STUDIES ON THE HYDROPTILIDAE (TRICHOPTERA): MORPHOLOGY, Phylogeny TAXONOMY AND DISTRIBUTION

By

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ABSTRACT

This thesis is an account of the morphology, taxonomy and distribution of the Hydroptilidae, a cosmopolitan family of small ('micro') caddis-flies, with special reference to the British fauna. Knowledge of the group, although well documented, has been very fragmentary and an attempt has been made to collate and correlate this data with new facts, mostly based on a study of material in the British Museum (Natural History), to present a more coherent picture of the family.

The introduction describes the general appearance and biology of all stages, their economic importance and collecting, preservation and examination techniques.

The external and internal morphology of the adult and case-bearing larval stages and the principal features of the young free-living larvae are described and illustrated.

The taxonomy, distribution and biology are described for the genera of the world (c. 50 with c. 600 species), for which a number of new synonymies have been indicated; three genera have been transferred to other families. The subfamily division into the primitive Ptilocolepinae and the more typical Hydroptilinae is retained but the latter has been split into six tribes. The phylogeny and position of the family within the Trichoptera are discussed and keys to all genera (adults and larvae where known) and a full species checklist are given in the Appendix.

The taxonomy, diagnostic features (adult), biology and distribution (with maps) of the 31 British species are described and discussed; Hydroptila martini Marshall and H. valesiaca Schmid are new additions to the list. Keys to and genitalia figures of the males and females of all species (except the female of H. tigurina Ris) are included.

In conclusion the Hydroptilidae, although superficially somewhat homogeneous, has been found to be perhaps the most morphologically and biologically diverse family of the Trichoptera.

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The following figures are photographs taken by the Photographic Section (BMNH): 66, 68, 69, 70, 71, 73, 75, 135, 136, 139, 140, 141, 142.

The serial sections of Hydroptilid larvae and adults were prepared by Mr D. J. Cooper of the Histology and Preservation Section (BMNH).

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22 *Ithytrichia lamellaris* Eaton
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29 *O. simplex* Ris
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31 *O. frici* Klapálek
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INTRODUCTION

SECTION I

"Trichoptera in general, but more especially the Hydroptilidae, are an annoyance to the Lepidopterist. If he lives near a river they are a constant source of disappointment to him whenever, on a summer evening, he inspects the entomological miscellany which accumulates upon his tablecloth beneath the gaslight. Down falls a crippled 'Micro-'; he has the trouble of looking at it; but his first glance detects the scabrous clothing of the anterior wings of a Micro-Trichopteron, whose hair looks as if it has been brushed the wrong way, in lieu of the scales of a Micro-Lepidopteron; and his only consolation is that he may leave the pinning of that kind of things to the Trichopterists."

The attitude of entomologists, including many Trichopterists, towards the Hydroptilidae, has changed very little since the above passage was written over 100 years ago by the Reverend A.E. Eaton in the introduction to his paper 'On the Hydroptilidae, a family of Trichoptera'. General collectors leave them for microlepidopterists, microlepidopterists leave them for trichopterists and the latter simply leave them. But this is perhaps a rather sweeping statement; a great deal has been published on the family since Eaton's time, the numbers of genera and species being increased from 6 and 21 to approximately 50 and 600 respectively and there have been numerous individual studies on various aspects of the group's morphology, biology and ecology for example. In general, however, this knowledge tends to be still rather fragmentary and there has, as yet, been no appreciation of the family as a whole. It is, perhaps, the small size of these insects which is the main deterrent to their collection and identification which consequently incur the use of slightly more delicate techniques than is usual for Trichoptera. The adults are inconspicuous in the daytime when they rest or scuttle about on vegetation, rocks, tree-trunks or the walls of bridges and they are only seen in large numbers on swarm-nights especially when they are attracted to m.v. light. When they have been collected and pinned or, preferably, preserved in alcohol, microscopical examination of potash-treated material is then usually required to identify the specimens to genus and species, the latter being particularly difficult if only females are present in the sample. Until now there has been no complete [family] key to all genera and therefore identification has relied principally on faunal keys, many of which, even where they are available, are often incomplete; such faunal keys usually refer to males only and in a number of instances stop at the generic level, in which case the original descriptions of the species already recorded from that particular region and its environs must be traced in the literature. Larvae are rather easier to identify, at least to the generic level, because each genus has a characteristic general appearance and case form, but species identification is almost impossible at present due to the paucity of correctly associated material and of reliable diagnostic features.

In comparison with the other families of Trichoptera, the Hydroptilidae has been somewhat neglected and, in my opinion, rather unjustifiably so because this cosmopolitan group probably has the greatest ecological, morphological and behavioural diversity within the whole order. However, despite the lack of an integrated understanding of the Hydroptilidae, a great deal has been discovered of the group's taxonomy and biology through the studies of numerous individual workers either in the description of new genera and species, generic reviews or in the morphology, ecology and behaviour of the larvae. The first review of the family was given by Eaton (1873) in which he erected 4 genera and described 6 new species, increasing the numbers known at that time to 6 and 21 respectively. Since then the numbers have steadily increased thanks to the work of such notable Trichopterists as McLachlan, Morton, Mosely and Kimmins in Britain; Ris, Klapálek, Ulmer, Martynov and Schmid on the Continent, and Ross and Flint in the U.S.A.. Amongst these, Mosely is perhaps best known for his singular contribution to the description of many new genera and species of Hydroptilidae not only from Great Britain and Europe but also many then less well known regions such as South America, Australia and New Zealand; indeed, according to Kimmins (1951), the Hydroptilidae was Mosely's favourite group. Kimmins, continuing the work of his predecessor, Mosely, also described a number of new taxa, but his most notable single contribution was probably his revision of the British species of Oxyethira, a genus with rather complex male and female genitalia, despite which Kimmins succeeded in providing descriptions, figures and keys to both sexes of almost every British representative. Of the Continental contributors, Schmid is perhaps best known for his descriptions of many new exotic genera and species from Ceylon, Iran and Pakistan (Schmid, 1958a, 1959a, 1960 respectively) and for his review of the genus Stactobia (Schmid, 1959) in which he gave a diagram of the basic configuration of the male genitalia and descriptions and figures of the males of all species, which he segregated into four distinct species-groups. Ross, as well as describing many new Nearctic taxa, was the first to break away from the classical use of wing venation in the taxonomy of the Hydroptilidae which, due to the small size of these insects, does not provide such reliable characters as it does in the larger groups of caddis flies; consequently Ross employed basic structures of the head, thorax and abdomen providing more stable features which could be used not only to differentiate genera but also to indicate possible phylogenetic relationships within the family. Finally, of the most recent workers, some mention should be made of Flint who has made impressive contributions to the knowledge of the Central and South American Hydroptilid fauna, especially in his reviews of the Leucotrichiini and the genus Ochrotrichia (Flint, 1970, 1972 respectively) and his studies of individual faunal regions.

The larvae, on the other hand, are less well documented, at least as regards specific descriptions, although a significant amount is known at the generic level thanks to the work of a number of authors of whom special mention should be made of Nielsen. In his monumental work on 'The biology of the Hydroptilidae', Nielsen (1948) describes the morphology, life-histories, feeding and case-building behaviour of five of the relatively more advanced Hydroptilid genera with such detail and accuracy that no subsequent works have ever surpassed or even equalled it; the only criticism that I can find with Nielsen's work is that it may tend to give a very restricted impression of the morphology and biology of Hydroptilid larvae in general, no stress being laid on diversity of the group as a whole.

The aim of this study has been to provide a broader picture of the family Hydroptilidae than has hitherto been available, by the collation and correlation of as much published information as possible, supplemented by numerous observations of my own. Consequently it will be seen that the group is, perhaps, a more important element of the caddis fly fauna than has previously been considered; it is also a very fascinating group in its own right. Finally, it is hoped that during the course of this work numerous lines of research will have been opened within the family which may have not been previously undertaken because of fundamental gaps in the knowledge of the group which possibly have been filled in here.

This study has been divided into a number of sections which, although they are interdependent to some extent for the explanation of certain morphological terms and taxonomic groupings adopted here, can be treated as distinct units which may be read separately each in its own context. Later in this introductory section a very brief account will be given of the general features of the Hydroptilidae, their feeding and habitat preferences, the economic importance of the group and, finally, methods of collection, preservation and examination. Section II describes the external and internal morphology of both the adult and larval stages and includes brief accounts of the early instar larvae and the pupal stage. Most of the information on the internal morphology is new, while the accounts of the external morphology are essentially summaries of descriptions given in the literature with attempts to unify the terminologies of certain body regions over which there has been some confusion in the past, such as the male and female genitalia and the larval head capsule. Section III is devoted to the systematics of the family in which, after a brief historical introduction, the genera are individually described and discussed, possible generic synonymies are indicated and three genera are transferred to other families of Trichoptera. To aid the presentation of this otherwise large and unwieldy section, principally for the purpose of this thesis, the system of grouping genera into tribes has been adopted although this is not a common practice in Trichoptera systematics in general and may be abandoned in any publications resulting from these studies. Finally, Section IV deals exclusively with the British species of the Hydroptilidae for which keys, descriptions and figures are given for the males and females of all species, except the female of *Hydroptila tigurina* Ris. References to larval descriptions are indicated and any additional information regarding biology and emergence periods is given where available. 10km sq distribution maps of the British Isles have been produced for each species in conjunction with the Biological Records Centre and the provisional distribution patterns indicated by these have been discussed in the text along with the Continental occurrences of the species and their possible British origins. Finally, as a result of these studies, two species have been added to the British list, one of which has only previously been recorded from Switzerland while the other was confused by Mosely (1939) with *Hydroptila occulta* (Eaton) and is provisionally redescribed here for the first time under the name of *H. martini* sp.n.; it is hoped that a paper discussing the *occulta*-complex in Britain will be published in the near future, thus establishing the identity of this distinct species.

The remainder of this introductory section will now be devoted to giving a general account of the family Hydroptilidae before the details of its morphology and systematics are discussed in more depth in the subsequent relevant sections.

General Appearance.

Adult Hydroptilids are minute caddis flies with an average body length of 3.5mm and which, as can be seen from fig. 1, bear a striking similarity to small moths due to the dense layer of pubescent setae on the forewings, at first glance resembling the overlapping scales of the Lepidoptera. The superficial affinity of the Hydroptilidae with microlepidoptera is reflected in the name Hydroptila tineoides Dalman (c.f. Tineidae), which is the type-species of the type-genus, but perhaps the most graphic allusion to this was made by McLachlan who, when relating to Stainton (in litt., 1880) how his 'Revision and Synopsis of the European Trichoptera' was progressing blandly replied that he was "in the process of finishing off the Hydroptilids - those nepticuliform little wretches"! (c.f. Nepticulidae).

The aquatic larvae, however, are unmistakably trichopterous although they do have a number of characteristic features which distinguish them from any other family and have resulted in the inclusion of the primitive Ptilocolepinae, the adults of which bear more resemblance to those of the Rhyacophiloid groups, with the Hydroptilidae. Unlike the more primitive Rhyacophilidae and Glossosomatidae, however, to which the Hydroptilidae are most closely related, the larvae are not free-living but construct transportable cases which may be composed of secretion only or may have various organic or inorganic particles attached. The form of the case is remarkably variable and Ross's collective term for the group, the 'purse-case builders', is rather misleading; apart from the basic purse-type case (of two closely apposed silken valves with slit-like anterior and posterior openings and which may be carried horizontally or vertically) some genera build strongly dorso-ventrally flattened cases, which may be temporarily or permanently fixed to the substrate, while some have fusiform or even distinctly tubular cases, the latter superficially resembling those of the higher Limnephiloid caddis families.

Life-cycle.

The Hydroptilid life-cycle is quite straightforward. After mating, which usually occurs during a swarming period, the female goes underwater and lays her eggs on submerged objects and aquatic vegetation. The minute plankton-like larvae soon hatch and the first four instars, which are of relatively short duration, are passed in the free-living state quite unlike the case-building final fifth-instars; this is regarded as a simple type of larval hypermetamorphosis and has so far only been recorded in Trichoptera in this family. The fifth instar (abbreviated henceforth to Vth-instar) is the principal feeding and growing stage in the life-cycle during which the abdomen becomes characteristically distended as food reserves are deposited for the development of the future adult tissues; the function of the case is probably to serve as protection for this large and vulnerable part of the body. In Britain the larvae usually overwinter as fully fed Vth-instars which pupate in the early spring and give rise to an adult generation from late May to June. Some species are bivoltine; the offspring of the spring brood pass through five relatively short larval instars and give rise to a second brood around August. Life-cycles vary considerably between species and with latitude, altitude and climate and are almost continuous throughout the year in tropical regions as has been recorded by Flint for a number of Central and South American regions, notably within the Caribbean area.

Feeding habits.

The larvae feed essentially on plant material and detritus, the primitive groups feeding macrophytically on mosses and liverworts while the more advanced genera are specialised for grazing on the substrate or for extracting the fluid contents of the cells of filamentous green (rarely red) algae. There have only been one or two reported cases of predation in the Hydroptilidae (Disney, 1972; Burton & McRae, 1972) in which larvae of species of Orthotrichia were seen to feed on Simulium larvae, but it is not known whether these were instances of true active predation or whether the Diptera were taken in mistake for algal filaments. Feeding has not been observed in the adult stages.

Habitat preferences.

The larvae exhibit a wide range of morphological adaptations (reflected also in the form of the larval case) associated with the nature of their fresh-water habitat and their feeding habits. Habitat preferences range from cool, shaded seeps and springs amongst damp moss in montane regions (the hypothetical environment of the primitive caddis larva); fast-running streams and rivers, often in sections exposed to strong current; thin surface films of water on rocks often near the splash zones of cascades and waterfalls (the specialised madicolous habitat); the larger, more slowly flowing lowland rivers and streams to, finally, the almost static but rarely stagnant natural lakes, fens, canals, reservoirs and artificial ponds. Within the two latter major categories are included the more advanced algal-feeding genera which occur in close association with their food source in thickets of aquatic vegetation. The adults occur on rocks, plants, tree-trunks and other objects by the side of the water near the habitat of the larvae, although the favourite daytime resting places appear to be the walls and undersides of bridges. At night the adults are usually readily attracted to m.v. light, especially during swarming periods when a single Hydroptilid species may easily outnumber any other group of caddis fly present. Adult Hydroptilids are very short-lived and have never been reported to undergo any form of reproductive diapause, nor is it likely that they overwinter in this stage in the temperate regions.

Methods of dispersal.

Very little is known of the natural means of dispersal employed by the Hydroptilidae but it is unlikely that the adults play a significant role here, due to their small size and consequently reduced powers of flight, except perhaps within a very restricted range. Factors such as the movement of the adults in the wind or as aerial plankton still need to be investigated but it is known from a number of ecological studies that drift is important in the downstream movement of the larval stages, particularly when they are on masses of floating vegetation. However, again little is known of the compensatory upstream movements of the adults and a recent investigation into this problem in a number of families of Trichoptera by Svensson (1974) failed to produce any significant results for the two species of Hydroptilidae studied (Agraylea sexmaculata Curtis and Hydroptila sparsa Curtis). In general, however, it would seem likely that in those genera with substrate dwelling larvae, which prefer montane rivers and streams and other such rheophilous environments, the dispersal of species is very slow and tends to progress gradually along the courses of the water systems; such groups would thus have very restricted distributions with many local species isolated by impenetrable natural barriers (e.g. the Ptilocolepinae, Stactobiini, Leucotrichiini, Neotrichiini and Ochrotrichiini). On the other hand, those groups in which the larvae are associated with aquatic vegetation tend to have very wide distribution, often being at least Holarctic if not having representatives in various regions of the southern hemisphere and thus implying that dispersal of the vegetation, whether by natural means or in some way influenced by man, plays a significant role in the distribution of these groups and, consequently, in their recent success (e.g. of the Hydroptilini and Orthotrichiini).

Economic importance.

It almost always seems necessary to try and justify purely morphological and systematic studies of groups of organisms by giving some indication of their economic importance and of the value of these studies from such a point of view. This is, however, rather difficult in the case of the Hydroptilidae, as for Trichoptera in general, since these insects have no direct effect on man; they are neither poisonous, parasitic, transmitters of disease nor harmful to any of his food sources or livestock, but merely fill a relatively unobtrusive niche (or niches) in the complex ecosystem of the fresh-water habitat. However, the larvae, pupae and even adults (when they return to the water to oviposit or die) form a small but significant element of the diet of fish, albeit from sheer numbers rather than individual bulk, and are often recorded in the reports of Fisheries and similar institutions concerning the stomach contents of various economically important species of fish. Also, in areas such as the more urban regions of the Great Lakes in North America, the Hydroptilidae may contribute a considerable percentage of the 'nuisance species' of Trichoptera; at certain times of the year certain species emerge in such great numbers that the pupal exuviae may clog up water inlets to factories and power stations while the adults may block up car radiators thus causing the engines to overheat. Finally, again on the adverse side, some people are allergic to the loose hairs, or 'caddis-dust', which easily brushes off the wings of caddis flies and is in such great abundance during swarming periods that it contributes a great deal to the overall 'pollen count' much to the irritation of hay fever sufferers.

From a more academic point of view, but one which may have some practical application in the future, the larvae of the Hydroptilidae are very good indicators of pollution, especially those groups which dwell in cool, clear, fast-flowing streams where the oxygen tension of the water needs to be high in order to provide for the respiratory needs of the organisms. Vegetation dwelling larvae tend to be more tolerant of static, sometimes even stagnant, water probably as a result of their association with the plants; some genera and species even seem capable of withstanding certain degrees of inorganic pollution as, for example, *Agraylea sexmaculata* Curtis of which, according to Barnard (1971), a small colony was found in a Berkshire lake which had a high natural content of iron. The distribution of the more advanced genera of Hydroptilidae is, however, very dependent on the distribution of the green filamentous algae on which they feed, and which themselves are indicative of pollution to a certain extent. Finally, recent studies on the effect of D.D.D. and other pesticides on trichopterous larvae in Canada by Fredeen (1972) have shown that the larvae of *Hydroptila spatulata* Morton are the most resistant species of caddis to the larvicide, although no conclusive reasons for this could be given at the time.

Techniques.

Adult Hydroptilids are readily attracted to m.v. light at night and, although they are capable of flying distances of several hundreds of yards, the best results are obtained when the source of light, preferably accompanied by a trap, is placed as close as possible to the water. During the daytime the adults may be swept from the vegetation along the banks of the water or picked off individually from the trunks of trees or the walls of bridges, in all cases the best method of actually getting the insects into a tube being to use an aspirator. Although past Trichopterists tended to pin and set every specimen the most efficient way of preserving adult Hydroptilids is simply to put them into 70% alcohol (or any other suitable fluid such as formalin or methylated spirits); pinned material tends to be very delicate and awkward to handle and usually involves removal of the abdomen for examination which must then be separately mounted on the pin in a phial of glycerol or permanently mounted on a microscope slide. In addition many more specimens can be collected in alcohol, as those which defy pinning and setting are not simply discarded; in any case pinning and setting are unnecessary because wing venation is of no taxonomic value in this group.

Hydroptilid larvae may be collected from most bodies of fresh water by searching the undersides of stones and rocks, submerged logs and aquatic vegetation; kick sampling and the use of nets and dredges may produce small numbers of individuals but these are comparatively inefficient and perhaps the best method (which also saves time in the field) is to collect masses of vegetation in large plastic bags which may then be taken back to the laboratory where they may be more leisurely, but meticulously, sorted through later. To aid the removal of cases from their substrate, fine forceps can be used; the larvae and pupae are then best preserved in alcohol unless their internal anatomy is to be studied, when the specimens should first be placed overnight in Bouin's fluid. Where only pupal material is available (and this is somewhat advantageous in that fully developed pharate adults may be identified to species by examination of the genitalia) the larval exuviae, which have been pushed to one end of the case, need to be carefully extracted and permanently mounted on a microscope slide. This basically involves leaving the exuviae in the pupal case while the latter is dehydrated by taking it up through the alcohols; the case is then placed on the slide in the mounting medium (preferably Euparal) where it is then opened and the exuviae removed and carefully arranged before the coverslip is put into place.

Where only larvae are available, it is recommended that, whenever possible, they should be kept alive until they have become fully developed pharate adults or have emerged as imagines to ensure positive identification of the species. Rearing techniques, at least for those genera and species associated with lakes, ponds and slowly flowing water, are relatively simple since the larvae can be kept in aquaria or in separately aerated tubes (air bubbles being injected into the water in the tube via a fine hypodermic needle connected to an air-pump). The groups inhabiting fast-flowing water may require special techniques such as the maintenance of a constant flow of running water but such methods have not been investigated in any great detail with respect to the Hydroptilidae. Finally the importance of rearing and field observations cannot be stressed enough since, not only are they invaluable for acquainting the student with the habits, life-histories and ecology of the organisms under observation, but they may also provide small but significant details of possible taxonomic value.

Before concluding this introductory section I would like to add one final personal comment in that, speaking from what may be considered to be the point of view of a general entomologist I have found the Hydroptilidae to be a most fascinating and rewarding group of insects to study. Not only did the investigations into the morphology of the adult and larval stages raise many points of general interest and controversy, but also the systematics of the group involved looking into a multitude of fundamental taxonomic and phylogenetic problems while, finally, the family as a whole possesses many features of general biological interest. It is hoped that some, if not all, of those lines indicated here will be pursued in the future with successful and significant results.

SECTION II MORPHOLOGY

IIA. ADULT EXTERNAL MORPHOLOGY

1. General Appearance

There is a marked difference between the two subfamilies of the Hydroptilidae in the general external appearance of the adults. The Hydroptilinae have what is normally regarded as the typical Hydroptilid form being small with narrow pointed wings, long costal fringes, reduced venation and overall pubescent appearance due to a dense setal covering of the wings and parts of the body (fig 1). The Ptilocolepinae, however, bear more resemblance to small Rhyacophilidae and Glossosomatidae (which, with the Hydroptilidae, comprise the superfamily Rhyacophiloidea) the wings being relatively broad with rounded apices, short costal fringes, an almost full complement of veins and a granulose, rather than pubescent, appearance due to the presence of more sparsely scattered short, unmodified macrotrichia typical of the Order Trichoptera.

The Ptilocolepinae tend to have a rather uniform dark-brown to black appearance, reflecting the basic colour of the wing membrane and body surface, whereas the coloration and markings of the Hydroptilinae are dependent on the arrangement of the relatively longer, broader and more densely packed setae annlagous with the scales of Lepidoptera although, in the Hydroptilinae, the setae are erect and do not overlap each other. Indeed, Hydroptilids are often mistaken for small moths such as Nepticulids and some Tineids (eg. Meessia Hofmann). The setae of the Hydroptilinae are usually white and black or dark-brown and give the insects what is often termed a 'salt and pepper' or 'mottled' appearance due usually to the arrangement of the setae although in Agraylea the wing membrane itself is lightly spotted. Distinct metallic hues are seen in some of the more tropical genera such as the deep violet of Moselyella, the green and silver of many of the Leucotrichiini and the black and silver of Stactobia. The forewings often have distinct patterns of stripes and spots, which may be generically characteristic, and most noticeable when the insect is at rest with its wings held back over the body. Unfortunately these patterns are not very practicable taxonomic features as the setae are very easily brushed off, especially in fluid-preserved material.

The Hydroptilidae are described as being small to minute insects and are often termed the "micro-caddis". The average forewing length (middle of mesothorax to apex of forewing) of the Ptilocolepinae is 5 mm, with a range of 4-6 mm, while that of the Hydroptilinae is 3.5 mm, ranging from 1.2 mm in Chrysotrichia and Neotrichia to 6 mm in Moselyella.

The following account of the external morphology of adult Hydroptilids aims not only to give a general description of the basic form of all body regions but also to point out those features of taxonomic and phylogenetic importance. Information from various sources in the literature has been brought together and summarised here for the first time for the family as a whole and detailed accounts have been given of some previously poorly described regions such as the thoracic pleurites. All descriptions have been supported and illustrated, where possible, by observations on material in the BMNH collections or loaned from various world institutions (see Acknowledgements).

2. The Head Capsule

Features of the Hydroptilid head capsule have been previously used in taxonomic and phylogenetic studies, the most notable being the dorsal post-occipital setate lobes or warts and the dorsal ocelli. The structures described below are shown in the posterior and anterior views of the head capsule of *Agraylea multipunctata* Curtis (figs. 2 & 3) and the dorsal views of the head of various representative Hydroptilid genera (figs. 9 to 25).

The head capsule of the Ptilocolepinae (fig. 9), as in the other Rhyacophiloid groups (eg. *Agapetus* Curtis, fig. 10), is well developed and strongly chitinised but in the Hydroptilinae ? it undergoes various degrees of reduction, associated with the relative decrease in size, the weakly sclerotised regions being clearly defined by narrow membranous boundaries.

The head is hypognathous, the ventrally directed mouthparts being simple and not produced into an elaborate suctorial proboscis (haustellum) as is found in the more advanced families of Trichoptera (Crichton, 1957). The prominent but unmodified compound eyes are situated laterally on the head giving it a broad appearance in frontal and dorsal views. The filiform antennae are inserted anterodorsally between the compound eyes and articulate in a membranous base, with the scape pivoting on a small antennifer arising from the head capsule. The antennae are typically shorter than the wings in the Hydroptilidae and are sometimes held back over the body in repose. They often have a banded appearance due to the alternating arrangement of rows of contrasting setae (fig. 1) and are rarely modified except in certain members of the Leucotrichiini such as the males of some species of *Costatrichia*, where the pedicel and basal flagellar segments are broad and flat (fig. 5), and the males of some species of *Zumatrichia* and *Abtrichia* (fig. 4) where the scape and pedicel are elaborately modified to form processes which sometimes cover the whole 'face'.

The Hydroptilidae have the basic Trichopteran complement of three dorsal ocelli. The lateral pair lie close to the compound eyes on the posterior epicranium (a characteristic feature of the Hydroptilidae when compared with the other Rhyacophiloid groups) while the single median ocellus lies relatively more anterodorsally between the antennal bases. In *Hydroptila* (figs. 1 & 18), *Dibusa* and *Orthotrichia* (fig. 25) the ocelli are completely absent while in some species of the

Leucotrichiini the median ocellus only has been lost, usually in correlation with the unusual developments of the head and antennae in the males but sometimes also in the associated, otherwise unmodified females.

The clypeus and frons are fused to form the frontoclypeus which is ventrally adjoined to the labrum along the distinct clypeolabral suture. There is no frontoclypeal or transclypeal (Kristensen 1966 p. 242) sulcus but, as a detailed study was not made of the internal anterior muscle insertions of the head capsule, the identity of these head regions was not fully investigated. The frontoclypeus is rather variable in shape but is basically pentagonal to hexagonal, the broad medial area tapering ventrally towards the clypeolabral suture and dorsally, as the sclerite passes between the antennal bases, towards the anterior epicranial border. There is a pair of sutures separating the frontoclypeus from the genae extending down from the antennal sockets to either side of the frontoclypeus and which Crichton (1957) terms the frontoclypeal sutures when dorsal to the anterior tentorial pits and clypeogenal sutures when ventral to the same.

The epicranium is well developed and extends posteriorly from the antennal sockets to the small occipital foramen. There is a reduced mid-epicranial line (or suture) which is usually confined to the posterior half of the epicranium and extends posteriorly between the occipital regions to the occipital foramen. It sometimes extends as far forward as the median ocellus (eg. Oxyethira, fig. 20) while in some genera (eg. Orthotrichia, fig. 25) it appears to be completely absent.

Ventrad to the lateral ocelli there is a pair of ovoid warts which lie to either side of the mid-epicranial line just dorsal to the occipital foramen. These will be termed the 'occipital lobes'* and are useful taxonomic features as their size and shape vary considerably between genera (figs. 9 to 25). In the males of the genus Hydroptila (figs. 1, 18, 75) they are modified to form the specialised pivoted caps concealing the eversible membranous structures which probably function as scent dispersing organs (see also Eltringham, 1920; Mosely 1919, 1923 and Moretti & Cianficconi, 1964). The Ptilocolepinae resemble the other Rhyacophiloid groups in having a smaller pair of medial ovoid warts anterior to the occipital lobes as shown in fig. 9 (cf. fig. 10 and see also Ross 1944 fig. 105 and Ross, 1956, p. 9).

The genae are distinct and are produced ventrally to form the subgenal processes. The postgenal regions are prominent in the Ptilocolepinae (fig. 9, Ptilocolepus) and some genera of the Hydroptilinae, notably Stactobia (fig. 12) and Tricholeiochiton (fig. 22) due to the reduction and antero-lateral disposition of the compound eyes. There is no ocular sclerite but there is often a distinct ocular ridge as in Hydroptila (fig. 18).

The tentorium is basically π-shaped, the cross-piece representing the posterior tentorial bridge which arises from

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* or 'post-occipital' lobes

the posterior tentorial pits lateral to the occipital foramen and which in turn gives rise to the anterior tentorial arms (fig. 2). The latter internally traverse the head capsule having arisen from the distinct anterior tentorial pits which lie ventrad to the lateral corners of the antennal sockets (fig. 3). In Ptilocolepus a short process arises anteriorly from each anterior arm (fig. 9, arrowed) which is not present in the Hydroptilinae and may represent a reduced dorsal arm.

The tentorium is strongly developed in the Ptilocolepinae (fig. 9) as in the other Rhyacophiloid groups (eg. Agapetus, fig. 10) and a number of Hydroptiline groups such as the Stactobiini, the Leucotrichiini, Agraylea, Moselyella, Ugandatrichia, Ithytrichia and Orthotrichia (figs. 11 to 17, 19, 24, 25 respectively). In the more specialised and smaller Hydroptiline genera the tentorium undergoes various degrees of reduction of sclerotisation such that some parts are represented only by fine connecting tendons that are difficult to discern in potash-treated specimens. The posterior reduction of the anterior arms can be seen in Hydroptila, Oxyethira, Paroxyethira and Tricholeiochiton (figs. 18, 20, 21 & 22 respectively).

The cervical membrane connects the head to the prothorax. The laterocervicalia are represented by a single pair of anteriorly tapering plates which articulate posteriorly with the propleura and anteriorly with the small occipital condyli (figs. 2, 6 & 7).

The Mouthparts

There have been no published reports on observations of feeding in specifically named adult Hydroptilids although Crichton (1957), in his work on the structure and function of the mouthparts of adult caddisflies, implies that they are capable of feeding. This would appear to be supported by the structure of the mouthparts and alimentary canal as will be described and explained below (and, subsequently, in the following section on the internal morphology of the adults). The mouthparts of *Agraylea multipunctata* are shown in figs. 2 and 3.

