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## MAP RECORDING OF BRITISH INSECTS

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As announced last June, the British Trust for Entomology is conducting a pilot scheme for the map recording of British Insects. The species chosen for the first attempt are *Aphantopus hyperantus* (L.), the Ringlet; *Pararge aegeria* (L.), the Speckled Wood; *Lysandra bellargus* (von Rottenburg), the Adonis Blue; *L. corydon* (Poda), the Chalk Hill Blue; *Tettigonia viridissima* L.; the Great Green Grasshopper; and *Leucorrhina dubia* (van der Linden), the White Faced Dragonfly.

The records should be entered on special cards such as the one enclosed in this issue of the *Entomologist*. As far as possible, two names should be given for the identification, one being the collector and the other a confirmatory signature. In the "LOCALITY" column grid references and vice county numbers would be welcome, and under "HABITAT" any remarks on the type of terrain or any observation throwing light on the localisation of a species would be valuable.

The time is now with us when we are sure you can spare a little time for what promises to be an interesting project. Results and maps will be published as they become available. If everyone helps, an almost complete picture of the *present* distribution of these insects, and changes which have occurred in past years, may be obtained. Jot down on the cards just where and when you have seen these species—we shall be delighted to hear from you.

Fresh supplies of cards are available from the undersigned, but please enclose a stamped addressed envelope—this last sufficiently large to suit your requirements.—F. HEWSON, 23 Thornhill Drive, Gaisby Lane, Shipley, Yorkshire.



# TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

VOL. 14

NOVEMBER 1960

PART III

## THE LARVAE AND PUPAE OF THE BRITISH TIPULINAE (DIPTERA : TIPULIDAE)

By ALLAN BRINDLE, F.R.E.S.  
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### 1. Introduction

Since the classical work of Beling (1873, 1878, 1886), who described the larvae and pupae of 39 European species of the Tipulinae, comparatively little attention has been paid to the taxonomy of the immature stages of this subfamily. Beling included a key to certain species, but no figures were given, and in some cases the descriptions were insufficient to separate closely related species. A few of the descriptions were based on mis-identifications of the adults which were reared.

Further descriptions of larvae and pupae have been published since the time of Beling, and for these reference should be made to the bibliography of Alexander (1920) and Hennig (1950-52). The first recent attempt to provide a key to the larvae of the British Tipulinae was made by J. R. Chiswell (1956) who described 36 species. A short illustrated key to 44 species of the genus *Tipula* was published more recently (Brindle, 1958). A short time ago I received from the author a copy of an account of the larvae and pupae of the West Palaearctic species of the Tipulinae by Theowald (1957), in which most of the British species were figured. Although the keys provided extended down to species groups only, it is a valuable publication; in particular, the author used the number of sternal spines on the pupae as a taxonomic character, which has been used in the present keys.

This paper includes 62 species of the subfamily, and includes all the larvae and pupae known, except for a few species, which are dealt with in the check list on pp. 111-113. The keys, in general, extend down to species, but it has not been found possible to separate a few closely related larvae and pupae. In particular, the female pupae of *Nephrotoma* are not keyed out; this genus is most difficult to separate in both larvae and pupae, but it is hoped to deal with it in detail in a future paper.

The figures have been prepared from *camera lucida* drawings of specimens killed by immersion in hot (60-70°C.) water, followed by preservation in Pampel's fluid. All the material studied has been obtained from the counties of Lancashire, Yorkshire, and Westmorland.

The figures of the anal segments of the larvae are usually drawn from a posterior view, but the ventral lobes have been shown depressed in order to illustrate the pigmentation. Normally, except for the aquatic species, the ventral lobes are directed backwards, horizontally or slightly dorsally. The marginal hairs of the spiracular disc or the lobes are not shown unless they are useful in taxonomy. No setae found on the anal segments are shown (except in fig. 22), since the scale of the drawings is too small for adequate representation. They are not, however, necessary for identification apart from the one exception quoted.

The figures of the pupae illustrate the eighth abdominal segment from the left side. Special features, such as the respiratory processes, are included where necessary. The spines are sometimes malformed, but the characters chosen for the key have been checked in a series of pupae and pupal exuviae in most cases and appear to be reasonably constant. Many characters, however, are very comparative, and Table 1 has been compiled in order to assist determination.

Three main methods have been used to collect the larvae.

- (1) Sieving: Wire mesh sieves, with a mesh of 16 to the inch, have been used to obtain larvae from soil near water. The soil is sieved in the water, when the solid matter is lost through the mesh, and the larvae retained. In sandy soils this method is extremely quick; in peaty soils too much debris is left behind in the sieve, but this can be dealt with by the flotation method. The larvae normally curl up, so even small larvae can be obtained by this means, though active ones can crawl through the mesh, where they may be recovered from the lower surface of the sieve. This method—though most useful—is restricted to the neighbourhood of free water, i.e., streams or ponds.
- (2) Orthodichlorobenzene: This method relies on the interference with the respiration of the larvae in the soil so that they come up to the surface. About  $\frac{1}{2}$  oz. of Orthodichlorobenzene is added to one gallon of water and poured over one square yard of soil. Any vegetation is cut down so that the larvae

can be seen when they surface, usually during half an hour after the mixture has been applied. The liquid orthodichlorobenzene is immiscible with water so the addition of a little liquid detergent is recommended. This produces a milky liquid which penetrates the soil well, providing the latter is porous. In marsh soil the water table is so high that the penetration of the solution is not sufficient. The strength of the solution can be varied a little, but more than 1 oz. per gallon can be fatal to the larvae.

- (3) Flotation: This method takes advantage of the specific gravity of the larvae which is only slightly greater than that of water. The addition of a little salt to a dish of water containing larvae will cause the latter to float. In practice, magnesium sulphate, at the rate of one pound per gallon of water, is used. The soil to be sampled is put into this solution and stirred thoroughly and gently, when any larvae present will float to the surface. This method is suitable for small larvae which are not easily seen in a sieve or on top of soil.

The larvae of the Tipulidae are usually long and cylindrical, with the head capsule massive and heavily sclerotised, or much dissected, and capable of being retracted within the prothorax. They often possess fleshy lobes around the spiracular disc, retractile anal papillae adjacent to the anus, and the respiration is metapneustic. The pupae are generally long, rather parallel-sided, and often possess projecting respiratory processes on the prothorax. The larvae and pupae of the three subfamilies of the Tipulidae may be separated as follows:—

#### *Larvae*

1. Spiracular disc with six anal lobes, the lobes flattened, cylindrical, sometimes reduced in size, rarely entirely sclerotised ..... Tipulinae.
- Spiracular disc with five or fewer anal lobes ..... 2
2. Body with prominent processes, either very long and filiform, or shorter and toothed or tuberculate, at least as long as half width of body. Larvae sluggish .....
- Cylindrotominae.
- Body smooth, without prominent processes, if tubercles are present they are small, not a quarter width of body. Larvae usually active .....
- Limoniinae.

#### *Pupae*

1. Sheaths of maxillary palpi recurved at apex; pupae with rows of small spines near posterior border of abdominal segments, no spines being very prominent ..... Tipulinae.
- Sheaths of maxillary palpi straight or slightly curved; pupae with or without spines .....
- 2

2. Pupae with pairs of long spines on abdominal tergites, at least on sixth tergite, the length of the spines at least equal to half width of pupae ..... *Cylindrotominae pars* (*Triogma*, *Diogma*, *Phalacrocera*).
- Pupae without pairs of long spines ..... 3
3. Mesonotum with a pair of flattened lobes directed cephalad; pupae attached to plant stems with last larval skin .....
- ..... *Cylindrotominae pars* (*Cylindrotoma*)
- Mesonotum without flattened lobes; pupae not free on plant stems ..... *Limoninae*.

## 2. Larval Characters

### *General*

The larva of the subfamily form a very homogenous group, being usually cylindrical, rarely depressed, with a tough, unpigmented cuticle. The cuticle is usually covered by short pubescence, the colour of which determines the colour of the larvae. If the pubescence is somewhat sparse, the larvae may appear translucent, as in *T. irrorata* Macq.; when the pubescence is totally absent, as on the abdominal segments of *T. flavolineata* Mg., the larvae is partially transparent so that the contents of the gut are visible. The pigment of the fat body seen through the cuticle is also visible so that the general colour of *flavolineata* larvae is white, and *irrorata* larvae may have a pinkish tint. In most species the pubescence is dense. The general colour varies with the type of soil in which the larvae occur, so that *T. lateralis* Mg., has larvae varying in colour from light yellowish-brown (from sandy soils) to dark grey (from clay soils). In some larvae, for example, the *lateralis* group (*lateralis* Mg., *montium* Egg., *couckeii* Tonn., *solstitialis* Westh.), longitudinal stripes of darker pubescence occur along the dorsum, and in others, such as the subgenus *Lunatipula* Edw., narrow transverse stripes of darker pubescence occur both dorsally and ventrally, the pleurae usually being unicolorous. In a few species dense tufts or bands of hairs on the anal segment form useful taxonomic characters, as in *T. varicornis* Schum., and *T. pruinosa* Wied.

Setae are arranged in a generally uniform pattern across the abdominal segments near the posterior border, both dorsally and ventrally; on the pleurae the setae occur both on the anterior and posterior halves of the segments (figs. 1, 2, 3). The setae are usually short, fine, and inconspicuous, but in *T. pabulina* Mg., they are very strong, though short, and project from raised tubercles on the abdominal segments. This larva thus feels spiny when handled. J. R. Chiswell (1956) has dealt adequately with the chaetotaxy of the larvae and further details can be obtained by reference to this publication.

The head capsule is massive and retractile, and probably has been derived from a primitively eucephalous non-retractile type such as occurs in the Ptychopteridae, Anisopodidae, etc.



The body consists of three thoracic and eight abdominal segments, the last abdominal being referred to as the anal segment. This segment provides the chief characters used in the identification of the larvae.

The respiration is characteristically metapneustic, with one pair of functional spiracles borne on the truncated end of the anal segment. The two dorsal tracheal trunks are often visible through the cuticle as two undulating whitish lines along the dorsum. The truncated end of the anal segment is separable into two parts, the upper part or spiracular field, and the lower part or anal field, the two portions being separated by a pigmented band (fig. 4). These two fields are usually in a plane at right angles to the longitudinal axis of the body (fig. 7); in the wood-feeding larvae, on the other hand, the plane of the spiracular and anal fields is at an angle with the longitudinal axis of the body, so that the anal field is produced posteriorly (fig. 8), the anal papillae acting as "pushers" to assist the larvae to travel along the tunnels in the dead wood in which they live. In aquatic larvae the plane of the spiracular disc only is inclined at an angle to the longitudinal axis of the body, and the anal field is completely ventral (fig. 9); when the larvae are horizontal, dorsal side uppermost, the spiracular disc points upwards, assisting the larvae to obtain air whilst immersed in water.

#### *Spiracular Field*

The spiracular field consists of the spiracular disc with the two spiracles, and the anal lobes. The disc is glabrous and varies in extent. In *T. pabulina* Mg., the glabrous area is restricted and just encloses the spiracles but extends on to the surface of the ventral lobes (fig. 41); in other species it is more extensive, reaching the bases of the lobes in *T. lunata* L. (fig. 30), and the tips of the lobes in *T. lateralis* Mg. (fig. 53); in *T. flavolineata* Mg. (fig. 14), the whole of the anal segment is glabrous.

The spiracles vary in size and shape, being large and circular in *T. melanoceros* Schum. (fig. 58) and comparatively small and elliptical in *Tanyptera atrata* (L.) (fig. 15).

The lobes are invariably six in number, consisting of the dorsal, lateral, and ventral pairs (fig. 4). This number is characteristic of the Tipulinae since no other larvae of the Tipulidae have more than five lobes. The ventral lobes are the most constant in size and shape, but the pigmentation varies, and this is useful in identification of certain larvae. The ventral lobes are generally directed backwards, horizontally or slightly dorsally, but in the aquatic larvae they are directed ventrally so that all the lobes are widely spread. The dorsal and lateral lobes are much more variable. They vary from the cylindrical, papillae-like processes of *Nephrotoma* and the reduced lobes of *Tanyptera* to the broad, flattened structures which are more typical of the genus *Tipula*. They are sometimes unpigmented, but more usually have dark margins or sclerotised patches, the

latter feature being well shown in the subgenus *Lunatipula*, where most of the dorsal lobes is sclerotised and produced apically into forwardly projecting hooks (fig. 7). In the extreme form, *T. livida* v.d. Wulp. and *T. juncea* Mg., the entire dorsal and lateral lobes are sclerotised and form long curved spines (fig. 31).

The spiracular disc can be withdrawn so that the anal lobes close over the disc forming a spiracular chamber. This serves to protect the spiracles against the ingress of soil particles but is evidently not used to prevent the ingress of water. When the larvae are immersed in water the lobes and disc are fully expanded, the ingress of water being apparently prevented partly by the hydrofuge hairs which surround the disc and partly probably by a glandular secretion covering the disc. The disc is often margined with hairs which may extend close around the spiracles, as in *Dolichozepe albipes* Stroem. (fig. 10), when the disc is restricted in size, or extend around the borders and tips of the lobes as in *Prionocera turcica* (F.) (fig. 56). The hairs are usually short, being very long only in the aquatic type of larva.

#### *Anal Field*

This consists of the anus and anal papillae, and is almost invariably separated from the spiracular field by a pigmented band. In the subgenus *Vestiplex* Bezzi (figs. 33, 36, 37), the anus is also separated from the anal papillae by a similar band. The anal papillae are primitively four in number and are rounded; this being the type in most species. The four papillae consist of the ventral and the lateral pairs (fig. 4). The anal papillae apparently serve an osmo-regulatory function and their development from the rounded type to long finger-like processes found in some larvae is correlated with the wetter habitats which the latter favour. A table illustrating the correlation between the type of anal papillae and the water content of the environment will be found in Brindle (1957). Though exceptions occur, each type of environment sampled for larvae will provide generally the species with the same type of papillae, e.g., woodland soil provides species with four rounded papillae; marsh soil provides species with four or six long papillae; and the larvae of *T. maxima* Poda and *T. fulvipennis* Deg., which have eight papillae, two pairs of which are very long, are sometimes found freely aquatic in small rivulets, though the lobes do not possess the very long hairs associated with the aquatic type of larva. The lateral pair only is elongated in *T. paludosa* Mg. (fig. 4). The anal papillae are contractile and are fully expanded, when the larvae are immersed in water. They are usually, but not always, fully expanded when the larvae are preserved by the method referred to before.

It is possible that some species may be dimorphic with regard to the anal papillae. Previous authors, quoted by Chiswell (1956) state that the larvae of *T. paludosa* Mg., *T. oleracea* L., and *T. czizeki* De Jong, are indistinguishable. All the larvae of the last

two species reared in connection with this study have been readily identified by the four elongated anal papillae (figs. 49, 50). The larvae of *T. paludosa* (fig. 4) has only the lateral pair elongated. This possibility of dimorphism should be borne in mind when this part of the larvae key is used. *T. pagana* Mg., also exhibits some variation. Most larvae of this species obtained from soil, and mosses on soil, in woods, have possessed four rounded papillae with small protrusions which suggested a possible affinity to the other moss-feeding larvae, which all have eight small pairs. Further specimens from semi-aquatic moss (*Hypnum*) on moors, have the eight small papillae fairly clearly distinguishable. This species, therefore, has been keyed out twice.

### *Specialisation*

Amongst the larvae of the sub-family, those of the genus *Nephrotoma* are the least specialised; all the larvae of this genus are very similar with regard to the anal segment, and since this is the chief structure used in taxonomy their identification presents some difficulty. The couplets given in the keys are by no means satisfactory since so many depend on a single comparative character.

This lack of specialisation in *Nephrotoma*, however, in a subfamily which exhibits a number of interesting specialised features, suggests that this genus should be regarded as having the more primitive larval type. The typical habitat of *Nephrotoma* larvae is damp soil, and this type of habitat could be regarded as the more primitive one.

It should be remembered, however, that the term "primitive" is used in a somewhat relative manner. The larvae of the Tipulinae are metapneustic, with one pair of functional spiracles on the anal segment. The usual type of respiration in Diptera larvae appears to be amphipneustic, with an additional pair of spiracles on the prothorax. It would appear that the metapneustic type has been derived from the amphipneustic type by the reduction of the prothoracic spiracles, and this reduction would appear to be most useful in aquatic larvae, since only the anal pair of spiracles would need to be protected, and only the anal segment would have to be thrust above the water surface to obtain air. For further discussion on this point, reference should be made to Theowald (1957) in which more evidence for the aquatic primitive larva is given.

It appears to be difficult, however, in reviewing the structure of the larvae of the Tipulinae, to form an idea as to the course of development from a hypothetical primitive aquatic type to the predominantly terrestrial types at present existing. The present aquatic larvae are greatly modified by the inclination of the spiracular disc to the horizontal, by the long marginal hairs of the widely spread anal lobes, and by the elongation of the anal papillae. Such larvae are *P. turcica* (F.), *T. luteipennis* Mg., *T. melanoceros* Schum., and *T. cheethami* Edw.

If the larvae of *Nephrotoma*, together with the typical habitat of damp soil, are taken as the more primitive type, an interesting series of developments have taken place in the rest of the sub-family, apparently along four main lines:—

- (a) In the larvae which have continued to inhabit damp soil, there has been a tendency to develop sclerotisation of the dorsal and (to a lesser degree) of the lateral anal lobes. If the series below is considered it is seen that the dorsal lobes undergo a steady increase in the degree and extent of sclerotisation:—

*T. nigra* — *T. hortulana* — *T. nubeculosa* — *T. vernalis*  
— *T. fascipennis* — *T. lunata* — *T. livida*.

In *T. lunata* L., most of the dorsal lobes have been sclerotised and, as in all the members of the subgenus *Lunatipula*, end in forwardly projecting hooks (fig. 7). In *T. livida* v.d. Wulp, the extreme form is reached by the conversion of both the dorsal and lateral lobes into long curved spine-like processes. The sclerotisation of the lobes evidently serves to stiffen them and presumably produces a more efficient protection for the spiracles against the ingress of soil particles. In *T. livida* the development appears to be rather retrograde, and the use of the dorsal hooks is obscure.

In this series, which might be lengthened by the inclusion of other species, the anal papillae are constant, being of the presumed primitive type, i.e. with four rounded papillae.

