid-iv to early vii. Locally common.

Genus **Dioctria** Meigen, 1803

Dioctria is the most familiar genus of British Asilidae, with six British species. It is essentially a genus of cool, temperate woodlands and nearby grassland. Even in the Holarctic region there is "a dense concentration of species in eastern and central Europe, and on the Pacific coast of the United States" (Hull, 1962 : 29). Hull also states that the European (and British) species *Dioctria baumhaueri* Meigen has been introduced into the United States though he does not say by what means. It has already been suggested above that *Dasypogon diadema* may have been introduced into Britain by ship, but the spread of an asilid across the Atlantic by human agency is more difficult to credit.

Dioctria is a genus of slender, bare, usually dark flies, somewhat resembling ichneumons. The antennae are elongate (fig. 199) and—somewhat unusually for an asilid—this is achieved as much by elongation of the first and second segments as of the third. The antennae stand on a prominence rather high up on the head, resulting in a small frons and a long face. The facial tubercle, on the other hand, is quite small, and the moustache is rather sparse and bristly. The postoccipital region of the head is very bristly, and there is a cluster of supra-alars on the thorax, but there are no marginal scutellars, and the body generally is rather devoid of strong bristles.

The stance of *Dioctria* gives an impression of powerful legs, and the robust prothorax, strongly anchored to the anterior region of the mesonotum, suggests a particularly firm attachment for the fore legs. Although the appearance of *Dioctria* is characteristic once it has been learned, the genus has no single diagnostic character, except perhaps for the antennae and their tubercle; this structure is rare among Asilidae, except in the N. American and Pacific genus *Dicolonus* Loew.

KEY TO SPECIES

1 Femora mainly or entirely yellow 2
– At least hind femora mainly black 3
2 Wings dark brown. Mesonotum black, with little or no trace of stripes. Beard and postoccipital bristles black. Large, shining species (15 mm.) **oelandica** (Linnaeus)

Not infrequent in old-established woodland in Wales, England from Westmorland southwards, and Scotland (Perthshire). Early v to vii.

– Wings clear. Mesonotum mainly covered with brassy tomentum, leaving two narrow, bare, shining black stripes, and broader lateral and posterior margins. Beard and postoccipital bristles pale. Smaller, more patterned species (10 mm.) **linearis** Meigen

Fairly common in southern counties of England, rarer in Midlands to S. Yorks., Doncaster (Skidmore). v–viii.

3 Antennal tubercle huge, rising well above level of ocelli (fig. 219). Fore and middle femora entirely yellow ..... **rufipes** Degeer
Widespread throughout Britain, locally common: "scrubland or woodland rides on light soils" (Skidmore). iv to mid-vii.
– Antennal tubercle not rising above level of ocelli (fig. 220). Fore and middle femora black, at most indistinctly yellowish ventrally 4
4 Face parallel-sided, densely covered in yellowish tomentum, rising into a prominent antennal tubercle. Frons not strongly divergent 5
– Face more square, with thin and inconspicuous tomentum, and with a bulge *below* the antennae; antennal tubercle vestigial. Frons strongly divergent, bare and shining ..... **cothurnata** Meigen
Rare and local in southern England; absent from northern England (Skidmore) but abundant in some Scottish localities (Inverness-shire). v–vii.
5 Postoccipital bristles and beard black. Wings of male black in basal half
5. atricapilla Meigen
Widespread, but local in southern and Midland England to Yorkshire; Welsh border and possibly Wales in suitable woodland localities. vi–mid-vii.
– Postoccipital bristles and beard pale. Wings pale in both sexes
baumhaueri Meigen
Southern England as far as S. Lancs. and Yorks. Local. vi–viii.

Genus **Laphria** Meigen, 1803

Laphria is a very large genus of bee-like asilids, widespread throughout the world, although—as with *Asilus* and *Dasypogon*—many species that were formerly placed in it have now been removed to other genera. In the British fauna, at least, *Laphria* may be recognized by the closed marginal cell of the wing, combined with the blunt antennae, in contrast to the aristiform antenna of the Asilini. *Laphria* in the strict sense, together with one or two close allies, has the proboscis flattened from side to side, with an edge dorsally and ventrally.

The larvae of members of the tribe Laphriini live in burrows in wood, sometimes following those of wood-boring beetles, sometimes making their own tunnels. Some genera, notably *Hyperechia* in Africa and *Mallophora* in Central America, closely resemble Carpenter Bees (Xylocopidae), and may even mimic particular species. Other genera such as the N. American *Bombomima* resemble bumble-bees. Most Laphriini have a general resemblance to bees or wasps.

Three species of *Laphria* definitely occur in Britain, and others cannot be entirely ruled out. *Laphria flava* (L.) is one of the hairy, bee-like species, and is associated with pine-forests in Scotland. The other two species, *L. marginata* (L.) and *L. gilva* (L.) belong to a large group of species in which the hairs of the abdomen are not erect and furry, but recumbent, forming a pile, and thus giving the fly a much more slender, bare appearance. This division into two groups is general throughout the *Laphria* of the world, and the second group is often segregated as either a subgenus or a distinct genus *Choerades* Walker (*Epholkiolaphria* Hermann). It is difficult to separate these two by characters that are valid on a world basis, but in Britain the distinction is clear: *L. flava* belongs to *Laphria* s. str.; *L. marginata* and *L. gilva* to *Choerades* (*Epholkiolaphria*).

Key to Species

1 A robust, furry, bee-like species (20 mm.), with golden pubescence on dorsum of abdomen and posterior half of thorax, black elsewhere ..... **flava** (Linnaeus)
Scottish Highlands north from Perthshire, breeding in pine-logs and stumps, and occasionally other woods. Locally frequent. vi–ix.

– Smaller (10–16 mm.), more elongate, and much less furry owing to recumbent abdominal pubescence. Golden hairs of thorax very short and inconspicuous . . 2

2 Dense, recumbent, golden pile on abdominal tergites 2–6; rest of fly with only black and white hairs (14–16 mm.) . . . . . **gilva** (Linnaeus)

Reputed British species before 1938*; then frequent locally for a few years. Berkshire: Windsor Forest and adjacent old woodlands; Silchester* (*Blair*, 1952 : 50). *Sussex: near Midhurst* (*Boyce*)*; Surrey: Oxshott and Ash Vale* (*Parmenter*). *vii.*

– Recumbent yellow hairs conspicuous on abdominal segments 1–5, and short, erect, yellow hairs scattered over mesonotum, legs and beard. Moustache of black hairs, surmounted by silky yellowish-white hairs which extend up to bases of antennae (10–12 mm.) . . . . . **marginata** (Linnaeus)

Southern and central England. Cheshire: Delamere Forest; Notts.: old oak woods. Local. vi–viii.

Genus **Rhadiurgus** Loew, 1849

The single species of this genus is easy to recognize by having the centre of face and frons, above and below the antennae, bare and shining black (fig. 197), and by the form of the genitalia in both sexes. The cylindrical ovipositor is unique among British Asilidae; and male genitalia, with their widely spaced upper forceps, can only be confused with *Philonicus albiceps*, and that species is larger, more sandy coloured, and has conspicuous bristles before the hind margin of each abdominal segment.

The relationships of *Rhadiurgus* to other genera are more difficult to determine. The absence of abdominal bristles, though apparently trivial, is in practice a valid distinction between certain genera of Asilidae, and is a feature which *Rhadiurgus* has in common with *Pamponerus* and *Asilus*, both genera of totally different appearance. *Rhadiurgus variabilis* most nearly resembles *Epitriptus cingulatus*, but is clearly separated by the characters given above.

Rhadiurgus contains only the one species, *R. variabilis* Zetterstedt. Three or four exotic species have been assigned to it, and have subsequently been removed. The N. American species *Asilus leucopogon* Williston and *Asilus cacopilogus* Hine were at one time regarded as belonging to *Rhadiurgus*, but are now in *Proctacanthella* Bromley, 1934.

Melin (1923 : 234–5) describes how the eggs of *R. variabilis* are attached singly to stems, and he associates this with the structure of the ovipositor.

One British Species

A small, slightly-built fly 10–12 mm. long, ashy grey and black, without any prominent pattern. Facial knob well developed, but occupying only lower half of face; upper half of face concave, and bare, shining black, with grey lateral margins; bare patch continued above antennae up to ocellar tubercle (fig. 197). Abdomen without any strong bristles, even along hind margins of tergites. . . . . **variabilis** (Zetterstedt)

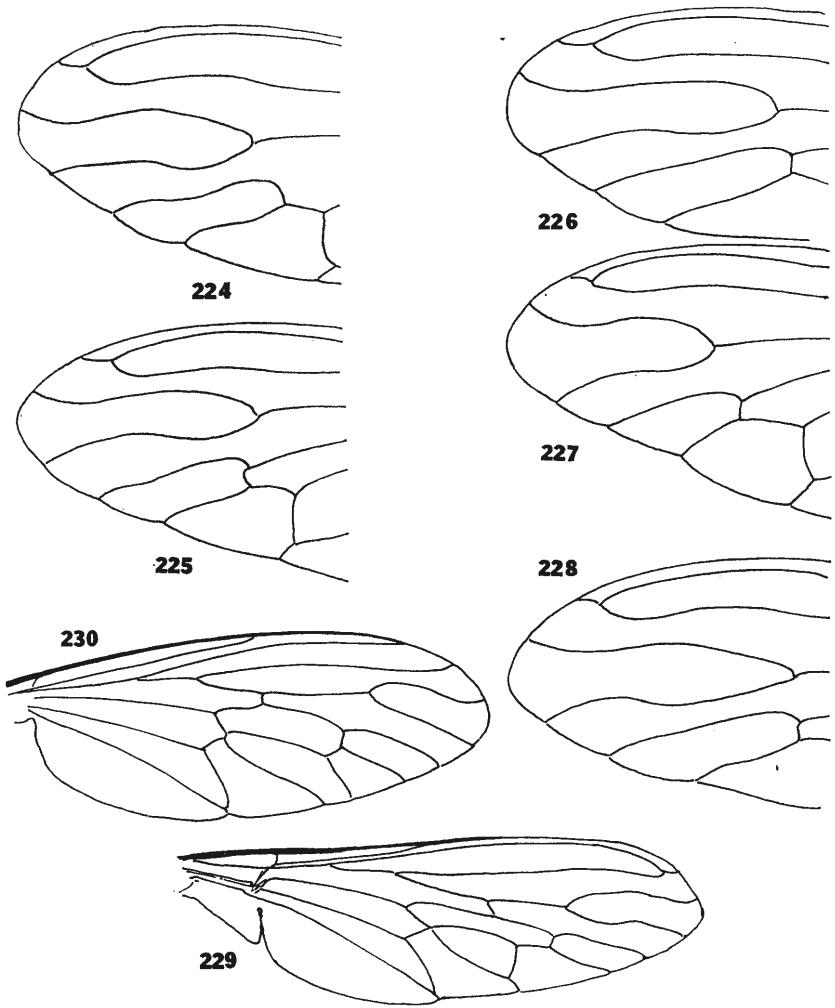
Scottish Highlands in pine forests. A northern species, also known from northern and central Europe and Siberia. Locally common. vi–viii.

Genus **Pamponerus** Loew, 1849

Pamponerus is a rather shiny, dark, compact asiline robber-fly, the male of which has the base of the wing conspicuously milky white, especially on the axillary lobe. In the Palaearctic Region only one species is recognized, *P. germanicus* (L.), with possibly one or two subspecies.

One or two species in other parts of the world have been placed in

Pamponerus because their males have a white-wing-base, but closer study usually shows that the resemblance is superficial. Thus a small group of species from Indonesia, including the *Philonicus areolaris* Bigot from Celebes mentioned by Verrall (1909 : 653) (which was really *Asilus areolaris*, Walker, 1860) were referred to *Amphiscolops* Hull (1962 : 552). *Asilus armatipes* Macquart from North China, also mentioned by Verrall in this context, is type species of *Hoplopheromerus* Becker, 1925.



FIGS. 224–230.—Wings of Asilidae. (224–228) wing-tips, to show differences in shape of radial fork. (224) *Machimus atricapillus*; (225) *Epitriptus cingulatus*; (226) *Philonicus albiceps*; (227) *Dysmachus trigonus*; (228) *Eutolmus rufibarbis*. (229, 230) comparison of general venation of *Machimus atricapillus* (229) and *Lasiopogon cinctus* (230).

ONE BRITISH SPECIES

Moderately large (20 mm.), compactly built, dark-coloured. Head with very large facial tubercle (fig. 231): third antennal segment elongate and tapering, ending in a two-segmented style rather than an arista. Thorax dull brown, with brassy yellow-brown margins and pleura. Abdomen dorsally shining black-brown, with yellow-grey tomentum and yellow bristly hairs at sides (note that *Pamponerus* is supposed to have no discal abdominal bristles). Femora black, tibiae and tarsi yellow, black-tipped. Wings with radial fork (R_{4+5}) displaced backwards, so that R_4 almost reaches wing-tip. In males wing-base is milky-white from base to beginning of discal cell; in females this area is clear, but not conspicuously white

germanicus (Linnaeus)

Western coastline: Devon, Wales, Lancs., Isle of Man. Scotland (Ayrshire, East Lothian, Forfarshire, Elginshire). Locally numerous. mid-v–vi.

Genus **Asilus** Linnaeus, 1758.

The old authors described many species of "Asilus", which have subsequently been removed to other genera as the generic concept has progressively narrowed. Bromley and some other modern authors have tried to revive "Asilus sensu lat." to avoid the difficulty of defining some of these genera, especially *Machimus*, *Tolmerus*, *Epitriptus* and so on.

Species of *Asilus* in the strictest sense are very few: only two in the western Palaearctic and one in N. America, with perhaps a few, little-known species in Asia. *Asilus barbarus* L. occurs in "Barbary", i.e. N. Africa, and the extreme south of Europe; *Asilus crabroniformis* L. is widespread throughout Europe, including Britain.

Asilus crabroniformis appears in later summer on cow pastures and commons in the south of the country. Eggs are laid in cowdung. Adult flies are conspicuous in collections, but not so easily seen when they rest on bare ground, and they are alert, and difficult to approach. Hence they give an appearance of being scarcer than they really are.

ONE BRITISH SPECIES

A large (20–25 mm.), brightly coloured black and yellow fly, with yellow wings smoky at the tip and along the hind border. First three abdominal segments black, rest bright yellow. Legs yellow, femora more or less dusky. As the name suggests, hornet-like (fig. 335) ..... **crabroniformis** Linnaeus

Southern England and Wales, northwards to Cheshire. Locally numerous, perhaps fluctuating over the years, both naturally and as a result of changes in land-usage. Late vii–early x.

Genus **Neoitamus** Osten-Sacken, 1878

(*Itamus* Loew, 1849)

A distinctive and wide-spread genus, of few species. The female has a telescopic ovipositor composed of the 6–10th segments, which are smaller in diameter than the preceding five segments, and are bare, shining black (fig. 214). The male also has one or two bare segments before the genitalia, and in both sexes the postoccipital bristles are proclinate, that is they bend forwards in a right-angle at their middle (fig. 234).

The only near relative of *Neoitamus* is the tropical genus *Astochia* Becker, 1913, which has a similar ovipositor, but the postoccipital bristles are no more than slightly curved forwards. *Astochia* has the basitarsi conspicuously swollen and bristly.

Melin (1923 : 238) showed that the telescopic ovipositor is used to insert eggs into the terminal buds of trees and bushes.

KEY TO SPECIES

1 Basitarsi black. Two pregenital segments of male steel-blue. Male genitalia with upper forceps more elongate than in *N. cothurnatus*.....**cyanurus** (Loew)
In oakwoods from Moray Firth southwards to Channel coast. vi–viii. Locally numerous.

– Basitarsi reddish-yellow, black at tip. Two pregenital segments of male shining black, but not steel-blue. Male genitalia with upper forceps bulbous
cothurnatus (Meigen)
Rare, known from only a few localities at the turn of the century. Berks: Tubney Wood; Oxon: Stow Wood. vi.

Genus **Philonicus** Loew, 1849

Females of the genus Philonicus are easily recognized by the two or more strong spines which curve upwards at the tip of the abdomen, from the anal lamellae, and which are actively used as a broom to sweep sand or dust over the eggs laid in the ground. Not all species have quite the same arrangement of spines as those of the typical species, *Philonicus albiceps* Loew, the only species to occur in Britain (fig. 215).