The labrum is joined to the frontoclypeus along the clypeolabral suture. It is relatively short in the Hydroptilidae and has a somewhat convex free ventral edge. The mandibles are reduced to weakly sclerotised processes arising beneath and to either side of the base of the labrum and, as noted by Crichton (1957) for *Agraylea* and *Oxyethira*, the mandibles may meet in midline between the labrum and the sitophore (labium). The maxillae are rather generalised having a basal cardo and stipes, the latter bearing a palp which is five-segmented in both sexes and a single medial lobe which Crichton (1957) interprets as the lacinia in Trichoptera on the basis of the presence of the cranial flexor muscle which originates in the occipital region of the head capsule in *Phryganea striata* Linnaeus. The first two segments of the maxillary palps are short while the three terminal segments are longer and subequal in length.

The hypopharynx is short and rounded and projects only a short distance ventrally beyond the labrum. In the twelve other British families of Trichoptera, in which the hypopharynx is known to function as a sucking proboscis, it is referred to as the haustellum (Crichton, 1957). As in the Hydropsychidae, Psychomyiidae, Philopotamidae, Rhyacophilidae and Glossosomatidae (Crichton, 1957; Klemm, 1966) the Hydroptilid hypopharynx has a granulose outer surface due to the presence of microtrichia, many of which are on small elevated processes of the wall (figs. 65, 66). It does not have the elaborate channelled surface seen on the elongate proboscis of the Sericostomatidae, Beraeidae, Molannidae, Odontoceridae, Leptoceridae, Polycentropidae and which is most highly develop̈d in the Phryganidae and Limnephilidae (Crichton, 1957).

The labium arises ventro-posteriorly from the head capsule. The basal part lies beneath the hypopharynx and bears a pair of three-segmented palps of which the two basal segments are short and subequal in length while the third is somewhat longer with a broad flattened medial area tapering apically. I agree with Crichton (1957) that there are no lobes between the bases of the labial palps.

The basic structure of the mouthparts appears to be constant throughout the family, as seen by the examination of material of all available genera, and closely resembles that of the other Rhyacophiloid groups.

3. The Thorax

The external structure of the thorax of adult Hydroptilidae is of great importance, both taxonomically and phylogenetically, as features of the nota and, to a lesser extent, the pleurites, vary differentially at the family, subfamily and generic levels. There have been few studies of the Trichopteran thorax, the most noteworthy being those of Tindall (1965) on *Limnephilus marmoratus* Curtis and of Schmid (1970) who figures and identifies the thoracic sclerites of *Rhyacophila torrentium* Pictet (see also Malicky, 1973). In addition there have been various references to Trichoptera in comparative studies of the insect thorax in general, a review of which is given by Matsuda (1970) in his extensive paper on this subject and whose terminology is adopted here. The thoracic structure of Hydroptilids has not been previously described in detail although Ross (1944, 1956) uses features of the nota and metapleurites in his family, subfamily and generic keys and figures the nota of the representative Nearctic genera.

In this study microscope-slide preparations and fluid preserved material from the BMNH collections were examined of the following species:- *Palaeagapetus celsus* Ross, *Ptilocolepus granulatus* (Pictet), *Agraylea multipunctata* Curtis, *Stactobia eatoniella* McLachlan and *Hydroptila sparsa* Curtis.

The features described below are shown in the diagrams of the lateral and ventral views of the thorax of *Ptilocolepus* *granulatus* (figs. 6 & 7), the dorsal view of the thorax and wing-base of *Agraylea multipunctata* (fig. 8) and the dorsal views of the heads and thoraces of representative Hydroptilid genera (figs. 9 to 25).

The lateral cervical sclerite (figs. 6, 7) articulates with the occipital condyle of the head and posteriorly with the anterior margin of the prothoracic anepisternum. Tindall (1965) interpreted this sclerite as the pre-episternum in *Limnephilus* Leach, a view supported by Matsuda (1970) who regards the lateral cervical sclerite as being a modified pre-episternum in Trichoptera and *Micropterix* Hübner (Micropterigidae, Lepidoptera). A small, unpaired, ventral cervical sclerite (Matsuda, 1970, fig. 149 B) is present between the bases of the lateral cervical sclerites in *Ptilocolepus* and is probably homologous with the anterior sternal sclerite of Tindall (1965).

The prothorax is a small ring-like segment of which the notum bears a pair of oval 'setigerous protuberances' (Matsuda, 1970), commonly referred to as warts (Ross 1944, 1956), which Matsuda (1970) homologises with the patagia of Lepidoptera. A characteristic feature of the Hydroptilidae, in comparison with the other Rhyacophiloid groups, is that these warts are close-set and meet almost in mid-line of the notum thus providing a useful taxonomic character at the family level (compare figs. 9 and 11 to 25 with fig. 10).

There is an additional pair of smaller lateral warts on the pronotum, just dorsal to the noto-pleural articulation (fig. 6, unlabelled).

The propleurites (figs. 6, 7) consist principally of two distinct sclerites, the dorsal anepisternum and the ventral katepisternum. In *Agraylea*, as in *Neuronia* Leach and *Limnephilus* according to Matsuda (1970), the epimeron is represented by a narrow, oblique bar alongside the posterior margin of the anepisternum (not figured for *Ptilocolepus* as its occurrence and position were not identified for certain). The anepisternum and katepisternum of *Limnephilus* are fused (Tindall, 1965) but are distinct in *Rhyacophila* Pictet although Schmid (1970) identifies the katepisternum as the pre-episternum and thus does not recognise the homology of the latter with the lateral cervical sclerite. In the Hydroptilidae the katepisternum articulates dorsally with the anepisternum and ventrally with the dorso-lateral rim of the coxa by distinct anterior and posterior processes termed, respectively, the trochantin and pleural process (Matsuda, 1970).

The prosternum is largely membranous with a distinct narrow median spina (fig. 7) extending from just behind the ventral cervical sclerite to the posterior basisternum which gives rise to two pairs of furcal processes, the anterior of which extends antero-dorsolaterally towards the anepisternum (figs. 6 & 7).

The mesothoracic and, slightly more so, the metathoracic segments are greatly developed to accommodate the wing musculature (see fig. 70). The two subfamilies of the Hydroptilidae show marked differences with respect to the form of the meso- and metanota, the Ptilocolepinae bearing more resemblance to the other Rhyacophiloid groups (compare figs. 9 & 10) while the Hydroptilinae are distinct and possess features which indicate the basic homogeneity of the group. Within the Hydroptilinae the shape of the metascutellum provides a useful taxonomic feature at the generic level as can be seen in figures 11 to 25.

In the Ptilocolepinae the mesonotum is convex with an anterior median suture, the prescutum is distinct and the subtriangular scutellum bears a large oval wart (Palaeagapetus) or two elongate lateral warts (Ptilocolepus, fig. 9). The metanotum is relatively shorter than in the Hydroptilinae anterior to the scutellum which has a distinctly convex anterior margin (fig. 9).

In the Hydroptilinae (fig. 8) the mesonotum is flat and has an anterior median suture, the prescutum is not distinct and the diamond- to kite-shaped scutellum has a warty texture (Ross 1956) along the edges only. The posterior margin of the scutellum is distinctly steep-sided and in a number of generic groups (Stactobia figs. 11 to 13, Leucotrichia fig. 14, and Ochrotrichia fig. 19) the dorsal surface bears a transverse median line or suture which serves as a useful key character.

In the Hydroptilidae in general the mesothoracic postnotum (fig. 8) is well developed and clearly separated from the scutellum by a membrane, as in Neuronia according to Matsuda (1970). There is also a distinct lateral postnotum (fig. 8) and the antero-lateral setate tegulae are well developed. In the Hydroptilidae the metapostnota appear to be represented only by the lateral pair (lateral postnotum III, fig. 8) unlike Neuronia in which, according to Matsuda (1970, fig. 143 C) the small antero-lateral postnotal processes are fused to the first abdominal tergite.

Both the meta- and mesonotal lateral margins possess anterior and posterior notal processes which are associated with the first and third (and fourth?) axillary sclerites respectively of the corresponding wings (fig. 8). The axillary sclerites of the forewing were difficult to interpret in this cursory examination but can be seen to agree basically with those of Limnephilus, as described by Sharplin (1963), except for the presence of a small distinct sclerite between the posterior notal process and the third axillary sclerite which I interpret as the fourth axillary sclerite. The relationships of the axillary sclerites require further detailed comparative study not only within the Hydroptilidae but in the Trichoptera as a whole.

The meso- and metathoracic pleurites are shown in figures 6 and 7, the terminology adopted here being that of Matsuda (1970). Their structure will not be discussed in detail since it conforms with the general Trichopteran plan as described by Tindall (1965), Schmid (1970) and Matsuda (1970) and is outlined in figures 6 and 7. One feature of taxonomic importance, however, is the absence of the mesothoracic posterior katepisternal suture (suture 'K', arrowed, figs. 6 & 7) in the Hydroptilinae. This suture is present in Limnephilus according to Tindall (1965), who refers to it as the pleural ridge (r 4), in Neuronia according to Matsuda (1970), although not specifically labelled, and, finally, in Rhyacophila although Schmid (1970) considers it to be the dividing line between the katepisternum and the postepisternum (1970, Plate I, fig. 3, K and PoE_2 respectively). It was Ross (1956) who first noted the 'general absence' of this suture in the Hydroptilinae but I have found this to be a consistent feature of this subfamily.

The thoracic sterna are shown in figure 7, but these have not been investigated here in very great detail. For a discussion of this region in Trichoptera and of the insect thorax in general reference should be made to Matsuda (1970).

The thoracic legs (fig. 28) conform to the typical Trichopteran plan, as described by Malicky (1973), being slender and elongate with the forelegs considerably shorter than the mid- and hindlegs, of which the latter are slightly the longer. The coxae are short and strong and closely associated with the pleurites in the meso- and metathorax (figs. 6 & 7). The femora and tibiae are long, the tarsi are five-segmented with segment I being the longest and segments II to V short and subequal. The pretarsus (fig. 29) bears two short distal curved claws, between which there is a small arolium and a pair of lateral pulvilli arising ventrally (see Dashman, 1953, for the comparative nomenclature of the parts of the insect pretarsus).

The legs are covered in long, fine setae which are sometimes strongly developed and aligned to form a distinct fringe, as along the outer coxal margin in some species of Stactobia (fig. 28). The males of Hydroptila tineoides Dalman are unique in possessing a covering of thickened black setae on their fore-femora which provides a useful specific character.

An important feature in the taxonomy of the Hydroptilidae at the generic level (and of Trichoptera in general) is what Trichopterists term the spur formula or spur count and which refers to the number of distinct tibial spines commonly present on each leg. The maximum number present on any one leg is four, with one pair originating at the apex of the tibial segment (the apical spurs) and a second pair arising some distance along the apical half of the segment (the preapical spurs). The spur formula consists of three figures which represent the number of spurs on each of the fore-, mid- and hindlegs respectively and is shown for Stactobia mclachlani Kimmins (figure 28) where it is 1 : 2 : 4.

Within the Hydroptilidae the genus Palaeagapetus is unique in possessing the spur formula 2 : 4 : 4 as typical of the Glossosomatidae (the Rhyacophilidae have the formula 3 : 4 : 4), all other Hydroptilidae, including Ptilocolepus, not having formulae exceeding 1 : 3 : 4 (0-1 : 2-3 : 3-4).

Spur counts are constant generic features but may be misinterpreted if spurs become detached although this can be overcome by careful examination of the tibiae for the basal spur sockets. Spurs may sometimes be reduced to very short, almost inconspicuous processes as on the apex of the foretibia of Madioxyethira which was first noticed by Kimmins (1964, fig. 30).

The legs of adult Hydroptilidae function as important locomotor organs both in running (Hydroptilids are often seen scuttling over plants, stones and other objects such as the underside of bridges by the waterside) and possibly also swimming in the females which go under water to lay their eggs (Nielsen, 1948).

The Wings

The form of the wings varies markedly between the two Hydroptilid subfamilies, the Ptilocolepinae retaining the generalised Trichopteran condition to some extent, as seen in the primitive members of the Rhyacophilidae and Glossosomatidae, while the Hydroptilinae have the narrow tapering wings and reduced venation normally associated with the family.

In the Ptilocolepinae (fig. 30) the wings are relatively broad with rounded, obliquely truncate apices. The hindwings generally resemble the forewings but are slightly shorter and narrower. The venation is strongly developed and closely resembles that of primitive Rhyacophilids as figured by Ross (1956, figs. 154 & 155) for Rhyacophila fuscula (Walker) and

Himalopsyche phryganea (Ross) from which it differs by the subcosta of the forewing and, from the Rhyacophilidae in general, by the fusion of various veins in the hindwing. The venation of the Ptilocölepinae differs from that of the Hydroptilinae by the presence of a discoidal cell (dc), separate M_3 and M_4 and a forked Cu 1 in the forewing (fig. 30, arrowed).

As previously stated the Hydroptilinae are noted for their narrow pubescent wings, reduced venation and well developed costal fringes. In the larger genera, such as Agraylea, Allotrichia, Moselyella and Ugandatrichia, the wings are slightly broader and less pointed apically than is usual in the subfamily, the costal fringes are short, the raised hairs are less dense and the neuration is more regular (figs. 31, 32). However, the wings of most Hydroptiline genera are long and slender with pointed apices, these often being highly acuminate, as in Oxyethira for example, and highly developed costal fringes which correspondingly increase in length as the area of the wing decreases. The forewings are covered in numerous semi-erect setae which give the Hydroptilinae their 'hairy' appearance. The hindwings are generally slightly narrower and shorter than the forewings (except in the smallest forms where they are subequal and their fringes are usually much longer than the breadth of the wing.) The venation is very irregular having undergone varying degrees of reduction involving the loss of apical forks and crossveins and the fusion of stems and branches. The most extreme examples of wing reduction occur in the genera Chrysotrichia and Neotrichia (fig. 33) where winglength averages 1.5 mm (1.2 mm in some cases) and the wings are so narrow that Schmid (1958) refers to them as "ribbon-like", the venation being reduced essentially to the main longitudinal branches R, M & Cu. The fringes are highly developed in compensation and thus provide the main functional wing area as seen in a number of other insect groups such as the Thysanoptera, the Trichogrammatidae and Myrmaridae (Hymenoptera) and the Ptiliidae and some Staphylinidae (Coleoptera).

Venational features of the Hydroptiline genera do not provide reliable taxonomic characters as, at such a reduced dimensions, small variations in the occurrence of certain crossveins, the point of origin of forks along main stems and the presence or absence of certain smaller forks (which all serve as critical generic and, sometimes, specific characters in the larger members of the Trichoptera) are not constant in the Hydroptilinae. Although there do seem to be distinct generic venational patterns these tend not to be employed by modern Hydroptilid taxonomists because, primarily, the finer details of venation are very difficult to see (even in dry-mounted wings) and, secondly, features such as the presence or absence of ocelli, thoracic notal structure, spur formula and basic genitalia form provide much more convenient and reliable characters. Taxonomists in the past tended to erect new genera solely on minor venational differences, such as the presence of a single crossvein (for example Agraylea and Allotrichia), and completely discounted similarities in the other features listed above (including larval form), even though they may have been aware of them and even remarked on them. Such instances will be discussed in Section III, especially with regard to certain genera described by Ulmer (1951) from the Sunda Islands and for which synonyms have here been proposed.

As previously noted, the forewings of the Hydroptilinae are densely pubescent and may be mottled or distinctly marked with stripes or spots. In species of certain genera the forewings of the males have definite regions of modified setae. In Abtrichia (fig. 34) and Acostatrichia there is a basal 'costal pouch' formed by a fold of the basal costal region of the forewing and which contains modified setae while in Costatrichia (fig. 35) there is a smaller 'costal bulla' (Mosely, 1937) which is merely a local thickening of the costa (these are the 'reflexed costal cells' of Flint, 1970). In a number of species of the angustella McLachlan group of Orthotrichia there is a row of small black, scale-like setae aligned basally below the subcosta and in Ugandatrichia there is sometimes a patch of modified flattened black setae in the middle of the apical half of the male forewing (fig. 31). All such modifications may function as scent-dispersing structures although this has not yet been shown in any Hydroptilid (a review of possible pheromone dispersing mechanisms in Trichoptera is given by Barnard 1977).

The wing-coupling mechanism varies within the family, the generalised condition being seen in the Ptilocolepinae which here resemble the other Rhyacophiloid groups. In this only a well developed jugal lobe is present on the forewing, with both the lobe and base of the wing lying on top of the hindwing and thus forming a relatively inefficient coupling device. In the Hydroptilinae the next stage in the development of this mechanism is seen in the larger genera such as *Agraylea* (figs. 8 & 32), *Moselyella*, *Ugandatrichia* and, to a lesser extent, *Ithytrichia* and *Hydroptila* where the jugum is still well developed and lies over the hindwing but the latter now bears a distinct humeral lobe with two or three short frenular setae which catch the basal membrane of the forewing. In *Stactobia*, *Madioxyethira* and possibly also *Catoxyethira* (although the base of the hindwing was damaged in the specimen examined) the jugum is reduced to a short process which does not project beyond the wing base although the three frenular setae are well developed and are relatively longer than in the previous group. In *Orthotrichia*, *Oxyethira*, *Paroxyethira* and *Neotrichia* the jugum has been completely lost and the frenular setae have become reduced or, in some cases perhaps, completely lost. In these cases, especially in *Neotrichia* and *Chrysotrichia*, the coupling mechanism is taken over by the overlapping marginal fringes which are well developed in these minute genera. According to Kimmins (1951) there is a row of bristles along the arched basal half of the costa of the hindwing in *Stenoxyethira minima* Kimmins which appear to engage with similar bristles along the anal vein on the under surface of the

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forewing and may thus represent an independently derived form of hamulate coupling. The latter could not, however, be investigated as the basal regions of the wings are damaged in the only specimen of this species known (the male type now mounted as a microscope slide preparation in the BMNH collection).

4. The Abdomen

The abdomen consists of the usual eleven basic segments (although X and XI are usually considered as one, the Xth) and, as in the Lepidoptera (Imms, 1957, [illegible] 519) the first segment is reduced to the tergite only (figs. 6 & 8, tA1). Segments II to VII or VIII are generally unmodified with distinct tergites and sternites separated on each side by the narrow pleural membranes which, for each segment, anteriorly bear the external openings of the abdominal spiracles (figs. 36 & 37). The sclerites of the posterior segments (usually VIII to X in the females and IX and X in the males) are variously fused or modified in other ways to form the external genitalia.

In all Hydroptilid genera examined there is a pair of small glands, of unknown function, which open anterolaterally on the fifth abdominal sternite in both sexes. The external structures associated with the openings of these glands differ markedly between the two subfamilies, the Ptilocolepinae as usual resembling the other Rhyacophiloid groups while the Hydroptilinae are quite distinct. In the Ptilocolepinae (figs. 36) there is a well developed sternal ridge which forms a continuous ventral connection between the two antero-lateral corners of the sternite, from each of which arises, in *Ptilocolepus* at least, a long slender posteriorly-directed membranous filament. According to McLachlan (1874, 1879) this filament may be branchial in origin or function and Betten (1934) believes it to be a tracheal gill persisting from the larval stages, but as Hydroptilid larvae do not have tracheal gills this would be very unlikely. However, the internal structure of this organ was not investigated in *Ptilocolepus* as it was in *Agraylea* (see Section IIB on Internal Morphology and fig. 71) where it has been shown to be glandular in structure, thus its true origin and function in the Ptilocolepinae remain unknown.

In the Hydroptilinae the structures associated with this region are very much simpler and are almost constant throughout the subfamily, thus indicating the homogeneity of the group. Basically the gland opens into a small, shallow sub-circular pit in the antero-lateral corner of the sclerite, from which there also arises a short, posteriorly-directed setate, finger-like process (fig. 37). The number and length of the setae on this process vary slightly between genera but there are usually three. *Tricholeiochiton fagesii* (Guinard) is unique in that there is no membranous process and the surface of the relatively broader and shallower pit is irregularly sculptured (fig. 38). *Ithytrichia lamellaris* Eaton presents an intermediate condition in which the surface is similarly, though less distinctly, marked but a short process bearing one very long main seta is also present (fig. 39).

In general the abdomen of adult Hydroptilids is relatively unmodified, except for certain species or species groups in which specialised structures may be present. In the females of Ugandatrichia cyanotrichia Mosely, for example, there is a pair of distinct setate patches on the sternite of segment VIII (Mosely, 1939). The males of Moselyella have a pair of extrusible finger-like processes from the apex of the pleural regions of the second abdominal segment (Kimmins, 1951) and, finally, the males of some species of Ochrotrichia (Metrichia) have pairs of internal 'sacs' or 'pouches' arising between abdominal segments IV and V, V and VI or VI and VII, according to species group (Flint, 1972).

The sternites of abdominal segments VI and VII in the females and segments VI to VIII in the males may variously bear posteriorly directed, unpaired, medio-ventral processes. These are usually short and spine-like but, as in the males of some species, they may be elongate and truncate with sculptured or setae-bearing apices (figs. 44, 46, 50, 55 and 59 to 60). Often they are totally absent or replaced by tufts of modified setae but on the whole provide useful taxonomic characters at both generic and subgeneric levels.

5. The External Genitalia

The external genitalia of the Hydroptilidae provide very useful taxonomic features as they vary considerably between species, especially in the males, while still retaining characteristic generic forms. Very little is known of the comparative morphology of Hydroptilid genitalia and, as may be expected, authors vary considerably in their terminology of the different structures involved.

Nielson (in Tuxen 1956 and 1970) in his general account of male and female Trichopteran genitalia, refers to the Hydroptilidae using *Hydroptila occulta* (Eaton) as his main example. Nielsen (1957) gives a more detailed account of male Hydroptilid genitalia (a similar work on female genitalia is, at present, in press) based on those of *Agraylea multipunctata* Curtis and *Orthotrichia costalis* (Curtis) (as *O. tetensii* Kolbe) in addition to *H. occulta*, but these are all very specialised representatives of the advanced Hydroptilini and Orthotrichiini tribes of the Hydroptilinae and therefore do not give an overall impression of the family as a whole. The following account therefore aims to give a summary of the basic forms of male and female Hydroptilid genitalia, with emphasis on the Hydroptilinae, together with some idea of the generic variations which occur (more detailed descriptions of which are given in the Systematic account in Section III) and the various terminologies employed.

Male genitalia

Contrary to what might be expected, the male genitalia of the Ptilocolepinae are not intermediate between those of the other Rhyacophiloid groups and the Hydroptilinae but are characteristically simplified and specialised in each genus (figs. 41 and 42). The following account essentially only refers to the Hydroptilinae except in the very basic features of the structures involved which are shown in the composite diagram of a hypothetical generalised Hydroptilid (fig. 40). Diagrams of generalised generic plans of the male genitalia have also been given (figs. 41 to 60).

The following components of Hydroptilid male genitalia are discussed below in turn: segment VIII; segment IX; segment X and the so-called 'Superior Appendages'; Inferior Appendages and 'Subgenital Appendages'; the Bilobed Process and the Aedeagus.

Segment VIII

The VIIIth abdominal segment is usually the last to have a distinct tergite and sternite except in the genus Oxyethira (fig. 56) where the sclerites are fused. In Stactobia (fig. 44) the VIIIth sternite is displaced posteriorly to lie ventral to the IXth tergite and, in Catoxyethira (fig. 46), it is greatly enlarged especially ventro-anteriorly. In Madioxyethira (fig. 45), according to Schmid (1960), the VIIIth sternite is interrupted medially by the unusual forward development of the inferior appendages which terminate beneath the VIIth sternite, although Kimmins (1964) considers the inferior appendages of Schmid to be formed from the fusion of the inferior appendages ('claspers') and sternites X and VIII.

Segment IX

In Trichoptera in general tergite and sternite IX are fused to form a distinct, strongly sclerotised, annular segment which is often referred to as the genital capsule. The boundaries between these sclerites are not distinguishable but, according to Nielsen (1957, pp. 5 & 6), secondary latero-dorsal or latero-ventral longitudinal sutures may be present. The posterior end of the segment (Nielsen, 1957) forms a membranous depression or genital chamber from which arise segment X and the inferior appendages, the aedeagus lying between the latter two structures. In the Hydroptilidae the genital capsule undergoes various degrees of reduction or development such that the anterior and posterior margins may be dorsally or ventrally excised or produced, internal apodemes may arise from the lateral anterior margins and various external processes may project posteriorly from the anal margin. The latter are termed the lateral or intermediate processes or side pieces according to Nielsen (1956) who considers them to be derived from segment X as will be discussed below. In Stactobia (fig. 44) the IXth sternite has been lost or fused with either tergite IX or sternite VIII, sternum IX being largely membranous and encroached upon by sternite VIII. In Oxyethira (fig. 56) the annular IXth segment is almost totally withdrawn into and concealed by the synscleritous segment VIII.

Segment X and the so-called 'Superior Appendages'

Segment X is generally considered to include segment XI and is represented by the tergite only, which projects posteriorly from the dorsal margin of segment IX and is commonly referred to as the dorsal plate. According to Nielsen (1957, 1970), venter X has 'to all probability been eliminated as an external structure by the formation of the ejaculatory duct'. It is usually entirely membranous, or weakly sclerotised, often with a pair of longitudinal supporting sclerotised rods, and its size and shape vary considerably between and within genera such that it provides a useful taxonomic feature, especially at the species level. The boundary between tergites IX and X is often difficult to interpret and, where apparently present, may really be a secondary development as Nielsen (1957) considers to be the case in *Orthotrichia*. The lateral processes of segment IX (intermediate processes, side-pieces) as stated above may, in *Hydroptila* and *Orthotrichia* according to Nielsen (1957, 1970) be derived from segment X.

The ventral face of the dorsal plate is generally concave and receives the aedeagus, forming what has occasionally been termed the 'supragenital plate'. Owing to his previous confusion of tergite X with what he later came to refer to as the subgenital plate, Ross (1948) states that tergite X 'must lie above the aedeagus'. Nevertheless, the ventral face of tergite X may fuse with structures ventral to the aedeagus (subgenital structures - see below) to form a distinct phallic tube (the phallocrypt of Nielsen, 1957) as described for *Agraylea* and also observed in *Moselyella* and *Ugandatrichia*. A specialised condition is seen in *Paroxyethira* (fig. 57) in which the dorsal plate is apparently entirely absent but the aedeagus is encased in a phallic tube which, according to Mosely (1924) and Mosely & Kimmins (1953) has a 'sleeve-like' base from which arise two asymmetrical 'lateral penis-sheaths'. The origin and homologies of this distinctive formation are uncertain but it probably again may represent a fusion of the dorsal plate with the subgenital structures (see below).

In Trichoptera segment X, according to Nielsen (1970), typically carries a pair of passively movable superior appendages, inappropriately termed cerci by some American authors. These appendages are basically absent in the Hydroptilidae, although various authors have applied the term to a number of non-homologous structures on account of their dorsal position relative to the aedeagus. These usually prove to be the lateral sidepieces of segment IX, the subgenital appendages commonly referred to by Mosely as the 'lateral penis-sheaths' and sometimes even the dorsally displaced inferior appendages. For example, in the *Hydroptila pulchricornis* Eaton group (including *H. kumas* Malicky and *H. phenianica* Botosaneanu) the inferior appendages correctly identified as such by Malicky (1974) have previously been termed 'superior (? inferior)' by McLachlan (1880) and 'intermediate' by Mosely (1939); however, Malicky's 'intermediate appendages' are really the fused subgenital plate, termed the 'lower penis cover' by Mosely. The homologies of the distinct forcipate 'superior appendages' which arise to either side of the Xth tergite in *H. forcipata* Eaton and the similarly positioned stout black spines in *H. vectis* Curtis are uncertain and could either be an example of the retention of the true superior appendages in these two species (unlikely, however) or secondarily developed structures. In many species of *Orthotrichia* there is a pair of asymmetrical lateral spines which arise from a semi-annular sclerite in *O. costalis* (Curtis) on the ventral side of segment X, according to Nielsen (1957), although their true origin and function are unknown. Finally, the dorsal plate of most species of the Nearctic subgenus *Ochrotrichia* (*Ochrotrichia*) is very elaborately developed with asymmetrical spines and processes and is termed the 'dorsal complex' by Ross (1938a) who later applied an arbitrary lettering system (fig. 29b) to aid descriptions.

Inferior Appendages and 'Subgenital Appendages'

The inferior appendages (the gonopods) or 'claspers' as they are more commonly known in Trichoptera, are associated with segment IX from which they arise ventrally or ventro-laterally. According to Nielsen (1957, 1970) they are typically two-segmented in Trichoptera with a proximal coxopodite and distal harpago, but in the Hydroptilidae, as in some genera of certain other families, the claspers are apparently one-segmented. However, Nielsen states that in Hydroptila occulta (Eaton) (fig. 54) the coxopodites are divided into two branches, one pair of which forms the true claspers, while the other pair has become dissociated from the latter and appears to arise laterally from segment IX and forms what have previously been termed the 'lateral penis-sheaths' by Mosely, the 'parameres' by Nielsen (1951, 1956, 1957, 1970) and also the 'lower penis cover' when fused medially (Nielsen, 1970). In this comparative study of male Hydroptilid genitalia a number of structures lying ventral to the aedeagus and dorsal to the claspers have been observed and, since a thorough investigation of their origins and homologies was beyond the scope of this work, I have referred to all such structures as the 'subgenital appendages' when paired (= 'lateral penis-sheaths', 'parameres', 'intermediate appendages') or the 'subgenital plate' when fused (= 'lower penis cover', 'ventral plate of X'). In this I am following Ross (1948) who first defined the term 'subgenital plate' applying it to the structure formerly referred to by him as the Xth tergite which, in his later opinion (1948), should only strictly apply to the structure above the aedeagus. In the diagrams of the generalised male genitalia of the principal Hydroptilid genitalia (figs. 41 to 60) the subgenital 'structures' have been labelled 'sg'.

The inferior appendages proper, or claspers (cl in figs. 41 to 60) vary considerably between and within genera in size, shape and the presence of additional branches, processes or setae and thus provide very useful taxonomic features at both levels. Ross (1948) introduced the term 'bracteole' (figs. 41 to 60, br) for the structure arising from the base of the clasper as seen in some species of *Stactobiella* and *Neotrichia* (fig. 52) but it has not gained widespread usage throughout the family. The bracteole does not appear to be associated with the 'parameres' of Nielsen (here generally termed the subgenital appendages) because a distinct subgenital plate is also present in both *Stactobiella* and *Neotrichia*, but it should be stressed that a thorough study of the homologies of the various structures of male Hydroptilid genitalia is required before any definite conclusions can be reached.

In certain species, especially of the genera *Palaeagapetus*, *Ptilocolepus*, *Madioxyethira*, *Oxyethira* and *Tricholeiochiton* (figs. 41, 42, 45, 56, 60 respectively) the claspers are fused in mid-line and, in the two last named groups, are so reduced as to be almost totally concealed within segment IX. *Madioxyethira* is also noted for the anterior prolongation of the claspers which, according to Kimmins (1964), truly represent a composite structure formed from the claspers and sternites VIII and IX.