- (b) In the larvae which have invaded steadily wetter soils, the lobes of the anal segment are never heavily sclerotised, usually with no more than dark borders to the sides of the anal lobes. In certain *Limnophila* larvae living in very wet soils, and which also have a dark border to the anal lobes (e.g. *L. nemoralis* Mg.) each lobe can be folded slightly lengthwise down the mid-line, the lobes when closed in towards each other forming a cup-like chamber which serves to contain air. By analogy it would appear that the Tipuline larvae in wetter soils would benefit from such a feature, and that complete sclerotisation of the lobes would prevent the folding down the mid-line. In almost all cases at least a middle line is totally unsclerotised on the dorsal and lateral lobes.

The anal papillae, however, show a steady increase in size and number. The series is:—

*T. nigra* (four rounded papillae)

|  
*T. unca* (the lateral pair of anal papillae elongated, the ventral pair rounded)

|  
*T. vittata* (all four papillae elongated)

|

*T. pruinosa* (four elongated papillae, with a small additional postero-ventral pair)

|

*T. lateralis* (six elongated papillae)

|

*T. maxima* (eight anal papillae, two pairs being very long)

In view of the osmo-regulatory function of the anal papillae, this increase in size and number in larvae inhabiting wetter soils would be expected.

It should be noted, however, that the larvae of a few widely distributed species can inhabit very different types of habitats, such as the common *T. paludosa* Mg., which is so common in pasture soils. These larvae also occur in damp woodland soil, in marshy soils, and even in aquatic mosses in running water.

- (c) In the larvae which have invaded dry hard dead wood, probably by way of detritus and fragmentary soft decayed wood, the lobes have been reduced in size, the anal papillae produced posteriorly to act as "pushers", and the pubescence on the cuticle reduced in amount. The series is:—

*D. bimaculata* — *C. pectinicornis* — *C. ornata* — *T. flavolineata* — *T. atrata*.

The last two species favour harder wood than the others, and are almost entirely glabrous. *T. irrorata* Macq. might be included at the beginning of the series since it is usually associated with soft decayed wood or detritus. The pubescence on the cuticle of this larva is much more sparse than the pubescence on the larvae of its close relatives, *T. hortulana* Mg. and *T. variipennis* Mg., which are always found in woodland soil.

- (d) In the larvae which have invaded mosses, the development has been less distinct. The lobes are rarely sclerotised, the anal papillae always eight, in four pairs, and they are the smallest of the Tipulinae. The series is:—

*T. pagana* — *T. signata* — *T. marmorata* — *T. rufina* — *T. subnodicornis*.

*T. pagana* Mg., mentioned previously, often appears to have four rounded papillae, but in some specimens the differentiation into four pairs of small equal papillae appears clearly. This larva is found in soil under moss (*Mnium*) in woods and in the moss itself, also occurring in moss (*Hypnum*) on moors. The next two species, and their relatives, are closely similar. *T. rufina* Mg. has the borders of the anal lobes slightly sclerotised, whilst *T. subnodicornis* Zett. has the surface of the lobes sclerotised and they appear reddish brown. The last species together with the similar *T. macrocera* Zett. are confined to moorland mosses.

Convergence has apparently occurred in several cases. In *T. cheethami* Edw., which lives in aquatic mosses, the anal papillae agree with those of the other moss-feeders, but the spiracular disc has long marginal hairs similar to those of *T. luteipennis* Mg. and *T. melanoceros* Schum.

The latter two species would appear to be most readily derived from a larva such as that of *T. lateralis* Mg., which possess the same number of anal papillae.

*T. pabulina* Mg. and *T. truncorum* Mg. are unusual in that they possess tubercles on the abdominal segments, a feature which occurs elsewhere in the Tipulidae in the *Cylindrotominae*, where the abdominal segments have short processes in *Cylindrotoma*, tooth-shaped processes in *Diogma* and *Triogma*, and long filiform appendages in *Phalacrocera*. Small tubercles also occur in some *Limoniinae*, e.g. in *Dactylolabis*.

### 3. Pupal Characters

#### *General*

The pupae of the Tipulinae (figs. 68-71) are greenish, yellowish, brownish, or blackish in colour, sometimes with an undulating lighter band along the pleurae, which may extend along the segmental borders. They are rather long in proportion to the width and are parallel-sided. They possess eight abdominal segments, most being clearly defined, the three thoracic segments are fused together. Anteriorly a pair of respiratory processes project from the prothorax outwards and slightly dorsally. Posteriorly the pupae are truncate in the male and pointed in the female, the latter feature being due to the sheaths of the cerci and sternal valves. The abdominal segments are furnished with spines which are larger on the sternites and they increase in size posteriorly. Two small spines are often present on the dorsum of the thoracic segments. The wing sheaths extend down to the posterior border of the second abdominal sternite. The leg sheaths lie side by side between the wing sheaths ventrally, the outer leg sheaths underneath those of the wings. They extend down to the posterior border of the third abdominal sternite in the female, and usually to the middle of the fourth sternite in the male. The antennal sheaths lie alongside the wing sheaths, and just below the eyes are the sheaths of the maxillary palps, which are always re-curved at the apex.

The pupae are found in or near the habitats of the larvae concerned, ranging from soil, dead wood, to mosses. The duration of the pupal stage varies from one to two weeks depending to some extent on the climatic conditions. When the adult is about to emerge, the pupa works its way up through the substratum by means of the abdominal spines and rests with its anterior half exposed and erect; the posterior half remaining fixed in the substratum by means of the posterior spines. The thorax of the adult first emerges by a longitudinal split in the

pupa skin, the head is freed and the withdrawal of the legs and abdomen commenced. This is accomplished by the head and thorax of the adult being moved gradually forward and slightly downwards, so that if the anterior half of the pupa is erect, the insect finally holds itself horizontally. The legs and abdomen are finally freed, and the insect climbs up some suitable support and rests. The wings are expanded during the emergence. This forward method of emergence causes difficulty unless the pupa is erect and the anterior half is free. If the pupa is lying horizontally, dorsal side uppermost, on the surface of the soil, as sometimes occurs during laboratory rearing, the insect buries itself deep into the soil as it emerges. In the rearing of moss-feeding larvae the moss is sometimes packed too loosely for the pupa to move up, and this also causes a faulty emergence.

The identification of the larvae of the Tipulinae is simplified by two main features:—(a) the variation in number and size of the anal papillae, and (b) the development of dark pigmented patches on the spiracular disc and the sclerotisation of the anal lobes. These, and other features, often environmental in character, are, to some extent, consequent on the long period passed in the larval stage and to the different environments preferred. The life cycle of most species occupies one year, with the larval stage accounting for ten months or so. The pupal stage is short, and its only active function is to move upwards through the substratum prior to the emergence of the adult. The pupae are thus much more constant in appearance than the larvae, and the characters used in separating them are chiefly (a) the arrangement of the spines on the abdomen and anal segment, (b) the length and form of the respiratory processes, (c) the arrangement of the leg sheaths, and (d) the length of the pupae, the time of year and habitat in which the pupae are found.

#### *Spine arrangement*

The spines on the pupae may be regarded as homologous with the larval setae. They occur in the same relative positions (cf. figs. 1, 2, 3, and 68, 69, 70, 71). The chaetotaxy of the larvae, however, is not particularly useful in taxonomy since it tends to be uniform within a genus and thus the arrangement of the spines would appear to be subject to a similar limitation. In practice the spine arrangement of the abdominal segments is remarkably constant, and only a few features are useful for taxonomic purposes. The final distinction in most species depends on the size, structure, and arrangement of the spines of the anal segment. The nomenclature of the spines of the pupae used in this paper is as follows:—

*Tergal spines*: on the tergites a row of small spines is present just anterior to the posterior border of each abdominal segment from the second to the seventh inclusive (fig. 69). These increase in size posteriorly.

*Pleural spines*: on the pleurae one spine occurs on the anterior half of each abdominal segment from the third to the seventh inclusive, and either one or two on the posterior half (fig. 70).

*Sternal spines*: on the sternites a row of larger spines occurs near the posterior border of each abdominal segment from the third to the seventh inclusive. In some species this row is preceded by a pair of smaller spines on the posterior half of the segment (fig. 71). This feature forms a useful taxonomic character.

In some species the number of spines in the row on the posterior border of the sternites 4 to 7 is constant, and reference is made to this in the key by quoting the number of spines on the fourth, fifth, sixth, and seventh abdominal sternites in that order. In the key they are simply referred to as "sternal spines", and the couplet "Sternal spines 2.4.4.4." means that two spines occur on the posterior hind border of the sternite of the fourth, and four spines on each of the sternites of the fifth, sixth, and seventh abdominal segments (fig. 68). Similarly the sternal spines of the subgenus *Lunatipula* Edw. are 4.6.6.5.

#### *Spines on the anal segment*

The anal segment, the eighth, usually has fourteen spines, and the diagram (fig. 72) represents the anal segment of a male pupa viewed posteriorly. On the dorsum are six spines, arranged in three pairs, distinguished as the antero-dorsal (AD), the medio-dorsal (MD), and the postero-dorsal (PD) on account of their usual positions. In some species the spines may form a single line or curve, and in this case the centre pair is regarded as the antero-dorsal, the middle pair as the medio-dorsal and the outer pair as the postero-dorsal. In the subgenus *Vestiplex* Bezzi and some other species, the antero-dorsal spines are small or absent (figs. 69, 70). In the male pupae two small spines occur near the apex of the abdomen and are referred to as the anal spines (A). One lateral (L) spine occurs on each pleurae; one ventro-lateral (VL) spine occurs near each sterno-pleural border; and a pair of ventral (V) spines occur on the sternum (fig. 72). In *T. varicornis* Schum. the lateral spines are very small; they are usually very large in *Nephrotoma*. In the latter genus there is only one ventral spine in the male pupae and none in the female. If the ventro-lateral spines appear to be rather ventral in position on the latter pupae, examination of the other spines soon discloses the absence of one pair. The postero-dorsal spine is often bifurcated (figs. 116, 117), the fork may be very deep as in *T. nigra* L. (figs. 134, 135) or shallow as in *T. fulvipennis* Deg. (figs. 114, 115).

#### *Respiratory processes*

The larvae of the Tipulinae are all metapneustic, having one pair of functional spiracles on the posterior truncated end of



the anal segment. By contrast the pupae are all apparently propneustic, with one pair of respiratory processes on the prothorax as in the pupae of the Culicidae. De Meijere (1902), however, in studies on the pupae of *D. bimaculata* (L.) and *T. irrorata* Macq., found little evidence to support the active function of these processes, and it appears probable that they are not functional in the Tipulinae, though detailed examination of this problem would be interesting. The variation in length of the processes in pupae inhabiting the same type of habitat strongly supports this view. They are usually about as long as half the width of the thorax (figs. 68, 69, 70, 71), and this is taken as normal in the key. In *Prionocera* they are much longer than the width of the thorax and accordingly could be assumed to be adaptive since the pupae occurs in wet *Sphagnum*. The pupae of *T. subnodicornis* Zett., however, which also occurs in wet moorland mosses has unusually short processes. Variation also occurs in the wood-feeding species. *Tanyptera* has short processes, *Ctenophora* slightly longer than normal, whilst *T. flavolineata* Mg. has long processes. The only adaptive feature of the processes in these species appears to be the fact that they are either very short, or are strongly curved, presumably as a protection against the hard wood forming the pupal chamber. Although usually constant within a species some variation has been noted in the pupae of *T. luteipennis* Mg., whose respiratory processes may be as short as *T. unca* Wied. (fig. 79) or may be of normal length. One female pupa examined has the processes of unequal length. This species is accordingly keyed out twice.

#### *Leg sheaths*

These are arranged side by side between the wing sheaths, the latter covering the outer leg sheaths. In the male the leg sheaths extend further than in the female, and this is correlated with the greater leg length of the male in the adult insect. There is no relation, however, between the actual length of the adult leg and the length of the sheaths, i.e. species with shorter-legged males have the same relative length of leg sheaths as do species with long-legged males. Presumably the legs are telescoped within the sheaths.

In most species the leg sheaths are straight at the tips, and the tips end at or about the same level (fig. 68); in some pupae the tips curve inwards and end at different levels (fig. 71). Variation occurs in this to some extent, e.g. some pupae of *T. marmorata* Mg. have the tips of the sheaths ending at different levels (figs. 178, 179), but in this case the tips of the sheaths are more or less straight and never curve inwards as in the case of *T. paludosa* Mg. (fig. 71). This character is used to separate the *maxima*, *vittata*, *oleracea*-groups from the *lateralis*-group.

#### *Length of pupae, time of year, and habitats*

The length of the pupa is usually used as a confirmatory character, though it is a major feature in *T. pruinosa* Wied, and

*T. maxima* Poda. It is given in all cases in the key, usually as the average for that species. Its infraspecific variation is generally small, sometimes, however, being between 3-5 mm.

The time of year when pupae occur is a useful confirmatory character since many species have a restricted flight period, and the duration of the pupal stage is short. A check on the likely date for any particular species of the adult can be made by reference to Coe (1950) in which the flight period is given. Pupae should be found within about a fortnight previous to the flight period, or during the early part of the latter if it is prolonged.

Many species have a restricted habitat, e.g. the pupae of *T. subnodicornis* Zett. are always found amongst moorland mosses or in the soil beneath. All habitats are included in both the larval and pupal keys. The value of this is only slightly reduced by the few species which inhabit several different habitats, e.g. *T. lateralis* Mg., *T. rufina* Mg., and *T. paludosa* Mg.

Table 1, combining these three features, appears opposite and contains most of the species, only such specialised habitats as that of *T. excisa* Schum. being omitted.

#### 4. General Life History

Mating occurs soon after emergence, and the female lays the usually black elliptical eggs in the soil or other material in a characteristic manner. The body is held vertically, and the ovipositor inserted by means of a rotary or stabbing movement, the posterior legs supporting the body tripod fashion. In some species the body of the female is inserted deep into the soil. From 200 to 500 eggs appear to be the usual number recorded from one female; the eggs hatching in from 7 to 14 days after laying.

The larvae are herbivorous, feeding on roots, decayed wood, or moss. Instances of cannibalism have been reported but appear to be due to close confinement in captivity. The first instar larva of *T. lateralis* Mg. has only two pairs of anal papillae (White, 1951), the third pair appearing in the second instar. A similar feature has also been recorded in the larvae of *T. maxima* Poda, and when the first instar larvae are better known this feature of the possession of the primitive number of anal papillae in very young larvae may be found to be general. There are four instars, and the larvae are active throughout the winter. In severe weather and in drought, larvae in exposed situations, such as moss on stone walls, may cease activity and resume normal functions on the return of milder or wetter weather. They are generally capable of withstanding a certain degree of dessication, varying in the species, for whilst shrivelled and inactive larvae of *T. marmorata* Mg. became active and normal after being immersed in water for some time, the young larvae of *T. paludosa* Mg. are apparently very susceptible to drought. The actual degree of dessication possible without death occurring is not, however, known for any species. The larvae are active and progress quickly, but retract

TABLE I. SHOWING SIZE, HABITATS, AND TIME OF YEAR WHEN PUPAE ARE USUALLY FOUND

| Size                                 | April              | May                                   | June                             | July        | August      | Sept.       |
|--------------------------------------|--------------------|---------------------------------------|----------------------------------|-------------|-------------|-------------|
| <i>Hard, dry, dead wood</i>          |                    |                                       |                                  |             |             |             |
| 25-30 mm.                            |                    | atrata<br>nigricornis<br>flavolineata | atrata<br>nigricornis            |             |             |             |
| „                                    |                    |                                       |                                  |             |             |             |
| „                                    |                    |                                       |                                  |             |             |             |
| <i>Softer, dead wood</i>             |                    |                                       |                                  |             |             |             |
| 25-30 mm.                            | bimaculata         | bimaculata                            | bimaculata                       |             |             |             |
| „                                    | pectini-<br>cornis | pectini-<br>cornis                    |                                  |             |             |             |
| „                                    |                    | ornata                                | ornata                           |             |             |             |
| <i>Detritus or very decayed wood</i> |                    |                                       |                                  |             |             |             |
| 20-22 mm.                            |                    |                                       | irrorata                         | irrorata    |             |             |
| 22-25 mm.                            |                    | selene<br>cava                        | selene<br>cava                   |             |             |             |
| „                                    |                    |                                       |                                  |             |             |             |
| <i>Damp soils in woods</i>           |                    |                                       |                                  |             |             |             |
| 15-20 mm.                            |                    | Nephrotoma<br>variicornis             | Nephrotoma                       | Nephrotoma  | Nephrotoma  |             |
| 20-22 „                              | pabulina           | pabulina                              |                                  |             |             |             |
| „                                    | hortulana          | hortulana                             | truncorum                        |             |             |             |
| „                                    | variipennis        | variipennis                           |                                  |             |             |             |
| 22-25 „                              |                    | fascipennis                           | fascipennis                      | fascipennis |             |             |
| „                                    |                    | brevispina                            | brevispina                       |             |             |             |
| „                                    |                    | pelio stigma                          | pelio stigma                     |             |             |             |
| „                                    |                    | lunata                                | lunata                           |             |             |             |
| „                                    |                    | scripta                               | scripta                          | scripta     |             |             |
| 25-30 „                              | nubeculosa         | nubeculosa                            |                                  |             |             |             |
| „                                    | rubripes           | rubripes                              |                                  |             |             |             |
| <i>Damp soils of river banks</i>     |                    |                                       |                                  |             |             |             |
| 20-25 mm.                            | lateralis          | lateralis<br>couckeii<br>montium      | lateralis<br>couckeii<br>montium | lateralis   | lateralis   |             |
| „                                    |                    |                                       |                                  |             |             |             |
| „                                    |                    |                                       |                                  |             |             |             |
| <i>Marshy soil</i>                   |                    |                                       |                                  |             |             |             |
| 15-20 mm.                            |                    | pruinosa<br>unca                      | pruinosa<br>unca                 |             |             |             |
| „                                    |                    | nigra                                 | nigra                            |             |             |             |
| 20-25 „                              | lateralis          | lateralis                             | lateralis                        | lateralis   | lateralis   |             |
| „                                    |                    | luna                                  | luna                             |             |             |             |
| 25-30 „                              | vittata            | solstitialis                          | solstitialis                     |             |             |             |
| „                                    |                    | oleracea                              | oleracea                         | oleracea    | czizeki     | czizeki     |
| „                                    |                    | fulvipennis                           | fulvipennis                      | fulvipennis | luteipennis | luteipennis |
| 30-35 „                              |                    | maxima                                | maxima                           |             |             |             |
| <i>Pasture soil</i>                  |                    |                                       |                                  |             |             |             |
| 20 mm.                               |                    | vernalis                              |                                  |             |             |             |
| 25 mm., etc.                         |                    |                                       | paludosa                         | paludosa    | paludosa    |             |
| <i>Aquatic or semi-aquatic moss</i>  |                    |                                       |                                  |             |             |             |
| 12-17 mm.                            | subnodi-<br>cornis |                                       |                                  |             |             |             |
| „                                    | macrocera          |                                       |                                  |             |             |             |
| „                                    |                    | cheethami                             |                                  |             |             |             |
| 20-25 „                              | rufina             | rufina                                | rufina                           | rufina      | rufina      |             |
| „                                    |                    | Prionocera                            | Prionocera                       | Prionocera  | melanoceros | melanoceros |
| <i>Terrestrial moss</i>              |                    |                                       |                                  |             |             |             |
| 15-17 mm.                            | Dolichopeza        | Dolichopeza                           |                                  |             |             |             |
| „                                    | rufina             | rufina                                | rufina                           | rufina      | rufina      |             |
| „                                    | alpium             | alpium                                | alpium                           | alpium      |             |             |
| „                                    |                    |                                       | marmorata                        | marmorata   |             |             |
| „                                    |                    |                                       |                                  |             | marmorata   |             |
| „                                    |                    |                                       |                                  |             | signata     | signata     |
| „                                    |                    |                                       |                                  |             | staegeri    | staegeri    |
| „                                    |                    |                                       |                                  |             |             | obsolata    |
| „                                    |                    |                                       |                                  |             |             | pagana      |

and curl up when disturbed. In general, the larvae are characteristic of damp situations and this explains the abundance of the adults during or after a wet summer or autumn.