Males are more difficult to define generically. They belong to the group of asiline genera with discal bristles in front of the hind margin of the abdominal segments, and are distinguished from all the British representatives of the group *Dysmachus–Eutolmus–Machimus–Epitriptus–Neoitamus* by the small facial tubercle. *P. albiceps* is distinctive in having the upper forceps of the male strongly convex when seen from above.

In Britain *P. albiceps* is best known as a species of coastal sand-dunes, and occurs abundantly all round the coasts of Great Britain and Ireland. It is occasionally taken in sandy areas inland.

ONE BRITISH SPECIES

Rather variable in size from 14 mm. (small male) to 22 mm. (large female). Colour light yellowish grey, of dusty appearance, cryptically coloured when resting on sand. Head with a much smaller facial tubercle than *Machimus* group. Thorax with fine black hairs, but with strong bristles not extending anterior to transverse suture, except for a pair of notopleurals on each side. Abdomen densely covered with yellowish-grey tomentum, and each segment with yellow bristles on each side. Ovipositor fig. 215 .....**albiceps** (Meigen)
Coastal sand dunes, and more rarely sandy areas inland. British Isles from Forth southwards. Common. Late vi–early x.

Genus **Dysmachus** Loew, 1860

Dysmachus is a somewhat stumpy asiline robber-fly, recognized by its abundance of hairs and bristles. A diagnostic feature is the ovipositor (fig. 222)with the anal lamellae embedded in the ninth tergite (*cf. Eutolmus*). Melin (1923 : 235) showed how this structure enabled *Dysmachus* to insert its eggs into spikelets of grasses.

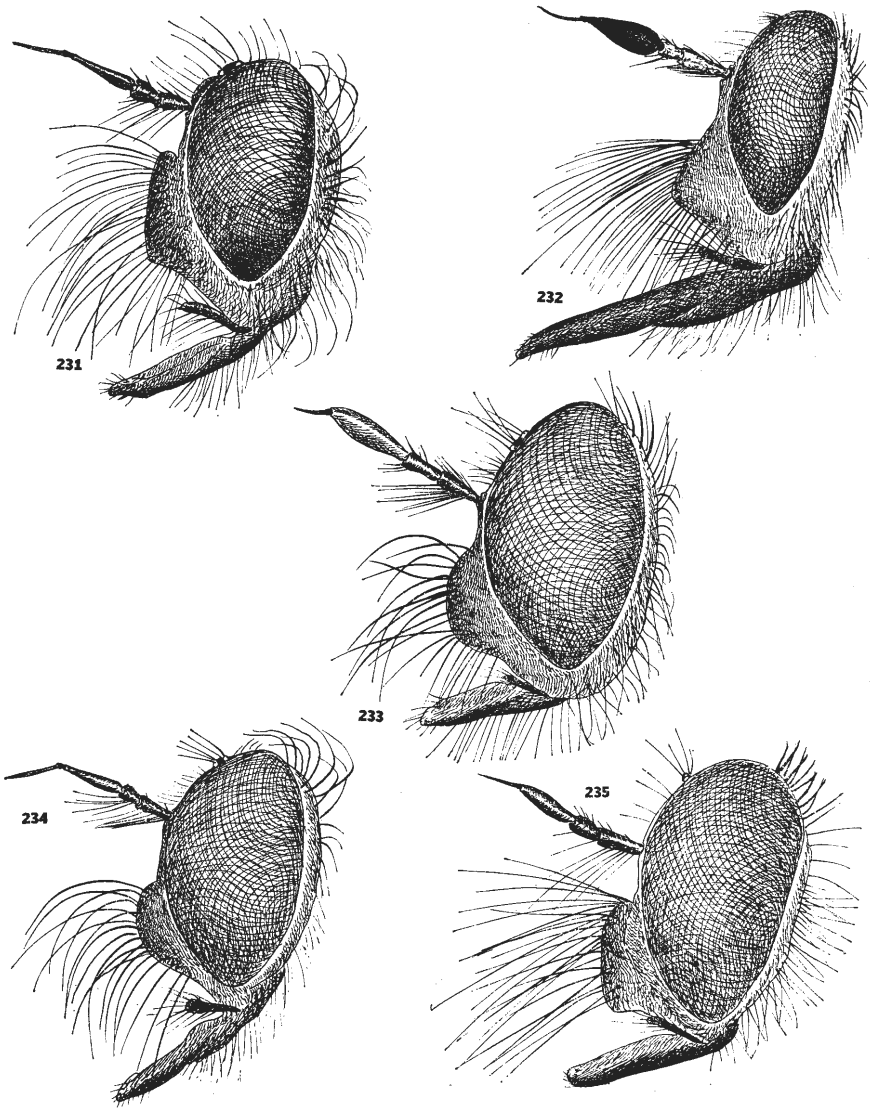
Dysmachus is essentially a Palaearctic genus. Tropical species with a "mane" of hairs and bristles on the mesonotum have been referred to *Dysmachus*, but most, if not all, of them belong to the *Neolophonotus*-group of genera, which are sharply distinguished from *Dysmachus* by having no hairs on the "metanotal lobes" underneath the scutellum.

ONE BRITISH SPECIES

Female genitalia as in fig. 222. A stumpy species covered with dense, yellowish-grey tomentum, with a rather indistinct, dull brown pattern on thorax, and dark triangles

on abdominal tergites, their bases anteriorly. Legs mainly black, but tibiae have a red ring at extreme base, extended on to dorsal surface of hind tibiae. Legs with numerous strong bristles, mostly white except for a single or double row of black bristles on fore tibiae. Wing venation differs from the related genera in the bell-shaped fork of R_{4+5} and the shorter, more divergent second posterior cell (figs. 224–28)

trigonus (Meigen)



FIGS. 231–235.—Heads of Asilidae in side view. (231) *Pamponerus germanicus*; (232) *Asilus crabroniformis*; (233) *Epitriptus cingulatus*; (234) *Neoitamus cyanurus*; (235) *Machimus atricapillus*.

All over Great Britain in sandy localities, both inland and on the coast.
(*Where it occurs with* Philonicus albiceps: "*As the dune becomes fixed, and the moss and flower carpet begin to cover the sand,* Dysmachus trigonus *appears*"—*Parmenter,* 1952 : 230.) *v–viii. Common.*

Genus **Eutolmus** Loew, 1849

The ovipositor of *Eutolmus* resembles that of *Dysmachus* (figs. 222, 223), but this would seem to be a convergent development associated with similar egg-laying habits; in other respects *Eutolmus* is much more nearly related to *Machimus*, and the male has a prolongation of the eighth sternite as have many species of *Machimus*. Both male and female *Eutolmus rufibarbis* are best distinguished from *Machimus* and *Epitriptus* by the form of the genitalia (figs. 2, 221–23).

One British Species

Moderately large (16–17 mm.), yellowish-grey, with strong bristles posteriorly on thorax, and a minimum of three strong notopleurals; bristles may be either black or yellow. Head, pleura, legs and abdomen rather densely covered with long yellow hairs
rufibarbis (Meigen)

Rare and local, known only from eastern England, from the New Forest to Suffolk and Lincolnshire. Late vi–end viii.

Genus **Machimus** Loew, 1849

The "*Machimus*-group" is a complex of species that are perhaps more characteristic of the asiline robber-flies than is the genus *Asilus* in the strict sense. They are slender, ashy-grey flies, usually with unpatterned wings, though often the tip and hind margin are greyish in the centres of the cells, as a result of microtrichiae. Distinctive characters are a well-developed facial tubercle, with dense moustache, hairs on the metanotal callosities, discal bristles on the abdomen, and a marked kink or step in the course of R_5 (fig. 229). This last is not confined to the *Machimus*-group, but occurs in a few other exotic groups.

In Britain we have two species with a prolongation of the eighth sternite in the male (*Machimus* sensu stricto), and three species without this prolongation (*Epitriptus*).

Key to Species

1 A smaller, more blackish species (11–14 mm.); femora black, with a subapical red ring which is extended into a posterodorsal stripe. Tibiae and tarsi dull reddish-yellow, hind tarsi and tip of tibiae blackish. Abdominal tergites with dense tomentum, which is black, with yellow posterior margin to each segment, but changes with shifting light. Most of tiny clothing hairs black. Male distinct from all other Asilidae by forked process of eighth sternite (fig. 2)
atricapillus (Fallén)

England south of the Lake District. Local in north, (Yorks.: Pocklington, Cheetham) but frequent and common in south. Particularly associated with limestone and chalk country. vi–x.

– A larger, more yellowish species (16–20 mm.); femora all black; tibiae and tarsi black, with only a narrow red ring at base of each tibia. Abdominal tergites with dense yellowish tomentum, which shows scarcely any trace of darker spots in any light, and which is covered with yellow clothing hairs. Male with eighth sternite triangular, hardly formed into a prolongation . . . . . **rusticus** (Meigen)

Extreme south of England, downland and coasts from Gloucestershire to the Isle of Wight. Rare, local. viii.

Genus **Epitriptus** Loew, 1849

Epitriptus is one of the segregates from the confused *Machimus*-group, and it is doubtful whether or not it is a valid genus on a world-basis. It is convenient, however, to recognize *Epitriptus* in the British fauna for three species which do not have the eighth sternite of the male prolonged into a definite process (*cf.* fig. 2).

In Verrall's time only one species, *E. cingulatus* (Fabr.), was definitely known from the British Isles; two others, *E. arthriticus* Zeller and *E. cowini* Hobby, were added by Hobby (1932, 1946).

Key to Species

1 Femora entirely black. Moderately large species (17 mm.), yellowish-grey, with unicoloured abdomen (*cf. Machimus rusticus*) ..... **arthriticus** (Zeller)
Known as British from only one female. Norfolk: Merton, 14.vii.1907 *(Darrant & Walsingham), and one male, Somerset: Berrow sand dunes,* 16.vii.1955 *(Fonseca).*

– Femora partly red 2

2 Femora extensively reddish behind. Smaller species (10–16 mm.), more slightly built. ..... **cingulatus** (Fabricius)
Widely distributed in England, Wales and Scotland, but only numerous in the south. vii–early x.

– Femora black with a subapical red ring. Bigger (15 mm. +), more robust. **cowini** Hobby
Isle of Man. vii–viii.

Family THEREVIDAE

One of the most enigmatic families of Brachycera. Adult Therevidae have the same general appearance as Asilidae, with which they are often confused, though familiarity with Therevidae will show them to be of a more dusty, and bristly appearance, with a more stumpy outline. Therevidae do not have the vertex of the head excavated between the eyes, and although this excavation is not universal in Asilidae, the distinction holds good for the British species. The face of Therevidae is deeply hollowed beneath the antennae, and the proboscis—more fleshy than that of Asilidae (figs. 236–39)—is curved upwards, and recedes into the facial hollow. This is in strong contrast to the facial tubercle and moustache of Asilidae (figs. 231–35).

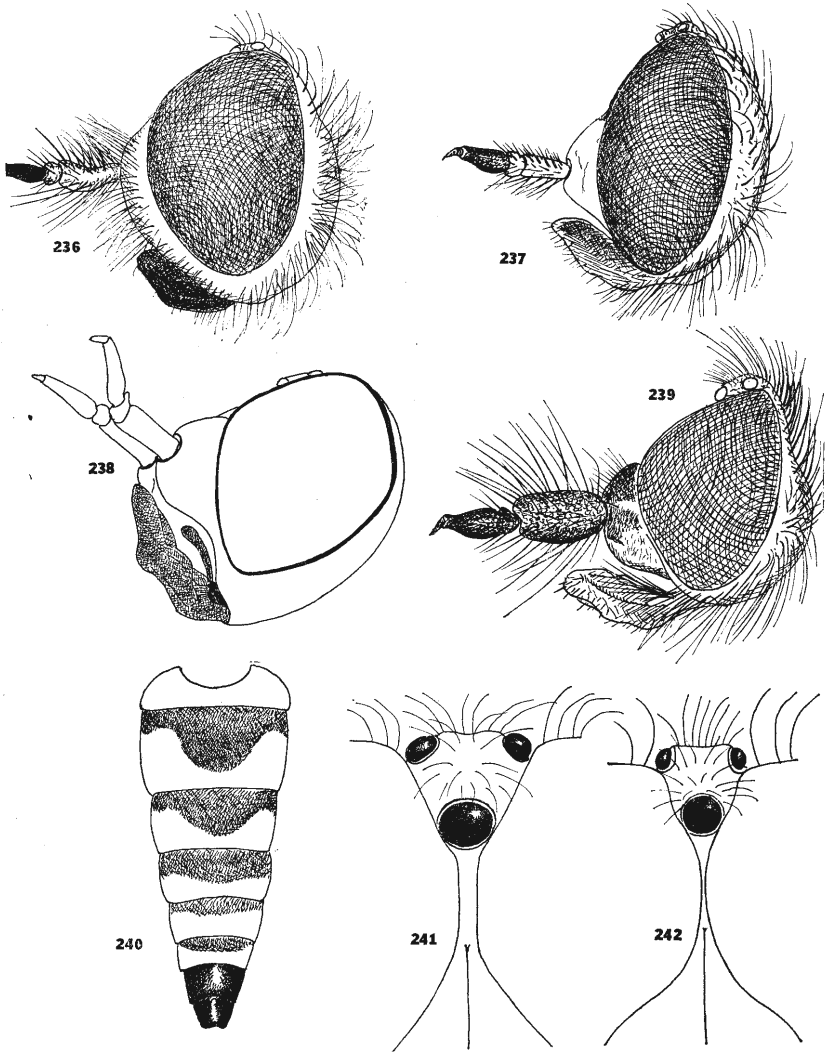
Whereas Asilidae hunt by sight, and have the eyes developed for this function, Therevidae have less prominent eyes, with the larger facets directed upwards instead of forwards. Perhaps this indicates a greater use of smell or hearing than of sight (fig. 336).

Morphology

Head (figs. 236–39).—Almost hemispherical, eyes rarely flattened antero-posteriorly as in many Asilidae. Males almost or quite holoptic, and usually with upper facets distinctly larger than lower, though not always sharply delineated; females dichoptic, with upper facets only slightly bigger than lower ones. In neither sex is the vertex excavated, and the ocellar tubercle is more or less sessile in females, but prominent in males. Ocelli always present. Frons of male is an approximately equilateral triangle, bare, with velvety tomentum in *Psilocephala*, and with hair-tufts, or densely hairy in

Dialineura and *Thereva*. Frons of female trapezoid, of varying proportions, and in most species of *Thereva* with a double callus (figs. 277–84), which is bare and shining black. Face deeply excavated in centre, with broad, rounded parafacials, which are densely hairy in *Thereva*, bare in *Psilocephala*.

The hairs of the face and frons have been given much significance in



FIGS. 236–242.—Therevidae. (236–239) heads in side view: *Thereva annulata* (236). *Psilocephala* sp. (238) showing how proboscis and palpi can be recessed into facial cavity; *Dialineura anilis* (239); abdominal pattern of *Thereva nobilitata* (240), (241, 242) comparison of breadth of frons in male *Thereva*: (241) *lunulata*; (242) *annulata*.

Therevidae (see Collin, 1948 : 95), but it is possible that this has been exaggerated.

There is extensive variation in the antennae of Therevidae, and in some exotic genera the first antennal segment, in particular, is dilated and elaborately equipped with bristles and other sense organs. The British genera are relatively conservative (figs. 236–39). Palpi and proboscis as in fig. 5. The component parts are the same as in Asilidae (fig. 6)—labrum; maxillae with palpi; hypopharynx; labium—but the structure and relative emphasis of the parts are different. Labium short and fleshy, upturned into the facial hollow, and with large labella and pseudotracheae, obviously developed into a spongelike sucking organ. Hypopharynx blunt-tipped, or even slightly spoon-shaped, overlain by a flattened labrum with a forked tip. Maxillae narrow, stylet-like, but apparently not very rigid, their palpi elongate with a conspicuous apical sensory pit (fig. 5). Occiput usually swollen or rounded, with dense hairs and a crown of strong bristles in *Dialineura* or *Thereva*; dorsally (postvertex) bare of hairs in *Psilocephala*, but with two or three irregular rows of strong bristles.