The Bilobed Process

The 'bilobed process' (figs. 41 to 60, bp) is a term introduced here to refer to the delicate membranous processes which have been seen in various forms in a number of genera lying just ventral to the subgenital plate. They have not yet been located in the members of the Stactobiini, Ochrotrichiini and Leucotrichiini (figs. 43 to 46, 48, 49), but in the Neotrichiini, Hydroptilini and Orthotrichiini the basic condition would appear to be that of a pair of short posteriorly directed processes each with a small apical seta. In Orthotrichia (fig. 59) they may be homologous with the single medial process of which the slightly dilated apex bears a pair of short setae possibly formed by the fusion of the two original processes. In Oxyethira (fig. 56) there are usually two pairs (rarely one) of short membranous processes each terminating in a seta apparently arising from the base of the subgenital plate. A number of species of the genus Neotrichia (fig. 52) and members of the sparsa-group of Hydroptila are depicted with a pair of short setae arising ventro-apically from the subgenital plate which could possibly represent the fusion of the bilobed processes to the underside of this plate. Bilobed processes have been seen in various forms in the following genera: Hydroptila, Agraylea (fig. 50), Ugandatrichia, Moselyella, Ithytrichia (fig. 51), Neotrichia (fig. 52), Oxyethira (fig. 56), Xuthotrichia (fig. 58), Dhatrichia, Orthotrichia (fig. 59) and Tricholeiochiton (fig. 60).

The Aedeagus

The copulatory organ ('penis' or 'phallus' of Nielsen) will simply be referred to here as the aedeagus as I have made no serious attempt to homologise the various structures seen in the Hydroptilidae. The term will thus apply to the whole length of the organ having a more or less sclerotised wall which is visible in prepared specimens and thus most likely to be figured and described in species descriptions. Nielsen (1956, 1970) gives general accounts of the Trichopteran 'phallus' and (1970) gives detailed descriptions of its structure in Agraylea, Orthotrichia and Hydroptila as representatives of the Hydroptilidae. As will be seen, however, these three genera are members of the more advanced Hydroptilini and Orthotrichiini and share (with the Neotrichiini) a common aedeagal form quite unlike that seen in the Stactobiini and Leucotrichiini, so that the conclusions reached by Nielsen (1970), although valid for the species studied, cannot be applied to the family as a whole.

The aedeagus is basically a long slender sclerotised tube surrounding the common ejaculatory duct which opens apically at the gonopore. In the Hydroptilini, Orthotrichiini and Neotrichiini (see fig. 40, 72) where the aedeagus is distinctly divided into two regions, the proximal muscular-walled region has been termed the ejaculatory duct (s.str.) and leads directly on from the common vas deferens, while the slender distal region has been termed the intromittent organ. In the other Hydroptilid groups where the aedeagus is apparently undivided or otherwise specialised, the homologies of this organ are unknown.

In the Ptilocolepinae the aedeagus is quite unlike that seen in any other Hydroptilid or Rhyacophiloid group, being reduced to a very short, broad structure with a slightly dilated membranous apex ('fan-like' in Ptilocolepus) and a small median (supporting?) sclerite (fig. 41).

The aedeagus of the Stactobiini is somewhat variable but is essentially a long narrow undivided tube. In Stactobia (fig. 44) and Plethus the apex is slightly dilated and is armed with a number of heavily sclerotised short spines. In the other genera (fig. 47a-e) a basic tripartite form may often be detected consisting of a slender central process (probably bearing the apical gonopore) flanked by two lateral processes, which are usually fused in midline to form a dorso-ventrally flattened plate projecting slightly beyond the median process. In Chrysotrichia (fig. 47b, after Schmid, 1960) the lateral processes are apparently free and in Pseudoxyethira (fig. 47d, after Schmid, 1958) two short divergent processes arise preapically on the common plate. The lateral processes may possibly be homologous with the paired parameres considered by Nielsen (1956, 1957, 1970) and Ross (pers. comm.) to be basic components of the primitive Trichopteran copulatory organ (not to be confused with the parameres of H. occulta as referred to by Nielsen, 1951 et seq.). However, as only a few species have been examined (and these not in any great detail internally), no definite conclusions regarding homologies can be reached.

In the Leucotrichiini (with the exception of Alisotrichia in which it is reduced to a simple narrow tube) the aedeagus has a very complex and distinctive structure which is a characteristic feature of the tribe. The basic condition (fig. 49b, adapted from Flint, 1970) consists of a proximal region (the 'ejaculatory duct' s.str.?) and a distal region, commonly termed the 'midlength complex' by Flint (1970), bearing a dilated membranous apex. The 'midlength complex' consists of a strongly sclerotised, posteriorly tapering tube, anteriorly bearing a fine 'basal loop' and with a pair of medio-dorsal lateral 'windows', or subcircular holes, in the aedeagus wall. These structures are almost certainly secondarily derived, being unique to the Leucotrichiini and unlike any other structures seen in Hydroptilid or Trichopteran aedeagi in general.

The form of the aedeagus in the genus Ochrotrichia varies between the two subgenera but is basically very simple in both. In the nominate subgenus the aedeagus (fig. 48a, Ae) appears to consist of distinct proximal region and a very slender distal region which apically bears a short curled process. This division is not so distinct in O. Metrichia (fig. 48c) in which the aedeagus bears two pre-apical stout spines, and a single longer spine arising anteriorly and projecting back alongside the aedeagus.

In the remaining Hydroptiline tribes (Neotrichiini, Hydroptilini and Orthotrichiini) the aedeagus has a common basic form which appears to have been simplified in certain genera such as Dibusa and Microptila Ris sensu stricto and Xuthotrichia (these genera being included here on the basis of various other adult and larval affinities). The structure described by Nielsen for Agraylea, Orthotrichia and Hydroptila (see figs. 50, 59, 72) is the one in which the aedeagus consists of the proximal muscular ejaculatory duct ('phallobase' of Nielsen) and distal intromittent organ ('aedeagus' of Nielsen) at the junction of which arises the spiral process or 'titillator'. The 'titillator' is the distinctive feature of this group and is a slender process of varying length which coils once or twice around the aedeagus near its point of origin before lying posteriorly alongside the intromittent organ. It has often erroneously been termed the paramere but, as Nielsen points out, it is probably not homologous with the paired parameres of other Trichoptera. According to Nielsen (1957) it is apparently a continuation of the phalloduct but the functional significance of this is unknown as the process appears to be immovable (Nielsen, 1970). This form of the aedeagus, with a spiral titillator and well developed intromittent organ which tapers posteriorly and then dilates slightly to form a truncate apex, is best developed in *Agraylea*, *Allotrichia* (fig. 50), *Ugandatrichia*, *Moselyella*, *Ithytrichia* (fig. 51), *Neotrichia* (fig. 52), *Hydroptila*, *Oxyethira* (fig. 56) and *Tricholeiochiton* (fig. 60) and *Dhatrichia*. Derived conditions may occur in *Paroxyethira* (fig. 57) and *Orthotrichia* (fig. 59) in which a titillator is present, but the intromittent organ is relatively slender and, in the latter genus, may have an additional lateral process.

It can thus be seen that the Hydroptilid aedeagus is a very variable structure and could provide a very interesting subject for more detailed comparative study from the taxonomic and phylogenetic points of view. The account given above is not exhaustive, serving only to indicate the basic forms encountered in the various groups such that a study of more species within each group could perhaps reveal evolutionary trends resulting in the derivation of various structures and the reduction of others.

Female genitalia

In the Hydroptilidae the female genitalia (fig. 61) are of the generalised Trichopteran condition which is of the simple 'teloscopic ovipositor' or 'oviscapt' form (Scudder, 1971). This essentially involves modifications of segments VIII to X (rarely VII) and the gonopore is situated ventrally between segments IX and X or, when the IXth sternite is reduced as in Oxyethira, apparently just behind segment VIII as noted by Nielsen (1956, 1970) for the order as a whole.

The posterior margin of the ring-like VIIIth segment bears a number of characters of taxonomic importance such as a row of short setae, dorsal or ventral excisions or processes or a pair of lobe-like setae bearing processes, a wide variety of which are seen in the genus Hydroptila. The anterior margin may bear a pair of slender lateral apodemes and the sternite may have patches of modified setae or, as in the case of Hydroptila occulta (Eaton), a distinctly shaped sclerite, termed the 'ventral plate' by Nielsen (1956, 1970). The long slender IXth segment forms a retractile 'oviscapt' (Nielsen, 1956 and Scudder, 1971) or 'false ovipositor' (Nielsen, 1970) which is chiefly membranous and has a pair of long, lateral, rod-like apodemal sclerites to which the retractile muscles are probably attached. Segment IX often bears a variously shaped anterior ventral sclerite, as seen in Hydroptila occulta (Eaton) (fig. 61) and termed by Nielsen the 'dorsal plate', and the distal end of the segment forms the lower lip of the genital opening. Segment X is very small forming the fleshy upper lip of the gonopore and bearing a pair of short unisegmented apical cerci.

In preparations of female Hydroptilid abdomens the form of the posterior genital ducts (the 'internal apparatus' of Nielsen) may be more or less discernible, the most noticeable structures being the sclerites of the vaginal wall. These are the 'trident-like' structures of Mosely and are often erroneously referred to as the 'bursa' or 'bursa-copulatrix' which are indiscriminately used terms previously applied to almost any part of the internal female reproductive system (see Section IIB.6, on Internal Morphology). The majority of the Hydroptilidae possess this generalised oviscapt form and many genera may be recognised by certain characteristic features such as the coil and loop in the posterior duct of <u>Madioxyethira</u> (fig. 64). The vaginal sclerites, as well as the dorsal and ventral plates and the posterior margin of the VIIIth segment, provide useful specific characters which, in my opinion, could be put to more use than has been done in the past.

The generalised oviscapt form may be modified in certain genera by the reduction of segment IX such that the genitalia are no longer retractile. A simple derived condition is seen in <u>Orthotrichia</u> (fig. 63) in which segment VIII is large and bulbous while segment IX has become relatively much shorter and has lost its oviscapt function (the position of the gonopore is not known for certain). More specialised conditions are seen in <u>Paroxyethira</u> and especially in <u>Oxyethira</u> (fig. 62). In <u>Paroxyethira</u>, according to Leader (1972), the tergite and sternite of segment VII are apparently fused with a small ventral posterior projection; the VIIIth tergite is excised postero-dorsally and elongated ventrally with a small VIIIth sternite; the IXth segment is small, cylindrical and partly concealed by VIII and, finally, segment X is very small with two cerci and a small median excision. In Oxyethira (fig. 62), according to Kimmins (1958), segment VII is fused and the ventral apical margin sometimes excised, tergite VIII is reduced to a narrow arched band, the sternite forming a short subgenital plate, segment IX is greatly reduced with the sternite apparently absent and the short hood-like tergite often fused to VIII and, finally, the Xth segment is short and broad, carrying the typical pair of short cerci. In both Paroxyethira and Oxyethira the gonopore appears to open just behind segment VIII, the whole form of the genitalia resembling the independently derived conditions as seen in such groups as the Polycentropinae and Hydropsychidae as described by Nielsen (1956, 1970).

IIB. ADULT INTERNAL MORPHOLOGY

Introduction

Apart from their inclusion in comparative studies of specific organ systems throughout the order Trichoptera, Hydroptilid adults have received very little attention regarding details of their internal anatomy. Past references include Eltringham (1920), Mosely (1919, 1923) and Moretti & Cianficconi (1964) on the cephalic scent-organs of Hydroptila males, Unzicker (1968) on the female reproductive system of Hydroptila hamata Morton and Ehnbom (1948) on the central nervous and stomatogastric systems of Agraylea sp.

The following account of the micro-anatomy of the internal organ systems is based on longitudinal serial sections (8µ thick) of male and female specimens of Hydroptila sparsa Curtis and a single male specimen of Agraylea multipunctata Curtis cut and prepared by the Histology and Preservation Section of the BMNH. Serial sections (longitudinal and transverse) prepared by Eltringham for his study in 1920 of the male scent organs in certain species of Hydroptila, and now in the BMNH collections, were also examined. Freshly killed males and females of Agraylea sexmaculata Curtis were dissected to investigate the basic arrangement of the main organ systems including the central nervous system which was removed whole and preserved in 80% alcohol.

The following systems will be described:

1) The Alimentary Canal and associated structures
2) The Central Nervous System
3) The Circulatory System

4) The Respiratory System
5) The Abdominal glands
6) The Reproductive System

1. The Alimentary Canal and associated structures

The Hypopharynx, Salivary glands and 'Sucking Pump'

The hypopharynx or, as it is commonly termed in adult Trichoptera, the haustellum (Crichton, 1957) is a short rounded projection of the gnathal region and is almost totally concealed anteriorly by the labrum. Its concave ventral surface appears granulose due to the presence of many microtrichia (figs. 3, 65, 66) and its entire form resembles that of Rhyacophila as described by Klemm (1966). The salivarium is a simple pocket formed by the posterior wall of the hypopharynx and the anterior wall of the premental labium and receives the opening of the common labial salivary duct. The paired salivary glands extend throughout the thorax as slightly convoluted thick-walled tubes each with a narrow lumen which is continuous anteriorly with the salivary duct. These ducts arise in the region of the prothorax and pass forward to either side of the ventral nerve cord between the prothoracic and suboesophageal ganglia. They then run along the floor of the head capsule and unite to form the common duct near the base of the hypopharynx from which short muscles inserting on the dorsal wall of the common duct were seen to arise. In the specimen of Hydroptila examined the lumen of the salivary gland appeared to contain a central core, the whole structure resembling a reduced larval silk gland with the core possibly representing the silk thread.

The anterior region of the alimentary canal of adult caddisflies is very muscular, both intrinsically and extrinsically, and functions as a powerful sucking pump (Crichton, 1957, Klemm, 1966). For comparative reasons this region will therefore be considered independently from the rest of the gut.

The sucking pump is derived from the cibarial and pharyngeal regions of the foregut as shown in figure 65. As the origins and insertions of the muscles associated with the foregut were not easy to make out without the necessary precise examination which was beyond the scope of this project, the exact definitions of its component regions were difficult to interpret. The use of the terms cibarial and pharyngeal will thus follow Snodgrass (1935). The cibarium lies anterior to the 'gut proper' and is merely a pocket formed by the anterior wall of the hypopharynx and the posterior wall of the labrum. Anteriorly it receives sets of muscles arising on the inner anterior walls of the labrum and frontoclypeus. The true mouth lies at the base of the cibarial pocket, marked by the insertion of the anterior oral retractor muscle arising on the frons, and leads into the pharynx which extends from the region of the frontal ganglion through the circumoesophageal connectives to the posterior region of the head capsule. The wall of the pharynx is surrounded by well developed longitudinal (inner) and circular (outer) layers of muscle fibres, the former extending throughout the length of the pharynx whereas the latter cease before the circumoesophageal connectives. A set of muscles originating posteriorly on the tentorium insert on the wall of the foregut, but their actual point of insertion was difficult to interpret (although Crichton, 1957, terms them cibarial in Phryganea).

The Alimentary Canal (Figs. 65 to 69)

The thin-walled, narrow, tubular oesophagus leads on from the pharynx to the metathorax or anterior abdominal segments where it dilates to form the small crop before it passes into the midgut (fig. 68). There is a poorly developed stomodaeal valve (fig. 68, stv) at the junction of the fore- and midgut formed by a short invagination of the slightly thickened posterior wall of the foregut into the anterior lumen of the midgut.

The midgut is the widest region of the alimentary canal and is a straight tubular section extending to the approximate region of the Vth or VIth abdominal segments where it tapers slightly before passing into the hindgut. The inner lining epithelial cells do not appear to have a well developed columnar appearance (although they were not completely degenerate) and no gut contents were observed in the specimens examined (fig. 68), thus implying that the insects had not fed. The thin layers of inner circular and outer longitudinal muscle fibres form a network over the surface of the mesenteron when seen in gross dissection and, although devoid of food, the midgut appeared to retain its normal shape, possibly due to the presence of air.

At the junction of the mid- and hindgut the pair of common ducts from the trifurcate Malpighian tubules lead ventrally into the poorly differentiated pyloric region, there being no distinct pyloric valve, the junction being simply marked by a slight infolding of the gut wall. Close to its point of entry into the gut each common Malpighian duct divides into two branches, one of which soon divides again so that, in all, there are three pairs of tubules. One pair lies anteriorly within the abdomen while the other two run posteriorly and are closely associated with the reproductive system.

The hind gut is differentiated into an anterior ileo-colon and posterior rectum, the former being narrow but relatively thick-walled and tubular with well developed intrinsic musculature whereas the latter is somewhat distended and thin-walled with six prominent rectal papillae (figs. 67, 69). The anus opens on segment X.

2. The Central Nervous System

A detailed description of the central nervous system of the imago of Agraylea has been given by Ehnbom (1948) and, as my observations agree with those of Ehnbom except where otherwise stated, only a brief account will be given here.

The system basically consists of the brain and the ventral nerve cord (fig. 67) the latter being made up of the suboesophageal, three thoracic and five abdominal ganglia. The Vth abdominal ganglion is a composite structure formed from the fused ganglia of segments V-VIII although Ehnbom states that in the Hydroptilidae segments III and IV are also involved.

The brain (supraoesophageal ganglion) and suboesophageal ganglion form a compact structure which occupies a large volume of the head capsule (figs. 65, 66, 67). Of the brain the protocerebrum and deuterocerebrum can be readily distinguished but the tritocerebrum has become unrecognisable due to fusion with the anterior regions and the circumoesophageal connections. The tritocerebral (suboesophageal) commissure is highly reduced and, according to Ehnbom, fused with the suboesophageal ganglion. Dorsally the protocerebrum bears a weakly developed median longitudinal groove and laterally gives rise to the nerves from the optic lobes. The latter nerves are very short and lie above the anterior tentorial arms. In *Agraylea* the three ocellary nerves arise dorso-medially and laterally from the protocerebrum. The deuterocerebrum is more or less fused with the protocerebrum lying dorso-lateral to the pharynx and it gives rise anteriorly to the antennal nerves. The tritocerebral region may be identified, according to Ehnbom, by the labro-frontal nerves which arise antero-ventrally and, although very fine, can be traced in serial sections.

The circumoesophageal connectives are greatly reduced in the Hydroptilidae and form a very narrow passage through which the pharynx and aorta pass (fig. 65). The suboesophageal ganglion lies postero-ventrally within the head capsule and is distinctly bilobed being seen, in ventral view, to gradually taper towards the origin of the ventral nerve cord. Anteriorly this ganglion gives rise to the mandibular, maxillary and hypopharyngeal nerves although in *Phryganea*, according to Crichton (1957) the mandibular nerves arise from the circumoesophageal connectives. The pair of connectives arising ventrally from the suboesophageal ganglion are separate but fuse midway before entering the prothoracic ganglion. This does not accord with Ehnbom's observation that the connectives unite directly on leaving the suboesophageal ganglion. The pro- and mesothoracic ganglia are similarly fused but along their anterior halves only. while the remaining ganglionic connectives are distinctly paired.

The stomatogastric nervous system was very difficult to interpret in these small insects, a detailed investigation being beyond the limited scope of this study. However the frontal ganglion is distinct (fig. 65), lying anterior to the protocerebrum and dorsal to the pharynx. In sections examined of Hydroptila sparsa, prepared by Eltringham, a pair of prominent spherical organs, probably representing the corpora allata, were located latero-ventral to the aorta and dorsal to the pharynx, just posterior to the brain (fig. 70).

3. The Circulatory System

The circulatory system consists simply of the dorsal vessel which extends throughout the length of the body. The cephalic aorta lies dorsal to the alimentary canal as it passes anteriorly as a closed tube through the oesophageal ring (fig. 65) from where it then appears to run dorsally, anterior to the brain, and terminates approximately at the level of the epicranio-frontal suture. There are no paired glands associated with the aortic ampullae.

4. The Respiratory System

The simple open tracheal system consists of two main lateral longitudinal trunks which give off segmental branches to the spiracles, of which there are three thoracic and seven or eight abdominal pairs (figs. 36 and 37). The abdominal spiracles are situated anteriorly on the membranous pleural region of each segment, where the sternites and tergites are not fused, and appear to have a simple, single-valve type of closing apparatus. There seem to be two main mechanisms present in the Hydroptilidae examined, the first being of the typical valvular type with both a dorsal and ventral muscle process and the second having the ventral process suppressed while the dorsal one functions as a lever (see Snodgrass, 1935, p. 442, fig. F & G respectively). The only accounts of Trichopteran spiracles are those of [illegible] (1912) and Hassan (1944), the latter stating that Limnephilus has a very simple regulatory apparatus with no ventral or dorsal processes which may thus represent a simplification of the more generalised condition as seen in the Hydroptilidae.

5. The Abdominal Glands

In the Vth abdominal segment of both sexes there is a pair of small ectodermal glands which open antero-laterally on the Vth sternite. The external structures associated with these glands have been described previously in section IIA, 4 (figs. 36 to 39). Internally the glands have the appearance of small, multicellular sac-like structures whose walls are just one cell thick and which lie ventro-laterally between the IVth and Vth abdominal segments (figs. 67 and 71). Each gland narrows posteriorly to form a short duct-like region which opens apically on or adjacent to the external process of sternite V. The cells of the gland wall have a granular appearance (fig. 71) but their secretory function is unknown and there seem to be no distinct structural differences between the sexes.

6. The Internal Organs of Reproduction

The male reproductive system of Hydroptilids has not yet been investigated although the female reproductive system has been described by Unzicker (1968). However, according to Barnard (pers. comm.), the terminology used by Unzicker was incorrect and thus has been modified here. The following account is based on dissections of freshly killed and alcohol-preserved specimens of Agraylea sexmaculata Curtis.

The Male Reproductive System (fig. 72)

The testes are a pair of small compact trilobed bodies lying ventrally in the approximate region of the VIIth abdominal segment (fig. 73). The vasa deferentia are narrow, thick-walled tubes which lead from the testes and dilate slightly just before they unite to form the median common vas deferens. The swollen base of each lateral vas deferens receives a tubular membranous accessory gland which lies antero-laterally within the abdominal cavity. The common vas deferens leads directly into what has here been collectively termed the aedeagus (see section IIA, 5) and which consists of a proximal thick muscular-walled ejaculatory duct and a distal slender intromittent organ, or penis. Before opening at the gonopore on the apex of the intromittent organ the phalloduct, according to Nielsen (1957) gives off a branch into the slender external spiral process or 'titillator' which arises approximately at the junction of the proximal and distal halves of the aedeagus.

The Female Reproductive System (fig. 74)

The fully mature paired ovaries occupy almost the whole of the abdominal cavity from approximately segments I-VII. Each ovary appeared to consist of seven polytrophic ovarioles (although the exact number was not noted) which unite basally to form a very short lateral oviduct. The paired lateral oviducts unite medially to form a common oviduct which opens posteriorly into the well developed highly muscular tubular vagina. The latter tapers posteriorly towards the apex bearing the gonopore which, in Agraylea, opens externally between sternites IX and X.

From the dorso-anterior vaginal wall just behind the entrance of the oviduct there arises a slender, narrow-lumened duct which apically bears a small globular structure, the id entity of which is uncertain (see discussion below) but has here been termed the 'bursa copulatrix?' (fig. 74). Posterior to this organ on the vaginal wall lies the entrance of the common duct of a pair of large, tubular colleterial glands which lie coiled in the abdominal cavity dorsal to the base of the ovaries. At the entrance of these various ducts there is a distinct sclerite in the dorsal vaginal wall which can be clearly seen in prepared female abdomens and is the 'trident-like structure' of Mosely and part of the 'internal apparatus' of Nielsen (1957, 1970).

In the first specimens of Agraylea sexmaculata examined in June the ovaries were small, the ovarioles containing one or two ova at the most, and the colleterial glands were relatively small and well defined. Specimens examined two weeks later from the same locality (Croydon, Surrey) had fully developed ovaries and enlarged colleterial glands which appeared to be actively secreting. By this time the males had started to emerge and many pairs were observed *in copula* in which the two sexes faced away from each other, the female often pulling the male along behind her. In this species, therefore, it would seem that the females emerge first with undeveloped ovaries which mature in approximately a fortnight to coincide with the emergence of the males.

The identity of the unpaired slender duct must remain subject to further investigation which was not possible during the course of this study. According to Khalifa (1949) and Barnard (pers. comm) the female reproductive system of Trichoptera consists basically of the median vagina from which arise paired ovaries and colleterial glands, a single structure of unknown origin or function (the 'pear-shaped gland' of Khalifa, 1949 and Korboot, 1964) and a well developed bursa copulatrix which receives the direct products of mating. In species in which a spermatophore is formed there is an additional bursal gland attached to the bursa and a receptaculum seminis which arises from the bursal duct and receives the sperms released from the spermatophore in the bursa. In the sense of the terminology as used here, therefore, a bursa copulatrix is always present in Trichoptera, although the 'pear-shaped gland', receptaculum seminis and bursal gland may be absent, the latter two structures being associated with the absence of a spermatophore. In the mature specimen of *A. sexmaculata* examined (which had been seen to mate) no spermatophore was found so that it would seem likely that the unpaired structure described above represents a simple bursa copulatrix, from which the spermatophore-associated structures have been lost, rather than the poorly understood 'pear-shaped gland' of Khalifa. For a general comparative account of the internal anatomy of female (and male) reproductive systems of Trichoptera see Barnard (1977, unpublished Ph.D. thesis).

In Hydroptila hamata, according to Unzicker (1968, fig. 20) there is well developed bursa copulatrix ('spermatheca' of Unzicker) and a smaller 'pear-shaped gland' ('bursa copulatrix' of Unzicker). This may reflect true generic/specific differences but, until more detailed comparative examinations can be made of Hydroptilid female reproductive systems, no definite conclusions can be drawn.

7. The Occipital Scent-organs of Hydroptila males (fig. 75).

As described in the account of the external structure of the head capsule, the occipital lobes of Hydroptila males are modified to form pivoted caps which conceal membranous 'scent-dispersing' organs, the structure of which has previously been described in some detail by Eltringham (1920), Mosely (1919, 1923) and Morotti & Cianficconi (1964).

According to Mosely, in his studies of certain Palaearctic and Nearctic species, two basic forms can be seen. In one each cap conceals eversible membranous tubular filaments, varying in number and possession of external modified setae ('scent-hairs') between species (e.g. H. sparsa Curtis, H. simulans Mosely, H. occulta (Eaton)). In the other form there is simply a membrane, 'capable of considerable dilatation' and externally bearing a 'few battledore scent-scales' and, usually, two tufts of scent-hairs (e.g. H. forcipata (Eaton), H. vectis Curtis).

The functioning of these organs or the effects of the presumed 'scent-scales' on females have not been described nor were their structure or function investigated here. A comparative study of these organs throughout the genus may prove to be of taxonomic and phylogenetic importance as well as a source of information on life-histories and behavioural speciation.

Figure 75 shows the position in transverse section of the uneverted scent organs within the head capsule of H. simulans in a slide prepared by Eltringham (and now in the BMNH collections).

SECTION IIC. LARVAL EXTERNAL MORPHOLOGY

Introduction

The Hydroptilidae is perhaps the most diverse family of Trichoptera regarding the form of the larvae (and their cases) which are structurally adapted to suit a wide range of aquatic environments. The constituent genera nevertheless do share a number of basic morphological and behavioural features which distinguish them from all other Trichoptera and have caused them to be grouped into a single natural family unit for which a hypothetical primitive ancestor possessing all of these characters can be deduced. Indeed, it is principally on the basis of the appearance of the larvae and their cases that the Ptilocolepinae has been placed in the Hydroptilidae since the adults look more like small Rhyacophilids and Glossosomatids rather than the typical narrow-winged, pubescent Hydroptilinae. In the following account an attempt has been made to present a picture of a generalised Hydroptilid larva and to indicate the wide variety of structural modifications which have contributed to the success of this group.

The classic work on Hydroptilid larvae is that of Nielsen (1948) which has never been surpassed either in content or detail but, nevertheless, tends to give a very restricted view of the family as it deals essentially with only the five representative Danish genera (Agraylea, Hydroptila, Oxyethira, Orthotrichia and Ithytrichia) which are all highly specialised algal-feeding members of the Hydroptilinae. This work has still, nevertheless, provided an excellent foundation for all studies (whether morphological, biological or behavioural) on Hydroptilid larvae and without it the following rather more general account would have been almost impossible to conceive. The following has been based on descriptions in the literature (of widely varying content, detail and standard) and my own observations on material in the BMNH collections or loaned from various institutions throughout the world. The following genera are known in their larval stages (brackets signify a proposed synonym of the preceding genus; a single asterisk, *, indicates material which I have examined; two asterisks, **, denote a previously undescribed genus):-

PTILOCOLEPINAE: *Ptilocolepus*, *Palaeagapetus** (fig. 76)

HYDROPTILINAE: *Stactobia** (fig. 77), (*Lamonganotrichia*, fig. 79), *Plethus* (fig. 78), *Stactobiella** (fig. 97), *Catoxyethira* (fig. 80); *Leucotrichia** (fig. 81), *Zumatrichia* (fig. 83), *Peltopsyche*** (fig. 84), *Anchitrichia*, *Alisotrichia* (fig. 82); *Ochrotrichia* *Ochrotrichia*, *O.* *Metrichia*, *Rhyacopsyche* (fig. 86); *Neotrichia** (fig. 87), *Mayatrichia** (fig. 88); *Agraylea** (fig. 89), *Allotrichia*; *Hydroptila** (fig. 90), (*Oeceotrichia*, *Pasirotrichia*, *Sumatranotrichia*); *Oxyethira** (fig. 91), *Paroxyethira* (fig. 93), *Xuthotrichia*; *Tricholeiochiton** (fig. 92); *Ithytrichia** (fig. 94), (*Saranganotrichia*); *Orthotrichia** (fig. 95), (*Javanotrichia*, *Baliotrichia*, *Orthotrichiella*); *Dibusa** (fig. 96); *Caledonotrichia*** (fig. 98); *Dicaminus* (case only).

A characteristic feature of the family is that the larvae undergo a simple form of hypermetamorphosis in which instars I-IV ("young larvae") are minute, free-living, caseless and of very short duration, while the Vth instar ("old larva") builds a portable or secondarily fixed case and is the principal feeding and growing stage of the life-cycle. The following account of external and internal larval morphology refers only to the almost fully grown Vth instars, the earlier instars will be described separately later.

Vth INSTAR LARVAE

1. General appearance.

Despite their case-building habits Hydroptilid larvae are prognathous and campodeiform as are the more primitive, free-living and 'saddle-case' bearing groups (see below and Ross, 1967) compared with the hypognathous, eruciform, 'tube-case' building Limnephiloid groups.