The life cycle of most species occupies one year; in *T. rufina* Mg., however, which has a long flight period, it seems probable that two generations occur in the year. In collections of larvae of *T. flavolineata* Mg., on the other hand, there are always at least two distinct size ranges, indicating that this species takes at least two years to become adult.

Apart from the first instar, young larvae can be identified by the key fairly readily, although it is based on fourth instar specimens, for the characters are surprisingly constant. After a moult the spiracles are often unusually large and colourful and the sclerotised patches indistinct; after a day or so the larvae takes on a normal appearance.

In laboratory rearing the larvae are subject to mould attacks, but this can be remedied by frequent changes of the pabulum. Occasional specimens occur containing nematodes of considerable size, and parasitic flies are only rarely encountered, though *Crocota geniculata* (Deg.) and *C. cristata* (F.) have been recorded from Tipuline larvae (Alexander, 1920).

The change to the pupa is preceded by a period of inactivity in which the size of the larva is reduced. The pupa is often only two-thirds of the length of the larva.

### 5. Ecology

The main habitat is soil with divergence in two directions:— (a) into decayed wood on the one hand, and (b) into mosses on the other. All larvae have been recorded from one or more of these habitats. The chief ecological factor in their distribution appears to be that of the moisture content of the environment. Table 2 shows the usual habitats of all the larvae included in the keys and illustrates the restricted habitats of many species.

The correlation between the type of anal papillae and the moisture content of the environment has been referred to previously, and the value of this for identification is not seriously affected by the very wide ranges of some common species.

*Pasture soil*: the soil of pastures is usually too dry to be a common habitat and the species normally found are those of the abundant *T. paludosa* Mg. and the less common *T. vernalis* Mg. The larvae of both *T. oleracea* L. and *T. czizeki* De Jong have also been previously recorded from pasture soils but have not occurred in this type during the present study. *T. paludosa* is common in all types of pasture soil (peat, clay, marl, sand, etc.) according to numerical counts per square metre undertaken in various localities, and this species has the widest habitat range in the Tipulinae. The numbers per square metre fall off rapidly, however, when wetter soils are sampled. The occurrence of this species in wet moss in hygropetricous situations is probably only sporadic.

*Damp soil*: woodland soil tends to be kept damp by the cover of vegetation, which prevents evaporation, hence the occurrence of most species in woods. Most species appear to favour black friable soil, rather than the heavy clay soil found in some areas, but the degree of acidity does not seem to be at all critical. *T. fascipennis* Mg., for example, was found in equal numbers in acid peaty soil under bracken, and in alkaline marl under grass. In limestone woodlands of North Lancashire, rich black soil is often developed under mosses (chiefly feather mosses) growing on boulders, and this soil has been found to be productive of the subgenera *Lunatipula* and *Vestiplex*. The damp soil amongst mountain screes is a specialised habitat, only *T. excisa* Schum. being found exclusively in this habitat, though associated species (*T. marmorata* Mg., *T. alpium* Bergr., and *T. rufina* Mg.) are found in the mosses also growing amongst the screes, and they often penetrate into the soil as well.

*River banks*: the larvae characteristic of this habitat are also often found in marshy soil. The soil of river banks, though not obviously marshy, evidently possesses a gradient of water content varying from saturation at or below the water level to dryer soil higher up the bank, the gradient being largely determined to the type of soil and consequent difference in capillarity. The larvae can thus inhabit the soil with the preferred water content, though no evidence for any stratification of larvae has been obtained. *T. couckeii* Tonn. and *T. montium* Egg. have occurred only in this habitat in the present survey, both in sandy soils.

*Marsh soil*: this is taken as soil with the water table near to the surface without any free water being present. Characteristic larvae are *T. lateralis* Mg., *T. luna* Westh., *T. solstitialis* Westh., *T. pruinosa* Wied., and *T. unca* Wied. All, except the last, have four or more long elongated anal papillae. Both *T. maxima* Poda and *T. fulvipennis* Deg. also occur. Again the degree of acidity seems immaterial, peaty soils often being as productive as limestone soils.

*Saturated soils*: this is marsh soil with free water, and obviously is hardly separable from the last since water content will vary according to the weather. Certain larvae, however, are invariably found with free water present, e.g. *T. luteipennis* Mg. This species occurs in the drainage ditches of fen country, i.e. in peaty soil, always at the water level or just below, and is equally common in saturated soil of marshes on limestone. *T. maxima* Poda and *T. fulvipennis* Deg., although showing no modification to a semi-aquatic life, are often most commonly found in this type of soil.

*Freely aquatic*: *T. maxima* Poda is the most usual species found freely underneath stones or pebbles on the beds of small streams, together with such larvae of the Limoniinae as *Pedicia* and *Dicranota*.

*Aquatic mosses*: the only larva confined to this habitat is that of *T. cheethami* Edw., which occurs in mosses (e.g.



*Eurhynchium*) in lotic water, either in streams or in hygropetricous situations. Other non-modified larvae which occur frequently are those of *T. rufina* Mg., *T. lateralis* Mg., and *T. oleracea* L. It thus appears that the long hairs bordering the lobes of the anal segment of *T. cheethami* Edw., which are apparently modifications for such a habitat, are by no means necessary.

*Semi-aquatic mosses*: these are taken as *Sphagnum*, *Hypnum*, etc., in partially submerged conditions in static water, often on moorlands. Characteristic larvae are those of *T. subnodicornis* Zett. and *T. macrocera* Zett., with the less common *T. melanoceros* Schum., and occasionally *T. pagana* Mg., and *T. rufina* Mg. *Prionocera turcica* (F.) also occurs here, though more often in almost completely submerged *Sphagnum*.

*Terrestrial mosses*: the mosses on walls, stones, etc., usually contain the larvae of the *marmorata*-group. The tendency of these mosses to become dry during a drought and their exposed situation during severe frosts appear to be the disadvantages of this habitat.

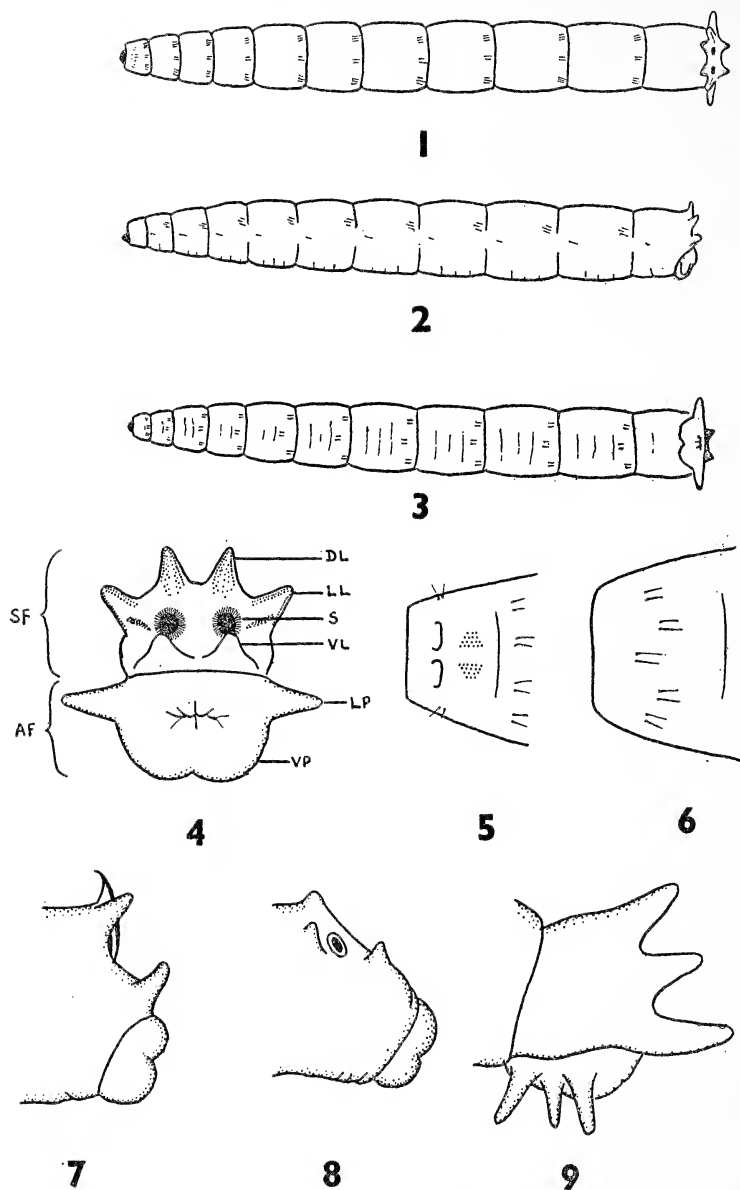
*Wood*: The larvae adapted for this habitat are *Ctenophora*, *Dictenidia*, *Tanyptera*, and *T. flavolineata* Mg., the latter two being the most advanced type. *T. flavolineata* appears to prefer the wood of small branches, and pupates immediately under the surface or under the bark when this is present. Predators of these larvae include the larvae of *Melanotus rufipes* (Hbst.), *Denticollis linearis* (L.) (Coleoptera, Elateridae), and of *Xylophagus ater* (Mg.) (Diptera, Rhagionidae).

The association of *T. irrorata* with decayed wood has been commented upon. It usually lives under moss on rotten logs, or inside the wood if this is sufficiently rotten. It also occurs in soil under moss on boulders in the woods of the Lake District.

Wood detritus, i.e. the soft fragmentary decayed wood which occurs inside old trees either when the tree is still vertical or when lying on the soil, is a material well suited to such transitional types as *irrorata*, or to certain of the damp soil type larvae, i.e. *T. scripta* Mg. *T. selene* Mg. and *T. cava* Ried. have both occurred in this material, and the latter species even in dung, another material which, when old, often contains soil-inhabiting larvae.

## 6. Key to Larvae

1. Spiracular disc with dorsal lobes closely approximated (fig. 10); colour green with undulating longitudinal dark brown stripes along the dorsum; in moss on trees, moss on soil, etc., usually near small streams in woods. Length 15 mm. ....  
*Dolichozepe albipes* Stroem.
- Spiracular disc with dorsal lobes clearly separated; colour not green (except in *T. macrocera* which lacks the darker stripes) ..... 2.

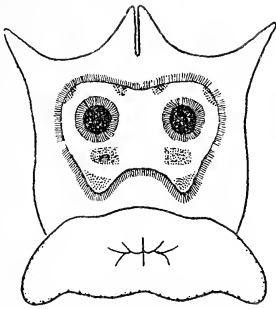


Figs. 1-4. *Tipula paludosa* Mg. 1, larva, dorsal view; 2, larva, lateral view; 3, larva, ventral view; 4, anal segment of larva, posterior view, DL—dorsal lobe, LL—lateral lobe, VL—ventral lobe, S—spiracle, LP—lateral anal papilla, VP—ventral anal papilla, SF—spiracular field, AF—anal field.

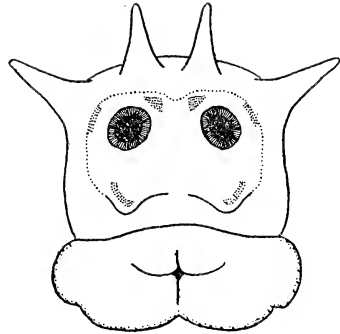
Figs. 5, 6. Dorsum of prothorax of larvae. 5, *Nephrotoma*; 6, *Tipula*.

Figs. 7-9. Anal segments, lateral view. 7, *Tipula fascipennis* Mg. 8, *Tanyptera atrata* (L.). 9, *Tipula luteipennis* Mg.

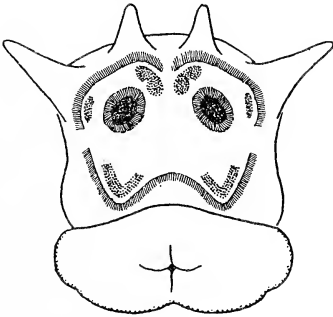




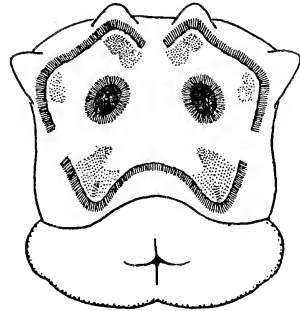
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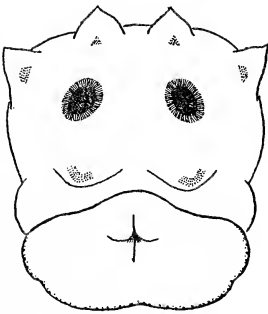
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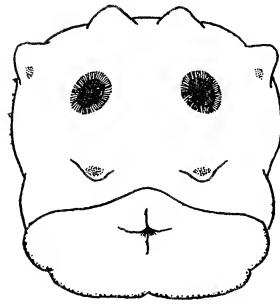
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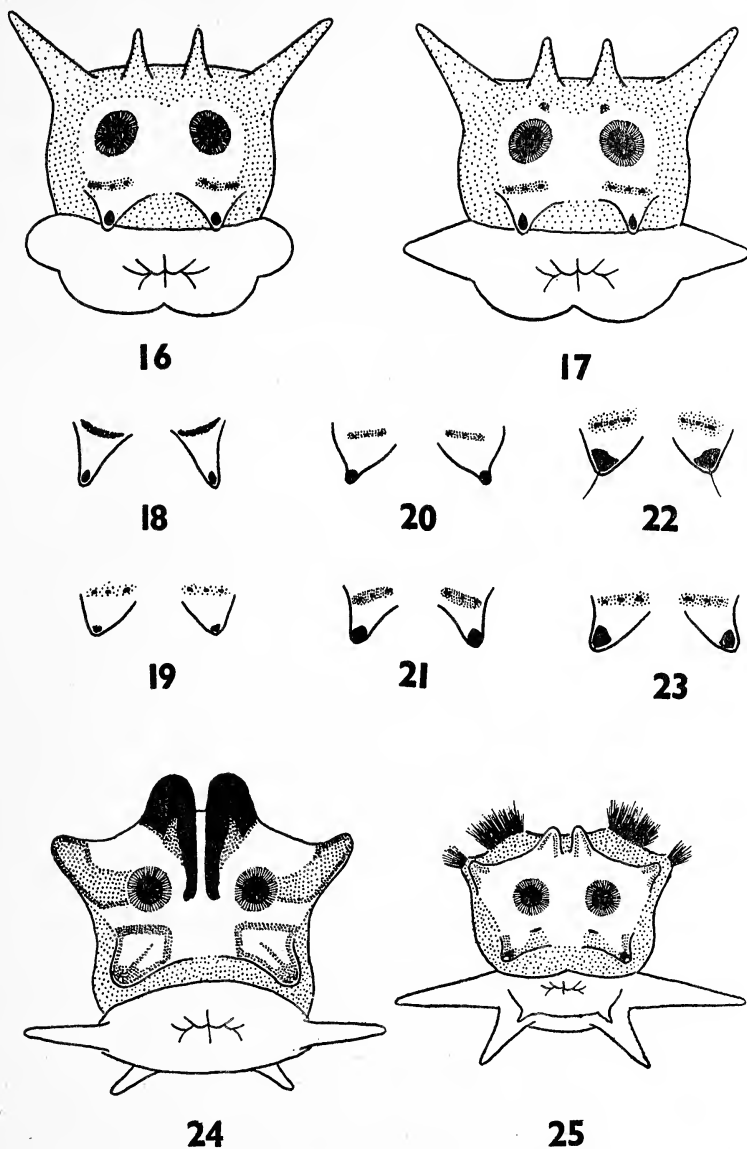
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Figs. 10-15, Anal segments, posterior view. 10, *Dolichozepe albipes* Stroem. 11, *Dictenidia bimaculata* (L.). 12, *Ctenophora pectinicornis* (L.). 13, *Ctenophora ornata* (Mg.). 14, *Tipula flavolineata* Mg. 15, *Tanyptera atrata* (L.), or *T. nigricornis* (Mg.).