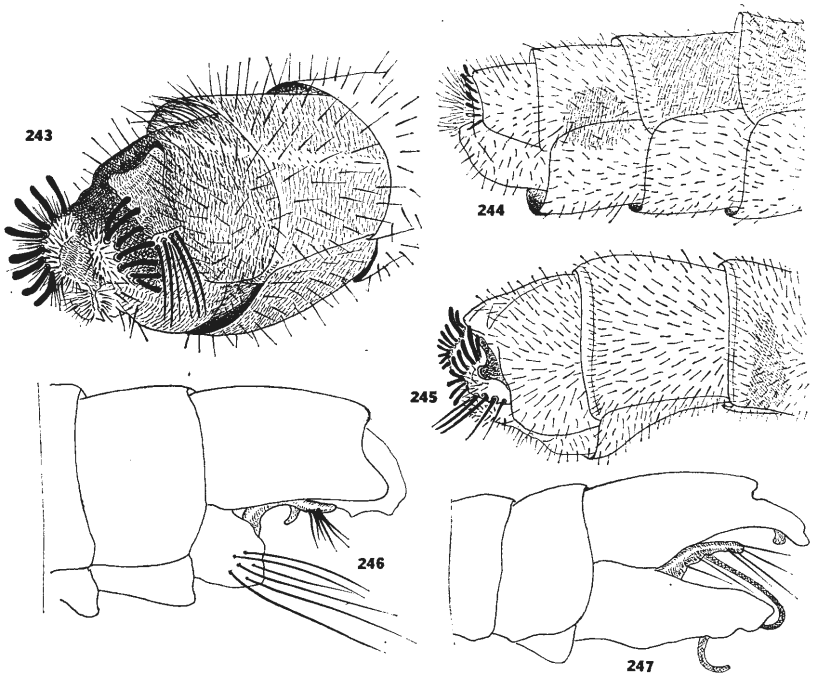
Thorax (fig. 336) with no special features in Therevidae. There are strong dorsal bristles, including four marginal scutellars, notopleurals, supra-alars, postalars and one or two pairs of prescutellar dorsocentrals. Prosternum—between fore coxae—bridged to pronotum (see Asilidae), and the presence or absence of hairs is sometimes used as a distinguishing character (e.g. in *Thereva lunulata*, by Collin, 1948 : 97). This is a difficult character to use, however, and should be avoided if possible.

Abdomen broad-based; i.e. not distinctly "waisted", though it is slightly broader on second segment, which is also the longest segment, but less so than in Asilidae. There is a general tendency for the extreme hind margin of each segment to be narrowly bone-yellow; Lundbeck (1908, II : 135 note) pointed out that it is misleading to rely upon this, since the effect partly depends upon how much of the intersegmental membrane is exposed to view. In most Therevidae the centres of the abdominal tergites are darker, with the hind margins and lateral triangles grey, but often any pattern is obscured by dust. Sometimes, as in the British *Dialineura anilis* and two species of *Thereva*, the whole insect may be covered in silvery hairs.

Male genitalia (figs. 246–54) bear a general resemblance to those of Asilidae, but differ from most Asilidae in having the epandrium complete, not divided into upper forceps, though it may be emarginated posteriorly. There is a sinuous aedeagus, flanked by lower forceps (hypandrium) and claspers; the latter may assume complex shapes.

Female genitalia (figs. 243–45, 255–58).—Eighth segment usually an obvious component, laterally compressed, often also bare and shining; even from fifth segment onwards short hairs are erect, and these segments often participate in penetrating soil or sand when ovipositing. Ninth segment smaller, obviously retractable within eighth segment. Visible beyond ninth tergite are a pair of hairy plates, which also bear two sets of spines: a posterior series, forming a double comb, of stout spines, often slightly dilated apically; and a small lateral comb of divergent, longer bristles, which may often be concealed under the eighth tergite. The whole structure forms an ovipositor which is used to push a way into sand or loose soil, holding this back until the eggs are laid, and then allowing it to fall in and cover the eggs.

LEGS unremarkable (at least in British species), and without any conspicuous features. Femora obscured by rather scaly, recumbent hairs, and by a second set of longer hairs, especially ventrally and posteriorly on fore-femora. Hind femora with a single—or irregularly double—row of moderately long, strong anteroventral bristles, and in some species a few posteroventral bristles near base. Collin (1948) makes use of these bristles in keys to species of *Thereva*, but there is confusing variation. Tibiae slender, with moderately long, strong bristles; hind tibiae with dorsal, antero-dorsal and anteroventral rows; fore and middle tibiae also with posteroventral row.



FIGS. 243–247.—Genitalia of Therevidae. (243) *T. plebeja* ♀; (244) *Psilocephala melaleuca* ♀; (245) *P. rustica* ♀; (246) *P. melaleuca* ♂; (247) *P. rustica* ♂.

WINGS.—Apart from a tendency towards a closed fourth posterior cell, the wings of Therevidae are generally closer to those of Tabanidae than those of Asilidae (figs. 207, 208). Vein R_1 enters the costa rather early (with a stigma; *cf.* Rhagionidae). R_{2+3} almost straight; radial fork wide open, and bell-shaped; discal cell relatively broad. Therevidae have none of the venational peculiarities of the Asilidae: elongate R_2; closed marginal cell; narrow, even constricted discal cell. The costa continues round the margin, even including the alula. There is a distinct trace of the axillary vein.

The wing-venation seems to be somewhat more plastic than it is in Asilidae, and the shapes of cells may vary within one species—notably the aperture of the fourth posterior cell.

Classification

Little subfamily or tribal classification has been carried out on Therevidae, partly because of scarcity of material, and partly because the family does not readily split into smaller units. The most striking differences between genera are in the antennae—shape, proportions of segments, and degree of bristleness—and there has been a tendency in the past to erect a new genus for every striking development. Kröber (1924 : 2) merely arranges the genera of the Palaearctic Region into three groups, two of which—the *Phycus*-group and the *Xestomyza*-group, both with elongate first antennal segment—do not occur in Britain. Our three genera, *Dialineura*, *Psilocephala* and *Thereva*, all belong to the *Thereva*-group.

Biology

Adult Therevidae sit about on vegetation and in bushy areas, on the edges of woods, or along rides in their interior. Some species occur especially in dry, sandy areas, inland or on the coast. Their behaviour somewhat resembles that of Asilidae and the larger Empididae, and so they have been thought to be predatory, though no-one seems actually to have seen a Therevid eating anything.

The structure of the proboscis, compared with that of Asilidae (figs. 5, 6) indicates that Therevidae do not pierce their prey in like manner, with the hypopharynx, because this is not developed into a piercing organ. If Therevidae are predatory they must engulf their prey in the labella, in the manner of Dolichopodidae, yet a detailed comparison of the respective pseudotracheal systems discounts this view (figs. 9, 10). In *Thereva*, the pseudotracheae are of the type that is familiar in Syrphidae and in the muscoid flies, with two main trunks dividing into closely packed, long, looped branches; both trunks and branches are supported by open rings of chitin which leave a groove along the length of the pseudotrachea. In *Dolichopus* the main trunks are absent, and the "branches" are few in number (as few as six per side). They are much shorter, no longer looped, and tapering sharply, and the rings of chitin have been conspicuously modified into large, interlocking teeth. The effect is uncannily like a zip-fastener. The labella have thus become a specialized device for crushing prey that has been enveloped in the labella, and rasping a way through its integument.

Therevidae show no trace of any evolution in this direction, and the structure of the labella, coupled with the lack of piercing stylets (*cf.* Tabanidae, fig. 7) give strong reason to suppose that the diet of adult Therevidae is confined to sucking fluids, probably nectar from flowers. The only activity of Therevidae that has been recorded is that in very hot weather males of *Therevidae* sometimes leap into the air and dance round each other, in the manner of certain Muscidae; and that small aerial swarms have been reported.

Larvae

The larvae of Therevidae share a characteristic appearance with those of Scenopinidae. They are elongate and vermiform, with a tough, shining white integument, and apparently consist of 20 segments, because the first six abdominal segments are secondarily divided into two. They live in

sand or soil, and feed actively on either vegetable or animal food. Fox Wilson (1924) conducted careful experiments, as well as field observations, on the feeding of *Thereva plebeia*. He found that the larvae fed on leaf-mould and humus in the soil, but that if humus was scarce, then they would attack growing plants. Cabbage plants and potato tubers both wilted under direct attack from *Thereva* larvae. On the other hand many authors have recorded that Therevid larvae are at times actively carnivorous, and even cannibalistic, if they are overcrowded, or food is insufficient.

The pupa, also found in sand or soil, is recognized by the thorn-like antennal sheaths on the head, and the long, curved thorn at the base of each wing.

KEY TO BRITISH GENERA

1 First antennal segment strongly swollen, longer and thicker than second and third segments, and with long, strong, bristly hairs. Antennae placed low on head; frons almost twice as long as face (fig. 239) fourth posterior cell wide open **Dialineura** Rondani (p. 98)

– First antennal segment not strongly swollen, and with strong bristles much shorter. Antennae placed higher on head; frons not much longer than face (figs. 236, 237). Fourth posterior cell usually closed 2

2 Face and frons bare. Antennae standing on an isolated callosity (fig. 237) **Psilocephala** Zetterstedt (p. 100)

– Face and frons densely hairy ..... **Thereva** Latreille (p. 100)

Genus **Dialineura** Rondani, 1856

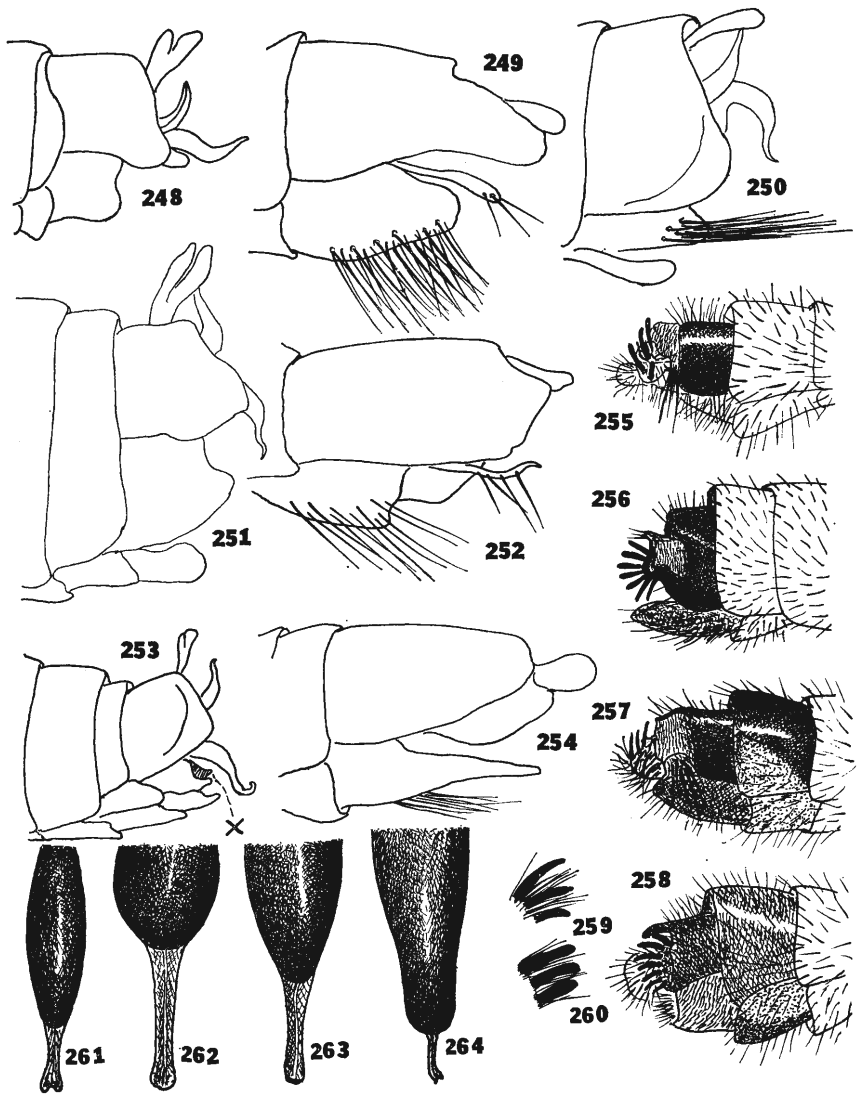
European dipterists long regarded *Dialineura* as a synonym of *Tabuda* Walker (1852), the type of which is the N. American species *Tabuda fulvipes* Walker, but the two genera are now separated (see *Catalog of the Diptera of America North of Mexico*, 1965 : 352).

This is one of those cases where the single British species is easily recognized, though the genus is difficult to define satisfactorily on a world basis. The swollen first antennal segment, with its abundant, long, bristly hairs, is greater in size and bulk than the rest of the antenna, and although this character is unique among British—and indeed among European—Therevidae, there are many exotic forms that are not congeneric with *D. anilis*.

Collin (1948 : 96) considers this character to be less significant than the bare face, coupled with the few hairs on the frons in both male and female, but he goes on to admit that *Dialineura* then becomes hard to separate from *Psilocephala*. In practice the antennal structure is sufficiently distinctive. Apparently the flies themselves find mutual recognition difficult: Verrall (1909 : 585) reports that Col. Yerbury collected a female *D. anilis* in cop with a male of *Thereva annulata* at Portishead, and a similar couple collected by Col. Yerbury at Barmouth, 27.vi.1902 is in the British Museum.

ONE BRITISH SPECIES

♂ Compactly built, with a stout, tapered abdomen which has silvery hairs over a grey tomentum. Thorax hairy, with yellowish hairs and black bristles: one pair dorsocentrals, three notopleurals; two supra-alars; one post-alar; four marginal scutellars. Legs reddish-yellow, with black bristles, femora somewhat darker. Wings with brown veins, and faintly spotted on forks and crossveins; fourth posterior cell wide open. Male genitalia, fig. 254. ♀ Lacking the conspicuous long hairs of thorax and abdomen, and hence more drab in appearance than male. Abdomen grey, with recumbent yellow hairs. Thorax dull yellowish-brown, with fine black hairs, and short, scaly



FIGS. 248–264.—Genitalia of Therevidae. (248) *T. fulva* ♀; (249) *T. lunulata* ♂; (250) *T. strigata* ♂; (251) *T. nobilitata* ♂; (252) *T. annulata* ♂; (253) *T. plebeja* ♂—X = inner flange of hypandrium, see key; (254) *Dialineura anilis* ♂; (255) *T. annulata* ♀; (256) *T. lunulata* ♀; (257) *T. nobilitata* ♀; (258) *T. plebeja* ♀. (259, 260) comparisons of spines of acanthophorites of *T. nobilitata* (259) and *T. bipunctata* (260). (261–264) aedeagus of *Thereva*, viewed from above, without dissection: *plebeja* (261), *valida* (262); *inornata* (263); and *strigata* (264).

yellowish hairs. Eyes separated at vertex by a distance equal to width across bases of antenna; frons and face diverging. No bare frontal calli. Legs as in male, or femora more yellow ..... **anilis** (L.)

Verrall (1909 : 585) *considered that this species might mimic the predacious Yellow Dung Fly,* Scatophaga stercoraria *L.*

Sandhills of Welsh Coast; Scotland, Sutherland (Fonseca). Common. v–vi.

Genus **Psilocephala** Zetterstedt, 1838

Distinguished from *Dialineura* by the more slender first antennal segment, and from *Thereva* by the bare sides of the face, with no hairs between the bases of the antennae and the rest of the proboscis; note that care is needed not to confuse the hairs of the palpi with those on the face.

Species in many parts of the world have been referred to the genus *Psilocephala* on account of the bare face, but it is by no means certain that this negative character is a reliable criterion. Two species occur in Britain, both extremely rare, little more than a score of specimens known.

Key to Species

1 Body, especially abdomen, densely covered with silky, silvery hairs. Genitalia as in fig. 246 ..... ♂ **melaleuca** Loew

– Body not densely silvery 2

2 Femora black, with a distinct yellow tip. ♀ coxae with short clothing hairs, leaving the black bristles conspicuous. Genitalia as in figs. 245, 247 ♂ ♀ **rustica** (Panzer)

(*confinis* Fallén; *ardea* F of Verrall and Collin, not of Fabricius)

Apparently rare and local, known only from a few localities on the Welsh Border: Cheshire, R. Bollin; Shropshire, Wyre Forest; Herefordshire, Monnow Valley. vii.

– Femora black, including tip. ♀ coxae with long hairs, which partly obscure the black bristles. Genitalia as in fig. 244 ..... ♀ **melaleuca** Loew

A few specimens, all bred from larvae found in rotting stumps, in the Windsor Forest–Ascot area of Berkshire. (Donisthorpe, Southwood, Crow). vi, early vii.