The Hydroptilidae may be distinguished from all other caddis larvae by a combination of the following characters: small size (2.0 mm - 7.0 mm body length), enlarged abdomen, three pairs of well-developed thoracic tergites, the absence of segmentally arranged tracheal gills and the fusion of the abdominal prolegs to the sides of segment X. The number of abdominal tergites is variable but there is always one on segment IX (the 'anal plate') and in the Hydroptilinae there is usually a pair of small sclerotised rings (sometimes fused) on the terga of segments II or III to VII or VIII which may be regions of modified chloride epithelia (see later).

As stated at the beginning of this section the general appearance of Hydroptilid larvae is highly variable owing to structural adaptations to different life conditions such that the genera may be classified in a number of ways according to habitat, feeding habits or case-form. These groupings, which are outlined below, are based purely on ecological and behavioural features (and their effects on larval form) and thus are not intended to have any phylogenetic significance although, as will be seen later, the evolution of the family has tended to follow a combination of these factors in what may simply be termed ecological radiation or diversification.

Larval Generic Classifications (non-phylogenetic).

Aquatic environment.

Springs and seeps, damp moss, thin film of water: unspecialised Ptilocolepinae; highly specialised Stactobia (with flattened case and body, protective sclerites and setae, clinging appendages).

Rapid to fast running water, in current: Leucotrichia group (flattened fixed cases and body with protective sclerites, clinging appendages); Rhyacopsyche (streamlined case, attached by thread to substrate); Caledonotrichia, Catoxyethira (fixed, "winged" cases).

Moderately fast to slow running water, on bottom: Hydroptila, Ochrotrichia, Neotrichia, Mayatrichia, Stactobiella (larvae unmodified except perhaps for clinging appendages, transportable case compressed laterally, usually with small sand grains attached for ballast).

Running to slow and static water, in plant thickets: *Agraylea*, *Oxyethira*, *Paroxyethira*, *Tricholeiochiton*, *Orthotrichia*, *Ithytrichia* (transportable case light, constructed of silk-secretion only, sometimes with incorporated algal filaments; larval thoracic legs tending to become very long and slender).

Food sources.

Large particle bryophyte-feeders ('browsers'): Ptilocolepinae (mandibles, labrum and legs simple).

Detriphages: *Stactobia*, *Plethus*, *Leucotrichia* group and the secondarily derived *Allotrichia* and *Ithytrichia* (mandibles adapted for scraping and scooping periphytic vegetation).

Filamentous algal-feeders: *Agraylea*, *Hydroptila*, *Oxyethira*, *Paroxyethira*, *Tricholeiochiton*, *Orthotrichia* (mandibles asymmetrical, forelegs often forming specialised chela, *Orthotrichia* with unique labral 'beak').

Disney (1972) has reported *Orthotrichia* 'preying' on *Simulium* larvae but it is likely that the Hydroptilids took the Diptera by chance in mistake for algal filaments and did not actively seek them out in preference for any other form of food.

Case Form.

Vth-instar Hydroptilid larvae construct distinctive cases of silk (secretion) which may be externally sculptured or into which may be incorporated various organic or inorganic particles such as bryophyte fragments, algal filaments and diatoms (reflecting the diet of the larvae) or small sand grains which are probably added to provide ballast. In his work on the phylogeny of the

Trichoptera, Ross (1967) used the term 'purse-type' for Hydroptilid cases to distinguish them from the 'saddle-cases' of the Glossosomatidae and the 'tube-cases' of the higher Limnephiloid groups. The 'purse-case' essentially consists of two silken 'valves' closely apposed and joined along the lateral margins (seams) leaving slit-like anterior and posterior openings. It may be laterally or dorso-ventrally compressed and in the latter instance may be temporarily or permanently fixed to the substrate or have a more fusiform shape (although still retaining the slit-like openings). As the abdomen of the Vth-instar larva increases in size the larva enlarges the case by splitting the dorsal and ventral seams and adding new layers of silk before closing them again (see Nielsen, 1948). Neotrichia and Mayatrichia are distinct in having a slightly tapering 'tube-type' case with circular oral and anal apertures, thus superficially resembling the higher Limnephiloidea, although the larvae are undoubtedly Hydroptilid. The genus Alisotrichia of the Leucotrichia group is also unique in that the Vth-instar larva appears to have lost the case-building habit and consequently retains the general appearance of the free-living early instars (fig. 82).

The cases of Hydroptilidae are generically very distinct and thus provide useful key characters in the identification of genera. An attempt has therefore been made below to classify the Hydroptilidae on the basis of case form.

(a) Transportable.

(i) Compressed, anterior and posterior openings slit-like:

- simple 'purse' or 'spectacle-type', dorso-ventrally or laterally compressed, rectangular to ovoid, constructed of secretion only (Stactobiella; Tricholeiochiton, fig. 92; Paroxyethira, fig. 93) or with incorporated material (Ptilocolepus; Palaeagapetus, fig. 76; Ochrotrichia, fig. 85; Allotrichia; Agraylea, fig. 89; Hydroptila, fig. 90; and Dibusa, fig. 96).

- 'bottle-', 'vase-' or 'jug-case' of Oxyethira (fig. 91), laterally compressed, constructed of secretion only.

- 'wheat-seed case' of Orthotrichia (fig. 94b) constructed of secretion only with longitudinal strengthening ridges.

- 'pumpkin-seed case' of Ithytrichia (fig. 95) constructed of secretion only, laterally compressed but carried horizontally.

(ii) Tubular, anterior and posterior openings circular:

- fusiform, anterior and posterior ends tapered, constructed of secretion only, floating free in current attached to substrate by silken thread (Rhyacopsyche, fig. 86).

- tubular, with straight sides gradually tapering posteriorly, openings wide and circular, with attached sand grains (Neotrichia, fig. 87) or just with sculptured external surface (Mayatrichia, fig. 88).

(b) Fixed.

(i) fusiform with wide lateral 'wings' or 'fringe' (Catoxyethira, fig. 80; Caledonotrichia, fig. 98), probably temporarily fixed only.

(ii) strongly dorso-ventrally depressed:

- seam in mid-ventral line, case 'barrel' or 'tortoise-shell shaped', probably temporarily fixed only (Stactobia, fig. 77; Lamonganotrichia, fig. 79; Plethus, fig. 78).
- seams along lateral margins; case sub-circular, 'water-penny' or 'leech-egg case' shaped; permanently fixed to substrate (Leucotrichiini, e.g. fig. 81).

(N.B. Dicaminus is known from the case only; therefore, as the true identity of the larva is unknown, the genus has not been included in the above list. However, the purse-type case is distinguished by its upright attachment to the substrate and pair of dorsal exit-holes or 'chimneys' thus giving it the appearance of a tunicate in lateral view.)

The function of the case in Vth-instar larvae is probably to protect the vulnerable, distended, highly conspicuous abdomen. The size of the abdomen increases considerably during this stage as food reserves are deposited for the development of the future adult tissues. The shape of the abdomen, as would be expected, is reflected in the shape of the case, i.e. it is compressed laterally or dorso-ventrally, fusiform, tubular or, as in the Leucotrichiini, has swollen middle segments.

2. The Head Capsule.

There has been some controversy over the homologies of the various regions of the head capsule of Trichopteran and endopterygotan larvae in general, especially with respect to the ventral sclerites and the maxillo-labial and hypopharyngeal complex. This account of the Hydroptilid cranium is based essentially on Hinton's work (1963) as illustrated (figs. 99 and 100) although the terminologies of Nielsen (1948) and Badcock (1961) will be discussed and have been summarised diagrammatically in fig. 101.

The head is basically a well-sclerotised, dorso-ventrally compressed, ellipsoidal capsule, with an anterior gnathal and posterior occipital foramen, composed of the dorsal apotome, the lateral parietal sclerites, an anterior ventral apotome and occasionally, as in Oxyethira, a small posterior ventral apotome. The dorsal apotome (fig. 99) is, according to Hinton, the facial area bounded by the dorsal ecdysial lines and may be the median part of the frons (frontal apotome) or the median part of the frons and clypeus (frontoclypeal apotome). The dorsal apotome is usually referred to as the clypeus or frontoclypeus in trichopterous larvae but, in Hinton's opinion, it is a secondary functionally derived region not necessarily homologous with these areas in other insect orders. In the Hydroptilidae the dorsal apotome is usually a subtriangular sclerite with a distinct median constriction, its wide anterior margin forming the dorsal edge of the gnathal foramen and its apex converging towards the mid-line posteriorly. The ecdysial lines may be fused in Agraylea and Hydroptila and the length of the apotome relative to that of the head varies considerably between genera (e.g. compare figs. 84, 87c, 88a and 99). The anterior tentorial pits are usually well developed and in one unidentified Oxyethira species examined, in which the dorsal ecdysial lines were distinct, the pits appeared to lie just anterior to the median apotomal constrictions, apparently on the ecdysial lines as in Drusus trifidus McL. according to Fotius-Jaboulet (1961). The parietal sclerites form the major surface area of the cranium and extend from the dorsal to the ventral ecdysial lines. The ventral apotomes, according to Hinton (1963), are those areas enclosed by the ventral ecdysial lines, although the latter may become partially or totally fused in some genera such as Agraylea and Hydroptila. The anterior ventral apotome has been termed the gula by Nielsen (1948) and the submentum by Badcock (1961) but, as Hinton points out, there is no functional necessity for the ventral apotomes of different insects to be homologous. The ventral apotome will be discussed below in relation to the sclerites of the maxillo-labial and hypopharyngeal complex but, essentially, it is a triangular or V-shaped sclerite (fig. 106) which may have a transverse (strengthening?) ridge as in Palaeagapetus and Oxyethira (figs. 102, 109) or may give rise to an antero-lateral pair of sclerites as in Orthotrichia (fig. 110). The absence of a ventral apotome (as in figs. 103, 104, 105, 107, 108) may be due to its fusion with the ventral cranium or its incorporation with the anterior 'postmental sclerites' (q.v.).

A small triangular posterior ventral apotome has only been observed in *Oxyethira* (fig. 109) and, although Hinton (1963) states that it is "present in all the Hydroptilidae .... examined" he does not list which genera and species were looked at. The posterior ventral apotome has previously been termed the anal gular sclerite (Nielsen, 1948) and the protogula (Badcock, 1961) as illustrated (figs. 100 and 101).

It should finally be noted that the process of moulting was observed in the early instars by Nielsen (1948) who records that the larval skin bursts between the head and prothorax with a partial splitting of the head capsule along the posterior parts of the frontal and gular sutures (ventral and dorsal ecdysial lines); ecdysed cuticles of Vth-instar larvae were seen (by Nielsen) to have split along the ventral and dorsal ecdysial lines in *Oxyethira*, *Orthotrichia* and *Ithytrichia*, although in *Hydroptila* and *Agraylea*, where the cranial sclerites are totally fused, the head is ecdysed in one piece.

The head capsule bears distinct sets of setae, the arrangement of which has been described by Nielsen (1948) for *Agraylea*, *Hydroptila*, *Oxyethira*, *Orthotrichia* and *Ithytrichia*. The form and number of the setae varies between genera but in general they are shorter and fewer in torrenticolous forms, e.g. *Stactobia* and *Leucotrichia*, and are longer and more numerous in vegetation dwellers, e.g. *Oxyethira*. The basic colour of the head ranges from pale yellow to dark brown and may vary considerably even within a single species. Markings of the head capsule sometimes provide useful diagnostic features in some genera such as Agraylea (see Lepneva, 1964 and Barnard, 1971) and Hydroptila (see Ross, 1944) although, especially in the latter genus, the range of variation in a species from a number of different localities needs to be examined before the constant characters can be defined.

The basic structure of the head capsule is seen in the Ptilocolepinae where the ecdysial lines and anterior tentorial pits are distinct according to Jacquemart & Coineau (1962) and Flint (1962), whereas in the Hydroptilinae variations in shape, sclerotisation and fusion of cranial regions occur. In Agraylea, Tricholeiochiton, Hydroptila and Oxyethira the dorso-ventral diameter of the head capsule is increased somewhat and in Stactobia it is strongly sclerotised and the sides are abruptly convergent anterior to the eyes (fig. 77). Mayatrichia is unique in having a distinct conical capsule which has an anterior rostrum-like form and, as in Neotrichia, the dorsal apotome is very elongate and extends back almost to the dorsal postoccipital margin. In genera such as Agraylea and Hydroptila and those in which the head capsule is strongly sclerotised and sculptured in association with torrenticolous habits such as Stactobia and the Leucotrichiini the ecdysial lines are partially or completely fused and at the most may be only faintly discernible.

There is a pair of small, round, darkly pigmented 'eyes' located antero-dorsally on the sides of the head capsule composed, as in general in trichopterous larvae, of six stemmata. There is usually an associated slight swelling of the cranium which is most noticeable in Stactobia (fig. 77) and Ithytrichia.

The short antennae are relatively well developed and lie anterior to the eyes on the parietal sclerites immediately behind the dorsal mandibular articulations (fig. 99). Each consists basically of a narrow, cylindrical, lightly sclerotised sensillum which projects anteriorly from its raised membranous socket on the epicranium. Distally each sensillum bears a small, thin-walled protuberance which is usually single but is paired in Ptilocolepus granulatus (Pictet), according to Jacquemart & Coineau (1962). There is also a single anteriorly directed seta arising from each sensillum, varying in length and point of origin between genera as does the length of the sensillum.

The labrum forms the upper lip of the pre-oral cavity and is basically a short broad flap attached to the leading edge of the dorsal apotome by the narrow, flexible anteclypeus (fig. 99). The dorsal labral surface is convex and is sclerotised except along the medially notched anterior margin which continues ventrally to form a membranous concave lower surface and bears various tufts and rows of short setae. There are a number of sets of dorsal labral setae directed anteriorly and varying in length between genera. The sides of the labrum are usually convex and the postero-lateral tormae are always well developed but are variable in shape, sometimes being inwardly curved as in Ithytrichia, S-shaped and directed outwards as in Oxyethira and Agraylea or S-shaped and strongly inwardly curved as in Hydroptila (see Nielsen, 1948). In Orthotrichia the asymmetrical labrum is very distinct and produced anteriorly as a slightly laterally directed 'beak' (fig. 94c) and the tormae are short and broad, the left being much larger than the right. The beak is used during feeding to keep open the hole in the algal cell wall, formed by the mandibles, while the larva sucks out the cell contents (this being a more efficient method than that employed by Agraylea, Oxyethira and Hydroptila in which the labrum is simple and not used in feeding). In Ithytrichia the labrum is rather long and narrow, broadest posteriorly and curving to a short, straight anterior margin. This structure may be correlated with the secondarily adopted detriphagous habits.

Mouthparts and Feeding Habits.

The mandibulate mouthparts are primitively used for biting through vegetable material as in the Ptilocolepinae but, within the Hydroptilinae, two main lines of feeding adaptations may be traced. The first line is seen in the Stactobiini and Leucotrichiini which are primarily detriphagous and feed by scraping diatoms and other small organic particles from the substrate in fast-flowing bodies of water, while in the second line the larvae have become associated with green filamentous algae (on the surface of stones or in plant thickets) on which they feed by biting a hole in each cell wall and sucking out the fluid contents (Hydroptilini and Orthotrichiini).

The mandibles are basically short and robust and are inserted laterally to lie immediately beneath the labrum (fig. 99).

They are moved in the horizontal plane by the abductor muscles (fig. 138) which originate on the lateral wall of the cranium and insert on the dorso-lateral posterior edge and ventral condyle, and by the strongly developed adductor muscles which originate on the dorsal and lateral cranial walls and are attached medially by a tendon directly to the mandible, there being no median condyles. The base of each mandible is broad and wide, tapering distally to a more or less pointed apex, and bears a pair of anteriorly directed setae. The inner concave surface is formed by the dorsal and ventral cutting surfaces which are primitively ridged or toothed but may be simplified as a single, straight cutting edge. The median concavity contains a tuft of hair-like spinules (the 'penicillus') which is usually absent or, at the most, only poorly developed in the right mandible where it may be replaced by a small membranous bladder (fig. 113); according to Jacquemart & Coineau (1962) a penicillus is present in the right mandible only of Ptilocolepus granulatus (Pictet), but this may be due to a confusion of the left and right sides. In the Ptilocolepinae, Stactobiini and Leucotrichiini the mandibles do not show the marked asymmetry typical of the algal feeding genera of the Hydroptilinae. In Palaeagapetus (fig. 111), Leucotrichia tubifex Flint and Stactobia caspersi Ulmer (fig. 112) (according to Flint, 1962; Flint, 1970 and Botosaneanu, 1956 respectively) a penicillus is present in each mandible and may thus reflect the primitive Hydroptilid condition.

In the Ptilocolepinae the mandibles are simplified as straight cutting edges and probably serve to cut fragments of moss and liverwort leaves (fig. 111). In the detriphagous genera of the Stactobiini and Leucotrichiini the cutting edges are reduced, the apices being broad, straight and bluntly toothed, and probably have a scraping or scooping function (fig. 112). In the algal-feeding genera the left mandible generally bears teeth on the upper blade only (rarely on the lower) while the right mandible has only one blade which is devoid of teeth but sometimes has a finely serrate edge; the apices are usually bluntly tapered but are distinctly pointed in *Orthotrichia* and *Ithytrichia* where the blades and teeth are correspondingly reduced (fig. 114). The former condition is seen in *Agraylea*, *Oxyethira*, *Tricholeiochiton*, some species of *Hydroptila* (e.g. *H. tineoides*) and *Orthotrichia* and is probably an adaptation for cutting 'scissors-like' into algal cells while in *Orthotrichia* the pointed apices may simply service to make a hole in the cell wall into which the labral 'beak' is inserted to keep it open while the fluids are sucked out. Some species of *Hydroptila* such as *H. vectis* (fig. 113), however, have robust strongly ridged mandibles which seem to suggest a scraping rather than cutting function and also indicate species differentiation within the genus. From my own observations the mandibles of Hydroptilid larvae, especially within the genus *Hydroptila*, may provide useful specific characters but it was not possible to investigate this in any detail due to the lack of positively identified material. *Ithytrichia*, according to Nielsen (1948), comes from the basic algal feeding stock but has secondarily become detriphagous as has *Allotrichia pallicornis* (Eaton), according to Giudicelli & Vaillant (1967), which is most closely related to *Agraylea* both in adult and larval features.

The maxillo-labial and hypopharyngeal complex and the ventral head sclerites.

The maxillae, labium and hypopharynx are fused to form a single compact structure which projects ventrally from the gnathal foramen to form the fleshy 'lower-lip' of the pre-oral cavity and which distally bears the spinneret (figs. 100, 101). It is largely membranous but bears small, isolated sclerites the identities of which are subject to some controversy. Nielsen (1948) described the maxillo-labium of *Agraylea*, *Hydroptila*, *Oxyethira*, *Ithytrichia* and *Orthotrichia* in great detail but, according to Badcock (1961), his interpretation of the maxillary segments and the ventral sclerites of the head capsule was incorrect. Fotius-Jaboulet (1961) independently came to the same conclusions as Badcock regarding the ventral sclerites but followed Nielsen's terminology of the maxillae. Finally, Hinton (1963), in his study of the ventral ecdysial lines of the head capsule of endopterygote larvae, discusses the origin of the ventral sclerites of the cranium from a functional point of view and reaches conclusions different from those of the above authors. The following account is a summary of these theories of which that of Hinton will be followed regarding the ventral sclerites while terminology of the maxillae as proposed by Badcock has here been accepted (figs. 100, 101).

The two large lateral lobes represent the maxillae while the median lobe consists of the ventral labium and dorsal hypopharynx, the latter projecting slightly disto-ventrally where it bears the opening of the silk duct (otherwise known as the 'spinneret'). The two sclerites at the base of each maxillary lobe represent the proximal cardo and distal st~~r~~ipes, the latter bearing the five-segmented maxillary palp and a median lobe or lacinia (the basal palpifer plus four-segmented palp and galea respectively of Nielsen and Fotius-Jaboulet).

As shown by Badcock (1961) and Fotius-Jaboulet (1961) the labium is divided into a distal prementum which bears the lateral palpifers and labial palps and the median bilobed ligula, and a proximal postmentum. The prementum has previously been termed the mentum by Nielsen (1948) but this cannot be so since it receives longitudinal sets of dorsal and lateral muscles originating on the ventral postocciput close to the tentorium whereas, according to Chapman (1969), there are usually no muscles to the postmentum (i.e. mentum). The 'postmentum' of Badcock therefore represents the 'submentum' of Nielsen which, so far, is quite acceptable, the confusion arising when the homologies of the sclerites of, or apparently associated with, the postmentum are considered. Badcock terms the principal postmental sclerite the 'mentum' ('submentum' of Nielsen) while any additional sclerites are regarded as originating posterior to the 'mentum' and are termed 'submental' ('gula' of Nielsen). Badcock also considers that a 'gula' is absent in Trichoptera but may be represented by a small mid-ventral sclerite on the posterior margin of the cranium as seen in *Oxyethira* which she terms the 'protogula' ('anal gular sclerite' of Nielsen). However, as has been previously discussed, Hinton (1963) simply regards the ventral sclerites of the head capsule as regions bounded by the ventral ecdysial lines and, therefore, of functional rather than morphological significance. Thus Hinton terms these sclerites the anterior and posterior ventral apotomes which are equivalent to the 'submentum' (where present) and 'protogula' of Badcock respectively (compare figs. 100 and 101). As I have not been able to make a thorough study of the sclerites of the postmental and ventro-cranial regions throughout the Trichoptera I have, for convenience, termed any additional sclerites which occur anterior to the anterior apotome simply the 'postmental sclerites' (i.e. the 'mentum' of Badcock). As can be seen from figures 102 to 110 illustrating the anterior ventral sclerites of representative Hydroptilids, the homologies are still not easy to follow. A generalised condition may be present in *Palaeagapetus* (fig. 102) where there is a distinct anterior apotome and a pair of 'postmental sclerites' (which may be distinguished by the insertion of an antero-lateral seta on each), while in *Ithytrichia*, *Oxyethira* and *Orthotrichia* (figs. 106, 109, 110) the 'postmental sclerites' appear to be fused, *Orthotrichia* apparently having an additional pair of lateral sclerites (possibly derived from the ventral apotome?). In the remaining genera figured (figs. 103-105, 107, 108) there appears to be only one set of sclerites, which may be paired or fused, and which may represent the fusion of the anterior apotome and the 'postmental sclerites'. The longitudinal sutures are not as well defined as indicated in figures 103 and 108 but are actually only faint fracture lines and, as such, may simply have been overlooked in Agraylea multipunctata and Tricholeiochiton (figs. 104, 105).

Dorsally the prementum and ligula are fused with the hypopharynx which, according to Badcock (1961), proximally bears a pair of sclerotised suspensorial rods, which receive the frontal muscles of the hypopharynx, and medio-distally bears the common opening of the labial silk duct, the whole structure being homologous with the spinneret of Lepidopterous larvae.

The general form of the maxillo-labial and hypopharyngeal complex of the Hydroptilidae varies very little although in Ithytrichia, according to Nielsen (1948), the anterior edge may be blunt and strongly developed to form a shovel-like structure used in scooping up detritus.

3. The Thorax.

The three thoracic segments are distinct and subequal in size, the metathorax being slightly the broadest. The prothorax is attached anteriorly to the postocciput of the head capsule by a short cervical membrane (fig. 65) which internally receives the dorsal, lateral and ventral longitudinal muscles ?

arising on the prothoracic wall and serving to maintain the attitude of the head and control its movements. Well developed tergites are present on all three segments and each has a distinct mesal suture which in the prothorax probably functions as an ecdysial line as observed in the cast cuticles of early instars by Nielsen (1948). This may account for the retention of the midline in the prothorax of larvae of the Leucotrichiini in which the meso- and metatergites are completely fused.

The protergite (fig. 115) completely covers the dorsum and extends laterally to overlap the dorsal margin of the pleurites and anteriorly to form a slight ridge over the base of the head capsule. The meso- and metatergites usually do not completely cover the dorsa so that they are completely surrounded by a membranous margin, although in Zumatrichia and Peltopsyche (figs. 83, 84) the sclerites are well developed and slightly overlap those preceding. The tergites are all approximately rectangular and dorsally arched, especially on the prothorax, and sometimes the antero-lateral angles may be produced as in the prothorax of Anchitrichia spangleri Flint (see Flint, 1970), the metathorax of Ochrotrichia (Ochrotrichia) (fig. 85) and the meso- and metathoraces of O. (Metrichia). Sets of setae, of varying lengths, are generally present on the tergites and are usually simple although, in the torrenticolous members of the Leucotrichiini and Stactobiini, they may be modified as short, stout spines in association with the increased sclerotisation of the tergites (fig. 77) and as an additional form of protection.

Pleurites are present on all three thoracic segments and basically consist of the fused episternite and epimeron (collectively termed the 'pleurite') separated by the raised pleural ridge which continues ventrally as a short pleural process and articulates with the antero-lateral coxal process (figs. 115-120). A small anterior sclerite, shown by Tindall (1963) to be derived from the episternite and which he terms the pre-episternite, may be present as a horn-shaped, distal seta-bearing process. This is termed the trochantin by Nielsen (1948) but, according to Tindall (1963) who studied muscle attachments in the theraces of caddis larvae, the true trochantin is incorporated into the coxal rim. The pre-episternite is usually free in the prothorax only in trichopterous larvae but within the Hydroptilidae various arrangements can be seen. In Palaeagapetus (fig. 116), Agraylea (fig. 117), Orthotrichia, Stactobia and Stactobiella the pre-episternite (pes) is free in all thoracic segments whereas in Oxyethira and Dibusa (figs. 119, 120) it is fused to the episternite. The epimeron is sometimes divided into what Nielsen (1948) terms the 'oral' region, which is always fused and a free 'anal' sclerite; the latter (aem) has been observed in the prothorax of Agraylea multipunctata (fig. 117), Oxyethira (fig. 118), Stactobiella, Ochrotrichia, Orthotrichia, Ithytrichia and Stactobia.

In the prothorax the tergite and pleurites are closely associated, although in the meso- and metathorax (fig. 115) they are usually widely separated. According to Nielsen (1948) there is no articulation between the protergite and propleurites, although he says that it may be suggested by two bulgings of the lateral margin of the tergite in <u>Hydroptila</u>. The absence of an articulation, according to Nielsen, resembles the primitive condition as seen in the Rhyacophilidae, the articulatory process in the more advanced groups such as <u>Limnephilus</u> (as described by Tindall, 1963) being formed by the ventral extension of the pleural ridge. As can be seen from figures 116 and 120, however, pleural processes would appear to be present in the Hydroptilid genera studied and although I have not examined these structures closely enough to comment on their function, they may serve as regions of attachment for muscles to the legs and sterna even though the actual articulatory associations have been lost (Tindall, 1963; Marshall, 1973). Nielsen (1948) states that in <u>Orthotrichia</u> there is a primitive articulation, not normally seen in caddis-larvae, between the meso- and metatergites and their corresponding pleurites. Again I cannot comment on this as I have not investigated these regions in any detail but, if such a condition does exist, perhaps the term used should be 'derived' rather than 'primitive' since <u>Orthotrichia</u> appears to be the only genus of Trichoptera in which it has been observed.

Apart from the Glossosomatidae where a single prosternite is sometimes present, the Hydroptilidae are unique within the primitive Rhyacophiloid groups in the possession of distinct sternites on some or all of the thoracic venters. Usually each segment has a ventral median bulge which sometimes bears a variously shaped unpaired 'oral' sternite and a pair of posterior lateral or 'anal' sternites may also be present, just anterior to the intersegmental constriction (figs. 122, 129). The prothorax usually possesses all three sternites which are fused in *Ithytrichia* (fig. 125), *Orthotrichia* and *Stactobia* (fig. 121) the last named genus having an additional pair of small posterolateral sclerites. In *Agraylea* (fig. 123) only the prothoracic 'oral' sternite is present whereas only the paired 'anal' sternites are seen in some species of *Plethus*, *Ochrotrichia* and *Caledonotrichia* (figs. 126, 127, 128). The presence, number, form and segmental occurrence of thoracic sternites varies greatly between genera and also, probably, species and thus may provide useful taxonomic features. According to Flint (1962, 1971a) thoracic sternites are totally absent in *Palaeagapetus* and *Rhyacopsyche*.

The Thoracic Legs.

The thoracic legs of Vth-instar Hydroptilid larvae are basically of the ambulatorial type which may be modified as short, robust clinging organs in torrenticolous forms or as long, slender appendages in vegetation-dwellers. The fore-legs are always shorter than the mid- and hind legs and are sometimes adapted for special feeding or case-construction purposes. The legs (fig. 115) consist of the six basic segments: coxa, divided trochanter, femur, tibia, tarsus and tarsal claw ('pretarsus') with its basal spine or spur.

In their most generalised form the legs are unmodified and the subequal mid- and hind legs only slightly longer than the forelegs, this condition being seen in the bottom-dwelling genera from slow to moderately fast-moving bodies of water such as *Ochrotrichia*, *Rhyacopsyche*, *Neotrichia*, *Mayatrichia*, *Hydroptila* and *Ithytrichia* (figs. 85-88, 90-95) and the vegetation-dwelling *Orthotrichia* (fig. 94). In the Ptilocolepinae, *Stactobiella* and *Dibusa* (fig. 96) the legs are shorter and more robust with reduced setae and are adapted for clinging to the substrate in fast-flowing water, being best developed in the torrenticolous forms such as *Stactobia*, *Plethus*, the Leucotrichiini (except *Alisotrichia*) and, to some extent, *Caledonotrichia* (figs. 77, 78, 81, 83, 84, 98). In these groups the tarsal claw is usually short and hook-like, with a well developed basal spur, and obviously suited for gripping the substrate. In vegetation-dwellers, such as *Agraylea* (fig. 89), the mid- and hind legs are substantially longer than the forelegs, a trend which continues in *Oxyethira* (fig. 91) and *Paroxyethira* (fig. 93) and is especially well developed in *Tricholeiochiton* (fig. 92). This elongation is brought about by a narrowing and lengthening of all segments, including both sections of the divided trochanter (the legs thus appearing seven-segmented) and the tarsal claw.

The attitude of the legs with respect to the body is also variable although two basic stances may be recognised. In the forms adapted for clinging to the substrate, such as the Ptilocolepinae, *Stactobia*, *Plethus*, the Leucotrichiini and *Caledonotrichia*, the cases are dorso-ventrally flattened and the legs are usually held out to the sides of the body. In the other groups, which possess laterally compressed, fusiform or tubular cases, the legs are held forward close to the body and often project beyond the anterior end of the case just as in the higher tube-case dwelling Limnephiloid larvae.

The setae of the legs are usually quite simple but in some genera may be modified to form distinct rows of hair-like bristles or spines; flattened, fan-shaped spurs (fig. 120) or small comb-like structures (as on the coxae of *Orthotrichia* and *Ithytrichia*). In species of *Hydroptila* the legs often have an overall covering of short, fine setae while in many of the torrenticolous forms the setae may be reduced in number and modified as short stout spines.