2. Larvae whitish, in decaying wood of trees or branches; lobes of spiracular disc not sclerotised ..... 3.
- Larvae usually grey or brown, not in decaying wood unless this is rotten; if larvae are whitish, then the lobes of spiracular disc are sclerotised ..... 7.
3. Spiracular disc with marginal hair fringe, hairs short; pubescence on cuticle short, pale brown, denser on dorsum of last abdominal segments, shortest and least dense on pleurae; in softer dead wood (*Ctenophora*) ..... 4.
- Spiracular disc without marginal hair fringe; in harder, often dry, dead wood (except *Dictenidia*) ..... 5.
4. Spiracular disc with dorsal and lateral lobes elongated, longer than broad at base; pigmented patches on disc darker (fig. 12). Length 30 mm. .... *C. pectinicornis* (L.).
- Spiracular disc with dorsal and lateral lobes short and rounded; pigmented patches on disc lighter (fig. 13). Length 35 mm. .... *C. ornata* Mg.
5. Spiracular disc with dorsal and lateral lobes elongated, longer than broad at base; pigmented patches on disc larger (fig. 11); pubescence yellowish-brown, very short, rather longer on thoracic segments and on dorsum of last abdominal segment. Length 32 mm. .... *Dictenidia bimaculata* (L.).
- Spiracular disc with dorsal and lateral lobes short and broad; abdominal segments glabrous ..... 6.
6. Dorsal and lateral lobes of spiracular disc pointed; dorsal lobes with small dark pigmented patch at base; ventral lobes with brown transverse mark at tip (fig. 14); short pale pubescence confined to thoracic segments. Length 30 mm. .... *Tipula flavolineata* Mg.
- Dorsal and lateral lobes of spiracular disc rounded; dorsal lobes without small dark patch at base; ventral lobes with small rounded mark at tip (fig. 15); short pale pubescence confined to prothoracic segment. Length 32 mm. ....  
*Tanyptera atrata* (L.).  
*Tanyptera nigricornis* (Mg.).
7. Dorsum of prothorax with two raised welts (fig. 5); lateral lobes of spiracular disc longer than dorsal lobes, and the lobes typically cylindrical and papillae-like; anal papillae either all rounded or with the ventral pair rounded and the lateral pair elongated. (*Nephrotoma*) ..... 8.
- Dorsum of prothorax without raised welts (fig. 6) (*Tipula*) (*Prionocera*). Lateral and dorsal lobes of spiracular disc usually subequal, and the lobes typically flattened and broad (papillae-like in *T. pabulina* Mg., *T. truncorum* Mg., and *T. nigra* L.); anal papillae variable ..... 15.
8. Spiracular disc without a small pigmented patch below the dorsal lobes; ventral lobes narrow with rounded black patch at tip, base of lobes with three black spots in a brown transverse stripe, the outer spot elongated (fig. 16); in damp soil. Length 22 mm. .... *N. flavipalpis* (Mg.).

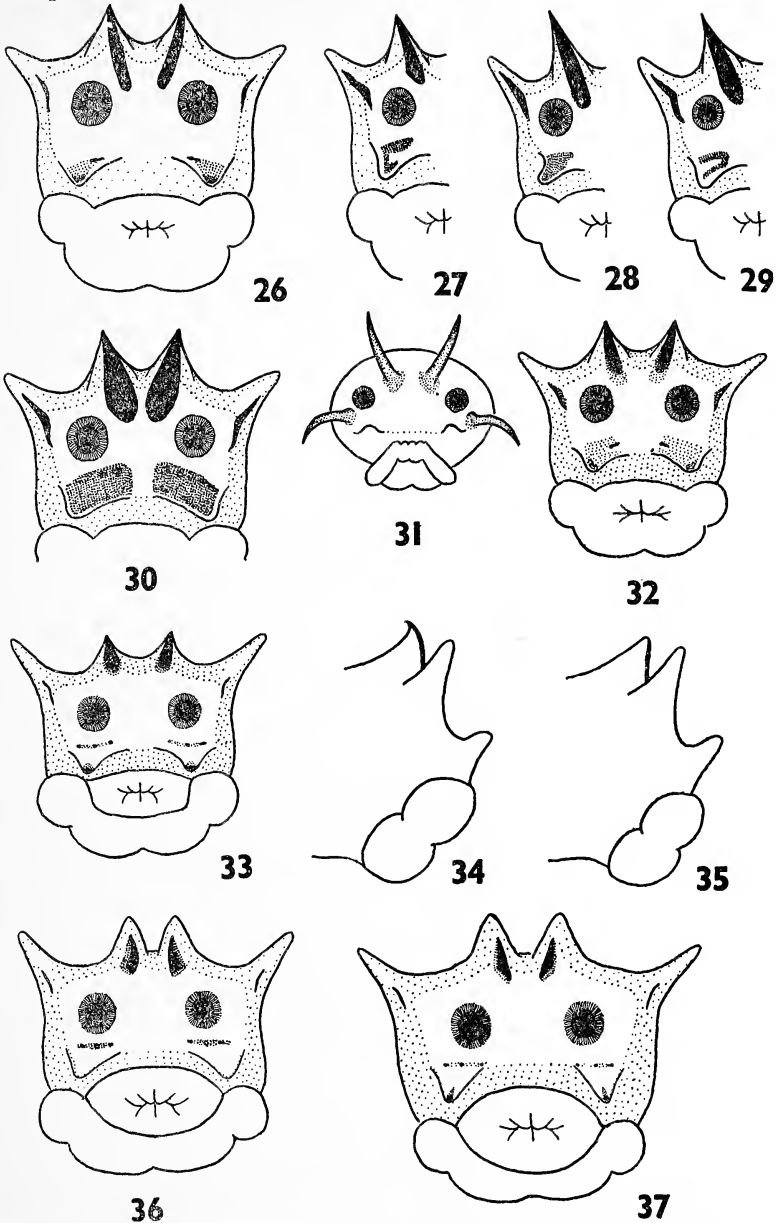


Figs. 16-17. Anal segments, posterior view. 16, *Nephrotoma flavipalpis* (Mg.). 17, *Nephrotoma analis* (Schum.).

Figs. 18-23. Ventral lobes, dorsal view. 18, *Nephrotoma crocata* (L.) (after Theowald). 19, *N. flavescens* (L.) or *N. maculata* (Mg.). 20, *N. scurra* (Mg.). 21, *N. cornicina* (L.). 22, *N. dorsalis* (F.) (after Theowald). 23, *N. quadrijaria* (Mg.).

Figs. 24-25. Anal segments, posterior view. 24, *Tipula varicornis* Schum. 25, *T. pruinosa* Wied.

- Spiracular disc with a small pigmented patch below the dorsal lobes; if indistinct then ventral lobes wider ..... 9.
- 9. Lateral anal papillae elongated, at least longer than broad at base (fig. 17) ..... 10.
- Lateral anal papillae rounded, not elongated (as in fig. 16) ..... 11.
- 10. Spiracular disc with small dark marks between spiracles; dorsal and lateral lobes narrow and very long, the lateral lobes almost twice as long as the dorsal lobes, and their length equal to two-thirds of the diameter of the anal segment; ventral lobes narrow with black patch at tip and with dark transverse stripe at base (fig. 18); in damp soil. Length 22 mm. .... *N. crocata* (L.).
- Spiracular disc without dark marks between spiracles; dorsal and lateral lobes shorter (fig. 17), the length of the latter hardly equal to half of the diameter of the anal segment; ventral lobes narrow with black patch at tip and with three black spots in a brown transverse stripe at base; in damp soil. Length 20 mm. .... *N. analis* (Schum.).
- 11. Ventral lobes lightly pigmented at tip (fig. 19); pigmented patch below dorsal lobes smaller; larvae grey, spiracular disc not differentiated sharply by reason of the colour from the rest of the anal segment; in damp soil. Length 18 mm. ....  
*N. flavescens* (L.).  
*N. maculata* (Mg.).
- Ventral lobes heavily pigmented at tip; pigmented patch below dorsal lobes larger and darker; spiracular disc usually much lighter than the rest of the anal segment ..... 12.
- 12. Ventral lobes narrow, or narrowed near tip ..... 13.
- Ventral lobes broad and blunt at tip ..... 14.
- 13. Ventral lobes narrowed suddenly near tip (fig. 20); larvae dark brown; in damp or sandy soil. Length 24 mm. ....  
*N. scurra* (Mg.).
- Ventral lobes narrowed gradually (fig. 21); larvae brown; in damp soil. Length 18 mm. .... *N. cornicina* (L.).
- 14. Transverse stripe at base of ventral lobes lighter; lobes longer and without any long setae at tips (fig. 23), in damp soil. Length 20 mm. .... *N. quadrifaria* (Mg.).
- Transverse stripe at base of ventral lobes darker; lobes shorter and with a long setae at tip (fig. 22); in damp soil. Length 22 mm. .... *N. dorsalis* (F.).
- 15. Dorsal lobes semicircular in outline when seen from behind, heavily sclerotised and black in colour; lateral and ventral lobes with marginal hair fringe and with extensive dark brown patches; four anal papillae, all elongated; anal segment with dense bands of hairs; colour yellowish-brown; in damp soil or amongst decaying leaves in damp places usually near small streams in woods (fig. 24). Length 22 mm. .... *Tipula variicornis* Schum.

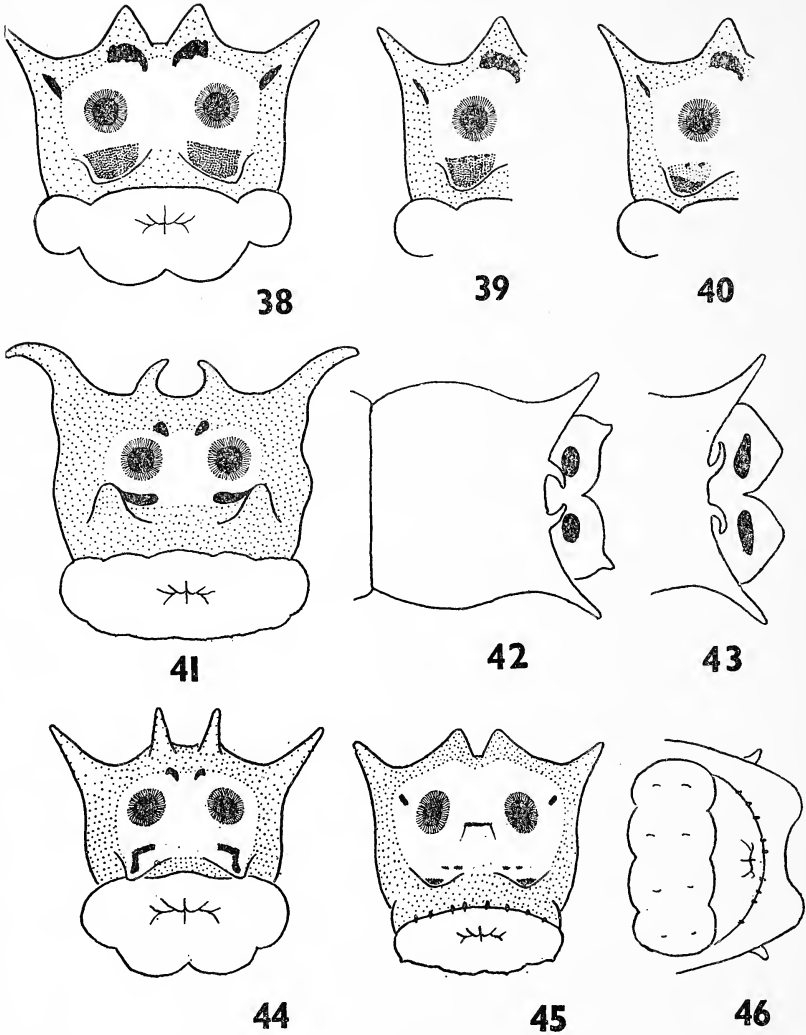


Figs. 26-33. Anal segments, posterior view. 26, *Tipula fascipennis* Mg. 27, *T. cava* Ried. 28, *T. selene* Mg. (after Chiswell). 29, *T. brevispina* Pierre. 30, *T. lunata* L. 31, *T. livida* v.d. Wulp (after Chiswell). 32, *T. vernalis* Mg. 33, *T. scripta* Mg.

Figs. 34-35. Anal segments, lateral view. 34, *T. scripta* Mg. 35, *T. excisa* Schum. Figs. 36-37. Anal segments, posterior view. 36, *T. nubeculosa* Mg. 37, *T. rubripes* Schum.

- Dorsal lobes not semicircular in outline; if heavily sclerotised then the lobes are pointed ..... 16.
16. Dorsum of anal segment with dense tufts of black hairs anterior to dorsal and lateral lobes; six anal papillae, all elongated but with the posterior ventral pair short; anal segment with bands of dense hairs; colour greyish-brown with darker longitudinal stripes along the dorsum; in marshy soil (fig. 25). Length 22 mm. .... *Tipula pruinosa* Wied.
- Dorsum of anal segment without any tufts of dense black hairs ..... 17.
17. Anal papillae four in number, all rounded (fig. 26) ..... 18.
- At least one pair of anal papillae elongated and usually longer than broad, or produced into tapering tips ..... 37.
18. Anus separated from the anal papillae by a dark pigmented band (figs. 33, 36, 37) (subgenus *Vestiplex* Bezzi) ..... 19.
- Anus not separated from the anal papillae by a dark pigmented band (figs. 26, 32) ..... 22.
19. Dorsal lobes sclerotised to extreme tip; ventral lobes heavily pigmented at tips; lateral lobes longer than dorsal lobes which are shorter than normal (fig. 33) ..... 20.
- Tip of dorsal lobes not sclerotised (figs. 36, 37); ventral lobes not, or scarcely pigmented at tips; dorsal lobes larger ... 21.
20. Dorsal lobes sclerotised to tip and ending in forwardly projecting hooks (fig. 34); larvae grey with darker, narrow, transverse bands; pubescence rather silky; in damp soil or detritus in woods. Length 24 mm. .... *Tipula scripta* Mg.
- Dorsal lobes sclerotised to tip but not ending in hooks (fig. 35); larvae grey with darker narrow transverse bands; pubescence silky; in soil of mountain screes. Length 24 mm. .... *Tipula excisa* Schum.
21. Sclerotised patches on dorsal lobes triangular, broad, and rather curved; ventral lobes unpigmented at tip but with dark transverse stripes at base (fig. 36); larvae brownish-grey with narrow transverse stripes on dorsal and ventral surfaces; in damp soil in woods. Length 32 mm. ....  
*Tipula nubeculosa* Mg.
- Sclerotised patches on dorsal lobes triangular, narrow, and straight; ventral lobes with pigmented tip and with lighter transverse stripes at base (fig. 37); larvae grey with narrow darker transverse stripes on dorsal and ventral surfaces; in damp soil in woods. Length 35 mm. *Tipula rubripes* Schum.
22. Dorsal lobes sclerotised to tips and ending in forwardly projecting hooks (fig. 7) (subgenus *Lunatipula* Edw.) ... 23.
- Dorsal lobes not ending in forwardly projecting hooks ... 30.
23. Dorsal and lateral lobes entirely sclerotised, forming long curved spines (fig. 31) ..... 24.
- Dorsal and lateral lobes not forming curved spines ..... 25.
24. Bases of dorsal lobes extending down between spiracles; lateral lobes curved upwards; ventral lobes black; larvae yellowish, in sand, e.g., clearings in dune forests. Length 26 mm. .... *Tipula juncea* Mg.

- Bases of dorsal lobes not extending downwards between spiracles; lateral lobes curved downwards; ventral lobes unpigmented (fig. 31); larvae whitish, in damp soil and detritus in woods. Length 30 mm. .... *Tipula livida* V. d. Wulp.
- 25. Stripe on lateral lobes narrow, usually about half the width of spiracular border; dorsal lobes with parallel-sided sclerotised patches (fig. 26); larvae grey with narrow dark transverse stripes dorsally and ventrally; in damp soil in woods, or soil under bracken. Length 24 mm. ....  
*Tipula fascipennis* Mg.
- Stripe on lateral lobes wider, as wide as spiracular border .....
- 26. Ventral lobes entirely pigmented .....
- Ventral lobes not entirely pigmented .....
- 27. Dorsal lobes with wide sclerotised patches which may unite ventrally; pigmented patches on ventral lobes extending on to the disc, extensive, only narrowly separated, the space between the patches less than the diameter of the spiracles; ventral lobes broad (fig. 30); larvae brownish-grey, with narrow dark stripes dorsally and ventrally; in damp soil in woods. Length 27 mm. .... *Tipula lunata* L.
- Dorsal lobes with narrower sclerotised patches; pigmented patches on ventral lobes extending on to disc but widely separated; ventral lobes narrow, longer than broad at base (fig. 28) .....
- 28. Larvae pale, or yellowish-brown, with narrow dark stripes dorsally and ventrally; patches on dorsal lobes not parallel-sided (fig. 28); sclerotised apex of dorsal lobes shorter, projecting forwards and upwards; in detritus inside old trees, etc. Length 25 mm. .... *Tipula selene* Mg.
- Larvae light greyish-brown, with narrow dark stripes dorsally and ventrally; patches on dorsal lobes parallel-sided; sclerotised apex of dorsal lobes longer, strongly curved forwards, so that the apex is projecting horizontally; in damp soil in woods. Length 30 mm. ....  
*Tipula peliostigma* Schum.
- 29. Sclerotised patches on dorsal lobes broad and long; ventral lobes pigmented as fig. 29; larvae greyish with narrow dark transverse stripes dorsally and ventrally; in damp soil or detritus in woods. Length 25 mm. ....  
*Tipula brevispina* Pierre
- Sclerotised patches on dorsal lobes narrow and short; ventral lobes pigmented as fig. 27; larvae pale brownish; in damp soil or detritus, etc., usually in woods. Length 22 mm. ....  
*Tipula cava* Ried.
- 30. Dorsal lobes sclerotised to tip (fig. 32), the patches becoming less black ventrally, being brownish as they extend on to the spiracular disc; larvae brownish, with narrow transverse darker stripes dorsally and ventrally; in pasture soils. Length 24 mm. .... *Tipula vernalis* Mg.
- Dorsal lobes not sclerotised at tip .....