Genus **Thereva** Latreille, 1796

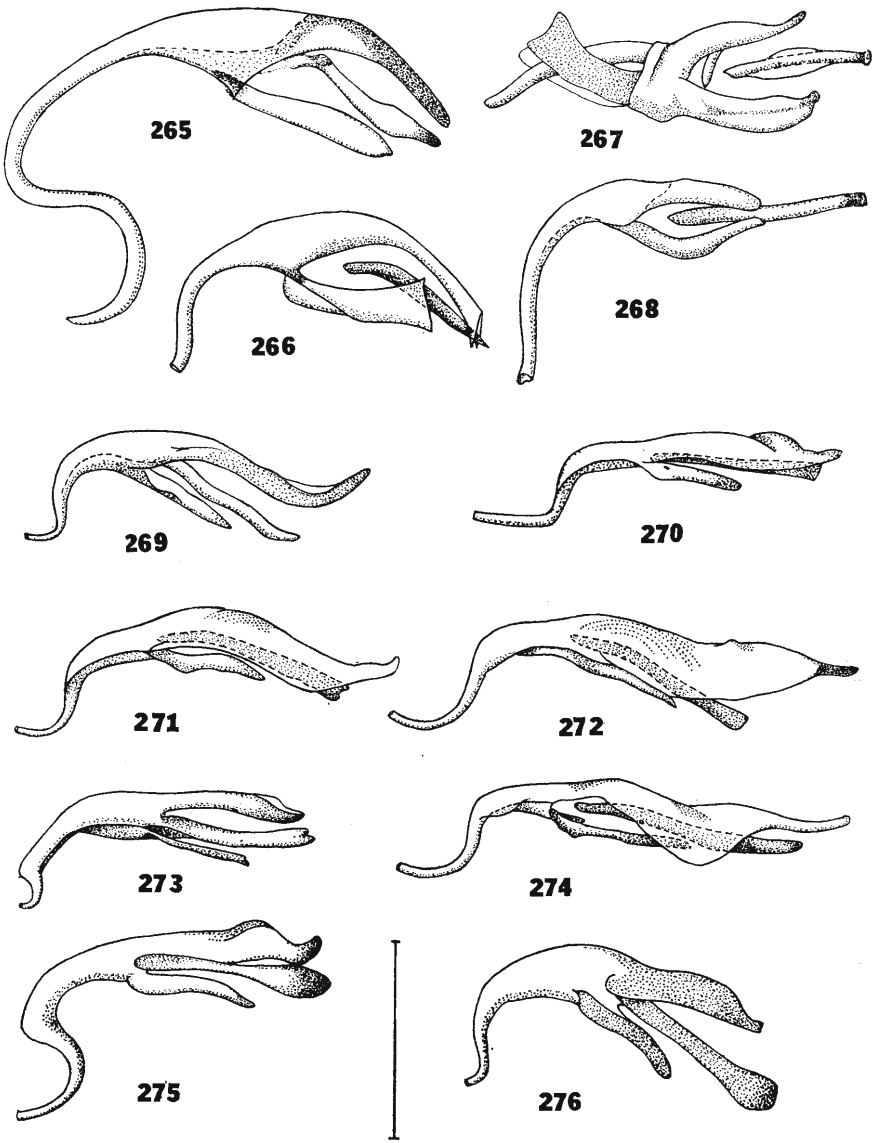
Squatly-built flies, with bushy hairs on the face, but without the swollen first antennal segment of *Dialineura*. The ten British species fall into two groups, with *annulata* F. and *lunulata* Zetterstedt being distinguished from the rest by the silvery appearance of the males (*cf. Dialineura anilis*), and by the absence of frontal calli in the females. The remaining species are difficult to name with certainty.

Collin (1948) rightly emphasizes the variability of colour characters in this genus, but instead makes much use of distinctions which involve bristles and fine hairs. These, again, are not easy to discriminate in single specimens, though they may be valuable in a comparison of ample material. Fortunately the male genitalia and the frontal calli of the female provide corroborative characters: see also Lyneborg, 1968.

Key to Species

1 Males silvery, with genitalia of the *Psilocephala* type (figs. 249, 252). Females with no bare frontal calli, and with only the eighth abdominal tergite shining black (figs. 255, 256) ..... **annulata**-group

– Males not silvery, with genitalia of the *Thereva*-type (figs. 248, 250, 251). Female with a pair of bare frontal calli, and with both the eighth and the seventh abdominal tergites shining black (figs. 257, 258) ..... **nobilitata**-group



FIGS. 265–276.—Aedeagus of Therevidae (from Lyneborg, 1968). (265) *Psilocephala rustica*; (266) *P. ardea*; (267) *T. annulata*; (268) *T. lunulata*; (269) *T. nobilitata*; (270) *T. fulva*; (271) *T. inornata*; (272) *T. handlirschi*; (273) *T. bipunctata*; (274) *T. valida*; (275) *T. strigata*; (276) *T. plebeja*.

annulata-group

1 Fourth posterior cell closed. Thorax with hairs all pale. Eyes of male more nearly touching (fig. 242) ..... **annulata** Fabricius
Widespread and common on sand-dunes throughout the British Isles, including Ireland. Chiefly coastal, but inland in suitable localities. Early v to late viii.
– Fourth posterior cell open. Thorax with abundant brown or black hairs dorsally. Male with eyes distinctly separated (fig. 241) ..... **lunulata** Zetterstedt
Local, in gravelly stream-beds left dry in summer. Chiefly Scotland (Spey Valley); but also Herefordshire (Monnow R.), Wales: Brecon, Llandrindod Wells. vi–viii.

nobilitata-group

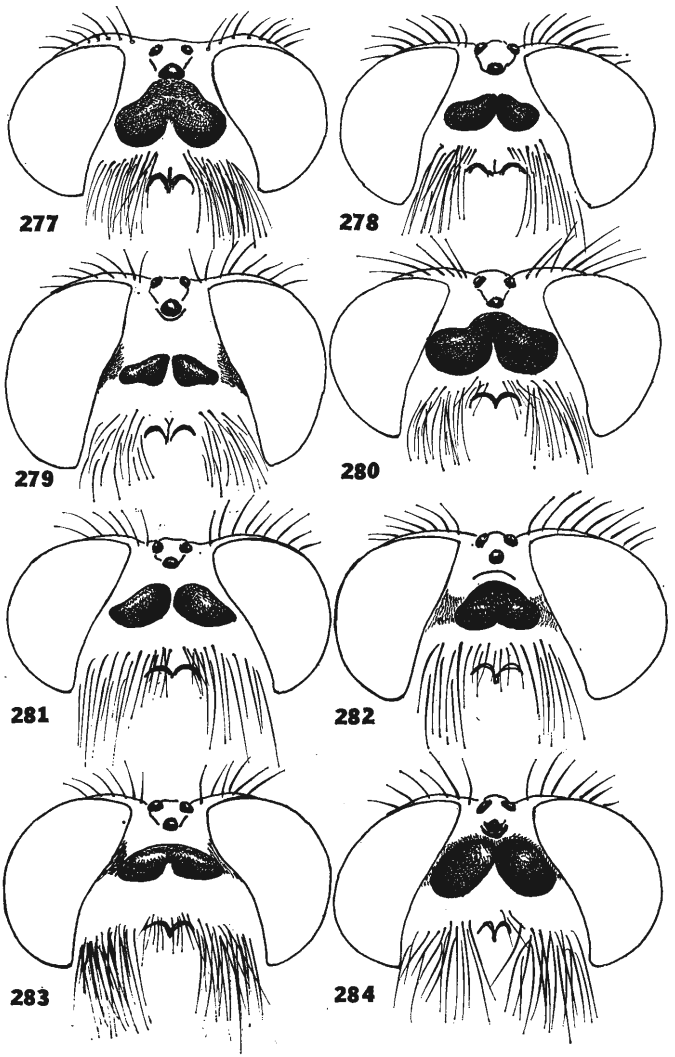
MALES

1 Abdomen with tomentum entirely yellowish, and long golden hairs, with a narrow strip of black hairs down middle ..... **fulva** Meigen
– Abdomen with dark patches of tomentum, and conspicuous black hairs 2
2 Mesonotum with golden yellow tomentum, even if hairs are black 3
– Mesonotum with ashy grey-brown tomentum 4
3 Fore femora posteriorly with a conspicuous tuft of hairs, twice as long as breadth of femur, sometimes chocolate-brown. Fore-tarsi entirely black **handlirschi** Kröber
– Fore femora posteriorly with shorter hairs, not predominantly blackish. At least first two segments of fore tarsus yellowish, with black tips. . **nobilitata** Fabricius
4 A small species (9 mm.), long hairs of abdomen pale greyish . . . **bipunctata** Meigen
– Larger species (12–13 mm.), long hairs of abdomen mainly black 5
5 Penis, *when viewed from above*, broad for most of its length, then suddenly narrowed (figs. 261, 264) 6
– Penis, viewed from above, broad basally, with long slender apical part (figs. 262, 263) 7
6 Penis in side view exposes inner flange of lower forceps (figs. 253, 276) **plebeja** Linnaeus
– Penis in side view as in fig. 275; inner flange of lower forceps concealed **strigata** Fabricius
7 Penis in side view as fig. 271. Tarsi mainly yellowish. One or more strong posteroventral bristles near base of hind femur ..... **inornata** Verrall
– Penis in side view as fig. 274. Tarsi mainly dark. No strong posteroventral bristles near base of hind femur ..... **valida** Loew

FEMALES

1 Frontal calli united into one, almost touching both eyes and ocelli (figs. 277, 280, 284) 2
– Frontal calli separate; or if united, then well separated from ocelli, and joined to eyes only by patch of dark tomentum (figs. 278, 279, 281, 282, 283) 4
2 Abdomen covered with yellow tomentum, yellow pile, and silky golden hairs. Only seventh and eighth segments shining brown. Erect hairs ventrally mostly yellow ..... **fulva** Meigen
Rare and local in southern England. Kent: Farningham, Dartford, Foots Cray. S. Wales, Glamorgan: Porthead. Easily confused with nobilitata. *Mid-vi–viii.*
– Abdomen entirely black-brown on each segment, with black hairs; only posterior margins and lateral triangles of each segment yellowish, with yellow hairs. Erect hairs of venter mostly black 3
3 Third antennal segment shorter. Mesonotum brown, with either two grey stripes or a divided dark brown longitudinal stripe. Ovipositor shorter (fig. 243). Frontal callus smaller (fig. 280) ..... **plebeja** Linnaeus
Southern England and Wales: frequent in all counties from Worcester and Cambridgeshire southwards. Verrall's Scottish records were rejected by Collin (1948 : 100). *v–viii.*
– Third antennal segment longer. Mesonotum grey, or blue-grey, with narrow grey longitudinal stripe. Ovipositor longer. Frontal callus bigger (fig. 284) **strigata** Fabricius
Rare in British Isles, perhaps an occasional migrant. Isle of Wight, Niton, vii 1909 (*C. J. C. Peel*).

4 Dark patches of second and third abdominal tergites semicircular, with only narrow lateral extensions (fig. 240). General colouring yellow. Frontal calli large, and tending to merge into one (fig. 278). Beard and parafacial hairs entirely yellow. Spines of acanthophorites pointed (fig. 259) ..... **nobilitata** Fabricius
Common and widely distributed in British Isles, including I.O.M. v–viii.
– Dark patches of second and third abdominal tergites more uniformly transverse ... 5
5 Frontal calli broadly united, almost touching eyes, and joined to them by patches of black tomentum (figs. 282, 283) 6
– Frontal calli not broadly united 7



FIGS. 277–284.—Heads of female *Thereva* in front view. (277) *fulva*; (278) *nobilitata*; (279) *inornata*; (280) *plebeja*; (281) *bipunctata*; (282) *handlirschi*; (283) *valida*; (284) *strigata*.

6 Frontal calli as in fig. 282 . . **handlirschi** Kröber (*praestans* Collin; *arcuata* Verrall)
N. Scotland: local. vii–ix.
– Frontal calli as in fig. 283 . . . . . **valida** Loew (*circumscripta* Collin, nec Loew)
Scotland, Nairn. vi. (*Much confusion about this species, see Collin*, 1948 : 101, *and Lyneborg*, 1968 : 170.)
7 Frons relatively higher, and less broad (fig. 279). Ventral hairs of abdomen all yellow . . . . . **inornata** Verrall
Scotland, Inverness-shire, Spey Valley, Bridge of Bron. vii, viii. Local.
– Frons relatively lower and broader (fig. 281). General colouring grey. Frontal calli distinctly separate (fig. 281). Beard and parafacial hairs often with some admixture of black. Spines of acanthophorites blunt-tipped (fig. 260). (*cf. nobilitata*) . . . . . **bipunctata** Meigen
Generally distributed in England, Wales and Scotland, on dunes and sandy banks, mainly coastal, sometimes inland. vi–viii. Common.

Family SCENOPINIDAE

Scenopinidae share with Anisopodidae the common name of "window flies", because the adults most often attract attention by appearing indoors, on windows. This applies particularly to *Scenopinus fenestralis*, of which Linnaeus (1758 : 597) wrote: "Habitat in Europa, frequens in fenestris." The larva of *S. fenestralis* is also a domestic insect, commonly found in carpets and other woolly materials, where it is predaceous on larvae of clothes moths and fleas. In grain mills, stables and food stores—any place, in fact, where moths, fleas and beetles may occur—*S. fenestralis* appears on windows. The natural habitat is probably birds' nests and dry debris (fig. 337).

Morphology

Body and legs entirely without strong bristles.

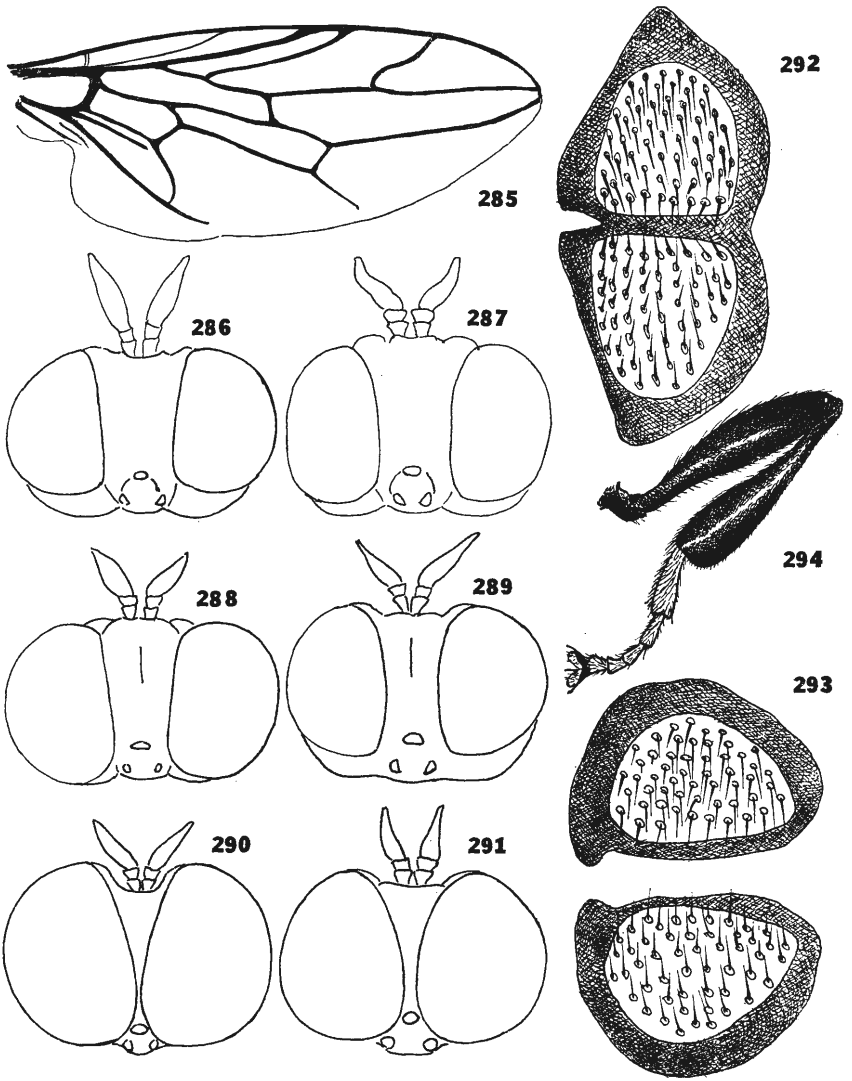
Head (figs. 286–91).—Resembling that of Stratiomyidae, with eyes that occupy a major part of the head, meeting in males of some species (only *fenestralis* in Britain), but leaving a prominent postocular flange, especially in females. Vertex level with eyes, three ocelli in a low tubercle. First two antennal segments short, subequal; flagellum merged into a single segment, elongate-conical, blunt, slightly swollen at tip but (in British species) without any apical arista or style. Facial area deeply recessed, concealing a short proboscis and cylindrical palpi, which are not normally visible in profile.