In *Agraylea*, *Oxyethira*, *Paroxyethira* and *Hydroptila* the foreleg (fig. 120) possesses a distinct modified seta-bearing tibial process against which the tarsal claw may be apposed, according to Nielsen (1948), thus forming a specialised chelate organ used in the manipulation of algal filaments. Also, according to Nielsen (1948), a larger chela may be formed by apposing the tibial process against the femur so that the filament is held between 'the distal end of the trochanter, the proximal end of the femur and the distal end of the tibial process on one side and the claw on the other ...' (vide Nielsen, 1948, p.142 for a fuller discussion); the modified setae on the foreleg probably serve to grip the algal filaments more efficiently.

Features such as the general form of the thoracic legs, as described above, and the presence of specialised tibial setae and tarsal claws have been used as taxonomic characters at the generic level and may, as further material is discovered, also prove to be of use in the identification of species.

4. The Abdomen.

The abdomen of Vth-instar case-bearing Hydroptilid larvae is uniquely distended and its shape, as well as that of the case, is usually characteristic for each genus. The abdomen consists of ten well defined segments (XI usually regarded as being fused with X) which are usually totally membranous, except for the distinct tergite of segment IX, and devoid of lateral tracheal gills or lateral lines (although the latter may be present in the Neotrichiini, fig. 87).

The larvae of the Ptilocolepinae are dorso-ventrally depressed, especially Palaeagapetus (fig. 76), in which there is a lateral pair of truncate, fleshy tubercles on each of segments I-VIII and small paired patches of setae on segment I, while in Ptilocolepus segment I has just a single large tergite. According to Flint (1962), the membrane of the abdomen of Palaeagapetus is 'white with reddish maculations dorsally' (fig. 76) which, from my observations, gives the larva the appearance of a small Rhyacophilid rather than a Hydroptilid in which such 'maculations' are totally absent.

In the torrenticolous forms, such as Stactobia, Plethus and the Leucotrichiini (figs. 77-84), the abdomen is dorsoventrally depressed to an even greater extent and each segment has a protective ovoid median tergite which usually bears protective spines on its dorsal surface or along its posterior margin; such spines may also arise directly from the abdominal membrane. The Leucotrichiini is further characterised by the great expansion of the middle abdominal segments as seen in Leucotrichia, Zumatrichia and Peltopsyche (figs. 81, 83) so that only the slender anterior segments are capable of protruding through the anterior opening of the permanently fixed case. Within this group the genus Alisotrichia (fig. 82) is unique in that it retains the free-living form of the early instars, in which the abdomen is not distended but remains narrow and tapers posteriorly, right through the Vth-instar until pupation.

A more generalised abdomen is seen in Ochrotrichia, Agraylea, Allotrichia, Hydroptila, Oxyethira, Tricholeiochiton, Paroxyethira, Stactobiella and Dibusa (figs. 85, 86, 89-93, 96) in which it is moderately to strongly laterally compressed and the intersegmental constrictions well marked, especially in Agraylea where there are additional transverse sulci on the venters of the middle segments (which are points of longitudinal muscle insertions). In Rhyacopsyche, Neotrichia, Mayatrichia and Orthotrichia (figs. 86-88, 94) where the case is tubular or fusiform, the abdomen also has a cylindrical shape and, except in Orthotrichia, the intersegmental constrictions are only weakly developed. Orthotrichia, like Ithytrichia (figs. 94, 95), has lateral processes on abdominal segment II which, according to Nielsen (1948, p. 185), resemble those present on segment I in eruciform, 'tube-case'-bearing larvae although I believe that they are functional analogues associated with the case-bearing habit rather than structural homologues as implied by Nielsen (ibid.). Ithytrichia (fig. 95) is unique in that the abdomen, although compressed laterally, can rotate 90° on segment I (plus the thorax) so that it is often held horizontally. This genus is also characterised by the deep dorso-ventral intersegmental constrictions and the bud-like processes on dorsa III - VII and sterna III - VI and VIII which, according to Lauterborn & Rimsky-Korsakow (1903), provide a greater respiratory surface area.

Segment X always bears a pair of well developed anal prolegs which are characteristically fused to the sides of the segment in Vth-instar Hydroptilid larvae (fig. 130) but project from the sides of the body in the free-living genus Alisotrichia and the 'tube-case'-building Neotrichiini (figs. 82, 87, 88) as in the typical early instars of all genera (fig. 131). The terminology used in figures 130 and 131 follows that of Nielsen (1948).

In Hydroptila and Ithytrichia there are long filiform caudal filaments, believed to have a respiratory function (hence termed 'caudal gills'), arising from segments IX and X (fig. 130). The median unpaired filament arises dorsally on segment IX, just posterior to the tergite, while in

Hydroptila there is an additional pair arising dorsally at the base of sclerite 'b' on segment X.

Hydroptiline larvae have dorsal sclerotised rings on abdominal segments II/III to VII/VIII and these seem to be a constant feature of the subfamily (figs. 77 to 98, not inclusive). Nielsen (1948) referred to them as the 'dorsal abdominal glands' but they do not appear to have a glandular structure internally and simply appear to be modified epithelial cells. According to Wiggins (1*976) they may be specialised chloride epithelial cells adapted for ionic absorption and osmoregulation as described for similar structures in the Limnephilidae by Wichard & Komnick (1973).

* in press

SECTION IID. THE YOUNG LARVAE: INSTARS I-IV

The Hydroptilid life-cycle is characterised by a form of larval hypermetamorphosis in which the first four instars (collectively termed the 'early instars' or 'young larvae') are free-living, case-less and of relatively short duration compared with the case-bearing Vth-instar ('old larva') which is the main feeding and growing stage. This type of development has been observed in all Hydroptilid genera for which the early instars are known, namely *Agraylea*, *Hydroptila*, *Oxyethira*, *Ithytrichia*, *Orthotrichia* (Nielsen, 1948); *Stactobia* (Botosaneanu, 1956; Danecker, 1961; Lepneva, 1964); *Ochrotrichia*, *Mayatrichia* (Ross, 1944) and *Paroxyethira* (Leader, 1970), and probably occurs throughout the family, although the primitive Ptilocolepinae, whose early instars are as yet unknown, may prove to be exceptional. Nielsen (1948) gives excellent descriptions of the early instars and their habits for the five genera listed above (including a key to genera) and these provide the basis of this comparative summary. Figure 132 shows a generalised early instar Hydroptilid larva adapted from the diagrams in Nielsen (1948) and Leader (1970) (no material being available for examination).

The young larvae are distinguished from the Vth-instars by their relatively smaller size (0.5 mm - 2.7 mm recorded for Ist and early Vth-instars respectively, see Table 1) and features associated with the absence of a case. Thus, the early instars of the Hydroptilidae resemble those of caddis larvae in general in having a narrow, posteriorly tapering abdomen and long anal prolegs which project freely from the sides of the Xth abdominal segment. In contrast, the abdomen of Vth-instar Hydroptilids is greatly distended with food reserves and the fusion of the anal prolegs is probably associated with the slit-like posterior opening of the case through which the end of the abdomen may project. In the Neotrichiini, where the case openings are circular, the anal prolegs of the Vth-instars are free and project through the posterior aperture of the case, while in Alisotrichia, where the Vth-instars retain the free-living habit, the anal prolegs also remain free.

TABLE 1: Body lengths in mm.
of Ist, early and pre-pupal Vth-instars of Hydroptilid larvae (after Nielsen, 1948 and Botosaneanu, 1956)

INSTAR GENUS	I	V (early)	V (pre-pupal)
Agraylea	0.75mm	2.70mm	5.10mm
Hydroptila	-	1.80	3.00-4.00
Oxyethira	0.55	1.50	3.40
Ithytrichia	0.55	1.10	2.65
Stactobia	-	1.50 (IV?)	2.80

External Morphology.

The head of an early instar Hydroptilid larva is prognathous, ovoid and slightly depressed dorso-ventrally and is covered in various long, fine, hair-like setae which give the larva a superficial resemblance to planktonic Crustacea. Nielsen (1948) does not mention the ecdysial lines of the head capsule but, according to Botosaneanu (1956), they are well developed in the young larvae of Stactobia although absent in the Vth-instars. According to Nielsen (1948) the mandibles retain a more 'primitive form' than do those of the older larvae, being more symmetrical, shorter and broader with many more pointed, distal denticles.

The size of the prothorax in relation to the head varies between young and old larvae according to genus but, in general, is narrower in the early stages where it also tends to be less well developed. None of the three thoracic tergites completely cover the nota and the setae are poorly developed as are the pleurites, according to Nielsen (1948), while thoracic sternites are totally absent. In generalised forms, such as Agraylea, Hydroptila, Oxyethira, Orthotrichia, Ithytrichia (Nielsen, 1948) and Paroxyethira (Leader, 1970), the thoracic legs of the early instar larvae are relatively longer and more slender with respect to the overall size of the body compared with those genera adapted for clinging to the substrate, such as Stactobia and Mayatrichia (Botosaneanu, 1956 and Ross, 1944).

Small unpaired tergites are present dorsally on all abdominal segments of the young larvae and are especially well developed in genera dwelling in fast-flowing water such as Mayatrichia and Stactobia, the latter retaining reduced tergites in the Vth-instars presumably to afford protection against the harsh torrenticolous environment. Abdominal setae are variable but in general are very long and fine, especially those arising laterally, in the 'natatorial' forms, whereas in Mayatrichia and Stactobia they are greatly reduced; in the latter genus there are two pairs of short spines on the posterior margins of tergites I-VII (Botosaneanu, 1956). The anal prolegs (figs. 131, 132) project freely from the sides of segment X and in the generalised forms bear very long setae. The caudal filaments described for the Vth instars of Hydroptila and Ithytrichia are also present in the early instars of these genera and also those of Orthotrichia.

Biology and Habits.

Nielsen (1948) studied the biology and habits of the early instars of Agraylea, Oxyethira and Orthotrichia. These small caseless larvae crawl about freely amongst algal filaments in masses of aquatic vegetation, the most active being those of Agraylea which are 'very bristled' and capable of curling their abdomens and their long flexible anal claws around the filaments. According to Nielsen, the larvae of Orthotrichia are more sluggish, their anal claws merely being dragged along during locomotion while the long-legged Oxyethira larvae do not use their anal prolegs at all during locomotion as the abdomen is always turned up ready to flick the long setae of the anal claws over the head to ward off predators when disturbed. The young larvae of all three genera swim backwards by horizontal undulations of the abdomen and 'walk-like movements', *Agraylea* being the most inclined to swim and having a positive phototaxis, while *Oxyethira* is the least inclined to do so. As noted by Lepneva (1964), swimming is usually a rare phenomenon in later developmental stages but is common in young larvae which, due to the larger surface area resulting from the dense covering of long, slender setae (thus offering greater resistance to sinking), resemble planktonic Crustacea and can remain suspended in the water for some time and move actively but slowly by curving the abdomen. I have noticed, however, that the early instars of those genera which live in torrents or thin surface films of water (such as *Stactobia* and probably also the Leucotrichiini) are relatively more 'robust' and dorso-ventrally flattened with short legs and few setae. These are therefore adapted for moving over the surface of the substrate rather than swimming freely as described for *Agraylea* above. The main purpose of these free-living early stages would appear to be that of dispersal over a restricted area to avoid concentration of the later predominantly feeding stages and thus allow better utilisation of the available food resources. This may not be so true, however, for those genera and species which tend to aggregate in the case-bearing stage, such as *Hydroptila* and *Stactobia*, but it does seem to apply to vegetation dwellers, such as *Agraylea*, *Oxyethira* and *Orthotrichia*, where the Vth-instars are more sparsely distributed.

SECTION IIE. LARVAL INTERNAL MORPHOLOGY, Vth INSTAR

Little is known of the internal anatomy of Hydroptilid larvae, the only study being that of Lauterborn & Rimsky-Korsakow (1903) on the gross features of the tracheal system, ventral nerve cord, dorsal 'abdominal glands' and pedal glands of Ithytrichia lamellaris Eaton, while Nielsen (1948) mentions the maxillary glands and illustrates the dorsal 'abdominal glands' of Hydroptila, Oxyethira, Orthotrichia and Ithytrichia. The following account therefore contains much new information regarding the internal organisation of Hydroptilid larvae. The principal studies on species of other trichopterous families are those of Branch (1922), Glasgow (1936), Satija (1959), Korboot (1964) and Gibbs (1967).

Material examined included transverse, horizontal and longitudinal serial sections of Agraylea multipunctata Curtis, Hydroptila sp. and Oxyethira sp. prepared for me by the Histology and Preservation Section of the British Museum (Natural History). Freshly killed specimens of A. multipunctata were dissected to investigate the arrangement and gross features of the principal organ systems which will be described in the following order:

1. The Alimentary Canal and Malpighian Tubules
2. The Salivary and Labial Silk Glands
3. The Central Nervous System and Lateral Stemmata
4. The Tracheal System
5. The Reproductive System.
6. The Circulatory System.
7. The Dorsal Abdominal Rings and Pedal Glands

1. The Alimentary Canal.

The gut is a simple narrow tube extending from the mouth to the anus (opening on abdominal segment X) and shows only the basic differentiation into stomodaeum, mesenteron and hindgut (fig. 133). The regions gradually pass into one another, the proventricular and pyloric valves being only very weakly developed, and there are no specialised sections such as a crop, proventriculus, caecal diverticulae or rectal papillae. However, the regions do show the basic histological differences: the stomodaeum and proctodaeum are lined throughout with a thin cuticular intima which lines a simple epithelial layer and is surrounded by inner longitudinal and outer circular muscles, while the mesenteron is distinguished by its slightly greater width, absence of a cuticular intima, the prominent layer of large epithelial cells and poorly developed inner circular and outer longitudinal muscles.

The stomodaeum (foregut) extends into the anterior abdominal cavity and consists of an anterior pharynx, which has well developed intrinsic and extrinsic musculature and which probably functions as a sucking pump during the uptake of algal cell fluids, and a posterior, narrow, delicate oesophagus which leads directly into the mesenteron (fig. 134). The short pre-oral cavity is formed by the ventral labral and dorsal hypopharyngeal walls and receives the laterally inserted mandibles. There is no further differentiation of the cibarium, the subregions being impossible to identify by muscle insertions as there is no recognisable clypeus in trichopterous larvae, the dorsal sclerite of the head capsule being a secondarily derived region formed by the dorsal ecdysial lines, according to Hinton (1963), and not necessarily being homologous with the clypeus or frontoclypeus of adult insects. The extrinsic muscles of the 'sucking pump' arise dorsally on the labrum and dorsal apotome and ventro-posteriorly on or adjacent to the postoccipital ridge. Although the number and attachment of the muscles of the anterior foregut have not been investigated or figured in full (partly shown in figs. 134, 138), the general arrangement appeared to accord with that as described for Hydropsyche sp. and Drusus trifidus (McL.) by Badcock (1961) and Fotius-Jaboulet (1961) respectively.

The entrance to the mesenteron is marked by a slight invagination of the oesophageal wall into the midgut and a change-over from stomodaeal to mesenteric tissue, there being a slight constriction here representing the stomodaeal (pyloric) valve (fig. 133). The mesenteron extends to approximately abdominal segment VI-VII, tapering posteriorly to the transition region which is marked by the entrance of the pair of common ducts of the Malpighian tubules. The columnar epithelial cells are well developed (figs. 135 to 137), being narrow and elongate with large nuclei and projecting into the lumen of the midgut (which was filled with green algal cell contents in all specimens examined).

The proctodaeum (hind gut) is a simple tubular region divided into three histologically distinct sections, namely the pylorus, intestine (ileo-colon) and rectum. The pylorus is the very short section immediately posterior to the pyloric constriction and receives the Malpighian tubules. The arrangement of the three pairs of tubules resembles that as seen in the adults; a single pair of common ducts arises dorsolaterally from the pylorus, each duct bifurcating close to its origin, one branch running anteriorly alongside the gut into the thorax while the other soon bifurcates again into two posteriorly directed branches which are closely associated with the highly convoluted silk glands. A similar arrangement has only previously been described for _Agapetus_ larvae (Glossosomatidae) by Satija (1959) and may indicate a phylogenetic relationship between the two families. In unidentified species of _Caledonotrichia_ I observed a curious arrangement of the Malpighian tubules through the transparent abdominal cuticle in which one of the otherwise posteriorly directed tubules runs anteriorly and dorso-laterally just below the surface and is thrown into a small loop in each of segments II-VIII.

The ileo-colon (figs. 136, 137) has a well developed, highly folded epithelium surrounded by distinct inner circular and outer longitudinal muscle layers and is divided subequally into the narrow tubular ileum and slightly dilated, sac-like posterior colon. There is no sphincter (the 'anterior sphincter') separating the ileum and colon as seen in

Hydropsyche colonica McL. by Glasgow (1936). The short, chamber-like rectum lies approximately within segments IX and X and is separated from the colon by a distinct rectal valve which receives a set of extrinsic muscles arising dorsally and ventrally on the lateral abdominal wall (figs. 137, 138). The rectal wall is very thin and there are no intrinsic muscle layers, rectal glands or rectal papillae. The anus is formed by a narrow sphincter receiving regulatory muscles from the wall of segment X and appears externally as a longitudinal infolded slit lying postero-ventrally between the bases of the anal prolegs (fig. 130).

It must be borne in mind that the representative species examined all belong to specialised genera which feed on the contents of the cells of filamentous green algae (and therefore may be described as fluid feeders), the gut being a simple, almost undifferentiated tube as seen also in, for example, the hymenopterous larvae (Imms, 1957, p. 123). The structure of the gut may vary slightly according to feeding habits and it would be interesting to compare its microanatomy with that of the bryophyte-feeding Ptilocolepinae and detriphagous genera such as Stactobia, Leucotrichia, Ithytrichia and Allotrichia pallicornis (Eaton) (the latter according to Giudicelli & Vaillant, 1967).

2. The Salivary and Labial Silk Glands.

In the Hydroptilid larvae studied only two distinct pairs of cephalic glands were observed, namely the maxillary salivary glands and the labial silk glands. There are no mandibular, antennal or dorsal cephalic glands as located in other caddis larvae by Branch (1922), Glasgow (1936), and Fotius-Jaboulet (1963).

The maxillary salivary glands (fig. 134) are a pair of well developed organs lying anteriorly within the head capsule lateral to the pharynx and ventral to the brain. Each consists of a mass of large, vase-shaped, uni-cellular glands whose ducts converge antero-medially into a short common duct which opens into the foregut adjacent to the base of the median mandibular process. Nielsen (1948) remarks on their relatively large size in this family due, he says, to an increase in the size of the cells rather than in the number of cells and, I expect, to the reduced size of the insects.

As in trichopterous and lepidopterous larvae in general, the labial glands have lost their salivary function and have become modified as silk producing organs. Owing to the reduced overall size of the Hydroptilidae these glands are greatly enlarged and occupy a major region of the abdominal cavity, extending well back into segment IX. There have been a number of anatomical, histological and histochemical descriptions of these glands in both Lepidoptera and Trichoptera but there has been no comprehensive comparative study throughout the two orders. The histology of the glands will not be discussed in great detail here as it appeared to conform to the basic structure as described by Glasgow (1936), Haller (1948), Barth (1962) and Lepneva (1964). However, the micro-anatomy will be described in full as it is somewhat distinct in the Hydroptilidae and there has been some confusion in past literature on Trichoptera regarding the possible homologues of Lyonet's gland as found in the Lepidoptera.

Each of the paired glands consists of a thick, tubular, highly convoluted glandular region and a narrow anterior duct, the latter uniting at the base of the labium to form a very short common exit duct (figs. 133, 138). The secretory regions lie alongside the gut and the coils are closely associated with the Malpighian tubules, the thickened walls being coarsely granular and the wide lumen containing the secreted silk thread (figs. 135, 136, 137). The gland tapers anteriorly towards the prothorax where it suddenly widens and shortly tapers once again to a very narrow tube (fig. 133) due to the anterior glandular wall folding back on itself slightly before passing into the non-granular narrow duct (figs. 138, 139). Internally, in the region of this fold, the thickened intima projects anteriorly into the lumen of the pre-duct region forming a 'valve' through which the silk appears to be moulded into a narrow thread and which may serve as a secondary posterior silk press. No additional glandular region was found to be associated with this structure as described for <u>Rhyacophila septentrionis</u> McL. by Fotius-Jaboulet (1963) and which she considered to be the Trichopteran homologue of Lyonet's gland (see discussion below).

The two narrow ducts continue anteriorly into the head capsule (fig. 138), a slight 'kink' occurring in each as they pass over the ventral postoccipital ridge in one specimen of Hydroptila sp.. The ducts pass to either side of the ventral nerve cord between the suboesophageal and prothoracic ganglia and from here they run side by side medially along the floor of the head capsule. Just prior to their entrance into the labial (premental) lobe the two ducts unite to form a short common silk duct which opens distally on the tip of the labio-hypopharyngeal complex (figs. 138, 141). Within the labial lobe there is a well developed silk press which receives dorsally and ventrally inserted muscles originating on the hypopharyngeal sclerite and premental sclerites respectively (the dorsal and ventral 'salivarial' muscles of Fotius-Jaboulet, 1963).

Adjacent and lateral to the junction of the two ducts there is a pair of poorly differentiated but distinct ovoid masses of nucleated tissue which have no definite connective sheath, glandular structure or ducts (figs. 138, 140). In my opinion these may be the true homologues of Lyonet's gland in Lepidoptera and not the prothoracic 'glandes annexes' surrounding the silk glands in R. septentrionis as described by Fotius-Jaboulet (1963) who also states that the structures described in the region of the junction of the silk ducts in Hydropsyche colonica McL. by Glasgow (1936) and in Philopotamus montanus (Donovan) by Lesperon (1937) are in no way homologous with Lyonet's gland. However, as a result of my observations on Hydroptilid larvae, the 'glandes annexes' of Fotius-Jaboulet are secondary structures associated with the folding of silk gland/duct wall in the prothoracic region of R. septentrionis.

This folding of the wall is also seen in the Hydroptilidae (*Agraylea*, *Hydroptila* and *Oxyethira*) although no associated glandular structure appears to be present. However, in the Hydroptilidae there are the small amorphous structures to either side of the junction of the silk ducts at the base of the labial lobe which positionally (and in accordance with the findings of Glasgow, 1936) are more likely to be homologues of Lyonet's glands than those in the prothorax of *R. septentrionis*.

It is therefore evident that there is a need for a thorough comparative study of the position, morphology, histology and function of 'Lyonet's gland' throughout the two orders. According to Packard (1909) there are two opinions concerning the function of these glands in Lepidoptera, the first being that they produce an adhesive substance which binds the two threads together to form a single common thread, and the second that they produce a lubricant to aid the withdrawal of the thread. Owing to the apparently reduced condition of Lyonet's gland in Trichoptera, Glasgow (1936) considers the second view to be the most likely since water penetrating into the anterior region of the common duct of the silk organ in Trichoptera would render the production of a lubricant unnecessary.

3. The Central Nervous System.

This consists essentially of the brain (supraoesophageal ganglion) and ventral nerve cord which is made up of the suboesophageal ganglion, three thoracic and eight abdominal ganglia. As this conforms to the basic Trichopteran plan, as illustrated in Lepneva (1964) and Malicky (1973), only those features of the microanatomy of the central nervous system which appear to be distinctive for the Hydroptilidae will be discussed in detail below. These features, however, may simply be due to the overall reduced size of Hydroptilid larvae compared with that of most other caddis families.

The supraoesophageal ganglion occupies a large volume of the head capsule (fig. 134). In one pre-pupal specimen examined the optic lobes could be seen to arise from the protocerebrum and lead to the dorso-laterally situated developing eye discs, lying just posterior to the antennae and medial to the larval stemmata, to which they are closely apposed. The supra- and suboesophageal ganglia are connected by the circumoesophageal connectives which thus form a narrow ring which is just wide enough to allow the pharynx to pass through. Posteriorly the suboesophageal ganglion gives off a pair of short connectives to the prothoracic ganglia which lie on the ventral pro/mesothoracic boundary.

The thoracic ganglia are all distinct, each lying postero-ventrally in its own segment and giving rise to lateral nerves to the legs and segmental muscles. The abdominal ganglia show a certain degree of forward displacement which becomes more pronounced as pupation is approached. In general, ganglia I-IV are distinct and V-VIII are fused and lie within segment V, whereas in a pre-pupal specimen of <u>Hydroptila</u> ganglia V-VIII appeared to have moved forward into segment IV with ganglion IV free and lying on the border with segment III. Each abdominal ganglion gives rise to pairs of lateral nerves to the muscles of the appropriate segment.

The stomodaeal nervous system was not studied in great detail although the frontal ganglion (fig. 134) and a pair of retrocerebral glands, presumably the corpora allata, were located in longitudinal sections.

The Larval Stemmata.

As in all trichopterous larvae the paired lateral eyes consist of six closely grouped ocellar units, or stemmata, which lie directly beneath a slight elevation of the antero-dorsal region of each parietal sclerite (fig. 99). The stemmata are darkly pigmented and connect internally with the medial developing imaginal eye discs. According to Ehnbom (1948) the larval stemmata are retained, in a much reduced condition, in the imago of Agraylea and lie outside the optic lobe on a level with the lamina ganglionaris and parallel with the anterior rear border of the compound eye from which they are always separated by a thin layer of cuticle. The reduced larval eye in the adult is thus represented by a narrow chain of a variable number of highly pigmented cells which has no nerve connection with the optic lobe.

4. The Tracheal System.

The basic arrangement of the principal tracheal trunks and branches of the body and head as traced in serial sections of Hydroptila sp. accorded well with that described by Novák (1952). Thus two longitudinal lateral trunks extend throughout the thorax and abdomen, giving rise to segmental branches to the thoracic legs, anal prolegs and internal body organs. Anteriorly the lateral trunks give rise to two cephalic branches which supply the nervous system, eyes, antennae, mouthparts and foregut.

In Hydroptilid larvae the tracheal system is closed, there are no gills and respiration is entirely cutaneous by diffusion. Fine branches arise from the main tracheal trunks in each abdominal segment and these in turn give rise to a branching system of even finer tracheoles which lie just beneath the thin membranous cuticle. Lauterborn & Rimsky-Korsakow (1903) give a crude diagram of the tracheal system of Ithytrichia lamellaris in which the tracheae can be seen to be highly branched within each abdominal 'papilla' and in the single caudal filament.

5. The Reproductive System.

In one specimen of Hydroptila examined, a pair of developing gonads were located dorso-lateral to the gut in the IVth abdominal segment. Each small ovoid body tapered to fine anterior and posterior filaments of which the latter was traced postero-ventrally as far as the VIth abdominal segment. These bodies probably represent the developing ovaries as suggested by their shape and internal arrangement of diagonal parallel sections (the ovarioles) and by their position in segment IV, the testes usually being present in segment V (Lepneva, 1964; Malicky, 1973; Dodson, 1935).

6. The Circulatory System.

The dorsal vessel was traced in transverse and longitudinal serial sections of Hydroptila sp. throughout the abdomen (as the 'heart') and thorax into the head capsule (as the 'aorta') as far as the supraoesophageal ganglion.

7. The Dorsal Abdominal Rings and Pedal Glands.

The sclerotised rings which occur dorsally on abdominal segments II/III - VII/VIII in Vth-instar larvae of the Hydroptilinae were first described in detail by Nielsen (1948) who referred to them as "peculiar unicellular glands" which, in relation to normal cells of the body, are gigantic and sometimes attain 90µ in diameter. He states that in Agraylea, Hydroptila, Oxyethira, Orthotrichia and Ithytrichia they are usually paired on segments II/III - VII/VIII, although in the two last named genera they form a complete ring around segment I and in some cases may fuse such that only a single sclerotised ovoid ring is apparent externally. Basically each cell is 'flask-shaped' with a short neck leading from the cuticle to a wide base in which can be seen a large granulated nucleus (fig. 142 and also fig. 137). The distal part of the 'neck' is covered by a thin cuticular plate (which is enclosed in the ring formed by the slightly thicker surrounding cuticle) and the 'neck' itself bears many fine longitudinal striations. Nielsen regards the latter as pore canals through which the glandular products of the cells are secreted although, by his own admission, he did not find any evidence of such secretions. Figures 137, 142 show the internal structure of these cells as seen in Hydroptila sp. and their basic form does suggest a glandular function (vis. the large granular nucleus and 'pore canals'). However, according to Wiggins (1976) they may be chloride epithelial areas specialised for ionic absorption in osmoregulation as discovered in the Limnephilidae by Wichard & Komnick (1973) and, although I have not investigated these cells in the Hydroptilinae with the histochemical techniques employed by these two authors, I am inclined to agree with Wiggins that they are chloride epithelia rather than secretory organs.

The Pedal Glands of Ithytrichia lamellaris Eaton.

Lauterborn & Rimsky-Korsakow (1903) described and illustrated a distinct pedal gland in each foreleg of I. lamellaris (fig. 95c) consisting of a large glandular region occupying approximately half of the femur and leading by a duct through the tibia and tarsus to open at the base of the latter adjacent to the spur of the tibial claw. I was not able to locate this organ in preserved specimens using transmitted light and, as no serial sections were available of this species for examination, its true identity and function must remain subject to further investigation.

SECTION IIF. THE PUPA

The general appearance of the exarate, decticous pupae of most Trichoptera is very uniform throughout the order and the cast pupal skins are difficult to identify below the family level unless they can be associated with their pupal cases or emergent adults. Features which reflect retained larval characters (such as abdominal gills and lateral lines) or those of the pharate adult as seen through the pupal cuticle (such as spur formulae and antennae) may aid identification in addition to the structural adaptations of the pupae themselves. It should be noted that the term pupa is here used in its widest sense to refer to the stage in the life-cycle between the 'larval-pupal ecdysis' and the 'pupal-adult ecdysis' except when the pharate adult is expressly referred to. Hinton (1971) gives a full discussion of the precise terminology of metamorphosis in the Endopterygota which will be adopted here where relevant.

Hydroptilid pupae are recognised by their lack of any positive distinguishing structural features which variously characterise the other families of Trichoptera. In addition to their relatively small size (1.5 - 6.0mm body length) the following features are useful in the identification of the Hydroptilidae:-

1. absence of abdominal gills or lateral lines (absent in larval stages)
2. presegmental dorsal abdominal plates on segments III-VII
   postsegmental " " " " " III-V

3. mandibles symmetrical, short with one or two small median teeth or long or short without teeth or with a fine serrate cutting edge
4. anal seta-bearing processes absent (these only occur in forms where the posterior end of the pupal case is open to admit a water current, the setate processes serving to keep the apertures clear of debris)

The following account of the external morphology of Hydroptilid pupae is a summary of the main features of all genera known and described in this stage. Most of the information is from Nielson's (1948) descriptions of Agraylea, Hydroptila, Oxyethira, Orthotrichia and Ithytrichia with additional data from Ullmer (1957), Flint (1962) and Danecker (1961). Figures 143 and 144 were drawn from an actual specimen of Hydroptila vectis (Curtis) although no new information has been added from my own observations.