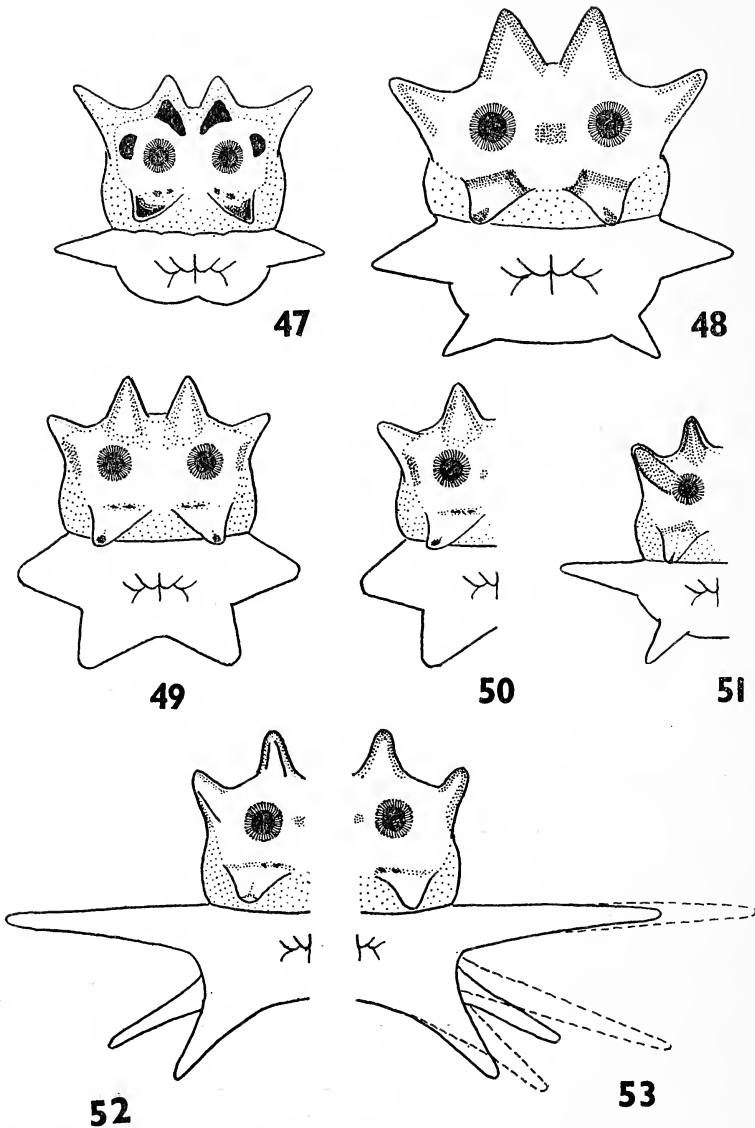


Figs. 38-41. Anal segments, posterior view. 38, *Tipula irrorata* Macq. 39, *T. hortulana* Mg. 40, *T. variipennis* Mg. 41, *T. pabulina* Mg.  
 Figs. 42-43. Anal segments, dorsal view. 42, *T. pabulina* Mg. 43, *T. truncorum* Mg. (after Theowald).  
 Figs. 44-45. Anal segments, posterior view. 44, *T. nigra* L. 45, *T. pagana* Mg.  
 Fig. 46. Anal segment, ventral view. *T. pagana* Mg.

- 31. Dorsal lobes with basal black patch which almost extends across the base (figs. 38, 39, 40) ..... 32.
- Dorsal lobes without, or with a much smaller black patch (figs. 41, 44, 45) ..... 34.

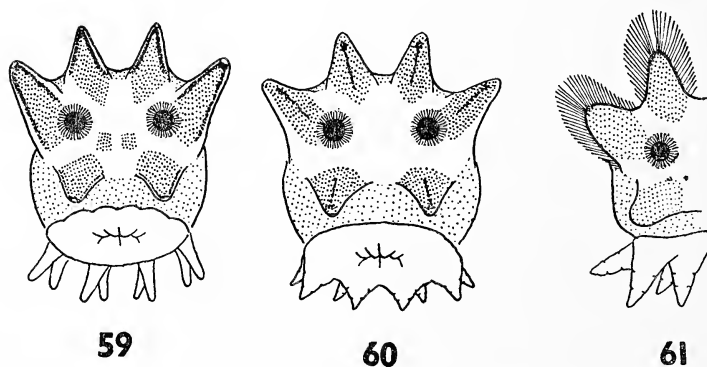
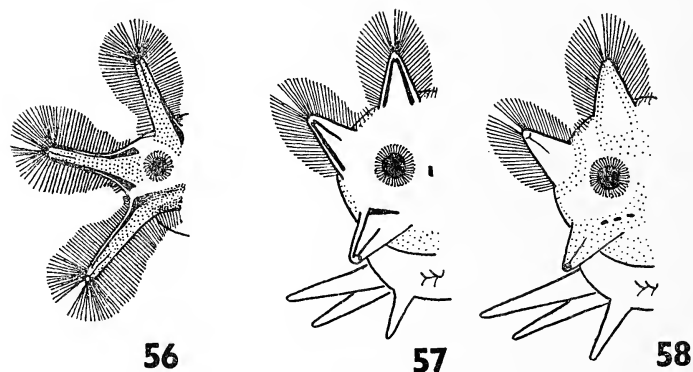
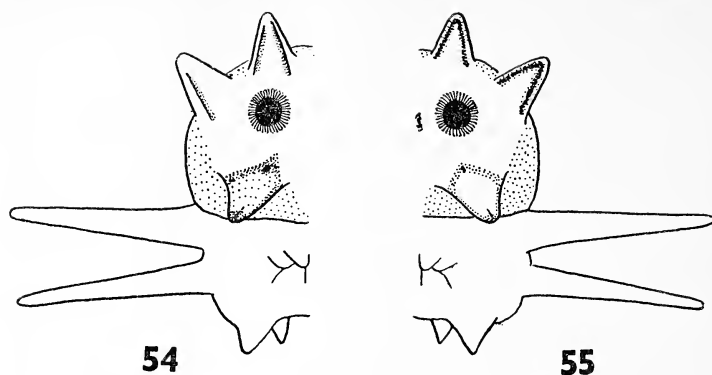


32. Stripes on lateral lobes wider, equal in width to width of spiracular border; ventral lobes entirely pigmented (fig. 38); larvae usually greyish, somewhat variable, though never brown, in rotten wood, or detritus in rotten wood, more rarely in woodland soil. Length 24 mm. ....  
*Tipula irrorata* Macq.
- Stripes on lateral lobes narrow, not wider than half the width of the spiracular border; larvae reddish-brown or brown, in woodland soil ..... 33.
33. Ventral lobes entirely and uniformly pigmented (fig. 39). Length 28 mm. .... *Tipula hortulana* Mg.
- Ventral lobes heavily pigmented at apex, lightly pigmented at base (fig. 40). Length 28 mm. ... *Tipula variipennis* Mg.
34. Larvae with tubercles on abdominal segments, from which arise short strong setae; dorsal and lateral lobes cylindrical, papillae-like, lateral lobes much the longer ..... 35.
- Larvae without tubercles on abdominal segments; setae weak, much less pronounced ..... 36.
35. Spiracular disc with small black patch at base of dorsal lobes (fig. 41); ventral lobes narrowed at tip and with ovoid black patch at base (fig. 42); larvae dark grey or grey, lighter between thoracic segments; in damp soil or amongst moss in woods. Length 20 mm. .... *Tipula pabulina* Mg.
- Spiracular disc without a small black patch at base of dorsal lobes; ventral lobes broad and blunt at tip and with elongated black patch at base (fig. 43); larvae greyish, lighter ventrally; in damp soil or moss in woods. Length 20 mm. ...  
*Tipula truncorum* Mg.
36. Dorsal lobes with a small black patch at bases; dorsal and lateral lobes cylindrical, the latter being the longer; ventral lobes with median dark band (fig. 44); larvae whitish-grey; in damp or marshy soil, often peaty. Length 25 mm. ....  
*Tipula nigra* L.
- Dorsal lobes without any small black patches at bases; angular dark mark to the outside of the spiracles; small triangular black spots along ventral margin of anal segment (figs. 45, 46); larvae brownish; in mosses on soil or in soil beneath mosses, sometimes in mosses in moorland marshes. Length 20 mm. .... *Tipula pagana* Mg.
37. Only one pair of anal papillae (the lateral pair) elongated or with tapering tips, the ventral pair rounded ..... 38.
- At least two pairs of elongated, tapering, anal papillae ... 39.
38. Spiracular disc with black pigmented patches to the outside of the spiracles, and below the dorsal lobes (fig. 47); larvae greyish-brown, with narrow darker transverse stripes dorsally and ventrally; in marshy or damp soils. Length 26 mm. ...  
*Tipula unca* Wied.



Figs. 47-53. Anal segments, posterior view. 47, *Tipula unca* Wied. 48, *T. vittata* Mg. 49, *T. oleracea* L. 50, *T. czizeki* De Jong. 51, *T. luna* Westh. 52, *T. montium* Egg. 53, *T. lateralis* Mg. (broken lines indicate length of anal papillae in *T. couchei* Tonn.)

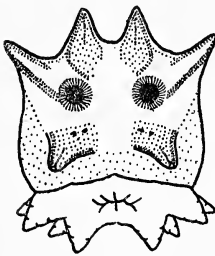
- Spiracular disc without any black pigmented patches; lobes margined with slightly darker colour; a brown elongated mark to outside of each spiracle (fig. 4); larvae greyish-brown, rather variable, somewhat translucent; in pasture soils, less commonly in marshy soils and aquatic mosses. Length 44 mm. .... *Tipula paludosa* Mg.
39. Anal segment with four elongated tapering papillae ..... 40.
- Anal segment with more than four elongated tapering papillae ..... 44.
40. Dorsum with longitudinal stripes; papillae longer and more slender; spiracular disc similar to that of *T. lateralis* Mg. (fig. 53); larvae greyish-brown; in marshy soils. Length 27 mm. .... *Tipula solstitialis* Westh.
- Dorsum without longitudinal stripes; anal papillae shorter and stouter ..... 41.
41. Dorsal lobes with sharply defined reddish-brown borders; ventral lobes heavily darkened across base (fig. 48); larvae dark brown or greyish-brown; in marshy or wet soils, usually by streams or riversides or in woods. Length 40 mm. ....  
*Tipula vittata* Mg.
- Dorsal lobes with vaguely defined borders only; larvae lighter in colour and smaller, not exceeding 36 mm. in length ..... 42.
42. Anal papillae slender and rather longer; ventral lobes with dark band across base and almost all the surface of the lobes pigmented (fig. 51); larvae brownish, with narrow darker transverse stripes dorsally and ventrally; in marshy soils. Length 29 mm. .... *Tipula luna* Westh.
- Anal papillae stout and shorter; ventral lobes with lighter stripes across base and surface of lobes not almost entirely pigmented ..... 43.
43. Colour grey, rather translucent, disc whitish, pigmented borders of lobes lighter, slight pigmented marks between spiracles often absent (fig. 49); in marshy soils. Length 34 mm. .... *Tipula oleracea* L.
- Colour yellowish-brown, not translucent, disc whitish-yellow, pigmented borders of lobes darker, two dark marks between spiracles prominent (fig. 50); in marshy soils. Length 35 mm. .... *Tipula czizeki* De Jong.
44. Six anal papillae ..... 45.
- Eight anal papillae ..... 50.
45. Lobes of spiracular disc margined with very long hairs, the length of the hairs at least equal to the breadth of the lobes at base; anal papillae completely ventral, spiracular disc at an angle with the longitudinal axis of the body (fig. 9) ... 46.
- Lobes of spiracular disc margined with much shorter hairs; anal papillae not completely ventral; spiracular disc in a plane at right angles to the longitudinal axis of the body ..... 48.



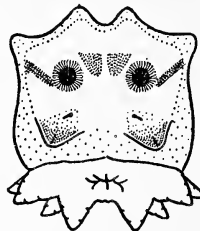
Figs. 54-61. Anal segments, posterior view. 54, *Tipula maxima* Pod. 55, *T. fulvipennis* Deg. 56, *Prionocera turcica* (F.). 57, *T. luteipennis* Mg. (hairs on ventral lobes omitted). 58, *T. melanoceros* Schum. (hairs on ventral lobes omitted). 59, *T. subnodicornis* Zett. 60, *T. macrocera* Zett. 61, *T. cheethami* Edw. (hairs on ventral lobes omitted).

46. Lobes of spiracular disc long and narrow, almost parallel-sided, more than three times as long as broad at base (fig. 56); larvae brownish or dark grey; in *Sphagnum* on moors, usually semi-aquatic. Length 35 mm. ....  
*Prionocera turcica* (F.).
- Lobes of spiracular disc shorter and broader, not twice as long as broad at base, tapering towards tip ..... 47.
47. Pigmented borders of dorsal lobes dark, usually well defined; disc yellowish, anal papillae shorter (fig. 57); larvae whitish-grey, long and thin, in marshy soils. Length 35-40 mm. ...  
*Tipula luteipennis* Mg.
- Pigmented borders of dorsal lobes lighter and ill-defined; disc whitish, ventral lobes slightly yellow; anal papillae longer (fig. 58); larvae grey, shorter and thicker; in *Sphagnum* or in wet peaty soil. Length 28 mm. ....  
*Tipula melanoceros* Schum.
48. Dorsal lobes with dark, well defined narrow lines internal to each border (fig. 52); larvae without or with only a faint pattern of longitudinal stripes along the dorsum, dorsum darker than ventral or pleural surfaces; in soils of river banks. Length 33 mm. .... *Tipula montium* Egg.
- Dorsal lobes with only a faint darker border (fig. 53); larvae greyish-brown with prominent dark stripes or spots along the dorsum ..... 49.
49. Anal papillae long and slender, the length of the longest (lateral) pair being greater than the width of the anal segment (fig. 53), pattern along dorsum usually broken up into ocellar spots; larvae lighter ventrally and along pleurae; in soils of river banks, usually lighter soils. Length 29 mm. ...  
*Tipula couckeii* Tonn.
- Anal papillae shorter and stouter, the length of the longest (lateral) pair not equal to the width of the anal segment (fig. 53); pattern along dorsum usually consisting of broken lines; larvae greyish-brown or darker; in marshy soils, in aquatic moss, etc. Length 28-30 mm. ... *Tipula lateralis* Mg.
50. Anal papillae of unequal length ..... 51.
- Anal papillae in four pairs all of about equal length ..... 52.
51. Dorsal and lateral lobes with sharply defined but not continuous borders; ventral lobes darker at base (fig. 54); larvae greyish-brown, rather variable; in marshy soils or freely aquatic amongst pebbles, dead leaves, etc., in small rivulets. Length 50 mm. .... *Tipula maxima* Pod.
- Dorsal and lateral lobes with vaguely defined darker borders which are continuous; ventral lobes lighter at base (fig. 55); larvae greyish-brown, variable; in marshy soils, in aquatic moss, amongst leaf mould by streams, etc. Length 40 mm. ...  
*Tipula fulvipennis* Deg.
52. Lobes of the spiracular disc margined with long hairs, the hairs longer than width of the lobes at base (fig. 61); lobes held out widely, spiracular disc at an angle with longitudinal axis of the body; dorsum darker, heavily marked with a

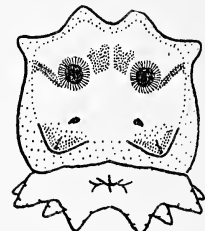
- pattern of longitudinal stripes; in aquatic moss in streams and waterfalls. Length 20 mm. .... *Tipula cheethami* Edw.
- Lobes of the spiracular disc margined with much shorter hairs ..... 53.
53. Posterior surfaces of the lobes sclerotised, of a reddish-brown colour; larvae in moorland mosses ..... 54.
- Posterior surfaces of the lobes not reddish-brown ..... 55.
54. Lobes of the spiracular disc with darker borders; anal papillae more or less parallel-sided, in pairs (fig. 59); larvae yellowish or greyish-white; in *Sphagnum* or *Polytrichum* on moors. Length 19 mm. .... *Tipula subnodicornis* Zett.
- Lobes of the spiracular disc with a median dark line and apical dark spot; anal papillae conical with narrow tips (fig. 60); larvae greenish or grey; in *Sphagnum*, *Hypnum*, etc., on moors. Length 22 mm. .... *Tipula macrocera* Zett.



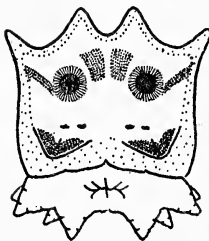
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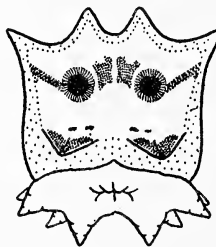
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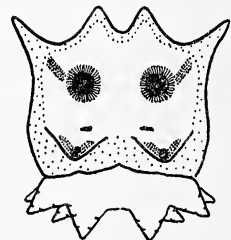
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Figs. 62-67. Anal segments, posterior view. 62, *Tipula rufina* Mg. 63, *T. marmorata* Mg. 64, *T. alpium* Bergr. 65, *T. signata* Staeg. 66, *T. staegeri* Niels. 67, *T. obsoleta* Mg.

55. Dorsum of larvae much darker than venter or pleurae; dorsum with at least a median dark longitudinal stripe; dark margins of lobes extending down to spiracles (fig. 62); larvae dark grey or greyish-brown; in mosses on walls, aquatic mosses on moors, etc. Length 20 mm. ... *Tipula rufina* Mg.