Thorax.—Mesonotum rather flat dorsally, with high sides, and a well-developed notopleural triangle. Scutellum unarmed. Propleura and prosternum reduced, so that forelegs are very mobile in front of a bulbous mesothorax. Postscutellum moderately prominent. No macrochaetae, only short, fine clothing hairs.

Abdomen.—Seven visible tergites in male, eight in female, most of them subdivided by a transverse groove. Second tergite as long as two others, and with a paired median sense-organ (figs. 292, 293) each half of which is covered with small pits, each with a short (? sensory) hair. In males, third and fourth tergites may have a very narrow, bone-white hind margin, which is sometimes concealed by the adjacent tergite, but which may become prominent when the male is hovering (*cf.* some Stratiomyidae). Ovipositor very short, triangular, with sclerites apparently fused strongly together. Male genitalia compact, upper and lower forceps forming a hemispherical container for aedeagus.

LEGS sturdy, obviously developed for walking (*cf.* Bombyliidae). Femora may be somewhat moulded to fit closely into the recessed pleura; male of *S. niger* with hind tibiae strongly clavate (fig. 294).

WINGS (fig. 285).—Radial veins thickened and concentrated anteriorly, somewhat in the manner of Stratiomyidae; R_5 reaching margin before wing-



FIGS. 285–294.—Scenopinidae. (285) wing of *Scenopinus niger* ♀. (286–291) heads of *Scenopinus* viewed from above: (286) *glabrifrons* ♀; (287) *niger* ♀; (288) *niger* ♂; (289) *fenestralis* ♀; (290) *fenestralis* ♂; (291) *glabrifrons* ♂. (292, 293) glandular organs visible on dorsum of second abdominal segment: *glabrifrons* (292) and *fenestralis* (293). (294) left hind leg of male *Scenopinus niger*.

tip. Discal cell remains large, and discal in position, and emits only two veins to form three posterior cells; these veins are strong almost as far as wing-margin, not faint as in Stratiomyidae. First posterior cell strongly narrowed at tip.

SIZE.—Scenopinidae are small, sturdy flies, about 5 mm. long.

DISTRIBUTION AND CLASSIFICATION

Scenopinidae are world-wide, but few in numbers of genera, species and individuals. In most areas of the world there are probably species and genera still undiscovered: e.g. Paramonov (1955), reviewing the Australian Scenopinidae, recorded *Pseudomphrale* from Australia for the first time, and described two new genera, bringing the total to five genera and 12 species. In Britain there are two well-established species and one rarity, all in the genus *Scenopinus*.

KEY TO SPECIES OF SCENOPINUS

1 Eyes touching, or very closely approximated (figs. 290, 291).....2
– Eyes separated by at least breadth of ocellar tubercle (figs. 286–89).....3
2 Eyes touching for a short distance (fig. 290). Frons black, shining through dull greyish tomentum.....**fenestralis** Linnaeus ♂
– Eyes separated by almost breadth of median ocellus (fig. 291). Frons reddish, shining.....**glabrifrons** Meigen ♂
3 Legs black, except for yellowish tarsi; frons as in figs. 287, 288. Male with inflated hind tibiae and narrow, ivory-white hind margins to segments three and four **niger** Degeer ♂, ♀

Recorded only from Southern England and Northern Ireland, but probably occurs elsewhere (cf. fenestralis). *Rather uncommon, but possibly mistaken for* fenestralis. *vi, vii.*

– Legs yellowish; frons as in figs. 286, 289.....4
4 Frons broader (fig. 286), shining black, with sparse whitish hairs **glabrifrons** Meigen ♀

Very rarely recorded from Britain. One female in B.M. from London, "larva in a Persian carpet, 28.x.1931."

– Frons narrower (fig. 289), shining black, but largely obscured by whitish hairs **fenestralis** Linnaeus ♀

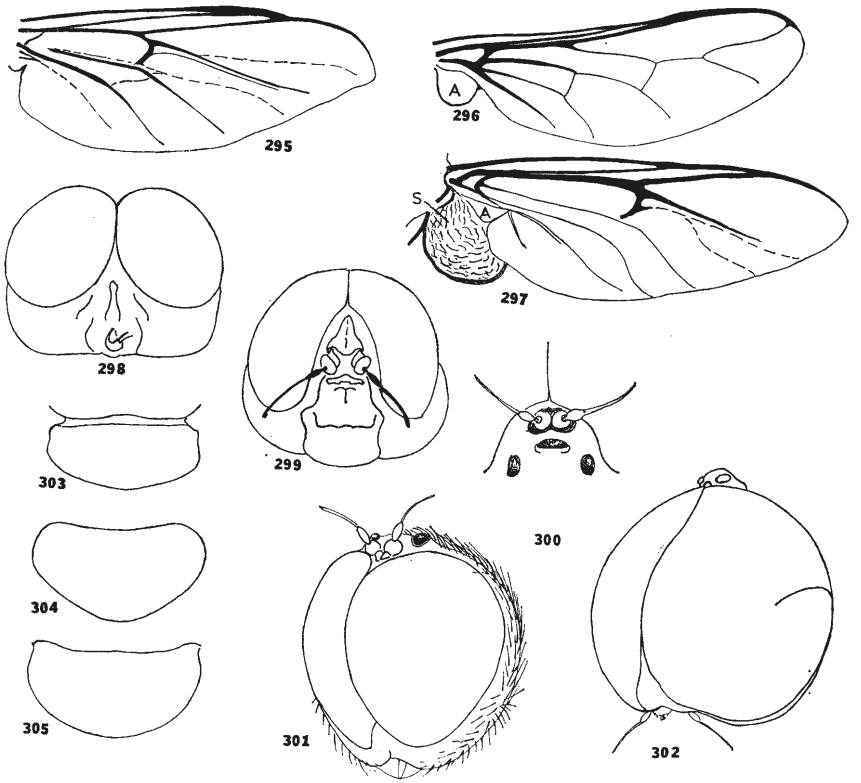
The common domestic species, found singly on windows at any time of year. Larva in carpets, and in dried goods of many kinds. Might occur anywhere, though records are apparently confined to southern England. Chiefly vi–viii.

Family ACROCERIDAE

(CYRTIDAE) (fig. 307)

This is a tiny family of unusual and interesting flies, which has suffered from problems of nomenclature. The best and simplest family name is the old one: Cyrtidae, from the genus *Cyrtus* (non-British). Current fashions use either Acroceridae, from *Acrocera*, or Ogcodidae, from *Ogcodes*. The last generic name, proposed by Latreille in 1796, was clearly based upon the Greek word ὄγκοδ, "the bulk, size, mass of a body" (Liddell & Scott: 1024), but was soon altered by Meigen (1822) to *Oncodes*, a more euphonious name to pronounce, and one that was used happily until some authors took the retrogressive step of going back to the original spelling. Since this spelling is used by Schlinger, the current world specialist, it would be absurd for us, with our insignificant representation to stand out, so we, too, must use *Ogcodes*. Fortunately we do not need to use the family name Ogcodidae, which is too adenoidal for words.

Along with Nemestrinidae, Acroceridae seem to be an offshoot from the evolutionary stock that led on to Bombyliidae. Some primitive genera feed from flowers, but more recently evolved genera have ceased to feed at all in he adult stage, and the mouthparts are vestigial, or completely absent. All necessary feeding is carried out by the larvae, which are internal parasites of spiders.



FIGS. 295–302.—Acroceridae. (295–297) wings: *Ogcodes pallipes* (295), *Acrocera globulus* (296), *Ogcodes gibbosus* (297). (298–302) heads: *Acrocera globulus* (298) showing reduced mouthparts; *Ogcodes gibbosus* (299) showing loss of mouthparts; *Acrocera globulus* (300), vertex and ocelli; *Acrocera globulus* ♂ (301); *Ogcodes gibbosus* ♂ (302). (303–305) scutellum: *Acrocera globulus* (303), *Oncodes gibbosus* (304) and *O. pallipes* (305).

MORPHOLOGY

There is a wide range of morphological variation in this greatly modified family, and the following remarks apply only to the British species. One conspicuous feature is the entire lack of any strong bristles on any part of the body (fig. 307).

HEAD.—Relatively small, dwarfed by the huge thorax; spherical, with the eyes contiguous in both sexes. Eyes sparsely covered with minute hairs, facets uniform in size, and in *Ogcodes* there is a short, curved line perpendicular

to the posterior margin, as in one section of Bombyliidae (Tomophthalmae: *cf. Villa modesta*). Frons and face have almost vanished, leaving the eyes touching, or virtually so, along a long, vertical line. In *Ogcodes* there is nothing at vertex except the triangle of three ocelli, the antennae being placed right down on the mouthmargin, with a triangular frons above them; *Acrocera* is markedly different, having the antennae crowded up against the ocellar triangle, which is long and broad, and the anterior ocellus transverse (fig. 300). Antennae with first two segments short, well-socketed; third segment seed-shaped, with a stout, moderately long arista, though the whole antenna is only about one-third as long as height of head. There are no palpi. Mouthparts entirely absent in *Ogcodes*, which has a large, square buccal cavity (fig. 299); in *Acrocera* there is a tiny, vestigial proboscis, with two fine bristles at its tip (fig. 298). Postverticals with dense, curly hairs, but (like rest of body) with no strong bristles.

THORAX.—Inflated, strongly convex on all sides. Pronotum tiny and inconspicuous; mesonotum bulging forwards and pushing head downwards (fig. 307). No trace of transverse suture; humeri and postalar calli well developed, but more conspicuous in *Acrocera* than in *Ogcodes* because of their bone-white colour. Pleural sutures often difficult to distinguish, since the thorax readily collapses after death, but there are no striking peculiarities. Spiracles small, circular; anterior spiracle well-defined; posterior spiracle and halteres completely concealed beneath enormous squamae.

ABDOMEN.—Broad, and inflated at base, narrowing rapidly. Male with five visible segments, female with only four; first tergite reduced in middle to a narrow band; posterior segments concealed, with only genitalia protruding. Abdomen unusually convex dorsally.

LEGS.—Rather small for such a bulky insect, but femora and tibiae are stout; tarsomeres relatively uniform, especially on fore-legs. Stout tarsal claws and a pad-like empodium as well as the two pulvilli ("three pulvilli"). No strong bristles, and only light clothing hairs.

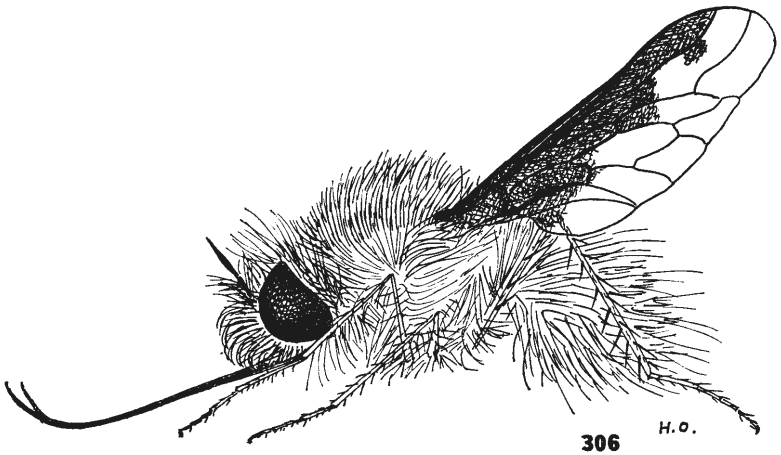
WINGS (figs. 295–97).—Costa, Sc. and R_1 strong, other veins largely evanescent, and those remaining are greatly modified from the generalized pattern (*cf.* with Tabanidae, fig. 209). Exotic genera of Acroceridae exhibit such a range of wing-venation that it is unprofitable to attempt to homologize the veins on the evidence of the British species alone. The huge squamae are possibly the biggest among Diptera, and a conspicuous feature of the family.

SIZE.—The three British species are similar in size, ranging from less than 3 mm. (smallest males) to almost 7 mm. (largest females), with the females noticeably more inflated than the males. Some exotic, primitive genera are much larger.

BIOLOGY

Acroceridae appear to have arisen from a flower-feeding family, perhaps a common ancestor with Bombyliidae. Some exotic genera, apparently primitive, have a long proboscis and feed from the nectar of flowers (e.g. *Lasia*, *Eulonchus*, *Panops*), but the more specialized genera—which include *Acrocera* and *Ogcodes*—have ceased to feed as adults, losing their mouthparts. This is presumably correlated with the parasitic habit of the larvae, which are able to store enough nutriment for the requirements of adult life as well as their own.

The larvae are internal parasites of spiders, particularly Lycosidae, but also Theridae and Drassidae. The black eggs are laid in great profusion on the tips of twigs, or just scattered on the ground, in areas where spiders' webs are numerous. An American species, *Pterodontia flavipes* Gray, is recorded as having laid up to about 4000 eggs. The first stage larva is an active form, recalling the planidium of the chalcidoid Hymenopteran *Perilampus*, or the triangulin of *Stylops*. The body is somewhat flattened, and has spiny processes pointing backwards. The first stage larva can progress by looping, crawling or leaping, springing by means of caudal processes and a sucker attachment. This instar remains active until it finds



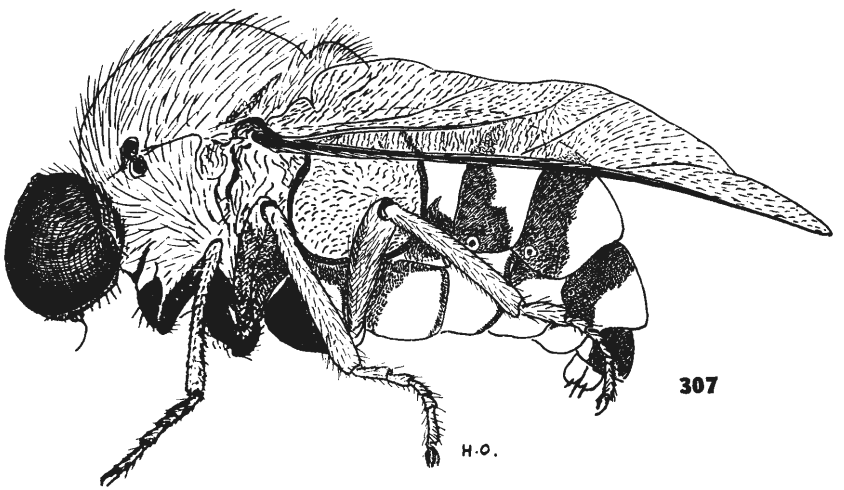


FIG. 306.—*Bombylius major.*
FIG. 307.—*Ogcodes gibbosus.*

a spider host, when it penetrates into the body of the spider, and comes to lie either in the cephalothorax or in the legs. The pupation and emergence of the fly coincides with the death of the host.

The *flight* of Acroceridae is peculiar, as might be expected from the abnormal body-shape, the reduced venation, and the huge squamae. They are sometimes known as "balloon-flies" (though this term is also applied to those Empididae that present their mate with a "balloon" of silk) in reference to their peculiar "floating" flight, which is rather a matter of keeping airborne than of purposive, directional flight.

The recorded distribution of the three British species of Acroceridae is little more than a record of the favourite haunts of certain collectors, and the coincidence of an interested observer happening to be there when the flies were about. Accounts of this family from all over the world emphasize that they are infrequently seen, but that occasionally they may suddenly appear in great numbers. This is consistent with the laying of such great numbers of eggs. Presumably in the normal way nearly all the larvae perish—either fail to find a host or fail to mature successfully—but sometimes all the factors happen to be favourable. Then a mass emergence takes place.

KEY TO GENERA AND SPECIES

1 Antennae at top of head, just in front of ocelli; posterior margin of eye intact, without dividing line. Wing venation as in fig. 296. Scutellum narrow, transverse (fig. 303) ..... **Acrocera globulus** Panzer
Chiefly known from scattered localities in England and Wales south of Herefordshire, Shropshire and Bedfordshire. Yorkshire: Lawland Moss; Skipwith Common. Generally rare, but occasionally locally abundant. Early vii–mid-viii.