The pupal cuticle is very membranous and transparent and closely follows the contours of the encased adult from which it differs in the possession of distinct pupal mandibles and the sheathed appendages which are closely apposed, but not cemented to, the body. The pupal skin has very few setae, those present usually being developed as pale spurs. The vertex of the head capsule bears a row of short setae and there is one pair on the antero-lateral margin of the fronto-clypeus. The compound eyes are plainly visible, the antennae are relatively short, as in the adults, and are directed posteriorly to lie dorsal to the eyes and ventro-lateral to the wings. The elongate, narrow labrum is semicircular to slightly tapered apically, according to Nielsen (1948), and somewhat emarginate in *Palaeagapetus*, according to Flint (1962), and bears a variable number of pairs of setae of which a maximum of four has been recorded in *Agraylea* by Nielsen (ibid.).

The pupal mandibles are highly developed compared with those of the adult and are structurally very different from those of the larvae. They are adapted for piercing and tearing open the pupal case, being distally flattened and curved slightly inwards with a narrow pointed apex. They lie across one another ventral to the labrum, each articulating with the genal areas of the head capsule ventro-lateral to the base of the labrum, and are worked by the muscles of the pharate adult. In the majority of the Hydroptilinae the mandibles are long and very slender with finely serrate inner blades, whereas in *Orthotrichia* (and *Baliotrichia*, *Orthotrichiella*, *Pasirotrichia*, *Leucotrichia* and *Rhyacopsyche* according to Ulmer, 1957) they are short, robust and strongly serrate. The Ptilocolepinae are distinct in that the mandibles are short and bear medial teeth (one in *Palaeagapetus* and two in *Ptilocolepus*) while in *Stactobia*, *Plethus*, *Lamonganotrichia* and *Saranganotrichia* there are neither teeth nor serrations. Each mandible usually bears two basal setae.

The wing-sheaths of Hydroptilinae pupae taper considerably and, according to Lepneva (1964), in *Stactobia* they are as long as or slightly longer than the abdomen although in some specimens which I have examined (e.g. the female Hydroptila vectis shown in fig. 143) they are shorter. This may be due to sexual differences in the lengths of the abdomen or in the state of development of the ovaries in the females. The legs are of the adult proportions (fig. 144) and, in the fore- and hind legs, the coxa, trochanter and femur are loosely attached to the body while the midlegs are entirely free and have fringes of natatorial setae medially and laterally on tarsal segments I-III or I-II. The adult tarsal claws and tibial spurs are separately ensheathed as illustrated.

The abdomen may be slightly longer and narrower in the adult and there are no gills, cuticular ridges, attachment or cleaning organs. Setae may be present but are few and confined to the dorsa of the anterior segments. The ventral processes of the posterior segments may be separately ensheathed even though they may not attain adult proportions as in Hydroptila tineoides Dalman according to Nielsen (1948). The arrangement of the dorsal plates is a constant and characteristic feature of the Hydroptilidae, including the Ptilocolepinae, the presegmental pairs occurring on segments II-VII and the postsegmental pairs on III-V. Each plate consists of an ovoid patch of backwardly directed, short, pointed 'teeth' and assists in locomotion, serving to grip the inner lining of the pupal case while the abdomen is rhythmically undulated (Hickin, 1967); they are thus often referred to as the 'organs of locomotion' (Lepneva, 1964).

Pupation and Adult Emergence.

According to Nielsen (1948) the Hydroptilidae resemble the Limnephiloid 'tube-case' dwellers in that the larvae pupate in the larval case. As the cases of the Hydroptilidae are generically distinct they provide the main guide to identification of pupae which have not yet passed into the pharate adult stage. The pupal case generally resembles that of the larva except that it is closed and attached to the substrate by means of various adhesive discs or threads of silk, the attitude of the fixed case often being characteristic of the genus and dependent on the nature of the environment. In the fixed larval case-dwellers, such as the Leucotrichiini, *Stactobia*, *Plethus*, *Catoxyethira* and *Caledonotrichia*, the larva merely seals up the case permanently except *Alisotrichia spangleri* Flint which, according to Flint (1970), spins a thread from the substrate to the anterior end of the case which is then detached and transformed into the torpedo-shaped 'cocoon' which floats freely just below the surface of the water as an adaptation to prevent desiccation if the water level alters. In those genera exposed to any sort of current the laterally compressed case is attached along its ventral seam and stands vertically upright in line (presumably) with the direction of current flow. This has been observed in *Hydroptila* (various authors), *Paroxyethira*

(Leader, 1972), *Allotrichia pallicornis* (Giudicelli & Vaillant, 1967) and also *Orthotrichia*. In *Agraylea*, *Oxyethira* and *Tricholeiochiton*, which live in vegetation thickets in almost static water, the case is attached at all four corners and lies broadside against the substrate which is usually the stem or underside of a leaf of an aquatic plant. *Ithytrichia lamellaris* attaches the pupal case by a single disc, on the plug of the anterior aperture, broadside against the underside of loose stones in running water, although it is sometimes found on the bases of the stems of aquatic plants and has also been found in dense masses of willow roots (Wallace, pers. comm.).

Once the case is fixed, the larva seals up the openings and spins a final internal lining before adopting the typical prepupal resting attitude in which, according to Barnard (1971) in *Agraylea sexmaculata* Curtis, the thorax becomes distended and the abdomen straightens, the intersegmental grooves becoming less distinct. According to Nielsen (1948), in genera where there is a distinct anterior and posterior differentiation of the larval case this becomes reversed in the pupal stage (e.g. *Oxyethira*, fig. 91). When the pharate pupa is fully developed, ecdysis takes place and the larval exuviae are pushed to the posterior end of the pupal case. The pupa (s.l.) possesses no special respiratory organs and, although active, does not make any definite respiratory or cleansing movements. Small openings, presumably for water circulation according to Flint (1964), have only been observed in the pupal case of *Alisotrichia hirudopsis* Flint but probably occur elsewhere in the family.

When the pharate adult is fully developed it cuts an exit hole in the case using the pupal mandibles and wriggles out with the aid of the dorsal abdominal hook plates. It then makes its way to the surface where, according to Nielsen (1948), it lies back uppermost and, using the fringed midlegs as oars, swims erratically until it reaches a support onto which it climbs and undergoes the final ecdysis. Usually, if no dry support can be found, the adult fails to emerge successfully.

A detailed account of pupation in *Agraylea multipunctata* is given by Watts (1976).

SECTION III SYSTEMATICS

IIIA. INTRODUCTION 1. THE HISTORY OF THE SUBFAMILY CLASSIFICATION OF THE HYDROPTILIDAE

Stephens (1836) erected the family Hydroptilidae for the genera *Hydroptila* Dalman, *Agraylea* Curtis and *Narycia* Stephens of which, however, the only species figured, *Narycia elegans*, subsequently proved to be a synonym of *N. monilifera* (Geoffroy), a Tineid moth of the family Psychidae. At that time the Hydroptilidae was distinguished within the Trichoptera by the unfolded posterior wings and filiform antennae of the adults and the 'cleft-like' openings of the larval cases. The latter, along with the larvae, had first been described and illustrated by Pictet (1834) for *Hydroptila pulchricornis* and *H. flavicornis* and, in fact, McLachlan (1880) considered Pictet to be the true founder of the family since he was the first to recognise the group as a distinct taxon under the name of 'les Hydroptiles'.

As the number of described genera and species of Hydroptilidae continued to increase no attempt was made until Nielsen (1948) to divide the resulting large heterogeneous group into subfamilies. Nielsen proposed the Orthotrichiinae for *Orthotrichia* and *Ithytrichia* and the Hydroptilinae for *Agraylea*, *Oxyethira* and *Hydroptila* on the basis of morphological affinities of the larvae but, although he was aware of the other genera known at that time, he only remarked on the possible positions of two other genera, *Ptilocolepus* and *Stactobia*, in his scheme. The Stactobiinae was erected by Botosaneanu (1956) for *Stactobia* and 'its immediate relatives' which, although not expressly mentioned, probably included *Stactobiella*, *Plethus*, *Plethotrichia*, *Lamonganotrichia* and, possibly, *Catoxyethira*. Ross (1956) proposed a new classification of the Hydroptilidae to include the Ptilocolepinae, a small subfamily of two genera with Glossosomatid-like adults but typically Hydroptilid-like larvae. Ross thus divided the family into the Ptilocolepinae and the Hydroptilinae of which the latter was further subdivided into the Hydroptilini and Neotrichiini. Flint (1970) subsequently failed to recognise Ross's (1956) classification when he proposed the subfamily Leucotrichinae (later amended to Leucotrichiinae by Flint, *in litt.*) for the neotropical genus *Leucotrichia* and its near relatives since he retained the Ptilocolepinae, Stactobiinae and Orthotrichiinae as distinct subfamilies thus leaving the Hydroptilinae still as a very heterogeneous group.

Table 2 shows the two principle approaches to the subfamily classification of the Hydroptilidae and compares them with the system adopted here. The latter is based on Ross (1956) in that the Hydroptilinae is split into a number of tribes corresponding to the subfamilies of Flint (1970) but which are here considered to exhibit a number of common features which unite them and which distinguish them from the subfamily Ptilocolepinae.

The following genera have been transferred from the Hydroptilidae to other families of Trichoptera and will be discussed at the end of the Systematic section (III): *Padunia* Martynov (*Uenotrichia* Tsuda); *Tsukushitrichia* Koboyashi and *Petrotrichia* Ulmer.

A full systematically arranged checklist of the Hydroptilidae is given in Table 3 in the Appendix (section VIII).

TABLE 2. Summary of the three main views of the subfamily classification of the Hydroptilidae

Nielsen (1948) Botosaneanu (1956) Flint (1970)	Ross (1956)	Proposed classification
PTILOCOLEPINAE	PTILOCOLEPINAE	PTILOCOLEPINAE
	HYDROPTILINAE	HYDROPTILINAE
STACTOBIINAE	HYDROPTILINI	STACTOBIINI
LEUCOTRICHIINAE		LEUCOTRICHIINI
ORTHOTRICHIINAE		ORTHOTRICHIINI
HYDROPTILINAE		OCHROTRICHIINI
		HYDROPTILINI
	NEOTRICHIINI	NEOTRICHIINI

IIIA. INTRODUCTION 2. THE HISTORY OF THE SYSTEMATIC POSITION OF THE HYDROPTILIDAE WITHIN THE ORDER TRICHOPTERA

It was Eaton (1873) who first recognised the relationships between adult Hydroptilids and Rhyacophilids after agreeing with Pictet's (1834) observations that the maxillary palpi of both sexes of the former are five-segmented thus placing the family in the old subdivision Aequipalpidae (later known as the Aequipalpia). McLachlan (1880) retained the Hydroptilidae in the Aequipalpia but, on the basis of the case-building habits of the larvae, placed it between the 'tube-case'-building families Sericostomatidae and Leptoceridae. McLachlan regarded *Ptilocolepus* as a member of the Glossosomatinae ('section III of the Rhyacophilidae') but noted that 'the affinities are certainly with *Agapetus*'(Glossosomatinae) 'but the thickened erect hairs of the anterior wings show an analogy in the direction of the Hydroptilidae'.

On the basis of adult features Mosely (1939) considered the family to be closely related to the Rhyacophilidae and had particular difficulty in assigning the Nearctic *Protoptila* group to the one or the other family , at first including it in the Hydroptilidae but later (Mosely, 1954) transferring it to the Glossosomatinae-Rhyacophilidae.

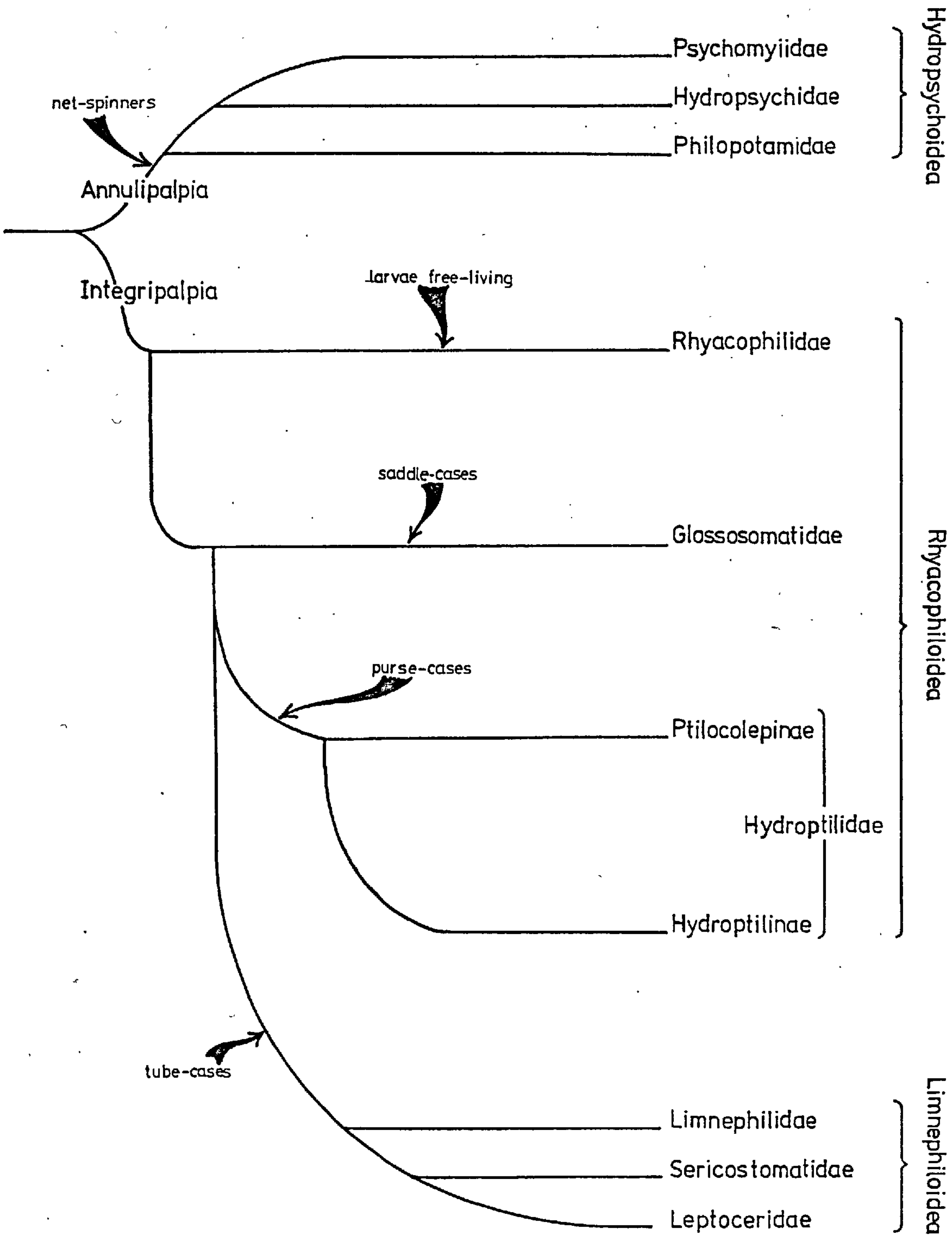
Nielsen (1948), on the basis of larval and pupal features, placed the Hydroptilidae between the 'saddle-case'-building Glossosomatinae and the 'tube-case'-building Integripalpia, the affinities with the latter being particularly exhibited by the form of the larval antennae and anal prolegs. Nielsen concluded that the subfamily Hydroptilinae sensu Nielsen (vide Table 2) was closest to the Integripalpia while the Orthotrichiinae sensu Nielsen retained the primitive features of the Rhyacophilidae. Nielsen's finding were, however, based purely on the external features of the larvae which may be subject to functional modifications correlated with the case-building habit and thus his views regarding affinities with the Integripalpia may have been influenced by superficially similar characters resulting from parallel evolution.

Milne & Milne (1939), on the basis of larval anatomy, behaviour and case-form, finally concluded this of the family: 'the Hydroptilidae is probably more closely related to the Glossosomatinae than the Glossosomatinae to the Rhyacophilinae..... Hydroptilid larvae being more specialised in the direction of the differentiation of the ends of the case (feeding from one particular end, etc.) than Glossosomatinids'.

The first serious attempt at a phylogenetic classification of the Trichoptera as a whole was made by Ross (1956) who based his conclusions on a comparative study of adult, larval and pupal morphology and case-making behaviour patterns. From these Ross deduced a set of primitive adult and larval characters and followed the development of these within each group, his findings regarding the evolutionary development of the Order being summarised below in Chart I (in which the realationships of the Hydroptilidae have been emphasised).

The ancestral caddisfly gave rise to two major evolutionary lines: the 'fixed retreat division', where the larvae simply spin silken nets in which they live and trap their food (the Philopotamidae and the Hydropsychidae-Psychomyiidae complex), and the 'case-maker division', containing all of the remaining families. Within the latter group the

Chart I. The position of the Hydroptilidae within the Order Trichoptera (after Ross, 1967)



most primitive representatives are considered to be the free-living Rhyacophilidae which build stone-covered silken pupal shelters. The early ancestors of the Rhyacophilidae gave rise to the primitive Glossosomatid-line, in which the larvae build transportable cases and which in turn gave rise to the more advanced 'saddle-case'-making Glossosomatidae and the 'purse-case'-making Hydroptilidae. The final stage in the evolution of the case-building habit was the adoption of the 'tube-case' form as seen in the higher Limnephiloid and Leptoceroid families. Ross considers this branch to have arisen from the same ancestor as that which gave rise to the Hydroptilid-line and not from the 'tube-case'-building Hydroptiline tribe, the Neotrichiini, which would appear to have evolved independently from the main branch of the Hydroptilinae. The Ptilocolepinae is considered to be an early offshoot of the Hydroptilid-line in which the adults retain many characters similar to those of the more primitive Glossosomatidae.

In conclusion, therefore, the Hydroptilidae may be regarded as a specialised but early offshoot of the case-making line of Trichoptera but is included in the Rhyacophiloidea, along with the Rhyacophilidae and Glossosomatidae, the other main subdivision being the Limnephiloidea which contains the Limnephilid and Leptocerid branches. The Hydroptilidae share a common ancestry with the Glossosomatidae with which they have both larval and adult affinities, the latter being most marked in the Ptilocolepinae which also exhibits pupal features intermediate between the Glossosomatidae and Hydroptilinae. The Hydroptilidae is also regarded as being an early offshoot of the line leading to the advanced Limnephiloidea.

IIIB. THE GENERA OF THE HYDROPTILIDAE - SYSTEMATICS

Family HYDROPTILIDAE Stephens

Hydroptilidae Stephens, 1836: 148. Type-genus: *Hydroptila* Dalman.

Distribution: Cosmopolitan (excluding polar regions).

Family diagnosis

Adult. Forewing length 1.2-6.0mm; forewings moderately to densely pubescent; wings primitively broad, with relatively complete venation and rounded apices, to narrow with highly reduced venation and tapering apices: ocelli 3, 2 or 0, lateral pair set close to compound eyes some distance posterior to antennal bases: post-occipital warts prominent, meeting postero-medially or represented by loosely hinged sclerites or 'lobes': ♀ genitalia usually an oviscapt with an elongate telescopic IXth segment and a small cerci-bearing Xth segment; IX rarely reduced, fixed: ♂ inferior appendages uni-segmented.

Larva. Campodeiform, prognathous: usually exhibiting hypermetamorphosis in which instars I-IV are free-living while V is case-bearing: dorsa of all three thoracic segments covered by paired nota: abdominal gills and lateral line absent; anal prolegs usually fused to sides of segment X in the Vth-instar (free in instars I-IV); abdominal tergites present or absent on segments I-VIII, always present on segment IX; dorsa of abdominal segments I-VIII variously with small cuticular rings which may be regions of chloride epithelia; abdomen usually greatly distended in Vth-instar.

Pupa. Mandibles usually short with one or two small median teeth (Ptilocolepinae) or with fine serrations along inner edge only (Hydroptilinae): abdominal gills and lateral line absent; apex of abdomen without lobes, processes or specialised cleaning appendages (apart from ventral membranous lobes containing the developing genitalia); presegmental hook plates present dorsally on abdominal segments III-VII, postsegmental plates on III-V.

A key to differentiate the larvae, pupae and adults of the Ptilocolepinae from the Glossosomatidae and Rhyacophilidae is given in the Appendix, section VIIIA.

A key to differentiate the adults and known larvae of the genera of the Hydroptilidae is given in the Appendix, section VIIIB.

A systematic checklist of the family Hydroptilidae is given in the Appendix, section VIIIC, Table 3.

Subfamily PTILOCOLEPINAE Martynov

Ptilocolepinae Martynov, 1913: 22. Type-genus: *Ptilocolepus* Kolenati.
Distribution: Holarctic.

The Ptilocolepinae contains two small montane genera which are confined to the Holarctic region, *Ptilocolepus* containing four extant Palaearctic species and *Palaeagapetus* which is known from the type-species in Baltic Amber and three extant Nearctic species. The adults look more like small Glossosomatids with which they were originally classified until features of their larval stages were seen to suggest that their true affinities were with the Hydroptilidae (Ross, 1956). *Rhyacophila granulata* Pictet was the first species to be described but, as Pictet himself noted, could [illegible] be distinguished from all other members of that genus by its 'rough wings and very ciliated legs'. *R. granulata* was later shown to be a senior synonym of *Ptilocolepus turbidus* Kolenati by Hagen (1855), the type-species thus becoming

Ptilocolepus granulatus. Thienemann (1904) described the larva of *granulatus* and noted its Hydroptilid affinities which caused Ulmer (1907) to place the genus in the Hydroptilidae. Subsequently, however, Martynov (1913) erected the Ptilocolepinae for the nominate genus only but retained the subfamily in the Rhyacophilidae; Ross (1956) eventually transferred the subfamily to the Hydroptilidae and redefined it to include the genus *Palaeagapetus* (earlier in that paper, chart 2, p. 18, Ross refers to the subfamily erroneously as the Palaeagapetinae), the inclusion of *Palaeagapetus* later being justified by the discovery of the immature stages of *celsus* described by Flint (1962) and shown to have many affinities with *Pt.granulatus*.

The following subfamily diagnosis is based on the literature and examination of adult material of *Pt.granulatus* and *P.celsus* in the BMNH collections and larvae of *P.celsus* loaned from the USNM collection.

Subfamily diagnosis

Adult. Forewing length 4-6mm; general body colour dark brown to black, wings somewhat iridescent: wings broad with rounded apices, very sparsely pubescent; costal fringes short; venation (fig.30) almost complete, resembling Glossosomatid and primitive Rhyacophilid condition- forewing with discoidal cell (dc) closed, Cu_1 forked and Cu_2 curved; head (fig.9) strongly sclerotised; π-shaped tentorium well developed; ocelli 3, lateral pair set close to compound eyes some distance posterior to bases of antennae; antennae short, of approximately 24-30 segments; post-occipital warts large, ovoid, meeting medially: pronotum (fig.9) with median warts close-set: mesonotum strongly convex; prescutum delineated by a row of punctate setal sockets; scutellum subtriangular, convex with a straight posterior margin and a large oval wart; katepisternal suture ('k') present (figs 6,7): metascutellum subtriangular: preapical spur absent from foretibia; spur formula 2.4.4 (*Palaeagapetus*), 1.3.4 (*Ptilocolepus*): abdominal sternite V (fig.36) with well developed ridge running from antero-dorsal fold (from which arise lateral membranous filaments in *Ptilocolepus*) posteriorly and ventrally to meet in midline; ventral processes variously present on sternites VI and VII: ♀ genitalia oviscapt: ♂ genitalia simplified but specialised in each genus (figs 41, 42) with segment VIII unmodified; segment IX fused, produced antero-ventrally with strongly developed oblique lateral ridges, strongly excised dorsally and ventrally, latter enclosing a triangular ventral plate in *Ptilocolepus* above which lie the fused, generally bifid, 'inferior appendages' (homology uncertain); 'inferior appendages' apparently fused with segment IX in *Palaeagapetus*; tergite X forming a simple dorsal plate, which in *Ptilocolepus* bears a pair of setose apical lobes; aedeagus greatly simplified, short, broad and membranous with a dilated apex and a median ventral sclerite.

Larva (fig.76a). Slightly flattened dorso-ventrally: head with distinct dorsal ecdysial lines; anterior ventral apotome large and triangular, postmental sclerites paired, posterior ventral apotome small and triangular (fig.102); labrum symmetrical, anterior margin strongly emarginate with a row of many short setae; mandibles (fig.11) not markedly asymmetrical, short and stumpy, medial brush present in both right and left, cutting edges strongly ridged: thoracic nota on all three thoracic segments, longitudinal median ecdysial lines distinct on each; thoracic sternites absent; legs short, subequal;

pre-episternite free on all thoracic segments (fig.116); abdomen entirely membranous except for the well developed tergite of segments IX and I in Ptilocolepus; anal prolegs fused to segment X; abdomen with prominent sucker-like tubercules on segments II-VII in Palaeagapetus.

Case (fig.76b). Purse-type, dorso-ventrally compressed (carried horizontally), constructed of two silken valves covered with small fragments of liverwort and moss.

Pupa. Mandibles long with two medial teeth in Ptilocolepus, one in Palaeagapetus.

Biology. The larvae occur in small montane springs and seeps, amongst luxuriant growths of moss and liverwort, on stones and other submerged objects; they are often found in the cold damp vegetation above the water level. Habitats in cool, shaded, montane coniferous forests, which favour the growth of bryophytes, are likely to support small colonies of these very local and primitive caddisflies; indeed, McLachlan (1880) noted that the adults of Ptilocolepus granulatus were found in European mountainous regions 'on driblets on faces of rocks' where water was soaked up by the moss. The habitat preferences of the Ptilocolepinae are thus very similar to those of the hypothetical ancestral caddis larva as postulated by Ross (1956).

The early stages (instars I-IV) of the Ptilocolepinae have not yet been discovered; the phenomenon of hypermetamorphosis has therefore not been verified in this subfamily.

Genus PTILOCOLEPUS Kolenati

Ptilocolepus Kolenati, 1848: 102. Type-species, *Ptilocolepus turbidus* Kolenati, by monotypy.

Distribution: Palaearctic.

Ptilocolepus occurs in the western Palaearctic region eastwards to the Urals, the Caucasus and Iran, the commonest and most widespread species being *granulatus* Pictet. The identity of *villosus* Navás from Spain is questionable due to the inadequacy of the original description (Navás, 1916); the species may prove to be synonymous with either *granulatus* or *extensus* McLachlan (N.B. *villosus* was not referred to by Schmid, 1949, in his paper on the Navás types).

The following key to the males of *colchicus* Martynov, *granulatus* and *extensus* is based on a study of material in the BMNH collections. Females of *granulatus* are in the BMNH collections but have not been described; the larva of this species has been described by Thienemann (1904) and Jacquemart & Coineau (1962).

Generic diagnosis

Adult. Branches R_2+R_3 and M_1+M_2 fused in hindwing (fig.30), spur formula 1.3.4.

Larva. Abdomen without lateral tubercules, segment I with small dorsal tergite.

Pupa. Mandibles with two medial teeth.

Key to *Ptilocolepus* males (excluding *villosus*)

1 Hindwing with patch of modified setae; 'inferior appendages' bifurcate with dorsal process not longer than ventral, ventral process broad; 'ventral plate' with process (fig.42b). Caucasus and Iran. . . . . *colchicus*

- Hindwing without patch of modified setae; 'inferior appendages' not as above; 'ventral plate' without process. . . . 2

2 'Inferior appendages' bifurcate, dorsal process longer than narrow ventral process; 'ventral plate' without process (fig.42a). Spain, Italy, Central Europe. . . . *granulatus*

- 'Inferior appendages' non-bifurcate; 'ventral plate' without process (fig.42c). Portugal, Spanish Pyrenees. . .*extensus*

Genus PALAEAGAPETUS Ulmer

Palaeagapetus Ulmer, 1912a: 35. Type-species, *Palaeagapetus rotundatus* Ulmer, by monotypy.

Distribution: Nearctic (and Baltic Amber).

Palaeagapetus rotundatus is known only from Baltic Amber and is probably therefore of western European origin (and thus possibly Eocene according to Ross, 1956). The three extant Nearctic species agree with the type form in features of venation, spur formula and male genitalia. *P.nearcticus* Banks and *guppyi* Schmid are western species*while *celsus* Ross occurs in the east from the western Appalachians of North Carolina and Tennessee, New Hampshire to the Laurentians of Quebec (Roy & Harper, 1975). According to Wiggins (in press) it is likely that *celsus* will be found in montane areas between these two extremes.

There is no key to the species of *Palaeagapetus* and only the larva of *celsus* has been described (Flint, 1962).

Generic diagnosis

Adult. Branches R_2,R_3 and M_1,M_2 free in the hindwing (c.f. fig.

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* From California to Vancouver Island.

30); spur formula 2.4.4.

Larva. Abdomen with lateral pairs of segmental tubercules, segment I without tergite.

Pupa. Mandibles with one medial tooth.

Discussion: the Ptilocolepinae

The Ptilocolepinae appears to represent a natural extant link between the primitive Glossosomatidae, with which the adults share many features, and the very specialised Hydroptilinae with which they are classified on the basis of the distinctive larvae and cases. The subfamily is confined to cool Holarctic regions, being found locally in clear, shaded montane springs in association with bryophytes as typical of primitive Trichoptera. The Ptilocolepinae probably thus arose from the main Hydroptiline stock very early in the evolution of the family, before the typical adult Hydroptilid form had been derived, and has since remained very little changed except with respect to the development of the highly specialised and characteristic male genitalia.

Subfamily HYDROPTILINAE Stephens

Hydroptilinae Stephens, 1896: 148. Type-genus, *Hydroptila* Dalman.

Distribution: Cosmopolitan (excluding polar regions).

The Hydroptilinae is a very heterogeneous subfamily considered here to contain six distinct tribes characterised by fundamental adult, larval and pupal morphological features which unite them and distinguish them from the Ptilocolepinae.