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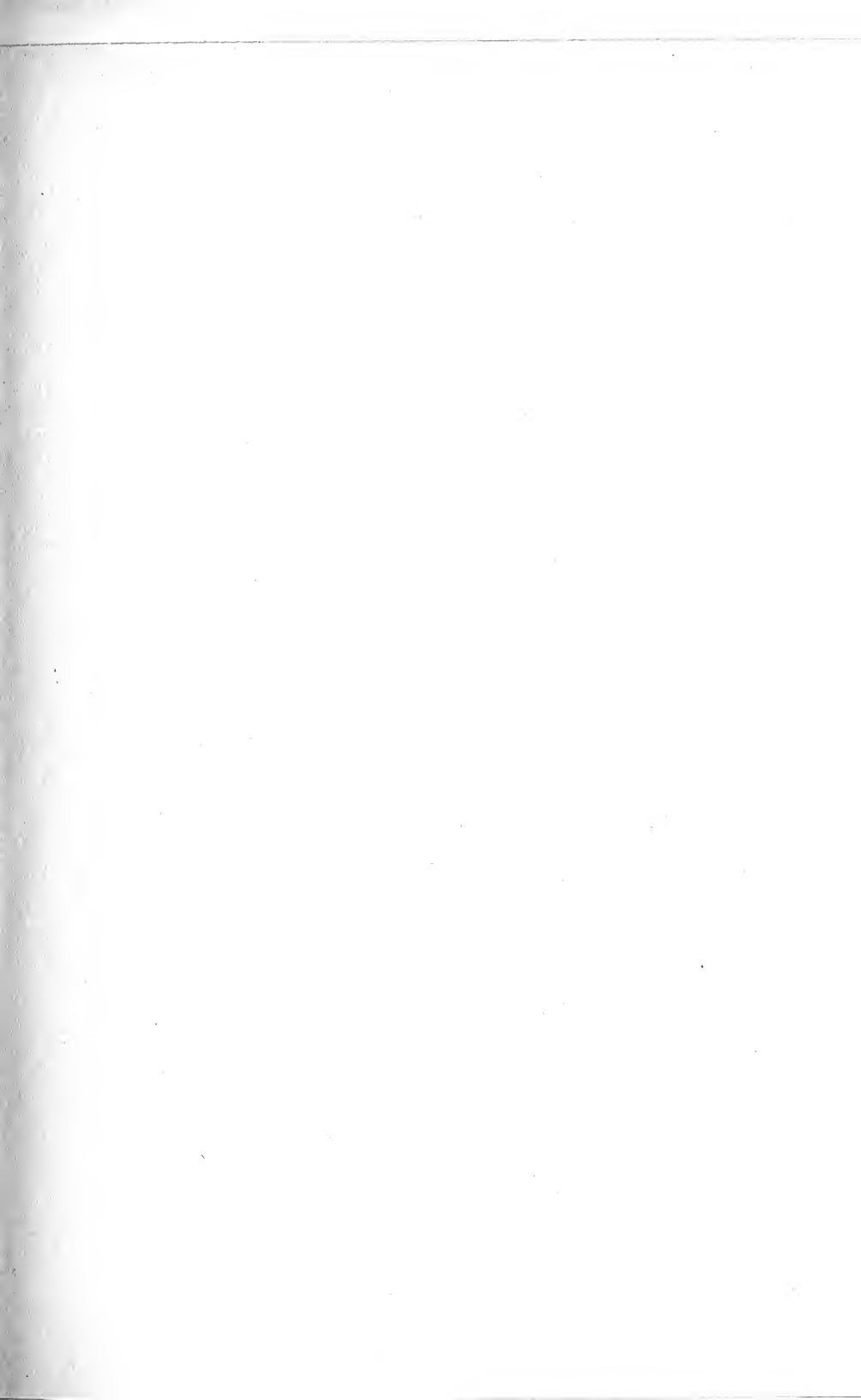
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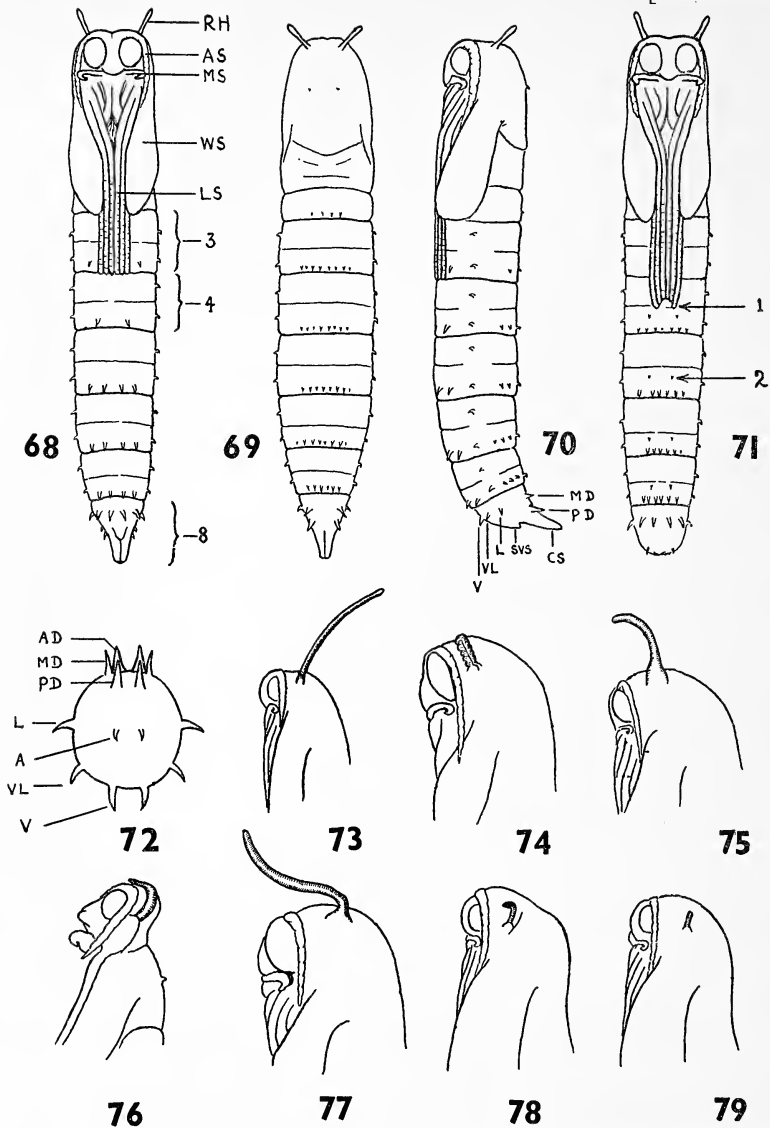


- Dorsum of larvae much lighter, without any trace of a dark longitudinal stripe; narrow transverse dark stripes on body, most pronounced dorsally, absent on pleurae; lobes without dark margins or with indistinct margins ..... 56.
- 56. Spiracular disc without any markings between the spiracles; or with a very small or narrow one ..... 57.
- Spiracular disc with extensive markings between the spiracles, covering most of the space between, although the markings may be faint ..... 58.
- 57. Markings absent between the spiracles; a short wide pigmented patch to the outside of the spiracles; lateral lobes elongated, rather longer than the dorsal lobes; larvae grey with dark transverse stripes prominent on dorsum; in mosses on walls, stones, etc., in woods (fig. 67). Length 20 mm. ....  
*Tipula obsoleta* Mg.
- A narrow horizontal line usually present between spiracles; a short dark wide pigmented patch to the outside of each spiracle; lateral and dorsal lobes subequal, shorter; larvae brownish with darker transverse stripes on dorsum; in mosses on soil in woods, or mosses in moorland marshes (fig. 45). Length 20 mm. .... *Tipula pagana* Mg.
- 58. Dorsal and lateral lobes short and rounded; ventral lobes with pale brown patches, the edges of which are not sharply defined. In mosses on walls, stones, trees, etc. .... 59.
- Dorsal and lateral lobes longer and more narrow; ventral lobes with dark brown patches, the edges of which are sharply defined. In mosses on walls, stones, etc., in woods ..... 60.
- 59. Markings between spiracles low down on disc so that the dorsal edge of the patches is about level with the dorsal edge of the spiracular border; ventral lobes pigmented between the basal black spots and the apical patch (fig. 63). Length 20 mm. .... *Tipula marmorata* Mg.
- Markings between spiracles higher and more irregular; ventral lobes unpigmented between the basal black spots and the apical patch (fig. 64). Length 20 mm. ....  
*Tipula alpium* Bergr.
- 60. Markings between spiracles regular, fan-shaped; lateral lobes slightly shorter; pigmented patches on ventral lobes darker (fig. 65). Length 20 mm. .... *Tipula signata* Staeg.
- Markings between spiracles irregular; lateral lobes longer; pigmented patches on ventral lobes lighter (fig. 66). Length 20 mm. .... *Tipula staegeri* Niels.

The distinctions between *T. marmorata* Mg. and *T. alpium* Bergr., and between *T. signata* Staeg. and *T. staegeri* Niels., are unsatisfactory since so many variations occur.

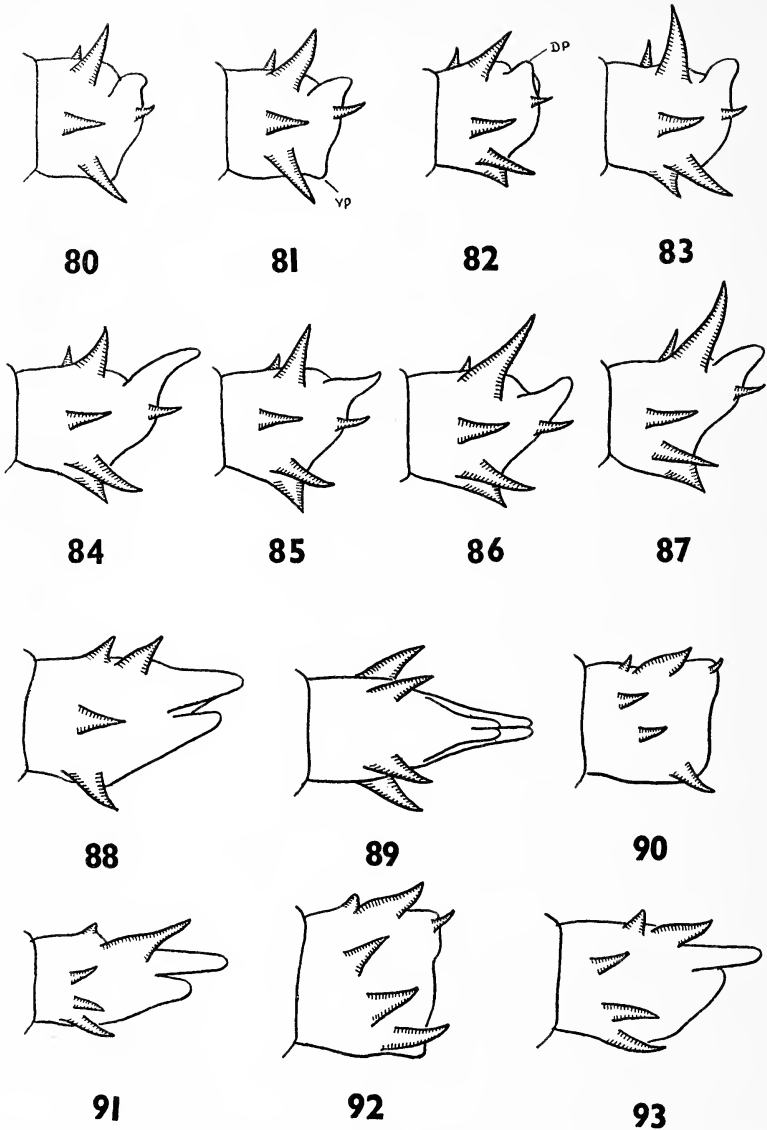
#### 7. Key to Pupae

- 1 Respiratory processes longer than normal or strongly curved (figs. 73, 75, 76, 77) ..... 2.



- Figs. 68-70. *Tipula excisa* Schum. ♀ 68, pupa, ventral view. RH—respiratory process, AS—antennal sheath, MS—maxillary palp sheath, WS—wing sheath, LS—leg sheath; 3, 4, abdominal segments; 8, anal segment. 69, pupa dorsal view. 70, pupa, lateral view. MD—medio-dorsal spine, PD—postero-dorsal spine, CS—cerci sheaths, SVS—sternal valve sheaths, L—lateral spine, VL—ventro-lateral spine, V—ventral spine.
- Fig. 71. *Tipula paludosa* Mg., ♂ pupa ventral view. Note (1) curved tips of leg sheaths which end at different levels, (2) pair of small spines anterior to row of sternal spines on posterior borders of sternites 4-7.
- Fig. 72. Diagram of anal segment of male pupa, posterior view, illustrating nomenclature of spines, lettering as in fig. 70, AD—anterio-dorsal spine, A—anal spine.
- Figs. 73-79. Pupa, anterior, lateral view. 73, *Prionocera turcica* (F.). 74, *Tanyp-tera atrata* (L.) (after Alexander). 75, *Dictenidia bimaculata* (L.) (after Theowald). 76, *Ctenophora pectinicornis* (L.) (After Coe). 77, *Tipula flavolineata* Mg. 78, *T. subnodicornis* Zett. 79, *T. unca* Wied.

- Respiratory processes of normal length (figs. 69-71) or shorter ..... 6.
- 2. Respiratory processes longer than width of thorax (fig. 73); in *Sphagnum*, etc., on moors. Length 25 mm., of which 5 mm. is the length of the processes ... *Prionocera turcica* (F.)
- Respiratory processes not longer than width of thorax, strongly curved; in dead wood ..... 3.
- 3. Respiratory processes curved anteriorly (fig. 77). Length 26 mm. .... *Tipula flavolineata* Mg.
- Respiratory processes curved ventrally (fig. 75, 76) ..... 4.
- 4. Respiratory processes placed near anterior end of pupae, projecting well above head (fig. 75). Length 25 mm. .... *Dictenidia bimaculata* (L.)
- Respiratory processes set lower down on side of pupae, more strongly curved (fig. 76) ..... 5.
- 5. Ventral, ventro-lateral, and lateral spines smaller (figs. 90, 91). Length 25-30 mm. .... *Ctenophora pectinicornis* (L.)
- Ventral, ventro-lateral, and lateral spines larger (fig. 92, 93). Length 27-28 mm. .... *Ctenophora ornata* (Mg.)
- 6. Respiratory processes shorter than normal (figs. 74, 78, 79) ..... 7.
- Respiratory processes of normal length (figs 69-71) ..... 11.
- 7. Respiratory processes short and broad (fig. 74); in dead wood. Length 25 mm. .... *Tanyptera atrata* (L.)  
*Tanyptera nigricornis* (Mg.)
- Respiratory processes short but narrow; in marshy soil or moorland mosses ..... 8.
- 8. Respiratory processes curved and broadened at tip (fig. 78); in moorland mosses ..... 9.
- Respiratory processes straight (fig. 79); in marshy soil ... 10.
- 9. Ventral and ventro-lateral spines larger and erect (figs. 94, 95). Length 14-16 mm. .... *Tipula macrocera* Zett.
- Ventral and ventro-lateral spines smaller and curved (figs. 96, 97). Length 12-14 mm. .... *Tipula subnodicornis* Zett.
- 10. Dorsal spines long and narrow; male anal spine placed more ventrally (fig. 98); female cerci sheaths much longer than those of sternal valves (fig. 99). Length 29 mm. .... *Tipula luteipennis* Mg.
- Dorsal spines shorter and broader; male anal spine placed more dorsally (fig. 100); female cerci sheaths hardly longer than those of sternal valves (fig. 101). Length 20 mm. .... *Tipula unca* Wied.
- 11. Only one ventral spine in males, none in females (figs. 88, 89); lateral spines very large (*Nephrotoma*) ..... 12. (Only the male pupae are keyed out; the female pupae appear to be hardly separable).
- Two ventral spines in both sexes; lateral spines not usually very prominent ..... 19.
- 12. Ventral spine represented by a rounded process ..... 13.
- Ventral spine normal and conspicuous ..... 14.



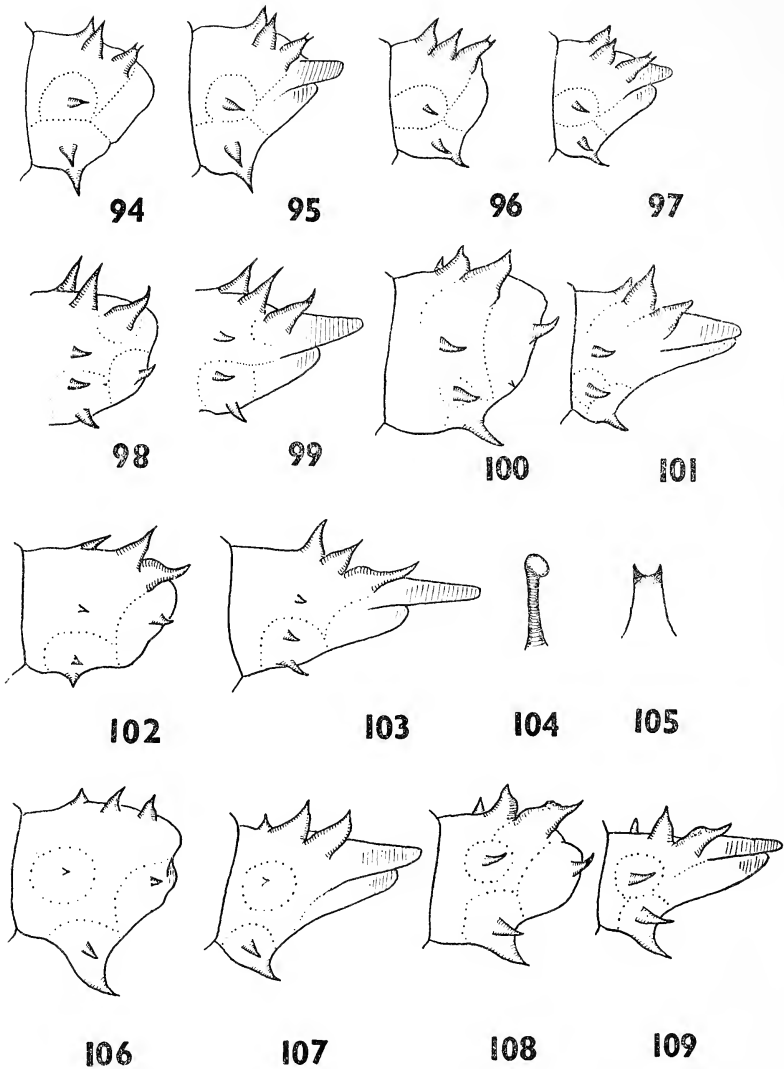
Figs. 80-88. Anal segments, lateral view. 80, *Nephrotoma flavescens* (L.) or *N. maculata* (L.). ♂ 81, *N. cornicina* (L.) ♂ VP—ventral process. 82, *N. quadrifaria* (Mg.) ♂ DP—dorsal process. 83, *N. scurra* (Mg.) ♂ 84, *N. dorsalis* (F.) (after Theowald) ♂ 85, *N. flavipalpis* (Mg.) ♂ 86, *N. analis* (Schum.) ♂ 87, *N. crocata* (L.) (after Theowald) ♂ 88, *N. flavipalpis* (Mg.) ♀

Fig 89. Anal segment, ventral view, *N. flavipalpis* Mg. ♀.