– Antennae placed very low, close to mouth margin. Posterior margin of eye with dividing line (fig. 307) (*cf.* Bombyliidae: Tomophthalmae). Wing venation as in fig. 297. Scutellum larger, triangular (figs. 304, 305). Genus *Ogcodes*..... 2

2 Femora brown with yellow tips. Squamae with pale border. Abdominal tergites with extensive bone-yellow patches, forming a distinctive pattern
Ogcodes gibbosus Linnaeus
Sometimes locally abundant in southern England, from Suffolk to Herefordshire, and southwards. Late vi to early viii.

– Femora entirely yellow. Squamae with blackish border. Abdominal tergites brown, with only a very narrow, pale hind margin.. **Ogcodes pallipes** Latreille
Uncommon. Recorded from scattered localities from Herefordshire southwards; Essex, Benfleet; Surrey, Bookham; Suffolk, Flatford (Parmenter); otherwise chiefly in western half of England, and in Wales. vii, viii.

Family BOMBYLIIDAE

Bombyliidae are called "bee-flies" because they are supposed to resemble bees, and because the larvae of some of them live in association with solitary bees, as parasites, carnivores or inquilines. Actually, the resemblance to bees is only a very general one, suggested partly by the furry coating of species of *Bombylius* and related genera, coupled with the long, but un-bee-like proboscis, and partly by the bee-like habit of hovering and darting over low-growing spring flowers, and close to the mouths of burrows of solitary bees.

Among Brachycera, Bombyliidae are recognized by the complete venation, with discal cell, but only four posterior cells, with the loss of a median vein (figs. 308–14). Bombyliidae are essentially aerial insects, with the legs thin

and obviously, as Verrall (1909 : 474) said: "used for alighting purposes only" (fig. 306); Tully (1946) noted that the fore-legs may be used to steady the fly when hovering to feed at a flower. The eyes are well developed, though not so outstandingly so as in Asilidae or Tabanidae.

Morphology and Classification

The range of external shape and structure in the family Bombyliidae is so great that it is difficult to generalize. As in some other families, notably Tabanidae, the appearance that is commonly associated with the family is that of successful modern genera, perhaps of relatively recent evolution, while a great many less characteristic genera remain little known, except to the specialist. The Bombyliidae that are known to occur in Britain are a pitiful remnant of this large and beautiful family, which are essentially flies of warm, dry climates, and are seen at their best when hovering low over a hot, stony hillside.

We have four species of *Bombylius* as representatives of one large section of the family, five species of *Villa*, *Anthrax* and *Thyridanthrax* representing a second, and *Phthiria pulicaria* as the sole representative of the rest of the family. The following account of morphology tries to emphasize what family characteristics these have in common, but of course is an altogether inadequate account of the family Bombyliidae in general.

Vestiture.—The striking difference in appearance between *Bombylius*, *Villa* (representing also *Thyridanthrax* and *Anthrax*), and *Phthiria* is partly due to the difference in vestiture. *Bombylius* (fig. 306) is covered with long, soft hair, so that even on the head the outline is really that of the tips of the hairs. There are some stiffer bristles, both long ones visible above the pile of the abdomen, and shorter ones on the legs, and a few small areas of white scales give pattern to some areas of the body surface (e.g. a short median white line on the dorsum of the abdomen), but the general effect is soft and furry. In *Villa* and its relatives, on the other hand, the vestiture of hairs is generally shorter and less dense, and clearly shows the body-surface, which is covered with close-lying scales. These scales are often rubbed off the dorsum of the thorax and abdomen when the specimen is handled for pinning, and then it is difficult to imagine what the insect looked like when it was alive. The scales are mainly black, but areas of white and yellow scales form conspicuous patterns, especially in the form of narrow bands on some of the abdominal segments. In *Phthiria*, the entire vestiture is much sparser, and the body-surface itself is more clearly visible.

Head (figs. 319–22).—*Bombylius* has a prominent face that is largely concealed beneath dense hairs; rather elongate, slender antennae; and a very long proboscis, which consists of an elongate labium, grooved dorsally to house an equally elongate labrum, and ending in a pair of labella with pseudotracheae. The labella are shown separated in fig. 306, but in life they are pressed together at the tip of the hypopharynx to form a sucking tube which can be inserted into flowers. At the vertex the eyes are widely separated in females, more closely approximated and almost touching in males. Three ocelli are always present, on a distinct ocellar tubercle.

In *Villa* the eyes of the male are closer together than in the female, but do not touch, and the ocellar tubercle is swollen. The rounded head is clearly defined under the scales and short hairs, and both antennae and

proboscis are shorter than in *Bombylius*. About half of the length of the proboscis is taken up by the fleshy labella, and the whole proboscis, when at rest, can be accommodated within the oral cavity. The head of *Phthiria* has a long proboscis (fig. 322), like *Bombylius* as well as a prominent face, which is the more obvious because it is not obscured by hairs. The third antennal segment is broadly spindle-shaped.

THORAX not remarkable, and its structure is largely concealed in *Villa* and *Bombylius*.

ABDOMEN.—In *Phthiria* the abdomen is elongate-oval, relatively bare, and unremarkable. In *Villa* it is also elongate, but oblong in outline, whereas the abdomen of *Bombylius* is broadly oval. In both *Bombylius* and *Villa* the so-called pattern of the abdomen is a superficial one, caused by different colours of hair and scales, and is only rarely and incompletely repeated in the pattern of the sclerites themselves. For this reason the characteristic appearance of a species can be completely lost in a rubbed specimen.

The MALE GENITALIA are being increasingly used to distinguish species of Bombyliidae from one another. As figs. 326–31 show, there are small differences between closely allied species, particularly in the penis and parameres of the complex aedeagus (shown in black). The females have a pair of fringed plates which are probably homologous with the acanthophorites of Asilidae and Therevidae (figs. 217, 255, 324).

LEGS are particularly slender in *Bombylius* (fig. 306), less so in *Villa* and *Phthiria*, though in these genera too the tarsi are conspicuously slender and tapering.

WINGS (figs. 308–14).—The one feature common to Bombyliidae in general is the reduction of the posterior cells of the wing to four, by loss of one branch of the median vein. It is difficult to say with certainty which branch has gone; in many genera which do not occur in Britain reduction of the medius has gone further, and some have even lost the discal cell. The broad division of the family into Homeophthalmae and Tomophthalmae (with *Bombylius* and *Phthiria* in the former and *Villa*, *Anthrax* and *Thyridanthrax* in the latter) is primarily based upon the intact or divided posterior border of the eye, but it is also correlated with a difference in the way that vein R_{2+3} originates from the stem of the radial sector. In Homeophthalmae, R_{2+3} arises at a shallow angle, except Lomatiinae; in Tomophthalmae, R_{2+3} arises close to the crossvein r–m, with a right-angled bend, and often with a short appendix (fig. 308). A similar right angle and appendix often occur at the base of R_{4+5} (fig. 311), but this is of common occurrence throughout the lower Brachycera, e.g. in many Tabanidae.

After the preliminary division into Homeophthalmae and Tomophthalmae, a number of subfamilies are recognized. Some, like Systropinae, are obvious because the body-shape is so characteristic—in this case extreme elongation of the body. Some subfamilies, such as Usiinae and Cyrtosiinae are less clearly defined assemblies of rather heterogeneous genera. Yet others, such as Exoprosopinae, are attempts to break down a large assembly into manageable units.

The subfamily assignments of the few genera found in Britain is as follows:

PHTHIRIINAE: *Phthiria*
BOMBYLIINAE: *Bombylius*
EXOPROSOPINAE: *Villa*: *Thyridanthrax*
ANTHRACINAE: *Anthrax*

Biology

Although adult Bombyliidae are well known from most parts of the world, the life-histories of only a small minority have been investigated. Whereas the adult flies take nectar from flowers—and perhaps pollen, too, in the manner of some Syrphidae (*Eristalis tenax*—see Müller, 1873 : 336–8) the larvae are all, as far as is known, carnivores, parasites, or scavengers among animal debris such as that in the nests of solitary bees. Blair (1920) bred *Bombylius minor* from cells of the bee *Colletes daviesana*.

It is not now thought, as was formerly believed, that the adult fly actively aims its egg into the burrow of the bee. Many observers, including Hugh Scott (1952 : 216), have reported that the female drops her egg on to the ground, often some distance from the burrow of the bee, though she does sometimes strike the ground with the tip of her abdomen, in the act of laying.

The first stage larva is an active, triangulin type, which searches for its food. The one or two later instars are less active, but feed vigorously. Larvae of *Systoechus*, a genus very closely allied to *Bombylius*, are active predators among the egg-pods of locusts, and larvae of *Villa* and *Thyridanthrax* attack larvae of Lepidoptera and pupae of tsetse flies.

It seems likely that the larval prey of Bombyliidae, in general, has no systematic relationship to match the relationship of the Bombyliidae. As with the prey of adult Asilidae, opportunity is probably the most important factor; obviously pupae of tsetse flies are available to *Thyridanthrax* only within the limited range of tsetse flies, in Africa, and must be replaced by something else throughout the rest of the world. In a particular area the simultaneous appearance in proximity of the Bombyliid and of a suitable host may account for such apparently specific predation as that reported by Yarrow (1937), who reported *Thyridanthrax fenestratus* "shadowing" *Ammophila sabulosa* L.

Much more direct observation is needed, however, before any coherent picture can be given of the biology of Bombyliidae.

Key to British Genera

(see also *Glabellula arctica*, discussed later)

1 Proboscis much longer than head, prominently projecting forwards. Posterior margin of eye intact, not indented, nor with a dividing line (figs. 306, 322) Homeophthalmae 2

– Proboscis short and fleshy, recessed into oral cavity. Posterior margin of eye distinctly indented, and usually with a short dividing line (figs. 319–21) Tomophthalmae 3

2 Tiny black flies, with elongate abdomen, not more than 4 mm. long, with clear wings ..... **Phthiria** Meigen (p. 115)

– Much larger, furry flies, with broad abdomen; sometimes with picture wings **Bombylius** Linnaeus (p. 116)

3 Wings with 3 submarginal cells (fig. 313) ..... **Exoprosopa** Macquart (p. 120)

– Wings with only 2 submarginal cells (figs. 308–12) 4

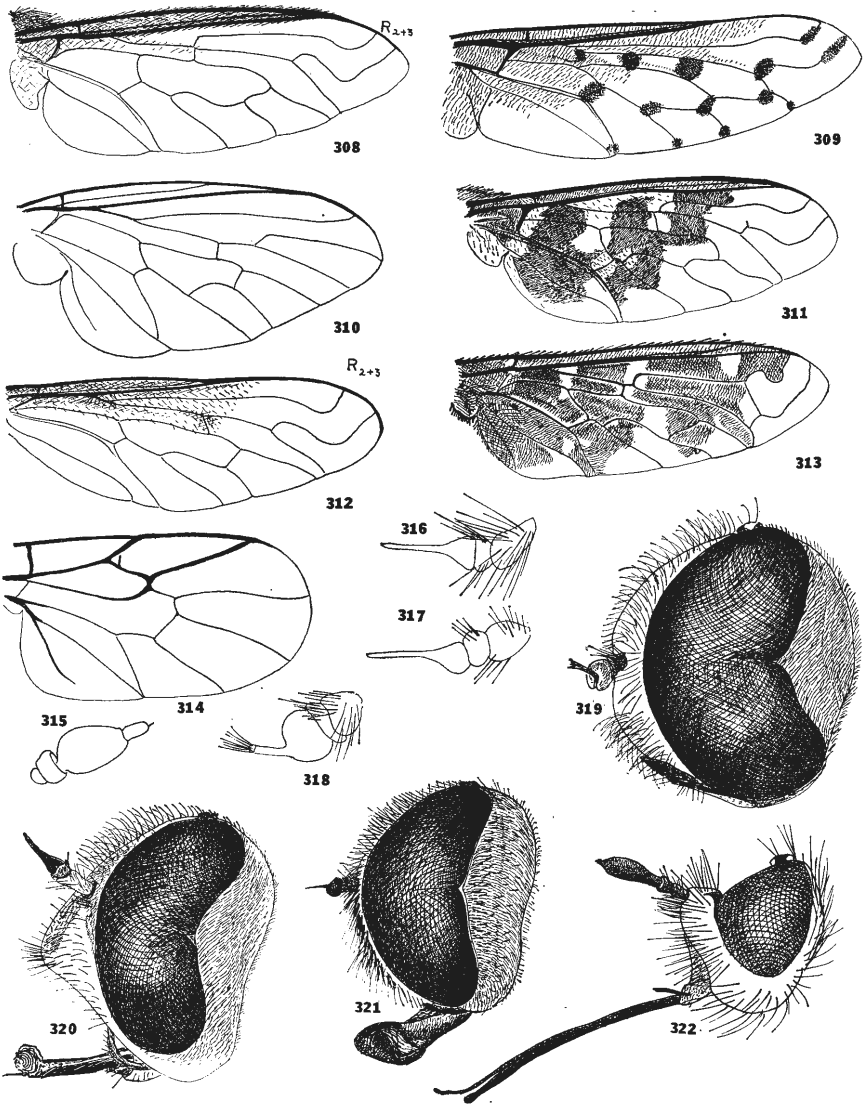
4 Wings clear, except for a little yellow colour in costal cell and nearby 5

– Wings distinctly patterned 6

5 Vein R_{2+3} originating opposite, or close to, small cross-vein (r-m), and bent sharply, almost into a right angle (fig. 308) ..... **Villa** Lioy (p. 117)

– Vein R_{2+3} originating far back, close to origin of R_3 from R_1, and at a very acute angle (fig. 312) ..... **Lomatia** Meigen (p. 120)

6 Wings distinctly fenestrate, i.e. with clear "windows" in the dark areas; radial fork, tip of R_{2+3}, and apex of discal cell all clear (fig. 311). Third antennal segment gradually tapering as in fig. 317 ... **Thyridanthrax** Osten Sacken (p. 119)



FIGS. 308–322.—Bombyliidae. (308–314) wings: *Villa modesta* (308); *Bombylius discolor* (309); *Phthiria pulicaria* (310); *Thyridanthrax fenestratus* (311); *Lomatia lateralis* (312); *Exoprosopa jacchus* (313); *Glabellula arctica* (314). (315–318) antennae: *Glabellula arctica* (315); *Villa modesta* (316); *Thyridanthrax fenestratus* (317); *Anthrax anthrax* (318). (319–322) heads in side view: *Anthrax anthrax* (319); *Thyridanthrax fenestratus* (320); *Villa paniscus* (321); *Phthiria pulicaria* (322).

– Wings more extensively and uniformly darkened. Discal cell entirely dark, as well as base of radial fork, and a brown border at tip of vein R_{2+3}
Anthrax Scopoli (p. 119)

Genus **Phthiria** Meigen, 1803

Distinguished from all other British Bombyliidae—and indeed from nearly all Bombyliidae in the world—by its small size of about 4 mm. Yet this small, black fly is immediately recognizable as a Bombyliid by reason of its head-structure (fig. 322), and by the presence of only four posterior cells in the wing (fig. 310).

HEAD (fig. 322).—With a similar profile in both sexes, the antennae borne forwards on a facial prominence. Males are holoptic, with a triangular supra-antennal region which is almost horizontal; females have the eyes widely separated, and the broad supra-antennal region connects with a frons that is almost twice as broad anteriorly as it is posteriorly. Both sexes have three ocelli. Antennae compact, with short first and second segments and a clavate third, ending in a short style. Proboscis narrow and elongate, almost twice as long as distance from mouthmargin to vertex: labium ends in short labella. Base of proboscis (and palpi) retractable into a large oral cavity, between the very prominent, hairy parafacials.

THORAX strongly humped, with a relatively large scutellum, but small humeral and postalar calli. No very strong bristles, but both sexes have abundant long hairs, some of which are rather bristle-like, and female has short clothing hairs as well (*cf.* Verrall, 1909 : 488). Sterno- and pteropleura strongly developed, pushing middle and hind coxae backwards. Abdomen with eight visible tergites (not seven as stated by Verrall). Long hairs, some of them bristly, extending along hind margins of segments. Male genitalia with divided epandrium and hypandrium, which when closed form an ovoid capsule; open, they reveal a stout aedeagus with coiled tip (fig. 323). Female with simple opening, scarcely developed into an ovipositor (fig. 325).

LEGS.—Thin and relatively long, without any special features. Tibiae with long spicules which are most obvious on hind legs; other clothing hairs sometimes stiff, but not bristly, except on hind coxae.