Subfamily diagnosis

Adult (fig.1). Forewing length 1.2-6.0mm: wings narrow with rounded apices and almost complete venation in the larger, more generalised forms (figs 31,32) to highly attenuate with consequently reduced venation in the smaller, more specialised groups (figs 33,34, 35); Cu_1 unbranched in the forewing (fig. 31, arrowed); wings densely pubescent, costal fringes usually long and well developed: sclerotisation of head capsule reduced in the smaller forms; π-shaped tentorium (figs 11-25) basically well developed, anterior arms reduced medially to weakly sclerotised filaments (scarcely detectable in KOH-treated specimens) in smaller, specialised genera; ocelli 3, 2 or 0, lateral pair close to eyes and some distance posterior to antennae; antennae usually short, of approximately 30 segments (rarely 40, sometimes 18); post-occipital warts well developed, ovoid to subspherical, often represented by distinct sclerites hinged to the head capsule which, in *Hydroptila* males, conceal eversible scent-organs; compound eyes of variable size but usually occupying whole width of head capsule: thorax (figs 8, 11-25) with close-set median pronotal warts; mesonotum flat, prescutum absent, scutellum with posterior half forming a triangular flat area with steep sides and a warty texture along edges only, anterior half triangular to arc-like, transverse suture present or absent; mesokatepisternal suture absent (fig.6, inset)(I have found this to be a constant feature of the Hydroptilinae, confirming Ross's (1956) view that it is 'usually' absent): fore-tibia with never more than one apical spur; meso-tibia with never more than one pre-apical spur (fig.28): abdomen with ventral processes variable (segments VI, VII or VIII); sternite V (fig.37) without postero-lateral ridge but with a pair of small dorso-anterior pits usually containing a short, posteriorly directed setose membranous process: ♀ genitalia on oviscapt; IXth segment usually long and telescopic (figs 61,64), rarely short and fixed with segment VIII modified (figs 62,63): ♂ genitalia variable but usually with a characteristic generic or tribe form (generalised form, fig. 40); segment VIII usually with tergite and sternite distinct, rarely fused; segment IX forming an annular 'genital capsule', sometimes with various postero-lateral processes, antero-lateral apodemes and dorsal and ventral excisions, sometimes concealed by segment VIII; inferior appendages usually present , size and shape variable, sometimes with baso-dorsal processes ('bracteoles'), sometimes fused and at times withdrawn into segment IX; tergite X reduced to dorsal plate (may be absent), size and degree of sclerotisation variable; subgenital plate or appendages present; bilobed process present ventral to subgenital plate, consisting of a membranous process with two short apical setae (sometimes appears to be fused to subgenital plate); aedeagus variable but basically a long narrow sclerotised tube enclosing the phalloduct which opens apically, a pair of lateral processes may occur along apical half (sometimes fused together or with central tube) which may be represented by a single spiral 'titillator' (homologies uncertain).

Larva. Early instars (I-IV) free-living (fig 132), Vth-instar case-bearing (figs 77-98). All three thoracic segments with paired nota completely covering dorsa; abdomen distended, membranous, compressed laterally or dorso-ventrally, rarely cylindrical, abdominal gills absent. Ecdysial lines of head distinct (figs 99-101), sometimes fused; ventral apotome and postmental sclerites variable (figs 102-110), small posterior ventral apotome sometimes present (fig. 109); labrum basically symmetrical; mandibles (figs 111-114) primitively symmetrical and each with mesal brush (in left mandible only in specialised groups), cutting edges ridged or modified as sharp blades or 'scoops' (figs 113-115): thoracic sternites variable (figs 121-129) with a maximum of three per segment (one median'oral' and two lateral 'anal'); pleurites primitively with pre-episternite free on all segments, usually free on segment I only; anal epimeral pleurite sometimes present (figs 116-119): legs variable, basically short and subequal, modified variously as robust, strongly clawed clinging organs (e.g. fig. 84b) or with mid- and hind-legs long and slender as in vegetation dwellers (e.g. figs 91-93): abdominal tergites present or absent, tergite IX always present; dorsal 'rings' usually present on segments I/II-VIII; anal prolegs usually fused to sides of segment X (except in early instars and Vth-instar of Alisotrichia and the Neotrichiini).

Case. Variable, basically purse-like of two silken valves with anterior and posterior slit-like openings (e.g. fig. 90), sometimes with incorporated inorganic or organic particles; usually held horizontally . Sometimes, however, the case may be cylindrical or fusiform with slit-like (fig. 95b) or circular (figs 87b, 88b) openings; in specialised torrenticolous or madicolous forms the case is greatly flattened dorso-ventrally and firmly fixed (temporarily or permanently) to the substrate (figs 77b, 78b, 81b) and may sometimes have lateral 'wings' (figs 79, 80, 98b).

Pupa. Of the typical Hydroptilid form (fig. 143); presegmental and postsegmental plates on abdominal dorsa III-VII and III-V respectively; mandibles without teeth, usually long. Case formed by sealing the larval case which has been previously attached to the substrate by adhesives discs at the corners or by one seam.

Biology. The subfamily contains both cool- and warm-adapted genera which occur in a wide variety of habitats; it is almost cosmopolitan in distribution being absent only from the extreme polar regions. Habitat preferences range from seeps, springs and splash zones of waterfalls to clear, fast-flowing montane streams, and from all sizes of rivers to still (but rarely stagnant) ponds in lowland regions.

The larvae are basically detriphagous but some groups have adopted specials methods for feeding on the fluid contents of the cells of filamentous green algae, the most specialised genus in this respect being *Orthotrichia*. The distribution and life-histories of the algal-feeding groups are dependent on those of the algae and genera vary as to whether they occur with the algae on the substrate or amongst vegetation. The primitive Nearctic genus *Dibusa* is unique in that it is associated with the red fresh-water alga, *Lemanea* (Wiggins, in press).

Tribe I STACTOBIINI Botosaneanu (stat.n.)

Stactobiinae Botosaneanu, 1956: 382. Type-genus, *Stactobia* McLachlan.
Distribution: Holarctic.

Botosaneanu (1956) erected the subfamily Stactobiinae for *Stactobia* and 'les genres étroitement apparentes' (*Stactobiella* etc.). Although Botosaneanu did not name these genera he probably intended the group to include *Stactobiella*, *Plethus*, *Plethotrichia* and *Lamonganotrichia* according to the knowledge of the group at that time. Ulmer (1957) considered *Plethus* and *Lamonganotrichia* to be closely related according to larval affinities but on adult features alone *Plethus* bears more resemblance to *Plethotrichia*,while *Lamonganotrichia* is more like *Orthotrichia*. However, Ulmer also considered the larva of *Plethotrichia* to have more affinity with that of *Hydroptila* and consequently placed it in the Hydroptilinae sensu Nielsen (1948) (*vide* Table 2).

Schmid (1959), despite recognising Botosaneanu's subfamily grouping, remarked on the relationships of *Stactobia* with *Stactobiella*, *Chrysotrichia*, *Medioxyethira*, *Pseudoxyethira*, *Parastactobia*, *Macrostactobia* and *Plethus* (of the latter of which Schmid considered *Plethotrichia* to be a possible synonym). Flint (1970), on the basis of larval morphology and case form, considered *Plethus* and *Lamonganotrichia* to belong in the Stactobiinae but placed *Stactobiella* in the Hydroptilinae sensu Nielsen (1948) along with *Hydroptila*, *Agraylea* and *Oxyethira*.

Idependently of my own findings, Morse (1974) has remarked on the relationship of *Catoxyethira veruta* Morse, from S. Rhodesia, with the Holarctic genus *Stactobiella* according to features of the adults.

Ulmer (1957) had previously noticed the relationship of the larvae of *Catoxyethira* and *Stactobia*.

Examination of adult type-material has revealed errors in the original diagnosis of the genera which are henceforth considered to comprise the tribe Stactobiini; such anomalies have occurred in the interpretation of spur formulae, presence of ocelli and wing venation features, all of which were once considered to be very important in deducing generic relationships. The present grouping is thus based on more reliable features such as the male and female genitalia, head and thoracic structures and amended ocellar counts and spur formulae; a number of previously unsuspected relationships and possible synonyms have also been discovered.

Since the constituent genera exhibit a number of larval and adult features which are unique to the Stactobiines I propose to treat the group as a distinct tribe although three main genus-groups may be recognised. These are A. the *Stactobia*-group (*Stactobia* and *Plethus*), B. the *Stactobiella*-group (*Stactobiella*, *Bredinia*, *Parastactobia* and *Chrysotrichia*)and C. the *Madioxyethira*-group (*Madioxyethira*, *Pseudoxyethira* and *Scelotrichia*). Within the tribe the genera show various lines of development and specialisation in either the larval or the adult stages or both, but they all share the basic common features (set out below) from which the principal characters of a hypothetical Stactobiine ancestor may be deduced. As more becomes known of the group, especially in the larval stages, the following tentative conclusions may accordingly require modification.

Tribe diagnosis

Adult (figs 11-13). Head with tentorium complete; antennae short, usually 18-segmented; ocelli 3: mesoscutellum with transverse suture; metascutellum with anterior edge approximately straight, parallel with posterior edge: Vth abdominal segment with typical short, lateral setose processes; ♀ genitalia an oviscapt; ♂ genitalia (figs 43-46) with tergite and sternite VIII distinct; IX reduced ventrally, sternite vestigial (absent or fused with tergite ?);inferior appendages small, distinct; paired subgenital structures ('subgenital appendages', Schmid, 1959) heavily sclerotised, arched downwards, sometimes represented by a fused sclerite (?); bilobed process absent; tergite X absent or reduced; aedeagus (fig. 47c-e) long, straight, without median constriction or spiral titillator, basically tripartite with a single apical process arising midlength beneath (or above) which are two flattened processes fused along most of their length (often only the apex reflects this form as a dilated, trilobed structure), sometimes rows of short apical setae or heavily sclerotised subapical spines may be present.

Larva. The larval stages are only known for *Stactobia*, *Plethus*, *Stactobiella* and *Catoxyethira* (including also *Lamonganotrichia* and *Plethotrichia*). The genera have different structural adaptations associated with their various habits and ecological preferences and do not appear superficially to be as homogeneous as the adults. The generalised larval form, as seen in *Stactobiella*, is that of the typical Hydroptilid with the Vth-instars inhabiting transportable purse-type cases, but the main evolutionary trend within the group has been the adaptation to life in fast-running water and the thin surface film of water on rocks (the madicolous, hygropetric or hydropetric habitat). Various degrees of specialisation may be seen but the basic trends are towards the dorso-vental flattening of the body and case, the attachment of the case to the substrate, the protection of the body by fusion and thickening of dorsal sclerites and the development of the thoracic legs as strong clinging appendages. The most advanced genus in this respect is *Stactobia*, which is truly madicolous, while *Plethus*, according to Schmid (1958), although morphologically similar to *Stactobia* does not share its 'hydropetric' habits; Schmid also states (1960) that *Medioxyethira milinda* is exclusively madicolous even though he did not examine the larvae of this species.

Pupa. Typically Hydroptilid with no distinguishing characters; mandibles long, without teeth.

Genus STACTOBIA McLachlan (Tribe I, group A)

Stactobia McLachlan, 1880: 505. Type-species, *Hydroptila fuscicornis* Schneider, by subsequent designation by Fischer (1961).

Afritrichia Mosely, 1939b: 35. Type-species, *Afritrichia aures* Mosely, by original designation. (Synonymised by Schmid, 1959).

Aratrichia Mosely, 1948: 76. Type-species, *Aratrichia fahjie* Mosely, by original designation. (Synonymised by Schmid, 1959).

Lamonganotrichia Ulmer, 1951: 68. Type-species, *Lamonganotrichia crassa* Ulmer, by original designation. (Syn. n.)

Distribution: Palaearctic, SW. Asia, Africa.

McLachlan erected this genus for *fuscicornis* and a new species, *eatoniella*, the true identities of which were subject to a careful investigation by Kimmins (1949). Larvae of the type-species were collected by Zeller from Messina (Sicily) along with the adults on which Schneider based his original description. Eaton (1879) referred to the biology of the larvae remarking that they '...at first roam at large, caseless; when they become corpulent they construct oval cylindrical cases of fine mud. They abound on rocks suffused with an extremely thin film of water resulting from the spray and dribbling of trickling streamlets, especially in places exposed to the sun!'; he was thus the first to record both larval hypermetamorphosis in the Hydroptilidae and the madicolous habits of *Stactobia*.

Prior to Schmid's (1959) paper on *Stactobia* the major contributions, albeit fragmentary, to the knowledge of the genus were by Mosely (1933), Vaillant (1951a, 1951b, 1952, 1956) and Botosaneanu (1956). Schmid subdivided the genus into four main species-groups, of which a summary of the main features is given below (partly adapted from Jacquemart, 1973). In the checklist (Appendix, section VIIIC, table 3) the species are arranged according to these groups with new species (i.e. post-1959) being assigned correspondingly. Examination of the type of *Lamonganotrichia crassa* reveals that this genus is synonymous with *Stactobia* according to structural affinities of the adult head, thorax and genitalia and similarities in the larva as described by Ulmer (1957).

Generic diagnosis

Adult. Forewing length 1.5-4.0mm: compound eyes relatively small; postoccipital lobes wide, ovoid (fig. 12): mesoscutellum narrow, deep (fig. 12): spur formula 1.2.4 (fig. 28)(0.2.4 in *radovanovici* Schmid); fore-coxae notched and fringed (fig. 28): ♂ genitalia (fig. 44) specialised; sternite VIII displaced posteriorly segment IX reduced ventrally, often produced anteriorly as a pair of lateral apodemes; inferior appendages small, rarely elongate; subgenital appendages strongly chitinised, arched; tergite X semimembanous: aedeagus long, straight, often considerably developed but sometimes thin and simple, usually with a dilated, heavily spined, membranous apex; ventral process of VII long, sinuous and thickened apically.

Larva. Early instars free-living, caseless, dorso-ventrally flattened and with tergites present on all abdominal segments. Vth-instars (fig. 77) case-bearing, dorso-ventrally flattened; sclerotisation well developed; setae modified as short, stout, protective spines. Sclerites of head fused; labrum symmetrical; mandibles (fig. 112) not markedly asymmetrical, massive, heavily ridged, 'shovel-like', brushes present in both left and right (Botosaneanu, 1956); anterior ventral sclerites paired (fig. 107): thoracic nota paired, medial lines distinct; pre-episternite free on all three segments; sternites as in fig. 121; legs short, subequal, robust, adapted for clinging: tergites present on all abdominal dorsa; posterior margin of tergite IX with 'crenallations' (modified flattened setae ?).

Case (fig. 77b). Dorso-ventrally compressed; transportable but usually temporarily fixed to substrate; barrel-shaped with dorsal and ventral longitudinal seams and slit-like anterior and posterior openings; constructed of silk and fine grains of mud or sand. The case of *Lamonganotrichia* (fig. 79, after Ulmer, 1957) is ovoid or shield-shaped, with a central rectangular section occupied by the larva and is bordered by a wide lateral folded fringe; a ventral longitudinal seam appears to be present.

Biology. The greatest contribution to the knowledge of the biology of *Stactobia* was made by Vaillant (1956) while detailed life-history data are given by Danecker (1961). The larvae are unique within the Hydroptilidae because they are madicolous (hygropetric, hydropetric), that is they are adapted to live in the tenuous habitat formed, according to Hynes (1970), by 'thin sheets of water flowing over rock faces and , although it is hardly a running-water habitat in the ordinary sense, it is often situated very close to one'. Thus the habitat often occurs at the edge of streams by the side of waterfalls and on rocky chutes, the faces of which may be almost vertical. Such conditions require very special structural adaptations of the inhabitants which can be clearly seen in the larvae and cases of *Stactobia* (fig. 77). Both are dorso-ventrally flattened and capable of maintaining a thin film of water over their dorsal surfaces by surface tension; the cases are temporarily fixed but may be moved if conditions become unfavourable; the larvae are protected dorsally by heavily sclerotised fused tergites and spine-like setae, and their short, robust legs are used in clinging to the substrate. The larval mouthparts are adapted for feeding on organic particles ('phytosaprophagous' according to Vaillant, 1956), the mandibles (fig. 112) being robust, strongly ridged and having a scraping function. According to Vaillant (1956) the larvae are exclusively petrimadicolous, that is they occur only on rocky substrates almost devoid of sediment and filamentous algae. The pupae are often gregarious forming a 'Puppenneste' (Danecker, 1961) in which the cases are closely packed in a single 'colony'.

Species-groups (after Schmid, 1959 and Jacquemart, 1973)

1 *furcata*-group (19 species): this is the largest and most homogeneous group, its main feature being the constancy of the form of the male subgenital appendages; its distribution extends throughout central and southern Europe, the Atlantic Islands, North Africa, Israel and Turkey.

2 *martynovi*-group (12 species): this is less homogeneous than the previous group and is characterised by the dorsal thickenings of tergite X and the anterior displacement of the inferior appendages of the males (most marked in *ulmeriana* Schmid to which, in my opinion, *schmidi* Kimmins from Nepal is most closely related); the group is restricted to southern Asia - Iran, Pakistan, Sri Lanka, Burma, Nepal and Turkestan (U.S.S.R.).

3 *nielseni*-group (6 species including *Lamonganotrichia crassa*): this group is distinguished by the modified VIIIth sternite and the absence of any subgenital appendages in the males; representatives occur in the southern Yemen (Aden), Iran, Pakistan and Indonesia (Java).

4 *vaillanti*-group (2 species): exclusively an African group with *vaillanti* Schmid from French Guinea and *aurea* (Mosely) from Uganda.

S. bolzei Jacquemart (Turkey) is considered by Jacquemart (1965) to be distinct although I believe that it may belong to the *nielseni*-group (original description inadequate for direct comparison).

S. japonica Iwata (Japan) is known only from the larva of which the case bears more resemblance to that of *Plethus* as figured by Ulmer (1957); the *japonica* of Tsuda & Nakagawa (1959) may be a distinct species since again only the larvae were examined.

S. megalatlantica Nybom and *mallorcensis* Vaillant are nomina nuda.

Discussion

Stactobia is a very specialised member of the Stactibiini. Although it is amongst the more successful of the Hydroptilid genera, its distribution is somewhat restricted in comparison with that of Hydroptila, Oxyethira and Orthotrichia because of its unique madicolous larval habits. It is the only Old World Hydroptilid genus to occupy this niche and is thus not subject to competition within the family and its continuous distribution indicates a relatively recent dispersal. The absence of Stactobia from the New World may be due to two factors: i. the slow rate of dispersal in comparison with lowland vegetation dwellers (see later discussions) and ii. its inability to compete with the highly successful Leucotrichiini which exhibits similar, but parallel, larval modifications and is confined to the American continent.

Stactobia could have arisen from temperate or subtropical Palaearctic stock which penetrated southwards into Africa and SE. Asia and northwards into central Europe. There are no species in the north of the region, the genus being totally absent from Scandinavia and the British Isles.

Genus PLETHUS Hagen (Tribe I. Group A)

Plethus Hagen, 1887: 643. Type-species, Hydroptila cursitans Hagen, by monotypy.

Plethotrichia Ulmer, 1951: 65. Type-species, Plethotrichia baliana Ulmer, by original designation. (Syn. n.).

Distribution: SE. Asia.

Plethus was erected for the type-species from Sri Lanka and now contains another five species from this island (Schmid, 1958), one from Pakistan (Schmid, 1960) and three from Indonesia (Ulmer, 1951); the larvae of *acutus* and *cruciatus* were described by Ulmer (1957). *Plethotrichia baliana* was originally considered to be closely allied to *Plethus* but was separated on account of the unmodified larval case (Ulmer, 1957); a close examination of the adult features, however, indicates that the two genera are synonymous. *Stactobia japonica* Iwata from Japan also resembles *Plethus* in the form of the larval case.

Generic diagnosis

Adult. Forewing length 1-2mm: head and thorax similar to those of *Stactobia* (c.f. fig. 12): spur formula 0.2.3: wing venation greatly reduced; veins of forewing confluent before margin; veins of hindwing reduced to the two main longitudinal subparallel stems of R and M; costal fringes well developed: o genitalia (fig. 43) simple, generalised without ventral processes; VIII unmodified; IX reduced ventrally although the sternite may be vestigial in some species, anterior apodemes short; inferior appendages unmodified; subgenital appendages heavily sclerotised, arched; tergite X variable; aedeagus long and straight without apical spines, sometimes with a pair of short basal processes: the anterior abdominal segments of the male may bear sensorial organs (Schmid, 1958) which, in *baliana*, occur on tergites V and VI according to Ulmer (1951).

Larva (fig. 78). Dorso-ventrally compressed; small abdominal tergites present, posterior margin of tergite IX simple; legs short, robust, subequal, unmodified; thoracic sternites as in fig. 126.

Case (fig. 78a). Dorso-ventrally compressed, barrel-shaped with dorsal and ventral seams and a lateral fringe ('wings').

According to Ulmer (1957) the larvae of Plethotrichia are more like those of Oeceotrichia (here synonymised with Hydroptila) in that they are not dorso-ventrally compressed, there are no abdominal tergites and the fore-tibia bears a short process. The case is of the purse-type, flattened laterally and constructed of secretion and diatoms. However, no pupae were collected to confirm the association of larvae and adults.

Biology. The larvae inhabit brooks amongst 'spongy algal masses' of Cladophora and 'siliceaceous' algae (Ulmer, 1957). According to Schmid (1958) the adults are abundant by streams, fast-flowing rivers and rocky streams and are not attracted to light. The larvae are not hygropetric although Schmid (1958) suspects that they lives amongst the rocks in shallow water. According to Ulmer (1957) the larvae of Plethotrichia live in flowing water, springs (including warm springs), waterfalls and brooks, often in moss and algae.

Discussion.

The adults of Plethus retain many primitive features of the generalised Stactobiine Hydroptilid, their main specialisations being their reduced size and wing venation and their abdominal sensorial organs (males). The larvae, although adapted to live in fast-flowing shallow water, are not as specialised as the petrimadicolous larvae of Stactobia. Plethus is essentially a warm-adapted genus confined to the Oriental region.

Plethus is most closely related to Stactobia and was probably an early offshoot of the Stactobia-group branch of the Stactobiini which has retained certain primitive attributes. Its main diagnostic features are the adult spur formula, overall reduced size and less specialised genitalia (i.e. with respect to *Stactobia*), larva and case.

Genus STACTOBIELLA Martynov (Tribe I. Group B)

Stactobiella Martynov, 1924: 57. Type-species, *Stactobia ulmeri* Siltala, by monotypy.

Tascobia Ross, 1944: 124. Type-species, *Stactobia palmata* Ross, by original designation. (Synonymised by Ross, 1944).

Distribution: Holarctic.

Stactobiella is a small Holarctic genus of six species, three of which are Palaearctic (northern and eastern Europe, Siberia) and three Nearctic which, according to Wiggins (in press), have been recorded over much of the American continent west to the Rocky Mountain states and north to Minnesota, Ontario and Maine. *S. risi* from Switzerland was first described in *Microptila* but was transferred to *Stactobiella* by Ulmer (1929); Döhler (1963) synonymised *risi* with *ulmeri* but the species were later considered to be distinct by Botosaneanu (1967) and are regarded as such here. Ross (1944) gives diagnostic characters for the males and females of *delira* and *palmata* and Ross (1948) gives a key to the males of all six species.

The species are grouped below according to features of the male genitalia.

1 *biramosa*-group: *biramosa* (Siberia, 'Russia'); *palmata* (Oklahoma, Wisconsin, Illinois, Kentucky, Maine, Tennessee, Oregon).

2 *ulmeri*-group: *ulmeri* (Finland, Germany, Poland, Rumania, U.S.S.R.); *risi* (Switzerland); *delira* (Wyoming, Colorado, Minnesota, Wisconsin, Maine, Kentucky, New Hampshire).

3 brustia (Wyoming).

Generic diagnosis

Adult. Forewing length 1.5-3.0mm: metascutellum narrow, as wide as metascutum (c.f. fig. 11): spur formula 1.3.4: ♂ genitalia (fig. 43) with segment VIII unmodified; IX well developed, especially dorsally, with long anterior apodemes; inferior appendages fused in brustia, sometimes with baso-dorsal bracteoles; subgenital plate strongly sclerotised, arched; tergite X absent or membranous; aedeagus (fig. 47a) simple, tubular, with fused lateral processes and a free median process in delira.

Larva (after Ross, 1944 and Wiggins, in press). Body slightly compressed laterally: abdomen without tergites (except on segment IX); dorsal abdominal 'rings' present (II-VIII): legs short, subequal, stout; tarsal claws distinct, sharply curved and with thickened basal spur nearly half as long as claw (fig. 97): setae unmodified: pre-episternite free on all thoracic segments, episternite and epimeron fused in meso- and metathorax.

Case (fig. 97). Purse-type, laterally compressed, constructed of silk only.

Biology. The larvae of palmata are found in small, fairly swift streams on stones in riffles and they mature in the early spring in Illinois (Ross, 1948). According to Wiggins (in press) it is therefore likely that this species overwinters as final-instar larvae.

Discussion

Adult features indicate that Stactobiella is related to Stactobia and Plethus although the metascutellum shows a close resemblance to that of Chrysotrichia, Parastactobia and Catoxyethira. The larvae, however, are unspecialised and exhibit the basic Hydroptilid form, the case being of the purse-type and laterally compressed. The genus thus appears to be an early offshoot of the Stactobiini which has retained many primitive larval and adult features . It is a temperate group which may have originated in the Palaearctic region and had at least two subsequent migrations into the Nearctic region (via the Bering route) as indicated by the relationships of delira with ulmeri and risi, and of palmata with biramosa. The affinities with the other genera of the Stactobiella-group will be discussed later.

Genus BREDINIA Flint (Tribe I. Group B)

Bredinia Flint, 1968c: 50. Type-species, Bredinia dominicensis Flint, by original designation.

Distribution: Lesser Antilles (Dominica).

The following diagnosis is adapted from the original description, the genus being known only from the type-series collected on Dominica in 1965. The larval stages are unknown.

Generic diagnosis

Adult. Forewing length 1.5mm: ocelli 3: mesoscutellum with transverse suture; metascutellum as wide as scutum, short and rectangular: spur formula 0.2.4: ♂ genitalia with sternite VIII divided midventrally; IX narrow, oblique, lateral halves divided ventrally by the inferior appendages and with long anterior apodemes; tergite X a large membranous lobe; inferior appendages small, quadrate; subgenital plate elongate, rectangular; aedeagus tubular, apex flat and tridentate, central tubule in apical quarter.

Biology. The adults were taken only near the larger lowland rivers of the island.

Discussion

Flint was uncertain of the relationships of this genus and placed it near *Neotrichia* due to the presence of ocelli, its minute size and the wing shape; near *Mayatrichia* by its spur formula and near *Alisotrichia* according to the transverse suture of the mesoscutellum and lateral apodemes of the male abdominal segment IX. However, although Flint noted the similarity of the shape of the thoracic nota of *Bredinia* to those of *Stactobiella*, he did not consider their possible relationships. In my opinion, from Flint's descriptions (1968c, 1970), *Bredinia* bears more resemblance to *Stactobiella* than to *Alisotrichia*, especially with regard to the thorax (c.f. figs 11, 14), the lateral apodemes of the male IXth segment and the tridentate aedeagus (figs 43, 47a-c c.f. 49b). The main distinction between *Bredinia* and *Stactobiella* is their spur formulae 0.2.4 and 1.2.4 respectively). As Flint rightly points out, however, the discovery of the larval stages is required to establish the true relationships of the genus.

Genus CHRYSOTRICHIA Schmid (Tribe I. Group B)

Chrysotrichia Schmid, 1958: 54. Type-species, *Chrysotrichia hatnagola* Schmid, by original designation.

Distribution: SE. Asia (Sri Lanka, India).

Five species described from Sri Lanka (Schmid, 1958) and India (Schmid, 1960) comprise this small SE. Asian genus. The immature stages are unknown but the adults appear to be closely allied to those of *Stactobiella* according to features of the head, thorax and male genitalia, although they may be distinguished by their distinctive spur formula and greatly reduced size and wing venation. The genera may prove to be synonymous but until more material, especially the larvae, can be examined they will be treated separately.The following generic diagnosis is based on original descriptions and examination of paratype material in the BMNH collections.

Generic diagnosis

Adult. Forewing length 1.25-1.50mm: head and thorax as in Stactobiella (fig. 11): ocelli 3 (N.B. absent according to Schmid, 1958): wings essentially reduced to thin 'ribbon-like' strips; venation represented by two main longitudinal veins only in the hindwings, veins of forewings reduced but not concurrent at the margin as in Plethus; costal fringes very long: spur formula 0.2.4: ♂ genitalia generalised as in Stactobiella and Plethus (fig. 43); segment VIII simple; IX reduced ventrally, anterior apodemes present; inferior appendages small; subgenital plate strongly sclerotised, arched; tergite X membranous; aedeagus (fig. 47b) long, simple, with a trilobate apex and sometimes with minute apical spines (as in hatnagola).

Biology. According to Schmid (1958) the adults occur along calm rivers at moderate altitudes. C. badhami from the Punjab was taken by a fairly large river rich in aquatic vegetation (Schmid, 1960).

Discussion

Schmid (1958) states that the male genitalia greatly resemble those of Plethus from which they may be distinguished by the small size and weak sclerotisation of the two terminal segments in comparison with the rest of the abdomen. The male genitalia are also similar to those of the ulmeri-group of Stactobiella; the diagnostic features at present used to distinguish this genus from Chrysotrichia (spur formula, wing size and venation) may not prove to be as critical as originally thought and the genera may prove to be synonymous.

Genus CATOXYETHIRA Ulmer (Tribe I. Group B)

Catoxyethira Ulmer, 1912b: 82. Type-species, *Catoxyethira* fasciata Ulmer, by monotypy.

Distribution: Africa.

Catoxyethira was erected for *fasciata* from Zaire by Ulmer (1912b) who described and figured the male genitalia and outlined the main features of the larva and case of an unidentified species (the generic identity of which is questionable since no positively determined adults were associated with it). *C. pinheyi* and *verxta* have since been described from the Victoria Falls and Rhodesia respectively and two new species (*ocellata* and *improcera*) are being described by Statzner (in press) from Zaire; undetermined material collected by Prof. J. Medler from Nigeria is in the BMNH collection.

Independently of Morse (1974) I noted the structural affinities of *Catoxyethira* adults with those of the Holarctic genus *Stactobiella* with regard to their spur formulae, thoracic nota and male genitalia; although the latter is very specialised in *Catoxyethira* it is derivable from the generalised Stactobiine form. As Morse points out, however, further studies are needed to clarify the taxonomic limits of the genera.

Hydroptila formosae Iwata (1928) from Taiwan (Formosa) was described from the larva and case only according to which Nielsen (1948) and Ulmer (1957: 186) suggested that the species might belong in *Catoxyethira*. However, neither Nielsen nor Ulmer formally transferred the species , this was done without reasoning by Fischer (1971) in his catalogue; thus the species remains in *Catoxyethira* until examination of additional material can establish its true identity.

The generic diagnosis is based on examination of the following material (all in BMNH collections except where stated otherwise):

fasciata (UHZIM); *pinheyi* (♂ type); paratypes of Statzner's new species; undetermined species (Medlar leg.).