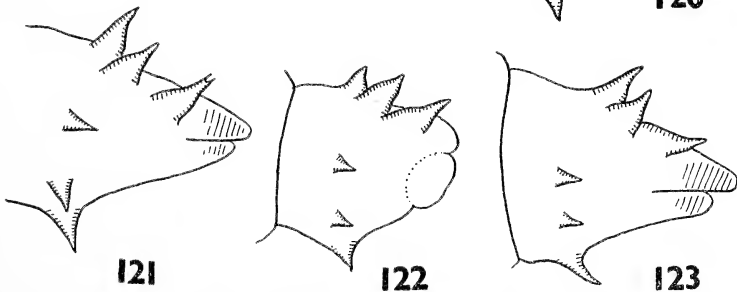
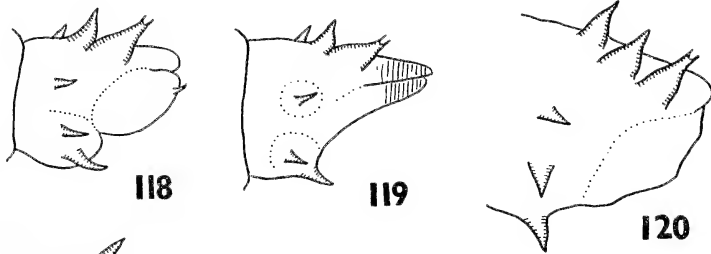
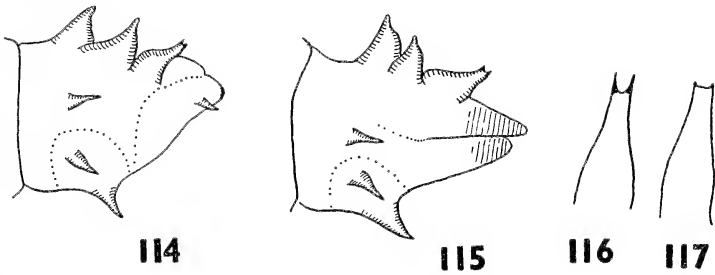
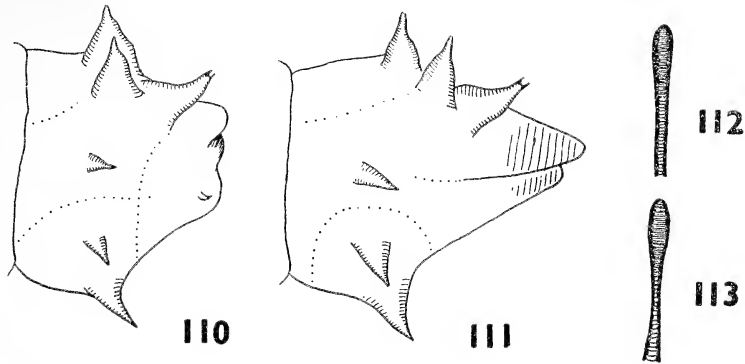
Figs. 90-93. Anal segments, lateral view. 90, ♂, 91, ♀, *Ctenophora pectinicornis* (L.) (after Theowald). 92, ♂, 93, ♀, *C. ornata* (Mg.) (after Theowald).



13. Ventral process small, in line with ventro-lateral spines, the latter posterior to the lateral spines (fig. 80); in woodland soil. Length 16-18 mm. .... *N. flavescens* (L.).  
*N. maculata* (Mg.)
- Ventral process large, posterior to the ventro-lateral spines, the latter in line with the lateral spines (fig. 81); in woodland soil. Length 18 mm. .... *N. cornicina* (L.)
14. Dorsal process small, not longer than breadth at base ... 15.  
 — Dorsal process large, at least twice as long as broad at base ..... 16.
15. Postero-dorsal spine shorter and oblique (fig. 82); in woodland soil. Length 16 mm. .... *N. quadrifaria* (Mg.).  
 — Postero-dorsal spine very large and erect (fig. 83); in damp (or sandy) soil. Length 20 mm. .... *N. scurra* (Mg.).
16. Dorsal process narrowed towards tip; postero-dorsal spines short, equal to half width of anal segment of pupae ..... 17.  
 — Dorsal processes blunt at tip; postero-dorsal spines very large, equal to width of anal segment of pupae ..... 18.
17. Dorsal process longer, curving ventrally (fig. 84); in damp soil. Length 18 mm. .... *N. dorsalis* (F.).  
 — Dorsal process shorter, curving dorsally (fig. 85); in damp soil. Length 18-19 mm. .... *N. flavipalpis* (Mg.).
18. Dorsal processes curved slightly dorsally, well removed from postero-dorsal spine (fig. 86); in damp soil. Length 20 mm. ...  
*N. analis* (Schum.).  
 — Dorsal processes curved slightly ventrally, close to postero-dorsal spine (fig. 87); in damp soil. Length 18 mm. ....  
*N. crocata* (L.)
19. Lateral spines very small and inconspicuous (figs. 102, 103, 106, 107) ..... 21.  
 — Lateral spines always prominent ..... 20.
20. Ventral spines small; tergal spines weak; tip of respiratory processes not enlarged; male without ventral process (figs. 102, 103); in peaty soil or *Sphagnum*. Length 22 mm. ...  
*Tipula melanoceros* Schum.  
 — Ventral spines larger; tergal spines strong; tip of respiratory processes enlarged (fig. 104); male with ventral spines placed on a ventral process (figs. 105, 106); female ventral spines widely spaced (fig. 107); in damp soil near streams in woods. Length 18 mm. .... *Tipula varicornis* Schum.
21. Two small spines anterior to row of sternal spines on abdominal segments 4, 5, 6, 7 (fig. 71); anterior dorsal spines prominent ..... 22.  
 — No small spines anterior to row of sternal spines on abdominal segments 4, 5, 6, 7 (fig. 68); anterior dorsal spines small or absent ..... 34.
22. Length 16 mm. Postero-dorsal spines assymetrical (figs. 108, 109); in marshy soil ..... *Tipula pruinoso* Wied.  
 — Length at least 20 mm. Postero-dorsal spines symmetrical ..... 23.

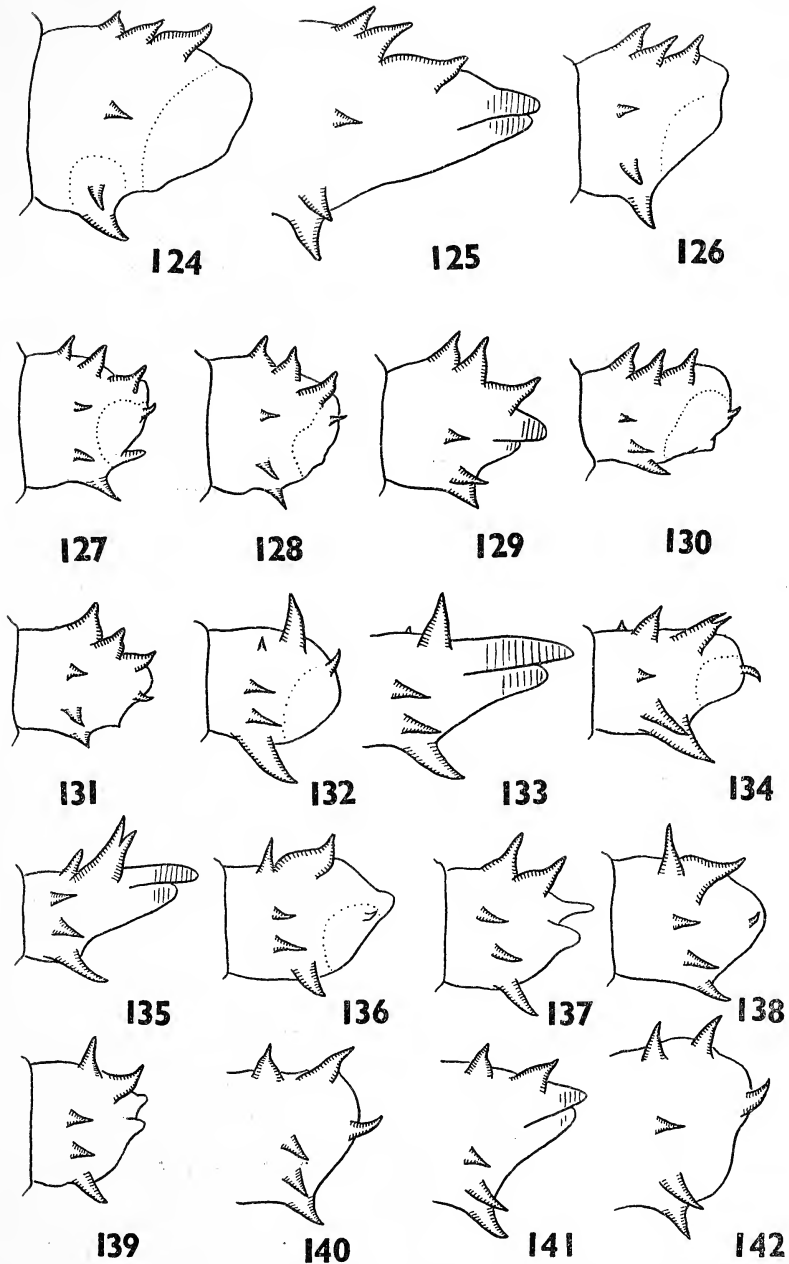


Figs. 94-103. Anal segments, lateral view. 94, ♂, 95 ♀, *Tipula macrocera* Zett. 96, ♂, 97 ♀, *T. subnodicornis* Zett. 98, ♂, 99, ♀, *T. luteipennis* Mg. 100, ♂, 101, ♀, *T. unca* Wied. 102, ♂, 103, ♀, *T. melanoceros* Schum.  
 Fig. 104. *Tipula variicornis* Schum, respiratory process.  
 Fig. 105. *T. variicornis* Schum. Ventral process, ♂, ventral view.  
 Figs. 106-109. Anal segments, lateral view. 106, ♂, 107, ♀, *T. variicornis* Schum. 108, ♂, 109, ♀, *T. pruinososa* Wied.



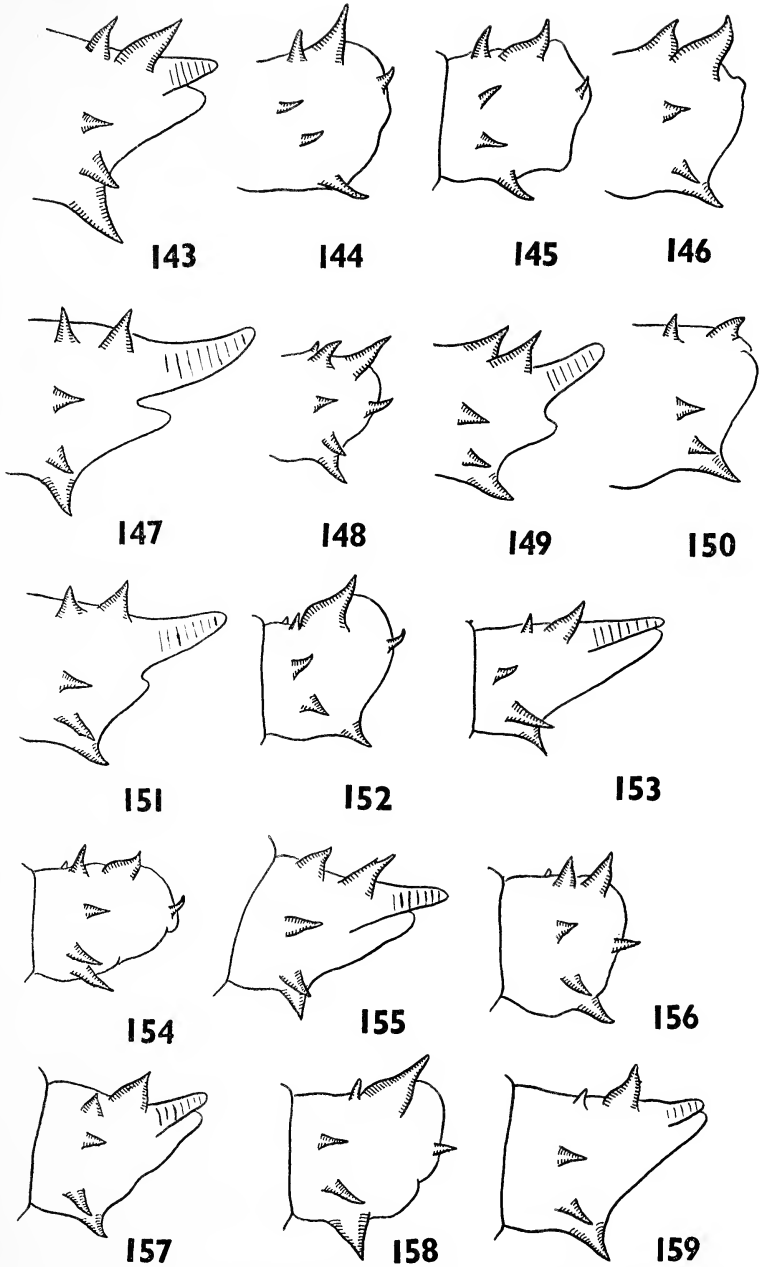
Figs. 110, ♂, 111, ♀. Anal segments, lateral view, *Tipula maxima* Poda.  
 Figs. 112, 113, respiratory processes. 112, *T. maxima* Poda. 113, *T. fulvipennis* Deg.  
 Figs. 114, ♂, 115, ♀. Anal segments, lateral view, *Tipula fulvipennis* Deg.  
 Figs. 116, 117. Bifurcate dorsal spines, showing variation.  
 Figs. 118-123. Anal segments, lateral view. 118, ♂, 119, ♀, *T. tuna* Westh. 120, ♂, 121, ♀, *T. vittata* Mg. 122, ♂, 123, ♀, *T. oleracea* L.

- 23. Tips of leg sheaths curved inwards and ending at different levels (fig. 71) ..... 24.
- Tips of leg sheaths straight and usually ending at about the same level (fig. 68) ..... 30.
- 24. Postero-dorsal spines bifurcate (figs. 116, 117) ..... 25.
- Postero-dorsal spines not bifurcate ..... 28.
- 25. Respiratory processes not spatulate, gradually widened towards tip (fig. 112) ..... 26.
- Respiratory processes spatulate (figs. 113, 114, 115); in marshy soil. Length 26-29 mm. .... *Tipula fulvipennis* Deg.
- 26. Length 32-35 mm. In marshy soil (figs. 110, 111) ..... *Tipula maxima* Poda.
- Length 30 mm. or less ..... 27.
- 27. Ventral spines smaller and curved; postero-dorsal spines smaller (figs. 118, 119); in marshy soil. Length 22-24 mm. ... *Tipula luna* Westh.
- Ventral spines larger and erect; postero-dorsal spines large (figs. 120, 121); in marshy soil. Length 27-30 mm. .... *Tipula vittata* Mg.
- 28. Male postero-dorsal spine almost reaching the end of pupa, on which a rounded process occurs (fig. 122); female cerci sheaths shorter, postero-dorsal spines almost reaching the end of the sternal valve sheaths (fig. 123); in marshy soil or aquatic moss. Length 26 mm. .... *Tipula oleracea* L.
- Male postero-dorsal spine not almost reaching the end of pupa; no rounded process; female cerci sheaths longer, postero-dorsal spines well anterior to tip of cerci or sternal valve sheaths ..... 29.
- 29. Male caudal tip angular (fig. 126); female similar to *paludosa* (fig. 125); in marshy soil in September. Length 28 mm. ... *Tipula czizeki* De Jong.
- Male caudal tip rounded (fig. 124); female cerci and sternal valve sheaths almost equal in length (fig. 125); in pasture soil usually, July to August. Length 28-30 mm. .... *Tipula paludosa* Mg.
- 30. Pupae narrower; dorsal spines long and narrow; female cerci sheaths much longer than those of the sternal valves (figs. 98, 99); in marshy soil. Length 29 mm. .... *Tipula luteipennis* Mg.
- Pupae broader, dorsal spines short and broad; female cerci sheaths shorter, not much longer than those of sternal valves ..... 31.
- 31. Prominence on anal segment of male (between ventral and anal spines) long and almost spine-like (fig. 127); female similar to *lateralis* (fig. 129); in soil of river banks. Length 24 mm. .... *Tipula montium* Egg.
- Prominence of anal segment of male much less produced .. 32.
- 32. Prominence on anal segment of male small and rounded (fig. 128); female cerci and sternal valve sheaths short (fig. 129). In marshy or drier soils, or in aquatic mosses. Length 22-23 mm. .... *Tipula lateralis* Mg.



Figs. 124-142. Anal segments, lateral view. 124, ♂, 125, ♀, *Tipula patudosa* Mg. 126, ♂, *T. czizeki* De Jong. 127, ♂, *T. montium* Egg. 128, ♂, 129, ♀, *T. lateralis* Mg. 130, ♂, *T. solstitialis* Westh. 131, ♂, *T. couckeii* Tonn. 132, ♂, 133, ♀, *T. livida* v.d. Wulp (after Theowald). 134, ♂, 135, ♀, *T. nigra* L. (after Theowald). 136, ♂, 137, ♀, *T. fascipennis* Mg. 138, ♂, 139, ♀, *T. vernalis* Mg. 140, ♂, 141, ♀, *T. brevispina* Pierre. 142, ♂, *T. lunata* L.