WINGS (fig. 310).—Venation simple. Anal cell closed, and often petiolate; anterior cross-vein rather long and erect, placed beyond middle of discal cell. A comparison of figures shows that *Phthiria* has none of the venational features that are characteristic of most Bombyliidae, notably the forward-turning of veins R_{2+3} and R_4. These latter, combined with the angulation of the roots of veins, and the appearance of distinct appendices (e.g. in fig. 311) suggest that most Bombyliidae require more support for the fore margin of the wing, and that *Phthiria* does not need this. Perhaps this is reflected in a different flight habit—but no-one knows the habits of these flies sufficiently well to say.

LENGTH only $3\frac{1}{2}$ mm., wings longer than the body.

ONE BRITISH SPECIES

Body generally black-brown, covered with grey dusting, and with some yellow areas. Frons of female with a yellow band along eye-margin, continued on posterior orbit. Sides of facial prominence, beside antennae, dark brown, with a yellow spot, and with stiff black hairs. Ocellar and occipital bristles, beard and lower facial hairs yellow. Thorax dull grey with yellow lateral margins and a yellowish spot on scutellum.

Metapleuron, immediately in front of haltere, entirely yellow. Abdomen ashy grey-brown, more greyish on hind margins of segment. Hairs of thorax and abdomen yellow. Legs dark brown, with hairs mostly whitish, especially on femora. Wings clear, only subcostal cell yellowish.....**pulicaria** Mikan

Coastal sand-dunes from the Channel to N. Scotland, feeding on Compositae. Locally not uncommon. vi, vii.

Genus **Bombylius** Linnaeus, 1758

These are properly called "bee-flies" because the dense, erect pubescence gives them a furry, bee-like appearance (fig. 306). Thorax and abdomen are rounded; head and wings relatively small; legs slender and weak; proboscis elongate. The general appearance is therefore that of an aerial insect, probably flower-feeding, with legs used for alighting rather than for walking.

Males holoptic, females dichoptic, with divergent frons. Proboscis slender, 2–3 times as long as head, held horizontally forwards. Palpi short and inconspicuous. Three ocelli on prominent tubercle. Antennae almost as long as length of eye, with an elongate, awl-like third segment.

Sclerites of THORAX and ABDOMEN obscured by dense pubescence, so that appearance and pattern are those of the tips of the hairs, except for a few areas where close-lying scales may show through the pubescence. Genitalia in both sexes concealed, not fully visible without dissection. Legs slender, femora dilated basally, with long and strong hairs and bristles ventrally in this area. Rest of femora, as well as tibiae, with strong individual bristles, or shorter spicules.

WINGS (fig. 309) rather elongate, and distinctly narrower beyond tip of R_1. R_{2+3} and R_4 sharply turned towards costa, and sometimes with distinct angles, or even adventitious appendages. First posterior cell closed. *Bombylius* is distinguished from some related genera by the position of the anterior cross-vein, which makes the first basal cell distinctly longer than the second. Anal cell narrowly open.

The variation in size among individuals of the same species, which is a common feature in Bombyliidae, is particularly noticeable in *Bombylius*.

Four species are commonly recognized as occurring in Britain, with several others reputed, or potentially British.

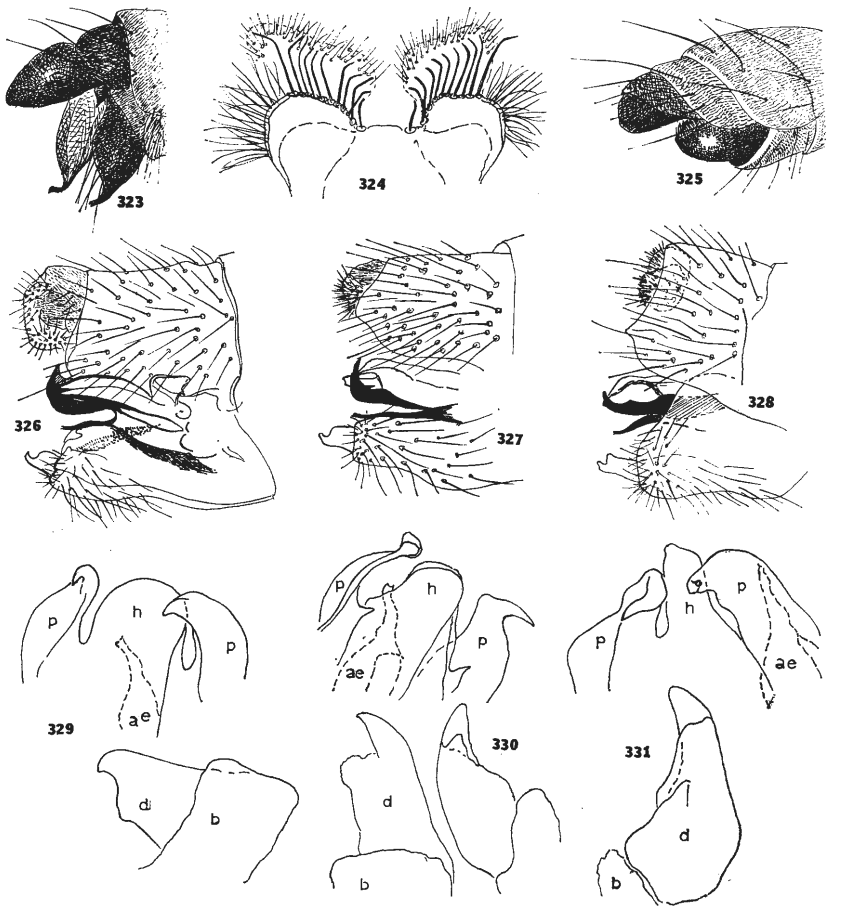
KEY TO SPECIES

1 Wings distinctly patterned or spotted 2
– Wings only indistinctly yellowish towards base 3
2 Wing with a clearly defined black-brown fore-margin (fig. 306)....**major** Linnaeus
England, Wales, and at least southern Scotland. Ireland (Stelfox). In early Spring (late iii to end of v), feeding from low-growing spring plants, primroses, bugle and violets. Usually singly, often moving along over paths and dry patches.
– Wings spotted (fig. 309).....**discolor** Mikan
Southern half of England and Wales, similar habits to B. major. *Mid-iii to mid-v.*
3 Upper cheeks and basal antennal segments with conspicuous black hairs, which also appear in post-ocular fringe.....**canescens** Mikan
Widespread throughout the British Isles, including Ireland and I.O.M. Local. Late v to mid-vii.
– Upper cheeks, basal antennal segments and post-ocular fringe with entirely pale hairs .....**minor** Linnaeus
Much rarer than canescens, *and its distribution inadequately known; Dorset, Studland and Corfe Castle (Andrewes); Devon, Newton Abbott, from pupae in burrow of* Andrena clarkella *(Parmenter). Occurs later, mid-vi to end of viii.*

Genus **Villa** Lioy, 1864

Clear-winged species of *Villa* are among the easiest Bombyliidae to recognize generically, but the most difficult to identify specifically. The shape is entirely different from that of *Bombylius*, with a relatively longer, more spherical head, and the body-hair still dense, but shorter, and mingled with conspicuous scales.

HEAD (fig. 321) more spherical than in *Bombylius*, with the eyes larger, and less concealed among long hairs. Face not noticeably prominent (ignoring short hairs, and comparing with *Thyridanthrax*, fig. 320). Proboscis short, fleshy, capable of being entirely concealed within the oral cavity.



FIGS. 323–331. Genitalia of Bombyliidae: (323) *Phthiria pulicaria* ♂; (324) *Villa modesta* ♀, acanthophorites; (325) *Phthiria pulicaria* ♀. (326–331) males of *Villa*: (326) *modesta*; (327) *circumdata*; (328) *cingulata*; (329) *modesta*; (330) *cingulata*; (331) *circumdata* ae = aedeagus; h = hypandrium; p = paramere; d = dististylus; b = basistylus.

Antennae short, third segment "onion-shaped", i.e. with a basal bulb, abruptly narrowing into a style-like prolongation.

THORAX and ABDOMEN unremarkable in shape; seen from above they are oblong in outline rather than rounded as in *Bombylius*. Covering of long hairs less furry than in *Bombylius*, especially on dorsum of abdomen, where ground colour is clearly visible between relatively sparse long hairs; here a covering of recumbent scales produces a pattern, mainly of black on disc of each segment, with various transverse bands of yellow or white scales. In perfect condition, this pattern would be a great help in identifying species, but in practice pinned specimens are usually very defective, with most of the scales rubbed off. Sides of abdomen with a fringe of tufts of long hair, some of which may be black.

Villa has a few strong bristles, but these may be difficult to distinguish among the long, softer pubescence.

LEGS with the scales perhaps denser and more conspicuous than in *Bombylius*; quite strong spicules present on femora and tibiae; tarsi slender and tapering, with pulvilli reduced, or evanescent.

WINGS distinctly shorter and broader, curves in principal veins more abruptly angular; this is especially true of R_{2+3}, which originates opposite, or close to, anterior cross-vein (r–m), and has a rectangular bend immediately after its origin. These abrupt angles may have a short appendix, perhaps only in one wing of a specimen. Basal comb of wing broad, and well furnished with both hairs and scales.

MALE GENITALIA seem to show some slight differences in shape of parameres, hypandrium and dististylus of clasper (figs. 326–31). Since material for dissection is limited it is difficult to indicate how much variation may occur within one species, and how much the appearance may depend on the angle at which the specimen is mounted. Females with acanthophorites (fig. 324).

KEY TO BRITISH SPECIES

1 Males (eyes touching ocellar tubercle) 2
– Females (eyes distinctly not touching ocellar tubercle) 4
2 Dorsum of abdomen with long, pale hairs and black clothing scales, but with no pale traverse bands of scales; tufts of black and white hairs at tip (*paniscus* Verrall nec Rossi) **modesta** Meigen ♂
– Dorsum of abdomen with bands of light and black scales, clearly visible between the longer hairs 3
3 Fore margin of wing darkened as far back as small cross-vein. Bands of pale scales on fore margin of second and third segments distinct, comparable with those on other segments ..... **circumdata** Meigen ♂
– Wing darkened only in costal and subcostal cells; small cross-vein clear. Bands of pale scales on second and third segments inconspicuous, or almost absent **cingulata** Meigen ♂
4 Brown fore margin of wing extending back to small cross-vein **circumdata** Meigen ♀
Southern half of England, on commons and waste-land. viii.
– Brown margin of wing extending only to costal and subcostal cells 5
5 Third abdominal segment with a distinct basal band of pale scales. Hind tibiae with distinct scales dorsally ..... **modesta** Meigen ♀
Coastal sand-hills in England and Wales, fairly common; rarely in Scotland. vi–ix.
– Third abdominal segment with only traces of a basal band of pale scales. Hind tibiae without distinct scales dorsally ..... **cingulata** Meigen ♀
Rare and local in southern England. vii, viii.

Genus **Thyridanthrax** Osten Sacken, 1886

Both generic and specific names of *Thyridanthrax fenestratus* refer to the more or less rectangular pale patches which occur in the dark area of the wing, and look like windows in a wall. This feature immediately distinguishes *Th. fenestratus* from all other species of Bombyliidae found in Britain, and so for our purposes it is convenient to recognize *Thyridanthrax* as a genus. When more species are compared it becomes difficult to classify the many gradations of wing-marking between this and the clear wings of typical *Villa*, and in both N. and S. America it has long been customary to merge them all into the genus *Villa s. lat.*, using the names *Villa s. str.*, *Hemipenthes*, *Thyridanthrax* and others as subgenera at most.

Besides the fenestrate wing, *Thyridanthrax* is recognized among British Bombyliidae by the prominent, conical face (fig. 320). The body is less oblong than that of *Villa*, but the wing-shape, the tendency for veins to bend at right angles, and the abundant covering of scales are shared by the two genera. Apart from the remote possibility of *Exoprosopa* (see below), any Bombyliid with fenestrate wings that is found in Britain may be assumed to be *Th. fenestratus*, unless there is some definite reason for doubt. One or two other Western Palaearctic species are very similar, and difficult to define *in absentia*, though the differences become apparent when specimens of the two species are placed side by side. For instance, *Th. perspicillaris* Loew has the wings broader and the infuscation paler, while a line of white hairs obliquely on the pleura helps to distinguish the two. Should a specimen be found with any notable differences in wing-pattern from that shown in fig. 311 it should be checked against continental works such as Lindner.

One British Species

Wings as in fig. 311. Body black, but subcallus conspicuously brown with a black basal band (visible, even in good specimens, through the covering of pale scales and black hairs, and often rubbed bare in preserved specimens). Mesonotum rather sombre dorsally, with black hairs, and a few pale scales, but pleura decorated with tufts of yellow and white, silky hairs. Abdomen dorsally black, with many black scales, and somewhat irregular banding of pale scales; venter brown, with scales more orange. Legs black and brown, with close-lying yellow scales. . . . **fenestratus** Fallén

Local, on sandy commons in central southern England, chiefly centering round the New Forest; Surrey, Frensham Little Pond. Wales, Barmouth. vi–end of viii.

Genus **Anthrax** Scopoli

This is one of those old names, like *Asilus* and *Tabanus*, which has been used loosely for a miscellany of species, nearly all of which are now placed in other genera such as *Villa* (above). As the name suggests, *Anthrax s. str.* applies to a small number of very black species, with predominantly black wings, and which are more familiar to European dipterists under the name *Argyramoeba* Schiner.

The most characteristic feature lies in the shape of the antenna, with the third segment ending in a tuft of hairs like a stencilling brush (figs. 318, 319). The only true *Anthrax* which concerns the British fauna is *A. anthrax* Schrank. Unlike other colourful rarities, *A. anthrax* was never a "reputed British species" before being recorded by the late Mr. P. A. H. Muschamp.

ONE BRITISH SPECIES

Can be confused only with *Th. fenestratus*. Abdomen black, with only small patches of white scales on segments 1, 2, 3 and 6. Wings extensively dark, without obvious fenestrae, and with several veins strongly rectangular. Alar squamae with white scales ..... **anthrax** Schrank

Known as British only from two specimens, caught singly in different years by P. A. H. Muschamp. Leicestershire: Woodhouse, ix.1929*; Cocklow Quarry, Mountsorrel,* 3.vii.1930 (*in H. W. Andrews coll. and in B.M.*).

Genus **Lomatia** Meigen, 1822

This is a reputed British genus, which is included in this work because one day it may be discovered here. *Lomatia* is a genus of rather small Bombyliids (body 8 mm.; wing 7 mm.), with spherical head; body rather like a sawfly, with yellow-banded abdomen; and long, paddle-shaped wings arising from a narrow base.

Lomatiinae are Tomophthalmae, with the posterior margin of the eyes very heavily notched, but are distinguished from other Tomophthalmae by the oblique origin of R_{2+3}, as shown in fig. 312. The subfamily occurs throughout the world, and includes a group of interesting genera (*Comptosia* and its allies) which have a "Gondwanaland" distribution in New Zealand, Australia and S. America. *Petrorossia*, a tropical genus, is characteristically to be found hovering over paths and bare patches of ground, much as *Bombylius major* does in this country.

Verrall (1909 : 761–2) refers to persistent rumours that *Lomatia lateralis* used to occur occasionally on sand dunes on both sides of the Bristol Channel. This is not one of the species figured by Stephens, yet I agree with Verrall that it should be regarded as a possible capture in Britain. Though *lateralis* is the most likely species to come over here there are related species that are not easy to separate without specimens for comparison. For the purposes of this present volume it is sufficient to draw attention to the distinctive venation of *Lomatia*: should any Bombyliid with this venation, and the general appearance of a sawfly, be captured in the British Isles it would be an important addition to the British List.

Genus **Exoprosopa** Macquart, 1840

Exoprosopa is one of the big genera of Bombyliidae, in its wide distribution, in numbers of species, and in the physical size of many individuals. Recognition is easy, since the appendix veinlet at the angle of R_{4+5} connects back with R_{2+3}, giving three submarginal cells (fig. 313). A number of species have a further cross-vein in this region, making four submarginal cells: these form a subgenus or genus under the name of *Hyperalonia* Rondani, or *Ligyra* Newman, according to the views of the specialist concerned.

Exoprosopa resembles other genera of Diptera that flourish in the tropics and subtropics, and dwindle away in mid-temperate regions. It is mentioned here because *E. jacchus* Fabricius is a reputed British species (Verrall, 1909 : 762). It was listed by Walker and Newman, and beautifully figured by Stephens (1846 : 27, pl. 46, fig. 4) as *Anthrax pandora* F. Once again, the coloured drawing is so precise in detail that it must clearly have been made from a specimen, and a well-preserved one at that.