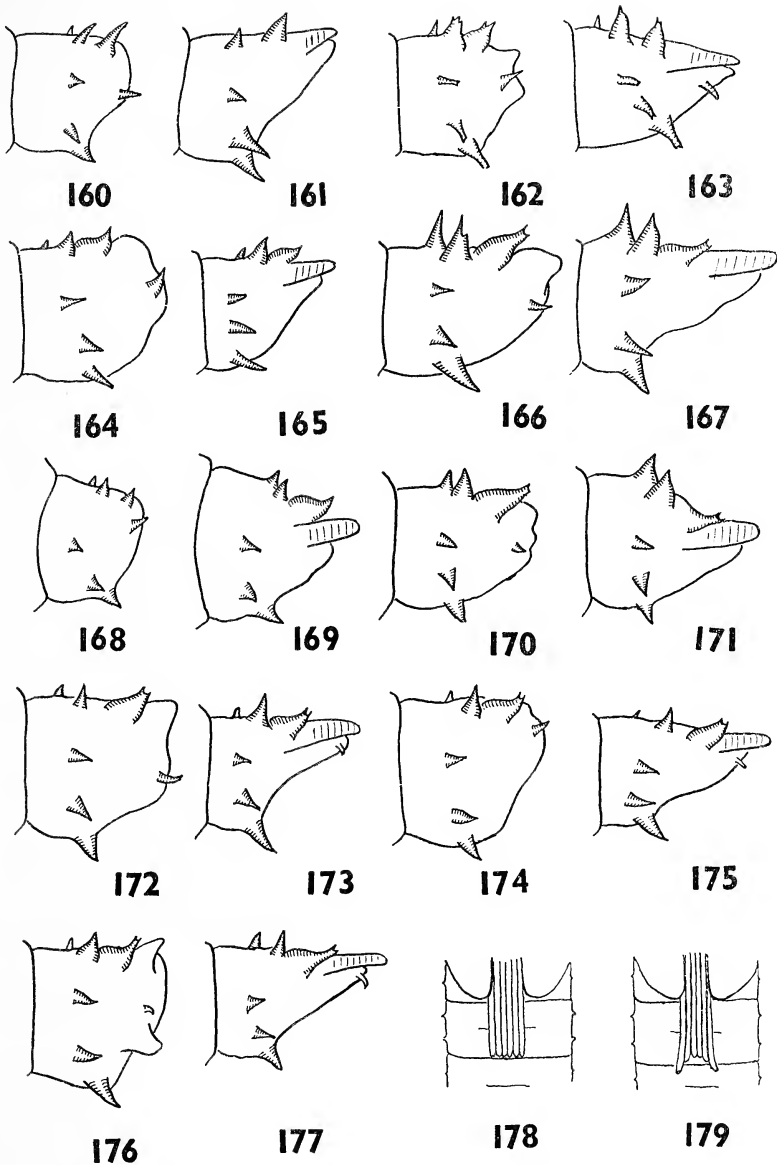
- Prominence on anal segment of male triangular ..... 33.
33. Prominence on anal segment sharply triangular; anal segment short (fig. 131); female similar to *lateralis* (fig. 129); in soil of river banks. Length 22 mm. ... *Tipula couckeii* Tonn.
- Prominence on anal segment bluntly triangular; anal segment long (fig. 130); female similar to *lateralis* (fig. 129); in marshy soil. Length 22 mm. ... *Tipula solstitialis* Westh.
34. Pupae 20 mm. or over ..... 35.
- Pupae 18 mm. or under ..... 50.
35. Sternal spines 6, 6, 6, 6; ventral spines large (figs. 132, 133); in woodland soil or detritus. Length 24 mm. ....  
*Tipula livida* v.d. Wulp.
- Sternal spines otherwise ..... 36.
36. Sternal spines 4, 5, 5, 5; postero-dorsal spines deeply bifurcate (figs. 134, 135); in damp or marshy soil. Length 16 mm. .... *Tipula nigra* L.
- Sternal spines otherwise ..... 37.
37. Sternal spines 4, 6, 6, 5 ..... 38.
- Sternal spines 2, 4, 4, 4 (there may be very small additional spines between the larger ones) ..... 43.
38. Male anal spine very small; female cerci and sternal valve sheaths well separated ..... 39.
- Male anal spine large; female cerci and sternal valve sheaths in contact, or almost so ..... 40.
39. Tip of male anal segment with rounded process (fig. 136); female cerci sheaths long (fig. 137); in woodland soil. Length 25 mm. .... *Tipula fascipennis* Mg.
- Tip of male anal segment without a process (fig. 138); female cerci sheaths very short (fig. 139); in pasture soils. Length 20 mm. .... *Tipula vernalis* Mg.
40. Ventro-lateral spines directed ventrally and close to ventral spines ..... 41.
- Ventro-lateral spines directed posteriorly and well separated from ventral spines ..... 42.
41. Lateral and ventro-lateral spines close to ventral spines; female cerci and sternal valve sheaths in contact (figs. 140, 141); in woodland soil or detritus. Length 24 mm. ....  
*Tipula brevispina* Pierre.
- Lateral and ventro-lateral spines not close together, only the latter near to ventral spines; female cerci and sternal valve sheaths separated at tip (figs. 142, 143); in woodland soil or leaf mould. Length 24 mm. .... *Tipula lunata* L.
42. Male anal segment rounded; postero-dorsal spine large and erect (fig. 144); female similar to *lunata* (fig. 143); in woodland soil or detritus. Length 24 mm. .... *Tipula selene* Mg.
- Male anal segment angular; postero-dorsal spine oblique (fig. 145); female similar to *lunata* (fig. 143); in woodland soil or detritus. Length 23 mm. .... *Tipula cava* Ried.
43. Sternal spines distinct, all large; female cerci sheaths curved (subgenus *Vestiplex* Bezzi) ..... 44.



Figs. 143-159. Anal segments, lateral view. 143, ♀, *Tipula lunata* L. 144, ♂, *T. selene* Mg. (after Theowald). 145, ♂, *T. cava* Ried. 146, ♂, *T. nubeculosa* Mg. 147, ♀, *T. rubripes* Schum. 148, ♂, 149, ♀, *T. scripta* Mg. 150, ♂, 151, ♀, *T. excisa* Schum. 152, ♂, 153, ♀, *T. truncorum* Mg. 154, ♂, 155, ♀, *T. pabulina* Mg. 156, ♂, 157, ♀, *T. hortulana* Mg. 158, ♂, 159, ♀, *T. varipennis* Mg.

- Sternal spines less distinct; often additional small spines between the larger ones; female cerci sheaths straight... 46.
44. Male dorsal spines large (fig. 146); female cerci and sternal valve sheaths longer (fig. 147); in woodland soil. Length 24-28 mm. .... *Tipula nubeculosa* Mg.  
*Tipula rubripes* Schum.
- Male dorsal spines small; female cerci and sternal valve sheath shorter ..... 45.
45. Male anal spine prominent (fig. 148); female dorsal spines oblique (fig. 149); in woodland soil or detritus Length 24-26 mm. .... *Tipula scripta* Mg.
- Male anal spine very small or absent (fig. 150); female dorsal spines erect (fig. 151); in soil amongst mountain screes. Length 25 mm. .... *Tipula excisa* Schum.
46. Male anal spine small and curved; female cerci sheaths longer ..... 47.
- Male anal spine straight; female cerci sheaths shorter ... 48.
47. Median dorsal spine much smaller than postero-dorsal spine; female cerci and sternal valve sheaths subequal (figs. 152, 153); in woodland soil or mosses. Length 20 mm. ...  
*Tipula truncorum* Mg.
- Median dorsal spines almost as long as postero-dorsal spines; female cerci sheath shorter than those of sternal valves (figs. 154, 155); in woodland soil or mosses. Length 20 mm. .... *Tipula pabulina* Mg.
48. Male medio-dorsal and postero-dorsal spines subequal; ventral spines placed posteriorly so that they are directly ventral to the postero-dorsal spines (fig. 156); female cerci sheaths longer than those of sternal valves (fig. 157); in woodland soil. Length 20 mm. .... *Tipula hortulana* Mg.
- Male medio-dorsal and postero-dorsal spines not subequal; ventral spines placed more anteriorly so that they are directly ventral to the medio-dorsal spines; female cerci and sternal valve sheaths subequal ..... 49.
49. Postero-dorsal spines very large, about three times as large as medio-dorsal spines (figs. 158, 159); in woodland soil. Length 20 mm. .... *Tipula variipennis* Mg.
- Postero-dorsal spines equal to or a little larger than medio-dorsal spines (figs. 160, 161); in decayed wood or detritus on decayed wood, or in soil beneath moss on stones. Length 20 mm. .... *Tipula irrorata* Macq.
50. Lateral and ventro-lateral spines bifurcate (figs. 162, 163); pupae green in life, in mosses on trees near streams in woods. Length 15 mm. .... *Dolichozeza albipes* Stroem.
- Lateral and ventro-lateral spines not bifurcate ..... 51.
51. Postero-dorsal spines not bifurcate ..... 52.
- Postero-dorsal spines bifurcate ..... 53.
52. Spines on anal segment smaller (figs. 168, 169); in mosses on soil or in soil beneath the woods, or in moorland moss. Length 16 mm. .... *Tipula pagana* Mg.





Figs. 160-177. Anal segments, lateral view. 160, ♂, 161, ♀, *Tipula irrorata* Macq. 162, ♂, 163, ♀, *Dolichopeza albipes* Stroem. 164, ♂, 165, ♀, *Tipula marmorata* Mg. 166, ♂, 167, ♀, *T. rufina* Mg. 168, ♂, 169, ♀, *T. pagana* Mg. 170, ♂, 171, ♀, *T. cheethami* Edw. 172, ♂, 173, ♀, *T. alpium* Bergr. 174, ♂, 175, ♀, *T. staegeri* Niels. 176, ♂, 177, ♀, *T. signata* Staeg.

Figs. 178, 179. *T. marmorata* Mg. Variation in leg sheaths.

- Spines on anal segment larger (figs. 164, 165); in moss on walls, stones, etc. Length 16 mm. ....  
*Tipula marmorata* Mg.
53. Males ..... 54.  
 — Females ..... 58.
54. Four equidistant processes on end of anal segment (fig. 176); in moss on walls, soil, in woods. Length 15 mm. ....  
*Tipula signata* Staeg.
- Two processes or none on end of anal segment ..... 55.
55. Anal segment rounded at tip (fig. 174); in moss on walls, soils, etc., in woods. Length 15 mm. ... *Tipula staegeri* Niels.  
*Tipula obsoleta* Staeg.
- Anal segment with processes or projections at tip ..... 56.
56. Anal spine small; small rounded projections at tip of anal segment (fig. 170); in aquatic moss. Length 15 mm. ....  
*Tipula cheethami* Edw.
- Anal segment with prominent process near dorsal tip of pupae ..... 57.
57. Anterio- and medio-dorsal spines large and prominent (fig. 166); in moss on walls, aquatic mosses, etc. Length 17 mm.  
*Tipula rufina* Mg.
- Anterio- and medio-dorsal spines small (fig. 172); in moss on walls, stones, etc. Length 15 mm. ... *Tipula alpium* Bergr.
58. Cerci placed low down, about halfway between dorsum and venter of anal segment (fig. 171) ..... *Tipula cheethami* Edw.
- Cerci placed higher, nearer the dorsum of anal segment ... 59.
59. Anterio- and medio-dorsal spines large (fig. 167) .....  
*Tipula rufina* Mg.
- Anterio-dorsal spines small ..... 60.
60. Anterio-dorsal and medio-dorsal spines subequal (fig. 177) ...  
*Tipula signata* Staeg.
- Anterio-dorsal spines smaller than medio-dorsal spines ... 61.
61. Medio- and postero-dorsal spines well separated (fig. 175) ...  
*Tipula staegeri* Niels.  
*Tipula obsoleta* Mg.
- Medio- and postero-dorsal spines adjacent (fig. 173) .....  
*Tipula alpium* Bergr.

Full descriptions of all larvae not included in Chiswell (1956) are to be found in Brindle (1958-60).

## Check List of British Tipulinae (from Kloet &amp; Hincks 1945)

*Tipula* L.

- S. Acutipula* Alex.  
*fulvipennis* Deg.                   figs. 55, 113, 114, 115.  
*maxima* Poda                       figs. 54, 110, 111, 112.  
*vittata* Mg.                         figs. 48, 120, 121.  
*S. Anomaloptera* Lioy  
*nigra* L.                               figs. 44, 134, 135.  
*S. Schummelia* Edw.  
*yerburyi* Edw.                       larva and pupa unknown.  
*variicornis* Schum.                 figs. 24, 104, 105, 106, 107.  
*S. Vestiplex* Bezzi  
*nubeculosa* Mg.                   figs. 36, 146.  
*excisa* Schum.                     figs. 35, 68, 69, 70, 150, 151.  
*rubripes* Schum.                 figs. 37, 147.  
*scripta* Mg.                         figs. 33, 34, 148, 149.  
*S. Tipula* s.s.  
*mutila* Wahl.                       larva and pupa unknown.  
*microstigma* Pierre               larva and pupa unknown.  
*variipennis* Mg.                   figs. 40, 158, 159.  
*pseudovariipennis*  
     Czizek                           larva unknown. Theowald has examined two exuviae of female pupae from Beling's collection. They resemble *hortulana* pupae in the length of the cerci sheath, but the posterior dorsal spine is large, and the median dorsal spine is very small as in *variipennis* pupae.  
  
*hortulana* Mg.                     figs. 39, 156, 157.  
*rufina* Mg.                         figs. 62, 166, 167.  
*irrorata* Macq.                   figs. 38, 160, 161.  
*unca* Wied.                         figs. 47, 79, 100, 101.  
*winthemi* Lacks.                 larva and pupa unknown.  
*macrocera* Zett.                 figs. 60, 94, 95.  
*cheethami* Edw.                 figs. 61, 170, 171.  
*marmorata* Mg.                 figs. 63, 164, 165, 178, 179.  
*alpium* Bergr.                   figs. 64, 172, 173.  
*bistilata* Lundst.               larva and pupa unknown.  
*serrulata* Lacks.               larva and pupa unknown.  
*obsoleta* Mg.                    fig. 67.  
*vafra* Ried.                      larva and pupa unknown.  
*staegeri* Niels.                 figs. 66, 174, 175.  
*signata* Staeg.                 figs. 65, 176, 177.  
*pabulina* Mg.                   figs. 41, 42, 154, 155.  
*truncorum* Mg.                 figs. 43, 152, 153.  
*oleracea* L.                     figs. 49, 122, 123.  
*czizeki* de Jong                 figs. 50, 126.  
*paludosa* Mg.                   figs. 1, 2, 3, 4, 71, 124, 125.  
*vernalis* Mg.                   figs. 32, 138, 139.  
*subnodicornis* Zett.           figs. 59, 78, 96, 97.

- marginata* L. larva and pupa unknown.  
*solstitialis* Westh. fig. 130.  
*couckeii* Tonn. figs. 53, 131.  
*caerulescens* Lacks. Larva and pupa unknown.  
*lateralis* Mg. figs. 53, 128, 129.  
*montium* Egg. figs. 52, 127.  
*pruinosa* Wied. figs. 25, 108, 109.  
*melanoceros* Schum. figs. 58, 102, 103.  
*luteipennis* Mg. figs. 57, 98, 99.  
*pagana* Mg. figs. 45, 46, 168, 169.  
*flavolineata* Mg. figs. 14, 77.  
*juncea* Mg. larva similar to *livida* (fig. 31);  
Theowald describes the sternal spines  
of the pupa as 2, 6, 6, 5. Median dorsal  
spines very small, posterior dorsal  
spines unusually large. Female cerci  
and sternal valve sheaths separated  
as in *vernalis* and *fascipennis* but  
cerci sheaths twice as long as the  
sternal valve sheaths.  
figs. 51, 118, 119.
- luna* Westh.
- S. Lunatipula* Edw.
- selene* Mg. figs. 28, 144.  
*fascipennis* Mg. figs. 7, 26, 136, 137.  
*brevispina* Pierre figs. 29, 140, 141.  
*cava* Ried. figs. 27, 145.  
*lunata* L. figs. 30, 142, 143.  
*poliostigma* Schum. larva similar to *selene* (fig. 28); pupa  
similar to *lunata*.  
*helvola* Loew larva unknown. Theowald describes  
the male exuviae of the pupa. Similar  
to the *lunata* group but with a very  
long anal spine—almost as long as the  
posterior dorsal spine.
- Additions to list (livida, Chiswell (1954): siebkei Collin (1954)).*
- livida* v.d. Wulp figs. 31, 132, 133.  
*siebkei* Zett. larva and pupa unknown.
- Nephrotoma* Mg.
- dorsalis* (F.) figs. 22, 84.  
*crocata* (L.) figs. 18, 87.  
*flavipalpis* (Mg.) figs. 16, 85, 88, 89.  
*quadristriata* (Schum.) larva and pupa unknown.  
*scurra* (Mg.) figs. 20, 83.  
*maculata* (Mg.) figs. 19, 80.  
*flavescens* (L.) figs. 19, 80.  
*aculeata* Loew larva and pupa unknown.

- lunulicornis* (Schum.) larva and pupa described by Beling as *dorsalis*; larva resembles *pratensis* (not British), ventral lobes as *crocata* but shorter, and basal line lighter in colour and shorter. Pupa in Brauns (1954).
- quadrifaria* (Mg.) figs. 23, 82.
- submaculosa* Edw. larva apparently similar to *quadrifaria* but with small black patch below dorsal lobes much smaller. Pupa unknown.
- sullingtonensis* Edw. Larva and pupa unknown.
- analisis* (Schum.) figs. 17, 86.
- guestfalica* Westh. larva unknown; male pupa with ventral spine rounded at tip, but with dorsal processes projecting far beyond caudal end of pupa (see figs. 80-81).
- cornicina* (L.) figs. 21, 81.
- Prionocera* Loew.
- turcica* (F.) figs. 56, 73.
- pubescens* Loew larva unknown; pupa similar to *turcica* but with dorsal spines longer.
- proxima* Lacks. larva and pupa unknown.
- Dolichocheza* Curt.
- albipes* Stroem. figs. 10, 162, 163.
- Dictenidia* Brulle.
- bimaculata* (L.) figs. 11, 75.
- Tanyptera* Latr.
- atrata* (L.) figs. 8, 15, 74.
- nigricornis* (Mg.) apparently indistinguishable from *atrata*.
- Ctenophora*
- ornata* (Mg.) figs. 13, 92, 93.
- pectinicornis* (L.) figs. 12, 76, 90, 91.
- flaveolata* (F.) larva and pupa unknown.

### 9. Acknowledgments

The drawings of the anal segments of the larva of *T. livida* v.d. Wulp and *T. selene* Mg. are from Chiswell (1956) by courtesy of the Royal Entomological Society of London. The pupa of *Tanyptera* is from Alexander (1920); the pupa of *Ctenophora* from Coe (1950); and the following from Theowald (1957): larvae and pupae of *T. truncorum* Mg., *N. dorsalis* (F.), *N. crocata* (L.), *C. pectinicornis* (L.), *C. ornata* (Mg.), and the pupae of *T. livida* v.d. Wulp, *T. selene* Mg., and *T. nigra* L. Details of *T. juncea* larva are from Hemmingsen (1959) and of *T. peliostigma* larva from Erhan and Theowald (1959).

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