This species is included in the present *Handbook* because it could easily be confused with *Th. fenestratus*, though abundantly distinct on direct comparison (figs. 311, 313). It would be a notable addition to British Bombyliidae if this, or any other *Exoprosopa*, could be taken here.

ONE REPUTED BRITISH SPECIES

A small, black fly (body 8 mm.; wing 10 mm.) with heavily patterned wings as in fig. 313 (compare with *Th. fenestratus*, fig. 311); note different venation at wing-tip, with additional crossvein forming three submarginal cells, and extension of dark colour into tip of marginal cell.....**jacchus** Fabricius (*pandora* Meigen, nec Fabricius)

One specimen in British Museum from Stephens' collection: "taken near Dover, in July." Verrall (1909 : 762) *reports that the same species was said to have been taken in the West Country.*

A NOTE ON **Glabellula arctica** Zetterstedt

This is a strange little black fly, only 2 mm. long, and therefore smaller than *Phthiria pulicaria*. It has never been recorded from the British Isles, or even from adjoining parts of Europe, and its known distribution is confined to Northern Europe and Siberia. Other species of *Glabellula* occur in Asia, including Asia Minor, and *G. unicolor* Strobl occurs in Spain.

Glabellula is mentioned here because it is possible that it might persist as an Ice Age relict, and have been overlooked because of its very small size. Any tiny black fly that is swept from mountain pastures in Scotland or Wales should be carefully examined. The Bombyliid head and the characteristic venation (fig. 314) should identify it.

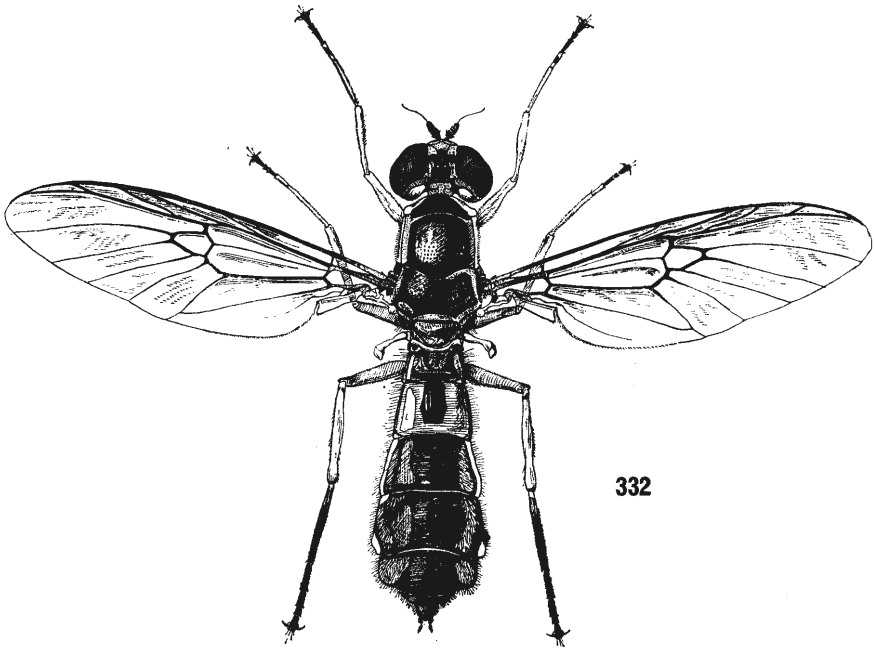


FIG. 332.—*Sargus bipunctatus* ♀.

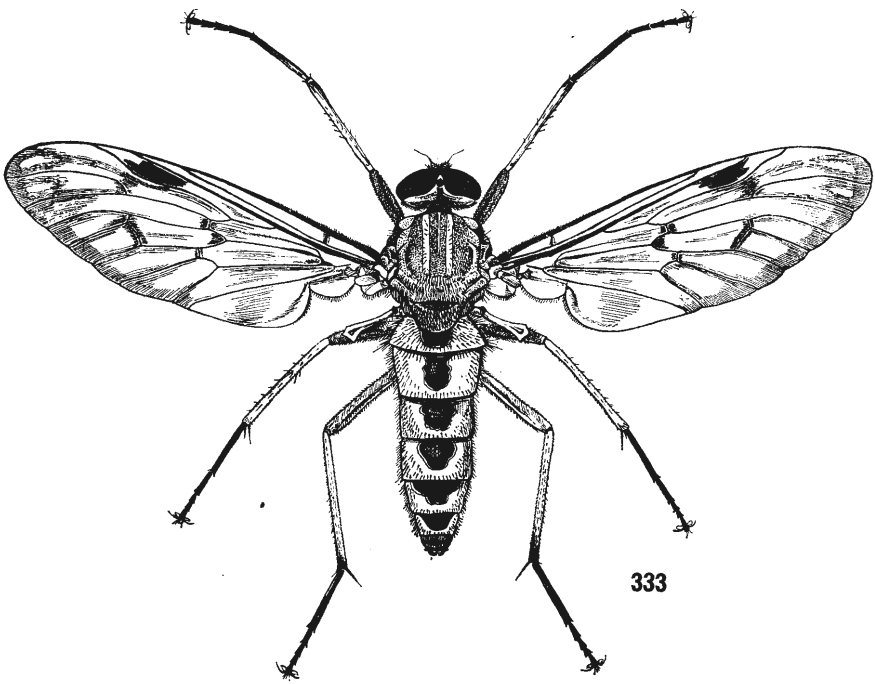


FIG. 333.—*Rhagio scolopaceus* ♂.

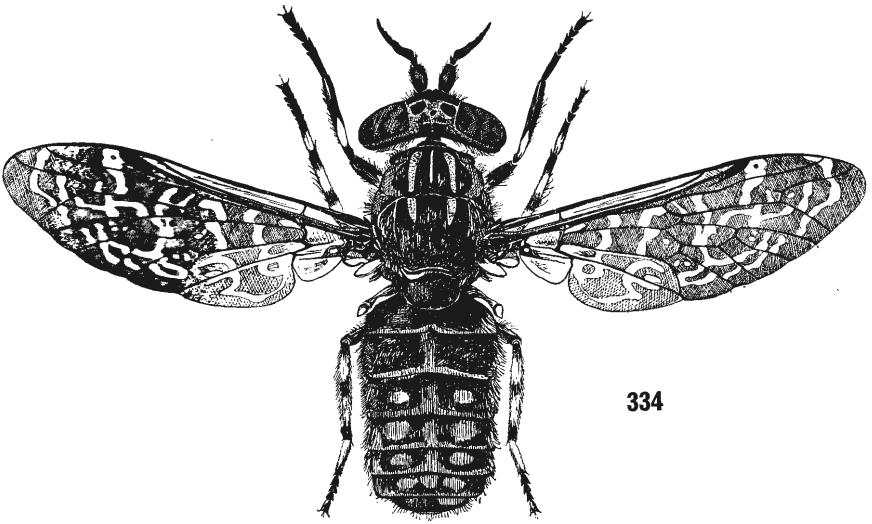


FIG. 334.—*Haematopota crassicornis* ♀.

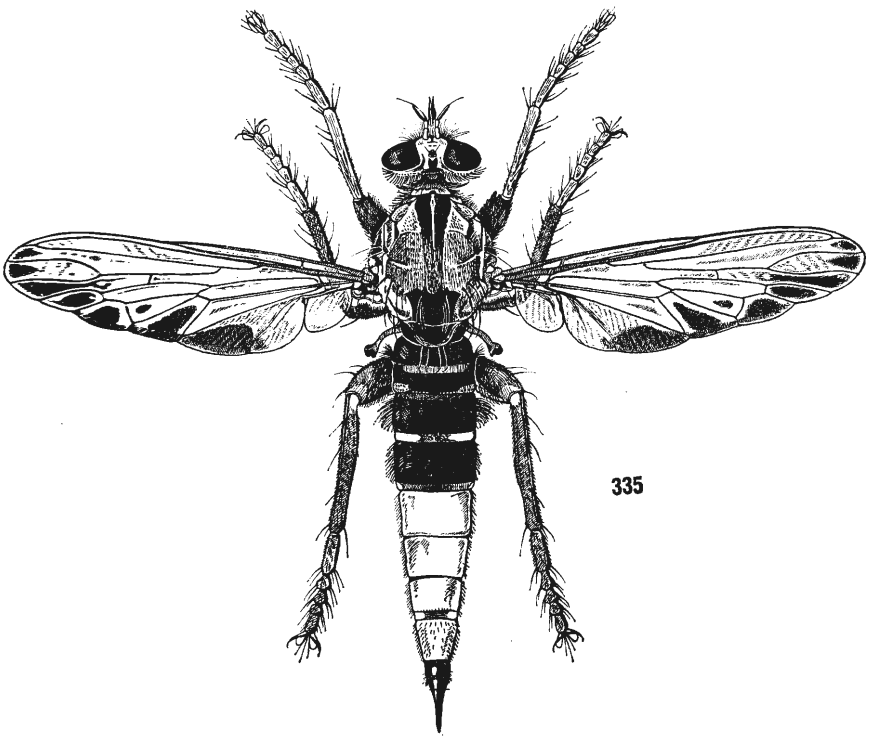


FIG. 335.—*Asilus crabroniformis* ♀.

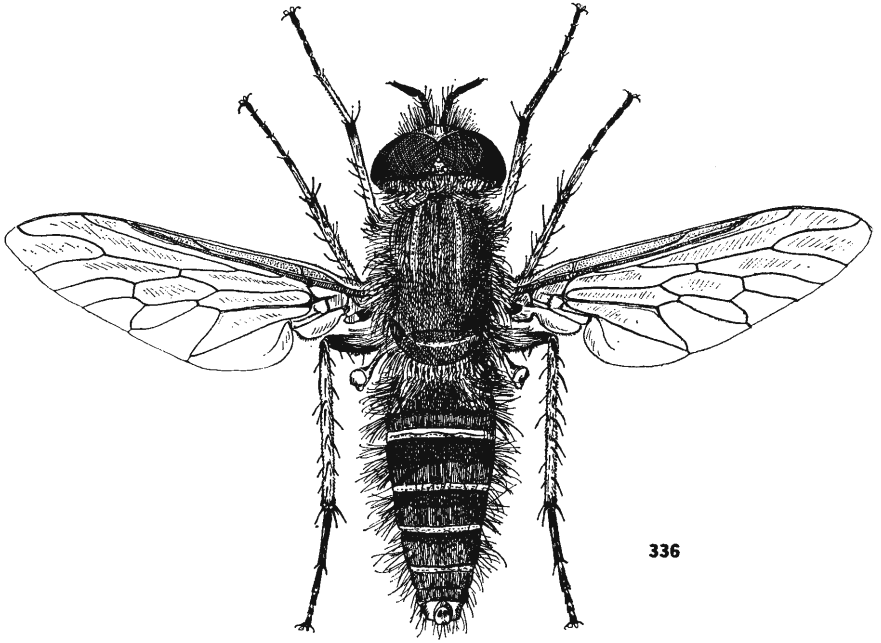


FIG. 336.—*Thereva nobilitata* ♂.

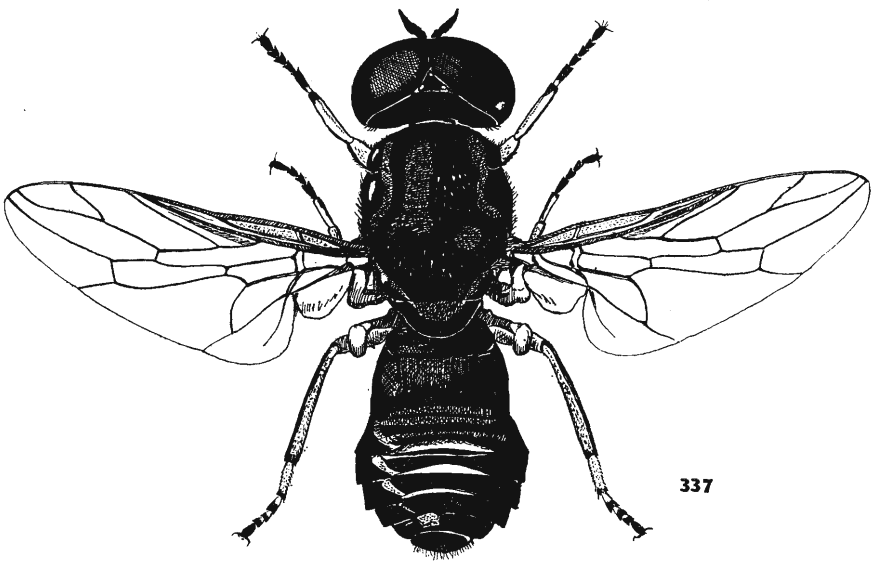


FIG. 337.—*Scenopinus fenestralis* ♂.

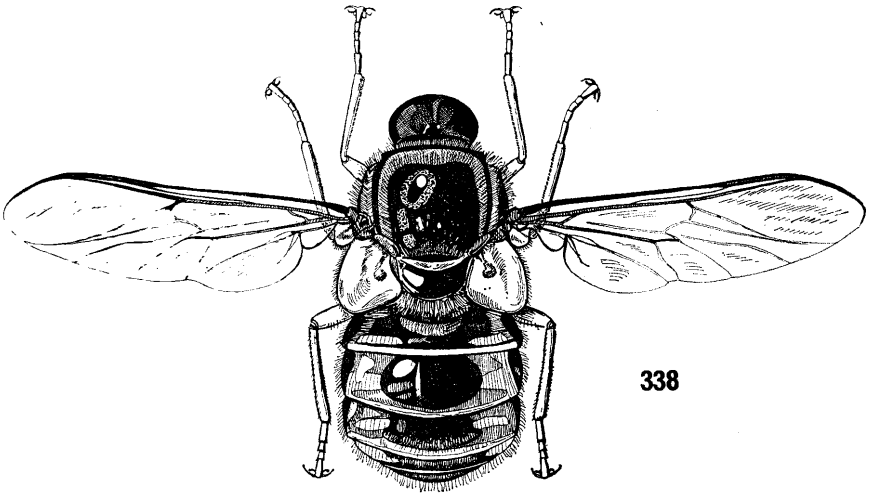


FIG. 338.—*Ogcodes gibbosus* ♂.

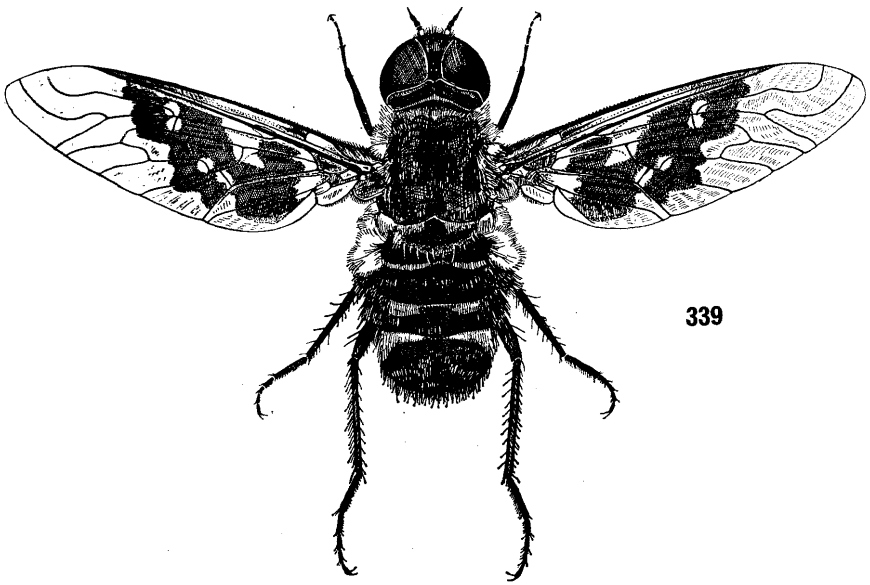


FIG. 339.—*Thyridanthrax fenestratus* ♀.

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3. The genus *Solva* Walker (*Xylomyia* Rondani). 1961, **94** : 202–5.
4. The genus *Atherix* Meigen (Rhagionidae). 1961, **94** : 218–20.

(5. Platypezidae; 6. Bibionidae.)

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(8. Chaoboridae; 9. Ptychopteridae.)

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(11. Trichoceridae & Anisopodidae.)

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