Generic diagnosis

Adult. Forewing length 1.5mm: head and thorax as in *Stactobiella* (fig. 11): ocelli 3 (c.f. absent according to Ulmer, 1912b): spur formula 1.3.4 (c.f. 0.3.4 according to Ulmer, 1912b): ♂ genitalia (fig. 46) very specialised (main diagnostic feature of genus); VIIIth sternite elongate with a pair of posterior dorso-lateral spines; IX reduced, withdrawn into VIII, sternite may be present although small and fused with tergite, anterior apodemes narrow and produced beyond VIII; inferior appendages may be present (fused with tergite X in *veruta*); tergite X semimembranous in *veruta*, membranous and covered in microscopic setae in *pinheyi*; aedeagus long, straight, tapering to acute apex (fig. 47c); (the characteristic features of the male genitalia of *fasciata*, *pinheyi* and *veruta* are summarised by Morse, 1974).

Larva. Young larva 1.2mm long, Vth-instar 2.5mm. According to Ulmer (1912b) the larva is somewhat similar in appearance to that of *Stactobia* from which it may be distinguished by the absence of the posterior 'crenellations' of tergite IX (c.f. fig. 77a), the short spines of the posterior margin of tergite VIII and stout spines on tergites VIII and IX. According to Iwata (1928) *formosae* has sternites on on abdominal segments III-V which do not occur in the African species of *Catoxyethira* and appear to be unique for the Hydroptilidae as a whole.

Case (fig. 80). According to Ulmer (1912b) this resembles the 'shield-case' of *Molanna* Curtis (Molannidae: Trichoptera) as it is dorso-ventrally flattened and has a central tubular region from which arise the lateral 'wings'. The case, constructed of silk and fine sand-grains, tapers anteriorly and posteriorly and is attached to the substrate by the edges of the 'wings'.

Biology. Nothing is known of the biology of Catoxyethira but from the dorso-ventrally flattened larva and case and the latter being fixed it would seem likely that the larva lives in fast-flowing water habitats such as swift streams (somewhat stony ?). Ulmer's (1912b) specimens were taken from a tributary of the Butagu, Ruwenzori West (Zaire) at 1800m, February 1908; the adults of Statzner's (in press) two new species were from a 'spring-brook' community (Kalengo stream, Zaire) and the larvae of formosae were taken in 'rapid mountain streams'(Iwata, 1928).

Discussion

The form of the adult head and thorax indicate that Catoxyethira belongs to the Stactobiella-group of the Stactobiini. Discounting the dubious Taiwan species formosae, Catoxyethira appears to contain five exclusively African species which are characterised by the highly specialised and distinctive male genitalia. The uniqueness of the latter within the Stactobiella-group suggests that the ancestors of Catoxyethira reached Africa quite early in the history of the group and there evolved as a more tropical, warm-adapted line in isolation from the basic temperate stock. The recent discovery of a number of new species (all collected in considerable numbers) indicates that the genus is more widespread and successful than may have previously been thought.

Genus PARASTACTOBIA Schmid (Tribe I . Group B)

Parastactobia Schmid, 1958: 48. Type-species, Parastactobia talakalahena Schmid, by original designation.

Distribution: SE. Asia (Sri Lanka).

Parastactobia is known only from the type-species in which the male genitalia are unique and difficult to homologise with those of any other Hydroptilid. Examination of the female paratype (loaned by the USNM) has revealed that, contrary to Schmid's original description, 3 ocelli are present and that the thorax most closely resembles that of the Stactobiella-group (assuming that the female had correctly been associated with the male type). The immature stages are unknown.

Generic diagnosis

Adult. Forewing length 1.75-2.25mm: head and thorax as in Stactobiella (c.f. fig. 11): ocelli 3: spur formula 0.3.4: ♂ genitalia distinct (after Schmid, 1958); segment IX with a large ventral notch (in which sternite VIII is completely encased) and a long asymmetrical dorsal spine and two tapering ventral appendages; tergite X reduced; aedeagus large with paired internal supports and a very complex apex.

Biology. Schmid (1958) records the adults from beside a small, stony, fairly calm river in a dense forest in a small montane locality.

Discussion.

Little can be said regarding the relationships of Parastactobia until more adult (and larval) material is available for study. If the female paratype examined had been correctly associated with the male type then the genus would appear to be a highly specialised member of the Stactobiella-group (with respect to the male genitalia) as suggested by the structure of the head and thorax. I do not agree with Schmid (1958) that the male genitalia resemble those of Macrostactobia (q.v.).

Genus MADIOXYETHIRA Schmid (Tribe I. Group C)

Madioxyethira Schmid, 1960: 89. Type-species, *Madioxyethira milinda* Schmid, by original designation.

Distribution: SE. Asia (Pakistan, Nepal); Africa (Zaire, Congo).

Schmid erected this genus for the type-species from Pakistan; Kimmins (1964) described *nepalensis* from Nepal and Statzner (in press) is describing a new species from Zaire (*marshalli*)which, on my recommendation (on the basis of affinities of the metascutellum and the male and female genitalia), he has placed in *Madioxyethira*. The occurrence of the genus in the African continent is supported by my belief that *Hydroptila trifurcata* Jacquemart from the Congo should rightly belong in *Madioxyethira* according to the form of the male genitalia (however, the figures given by Jacquemart (1962) are not easy to compare with those of established species). The immature stages are unknown.

The following diagnosis is based on examination of the male type of *nepalensis* and a female paratype of Statzner's new species (BMNH coll.)

Generic diagnosis

Adult. Forewing length 2.25-3.25mm: head and prothorax typical of the Stactobiini although the metascutellum (fig. 13) is intermediate between those of *Stactobia* and *Stactobiella* (figs 11, 12) and the post-occipital lobes are characteristically narrow:ocelli 3: spur formula 1.2.4; fore-tibial spur reduced to a small subspherical process (diagnostic): ♀ genitalia a typical oviscapt but with a characteristic loop in the anterior duct of the internal system (fig. 64): ♂ genitalia highly modified and difficult to homologise (fig. 45); segment IX relatively small but produced anteriorly into the preceding segments as a long point; inferior appendages large, concave and ventrally prolonged as a long unique plate which terminates on sternite VII; segment X forming two lateral obtuse plates ('bourrelet bombé of Schmid, 1960) which Kimmins (1964) cosiders to be prolongations of tergite IX . (Kimmins also considers that the 'inferior appendages' may have arisen from the fusion of sternites VIII and IX and the true inferior appendages); The aedeagus is narrow and simple in *milinda* while in *nepalensis* it has a complex apex divided into two narrow foliate lobes with two narrow divergent spines (fig.47c).

Biology. According to Schmid (1960) *milinda* is common and abundant in parts of Pakiistan between 4800 and 10000ft and its habits are exclusively madicolous (although Schmid did not collect larvae).

Discussion

As will be shown later, *Madioxyethira* may prove to be synonymous with *Pseudoxyethira* Schmid and *Scelotrichia* Ulmer (in which case the last name takes priority). Schmid (1960) remarked on the possible synonymy of *Madioxyethira* and *Pseudoxyethira* since he could only distinguish these genera (apart from using genitalic features) on the venation of the hindwings especially with respect to vein SR.

Genus PSEUDOXYETHIRA Schmid (Tribe 3. Group C)

Pseudoxyethira Schmid, 1958: 4 4. Type-species, *Pseudoxyethira asgiriskanda* Schmid, by original designation.

Distribution: SE. Asia (Sri Lanka).

The adult stages only of this highly specialised genus, representedd by a single species from Sri Lanka, are known. Examination of a paratype female (USNM loan) reveals that the mesoscutellum and post-occipital lobes are identical to those of *Madioxyethira* (q.v.) (the loan was returned before the significance of the fore-tibial spur and genital-

[illegible]

duct loop were discovered and these were therefore not investigated).

Generic diagnosis

Adult. Forewing length 2.75-3.00mm: head and thorax as in *Madioxyethira* (fig. 13): ocelli 3: spur formula 0.2.4 (according to Schmid, 1958): ♂ genitalia very specialised with the ventral half of segment IX extending anteriorly as a plate to the middle of sternite VII, but not invaginated into the preceding segments; dorsal half of segment IX massive; appendages absent; aedeagus 'long and spiniferous' (fig. 47d).

Biology. According to Schmid (1958) the adults frequent rivers at moderate altitudes and also elevated regions ; they run about on rocks on the river banks.

Discussion

If, as Schmid (1960) suggests, this genus is synonymous with *Madioxyethira* (q.v.) the name *Pseudoxyethira* takes priority. However, this is complicated by the possibility that *Scelotrichia* (see below) may also be a synonym since this would take date precedence.

Genus SCELOTRICHIA Ulmer (Tribe I. Group C)

Scelotrichia Ulmer, 1951: 73. Type-species, *Scelotrichia saranganica* Ulmer, by original designation.

Distribution: Indonesia (Java).

Only two male specimens of the type-species of this genus are known. The type-specimen of *saranganica* (UHZIM loan) was examined but was not in a condition favourable for the recognition of critical features; however, the post-occipital lobes appeared to resemble those of *Madioxyethira* and the mesoscutellum had a transverse suture. The following diagnosis is partly adapted from Ulmer (1951).

Generic diagnosis

Adult. Forewing length 2.8mm: head as in *Madioxyethira* (fig. 13): thorax with transverse mesoscutellar suture (c.f. fig. 11): ocelli 3: spur formula 1.2.4, fore-tibial spur minute (Ulmer, 1951, pl.II, fig. 31 B & C): ♂ genitalia difficult to interpret from Ulmer's figures.

Discussion

According to features of the head and mesothorax, *Scelotrichia* is a member of the Stactobiini. The shape of the post-occipital lobes and the presence of a small fore-tibial spur (and also the general appearance of the male genitalia) indicate that the genus may be very close to, if not synonymous with, *Madioxyethira* and *Pseudoxyethira* (see above); in that case the senior name would be *Scelotrichia*. Further examination of material and discovery of the larval stages are required to establish the true identities of these genera.

DISCUSSION: THE TRIBE STACTOBIINI (I)

On the basis of adult and, to a lesser extent, larval affinities the genera of the Stactobiini as defined here appear to fall into three natural groups each with both generalised and highly specialised representatives of which the former exhibit the basic features by which the relationships of the three groups may be recognised.

The *Stactobia*-group is distinguished by the shape of the metascutellum and the general form of the larvae. *Plethus* would appear to be the most typical and generalised representative on account of the unmodified male genitalia, which is highly specialised in *Stactobia*, and the larvae which, although obviously adapted for life in running water are not, according to Schmid, as hygropetric in their habits as are those of *Stactobia* (Schmid, 1958). *Plethus* is restricted to the SE. Asian region while *Stactobia* appears to be a more successful group with a continuous recent temperate distribution in the Old World (also somwhat sub-tropical). The *Stactobia*-group appears to fill the Old World niche occupied by the Leucotrichiini in the New World (Tribe II). *Lemonganotrichia* is grouped with *Stactobia* and *Plethus* on the basis of larval affinities whereas *Plethotrichia*, although almost identical with *Plethus* in male genitalic features, most closely resembles *Stactobiella* in larval features; the latter may simply be due, however, to both these genera retaining the generalised Hydroptilid form.

The *Stactobiella*-group is characterised by the distinctive, narrow, strip-like form of the metascutellum of the adults. *Stactobiella* , *Brodinia* and *Chrysotrichia* have generalised male genitalia very similar to those of *Plethus*; *Catoxyethira* and *Parastactobia*, however both have very unusual, specialised genitalia. The group as a whole has a wide distribution with Palaearctic, Nearctic, Oriental and African representatives. Only the larval stages of two genera are known, *Stactobiella* from a single Nearctic species (which has the unmodified Hydroptilid form) and *Catoxyethira* from essentially an unidentified African species (which, according to Ulmer (1912b, 1957), resembles that of *Stactobia*). It may thus be that the larvae of *Stactobiella* (and *Plethotrichia*) have retained the basic Hydroptilid form while those of *Stactobia* (*Lemonganotrichia*), *Plethus* and *Catoxyethira* have become adapted and structurally modified for life in fast-running water conditions.

Madioxyethira, *Pseudoxyethira* and *Scelotrichia* are African and SE. Asian genera grouped according to the shape of the mesoscutellum, the reduced apical process of the fore-tibia, the shape of the post-occipital lobes and the unique forms of the male genitalia (and possibly also the genital-duct loop of the female). The larvae of these genera are completely unknown but they are included in the Stactobiini because of the form of the thorax, the short antennae and because the male genitalia may be derived from the basic Stactobiine form.

It would thus appear that the Stactobiini is essentially an early offshoot of the main Hydroptilinae branch with representatives which have become isolated in the now equatorial regions of Africa and SE. Asia while Stactobiella has a more northerly Holarctic distribution with local species in montane habitats extending from Central Europe to the eastern United States. The most successful and best represented genus is Stactobia which may result from its specialised larval habits; these may allow it to fill a unique niche with no competition from any other Palaearctic Hydroptilid. Stactobia also has a continuous Palaearctic distribution.

The Stactobiini may have arisen from originally 'cool-adapted', montane stream-dwelling ancestors which gave rise to two main lines, the first (1) becoming 'cool-temperate-adapted' while the second (2) became more 'warm-adapted'. Line 1 is the Stactobiella-group containing the 'cool-adapted' genus Stactobiella which has retained a northerly distribution and appears to have crossed (via the Bering route) down into the North American mountain chains of the western 'Rockies' and eastern Laurentians and Appalachians. From line 1 may have arisen a more 'temperate-adapted' line leading to the African and SE. Asian genera Chrysotrichia, Catoxyethira and Parastactobia. The North American

Stactobiella line may have given rise to (if it is not synonymous with) the Central American genus Bredinia.

Line 2, consisting of the Stactobia- and Madioxyethira-groups, became more 'warm-adapted' and probably had a past continuous distribution extending from Africa through North Africa, SW. Asia to SE. Asia at a time when these areas were linked by one great forest. When the climate became drier and severed the links between these two continents, representatives of these once widespread genera became isolated in the Oriental and African regions where the original conditions were (are) maintained. In the latter continent these areas occur in the forests surviving in western Africa, the mountain slopes of eastern Africa and along the rivers through to southern Africa which are precisely the regions from which these Hydroptilids have been recorddd, namely Nigeria and Zaire (compare also the distribution of Ugandatrichia, Tribe V). The most recent successful representative of line 2, Stactobia, now has a continuous sub-tropical Palaearctic distribution in the mountain ranges extending from eastern Asia (Japan) through Asia Minor, the Mediterranean region and North Africa out to the Atlantic Islands. Some species of the furcata-group have spread northwards up into the more temperate Central European regions while the vaillanti-group has been discovered in Africa (Guinea and Uganda).

In conclusion, the Stactobiini appears to have arisen from an ancestor which evolved early in the history of the Hydroptilinae. The tribe is quite distinct from any other belong to this subfamily and its possible relationships with the New World tribe Leucotrichiini will be discussed later (end of the account of Tribe II).

Tribe II LEUCOTRICHIINI Flint (stat. n.)

Leucotrichinae Flint, 1970: 2. Type-genus Leucotrichia Mosely. (Here amended to Leucotrichiinae).

Distribution: North, Central and South America.

Flint (1970) erected the subfamily Leucotrichiinae (as Leucotrichinae) for the distinct group of Nearctic and Neotropical Hydroptilids consisting of Leucotrichia and its closely related genera. Since the group has many of the characteristic features of the Hydroptilinae in general it is considered here at the status of tribe and will thus be referred to as the Leucotrichiini.

The tribe is predominantly of Central American distribution (including the West Indies) although a few species occur in North America while some are found as far south as Chile in South America; the latter continent is very under-collected and will undoubtedly yield many new species.

Flint (1970) stated that he could give no single character by which the group could be distinguished from other Hydroptilids in the adult stages but he did list the following as being diagnostic when present: ocelli reduced to 2; head modified; antennae modified; reflexed costal cell (basal costal 'pouch' or 'bulla') present on male forewing. Flint did not define the basic structure of the male genitalia although, in his words, 'there is....something characteristic' about their form. As will be shown in the diagnosis given below, the adults of the Leucotrichiini do posses a number of distinguishing features which clearly set the group apart from the other Hydroptiline tribes; the larvae (at least in those genera which are known) also appear to be very distinct due to their structural modifications associated with their torrenticolous habits. The following list of diagnostic adult and larval characters has been based on an examination of Mosely's type material (BMNH) and a study of Flint's papers on *Leucotrichia* and related genera (1970, 1972c, 1974).

The Leucotrichiini is considered to contain those genera originally included by Flint (1970), with the addition of *Celaenotrichia*, of which Flint considered *Alisotrichia* to be distinct according to features of the male aedeagus, the female genitalia and the larval stages. The tribe thus contains the *Leucotrichia*-group (A): *Leucotrichia*, *Zumatrichia*, *Peltopsyché*, *Anchitrichia*, *Costatrichia*, *Acostatrichia*, *Betrichia*, *Abtrichia* and *Celaenotrichia*, and the *Alisotrichia*-group (B): *Alisotrichia*.

Tribe diagnosis

Adult. Forewing length 1.2-4.0mm; wings* brilliantly coloured, sometimes spangled with green and silver; head and tentorium well developed, former often with modifications in the male; antennae generally short, of approximately 13-20 segments, male basal or median segments sometimes modified; ocelli 3, often reduced to 2 in the male (rarely also in the female): mesoscutellum with transverse suture; metascutellum pentagonal or subtriangular: spur formula 1.3.4 (except *Alisotrichia*, $0.^{2}/3.^{3}/4$): Vth abdominal segment with typical lateral setose processes: ♀ genitalia a simple oviscapt, internal apparatus well developed (in *Alisotrichia* segment VII is modified and the internal apparatus is simple and 'ring-like'): ♂ genitalia (fig. 49) often with ventral processes; sternite VIII distinct, produced posteriorly beneath segment IX, sometimes with postero-lateral processes;, segment IX fused, incomplete ventrally, sometimes with postero-lateral processes; inferior appendages narrow, short, rod-like, basically unmodified but sometimes fused medially and bearing baso-dorsal bracteoles; tergite X membranous or well sclerotised, fused latero-

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* the male forewing sometimes has a basal costal pouch (bulla) which may contain modified setae

N.B. p.188 placed after p.190.

sometimes bears enlarged spine-like setae; the anal prolegs are fused to the sides of segment X, the claws alone being free. The genus Alisotrichia is unique in that the Vth-instar larva does not construct a case until just prior to pupation. The larva accordingly retains the structural adaptations of the earlier stages (c.f. figs.82 and 132) with a slender, tapering abdomen, large abdominal tergites (i.e. relative to the size of the segments) and long, slender, freely projecting anal prolegs which are not fused to the sides of segment X.

Case (fig. 81b). The 'penny-wort' cases of the Leucotrichiini are also said to resemble leech egg-cases. They are strongly depressed dorso-ventrally and composed of tough secretion, rarely embedded with small inorganic particles, and sometimes with transverse strengthening ridges; the dorsal surface is slightly vaulted while the flat ventral surface is firmly attached to the substrate;there is a small circular openings at either end.

Pupa. Typically Hydroptilid: mandibles long, without teeth. The pupal case varies between genera and species but basically resembles the larval case with sealed anterior and posterior ends. In Alisotrichia hirudopsis, where the case is not built until just before pupation, the central ovoid region is surrounded by an irregular flange by which the case is attached to the substrate and which has two to six small round openings (possibly for water circulation according to Flint 1964d, 1970). In A.spangleri the pupal case is torpedo-shaped and is attached to the substrate from one end by a silk thread 2-8mm long (Flint, 1970); in this way the case floats freely just below the surface of the water and this may serve to prevent desiccation due to fluctuating water levels (Flint, 1970).

Biology. The larvae (early and Vth-instars) are adapted to live in torrenticolous conditions, usually being found in great numbers on boulders in the rapid sections of fast-flowing rivers. Some are also found in the thin surface films of water on partly exposed rock surfaces moistened by water from nearby cascades (which may be considered to be similar to the madicolous habitat of *Stactobia*). Structural modifications include dorso-ventral flattening, fixed cases, well developed and fused sclerites, protective spinose setae and short robust clinging legs.

The larvae are reported to feed on 'periphyton' and small particles of detritus on the surrounding rock surfaces. In the case-dwelling forms the larva extends its slender anterior end through either of the narrow case openings and grazes on the immediate surroundings. The larva never leaves the case and this, in the later stages of the instar, would be impossible anyway due to the distention of the middle abdominal segments. The retention of the free-living habit by the final instar of *Alisotrichia* may be an adaptation serving to increase the feeding range of the larva. In all genera the mandibles are adapted for scraping and grazing as they are strong with blade-like, sometimes dentate, edges.

The adaptation of the pupal case of *Alisotrichia spangleri* for the prevention of desiccation due to fluctuating water levels shows a remarkable parallelism with that of the larva of *Rhyacopsyche hageni* which also inhabits a torpedo-shaped case anchored by a thread to the substrate; however, in this species, the pupal case is fixed.

Adult Leucotrichiini are reported to be most active on the exposed parts of the rocks on which the larvae dwell. They prefer bright sunlight and congregate on the rock surfaces and run around often describing semicircular paths. Such habits are typical of Hydroptilids in general.

ventrally with the subgenital appendages which may be indistinct or developed as heavily sclerotised plates; latter fused ventrally with subgenital plate which may be produced ventrally and may articulate with an unidentified structure lying between the inferior appendages; aedeagus (fig. 49b) an elongate tube with a median constriction and (except in *Alisotrichia*) a complex medial structure consisting of a basal loop and a pair of basally directed processes, sometimes with a pair of circular 'windows' in lateral view, apex membranous with various spinose processes and lateral plates.

Larva (figs 81-84). Larvae have been associated with *Leucotrichia*, *Zumatrichia*, *Peltopsyche*, *Anchitrichia*, *Abtrichia* and *Alisotrichia*; they typically exhibit hypermetamorphosis (Flint, 1970), the early instars being entirely free-living and caseless. From a specimen of what would appear to be a young larva from a small collection of *Peltopsyche sieboldii* Müller (BMNH), the early stages are dorso-ventrally flattened with slender, tapering abdomens and short, robust clinging legs; there is a single tergite on each abdominal segment and the long, slender anal prolegs project laterally from the sides of segment X. In all genera (except *Alisotrichia*) the final (Vth) instar builds a permanently fixed case in which it remains throughout the stage. The Vth-instar exhibits structural modifications suiting it for such a sedentary existence in comparison with the earlier free-living stages: the body again is dorso-ventrally flattened; the ecdysial lines of the rugose or papillate head are variously fused, as are those of the meso- and metathoracic nota; the legs are short and robust; the abdomen is distended, especially segments V and VI which are abruptly enlarged, and small tergites are present on segments I-VIII while tergite IX is large, shield-shaped and

Genus LEUCOTRICHIA Mosely (Tribe II. Group A)

Leucotrichia Mosely, 1934a: 157. Type-species, *Leucotrichia melleopicta* Mosely, by original designation.

Distribution: North and Central America and the Antilles.

Leucotrichia contains ten species of predominantly Central American distribution although *sarita* and *limpia* have been recorded from the southern United States while *pictipes* is widespread throughout the U.S.A. although not so far recorded from Canada. The larva of *pictipes* was first described by Lloyd (1915)(as *Ithytrichia confusa*) and larvae have now been associated with all species except *melleopicta*, *viridis* and *fairchildi*.

Generic diagnosis

Adult. Forewing length 2-3mm: dorsal region of head sometimes modified; ocelli 3 or 2 (♂ only): metascutellum pentagonal: wings unmodified: spur formula 1.3.4: ♂ genitalia simple (fig. 49) with a single posterior spine or paired setal brushes on sternite VII; sternite VIII posteriorly produced beneath segment IX; IX completely open ventrally, postero-lateral margin with a row of stout setae; tergite X heavily sclerotised; subgenital plate connected dorsally to tergite X and produced ventrally as a narrow, elongate mesal sclerite which projects down to the base of the inferior appendages; subgenital appendages small, semimembranous; inferior appendages unmodified, elongate and usually fused meso-ventrally; aedeagus with median complex and spinous, membranous sac-like apex (fig. 49b).

Larva (fig. 81). Typical of the Leucotrichiini but with the following characteristics: head rugose or papillate; pronota with antero-lateral angles not produced; femora with spiniform dorsal setae, tarsal claw single; abdominal tergites II-VII smaller than in *Zumatrichia*.

without central pores; tergite IX rarely with enlarged basal setae (after Flint, 1970).

Case (fig. 81b). Typically flat, silken, ovoid and slightly domed.

Biology. According to Wiggins (in press) the larvae occur on rocks in strong currents of running water where they graze on the surrounding periphyton and detritus. Collection data indicate that *pictipes* probably overwinters as a final instar larva and pupates from May to August.

Species-groups. Flint (1970) splits the genus into two main species-groups on the basis of adult features:

1 the *melleopicta*-group is characterised by the 3 ocelli in both sexes, the unmodified male head (except in *chiriquiensis*) and the single process of sternite VII in the male.

2 the *pictipes*-group is distinguished by the males having only 2 ocelli, a modified head (except in *imitator*) and a brush of setae or a point on sternite VII.

Flint (1970) gives keys to the males of all species and to all described larvae.

Genus ZUMATRICHIA Mosely (Tribe II. Group A)

Zumatrichia Mosely, 1937: 187. Type-species, *Zumatrichia filosa* Mosely, by original designation.

Distribution: North and Central America and the Antilles.

Zumatrichia contains nineteen species of essentially Central American distribution although *notosa* is known from Montana only and was originally described in *Leucotrichia*. The immature stages are known only for *antilliensis*, *anomaloptera* and *multisetosa*.

Generic diagnosis

Adult. Forewing length 2.5-4.0 mm: head unmodified; ocelli 2 (♂), 3 (♀); male basal antennal segment elongate, enlarged, with a 'button-like' appendage which covers half of the slightly concave face (c.f.fig. 4): mesoscutellum pentagonal: wings unmodified: spur formula 1.3.4: ♂ genitalia with a short ventral process on sternite VII; sternite VIII produced beneath segment IX, sometimes with a pair of lateral processes; segment IX open ventrally with a postero-lateral lobe or process; tergite X heavily sclerotised and sometimes produced posteriorly; subgenital appendages large and plate-like, fused with subgenital plate ventro-medially; inferior appendages usually fused baso-medially and often with a baso-dorsal bracteole; aedeagus with median complex and membranous apex bearing spines and plates.

Larva (fig. 83). Typical of the Leucotrichiini but distinguished by the rugose, but non-papillate, head; simple pronota; femora with spiniform baso-dorsal setae (according to Wiggins, in press, paired tarsal claws are present in *antilliensis*); abdominal tergites larger than those of *Leucotrichia* and with paired contiguous central pores; tergite IX covered in short, stout, spinous setae.

Case. Typically flat, silken (sometimes with embedded sand-grains), ovoid and dome-like (c.f. fig. 81b).

Biology. Wiggins (in press) states that the larvae inhabit fast-flowing sections of running-water (preferring larger rivers according to Flint, 1968a). The larvae of *antilliensis* have successfully adapted to living on boulders in the fast-flowing sections of the larger lowland rivers of Dominica (Flint, 1968a).

Species-groups. Flint (1970) splits the genus into five species-groups (here reduced to four) on the basis of features of the male genitalia:

1 the *multisetosa*-group (lobe of segment IX multisetate)

2 the *galtena*-group (sternite VIII without lateral processes, bracteole present)

3 the *filosa*-group (sternite VIII with lateral processe,no bracteole)

4 the *palmara*-group (sternite VIII with lateral and ventral processes, bracteole present; Flint, 1970, distinguishes *anomaloptera* and *palmara* on the colour and structure of the forewing only)

Genus PELTOPSYCHE Müller (Tribe II. Group A)

Peltopsyche Müller, 1879b: 144. Type-species, *Peltopsyche sieboldii* Müller, by subsequent designation by Fischer, 1961.

Distribution: Brazil.

This genus is known only from descriptions and crude figures of two species collected by Müller from the Santa Catarina region of southern Brazil. Although Müller (1879a, 1879b, 1880) gave a general account of the habitat and adults he only figured the general larval form and the basal antennal segments of the males of both species. Thus, since Müller's original adult specimens have not been traced, the genitalia and, therefore, the true identities of the two species remain unknown. However, I have been able to examine larvae and cases of *sieboldii* which were sent to McLachlan by Müller and are now in the BMNH collection.

The actual spelling of the name of the type-species is in need of clarification. Müller continually used *sieboldii* except in a communication to McLachlan which was published in the Proceedings of the Royal Entomological Society (Müller, 1879a) where he used *sieboldi*. *P.sieboldi* was used by Ulmer (1907) and Fischer (1961) lists the species under this name with all of Müller's references to *sieboldii* being treated as synonyms even though Fischer was aware that *sieboldii* was the first published name. I propose to accept Müller's original orthography and suggest that Fischer's (1961) catalogue and all subsequent references amend the name to *sieboldii*.

The following diagnosis is based on Müller's original descriptions with additional observations on the larvae in the BMNH collection. The genus is clearly a member of the Leucotrichiini according to the general appearance of the larvae and the modified male antennae.

Generic diagnosis

Adult. According to Müller the adults are distinguished by the modified basal segments of the male antennae (13-segmented, longer in the female). In *maclachlani* the second segment is merely somewhat longer and wider than the others, but in *sieboldii* this segment is enlarged, ovoid and bears a small, rounded process as in *Zumatrichia*. Müller suggests that these structures may have an 'odoriferous' function. The spur formula is quoted as 2.4.4 but this may be an error, the usual Leucotrichiine count being 1.3.4.

Larva (fig. 84). According to Müller's descriptions and figures the abdomen of the larva is greatly distended in segments V-VII and fills nearly the entire case (c.f. figs 81, 83) and is thus typical of the Leucotrichiini. Examination of the BMNH specimens of *sieboldii* (dried and originally glued to card) reveals that the general morphology is very similar to that of *Zumatrichia* with respect to the head, legs, thoracic nota, wide abdominal tergites (with their paired contiguous central pores) and the short, stout spines of segment IX; unlike Z. antilliensis, however, (according to Wiggins, in press) the tarsal claws are unpaired.

Case. This is identical to that of Leucotrichia being ovoid and flattened ('penny-wort' case); the dorsal surface is transversely ridged in sieboldii and smooth in maclachlani.

Pupa. According to Müller this is remarkable for the unusually great difference in the 'complicated corneus patches dorsally on the abdomen' between the two species. He is probably referring to the pre- and postsegmental dorsal abdominal plates but since Müller does not describe the specific differences I cannot comment on their significance.

Biology. The cases were found in very large numbers fixed to the upper side of stones in rapids in the larger tributaries of the Itahajy (Garcia, Encana, Warnow etc), Santa Catarina. P. maclachlani was only found in a single rapid near the mouth of the Warnow along with sieboldii.

Discussion

Peltopsyche may prove to be a senior synonym of one or more genera of the Leucotrichiini described subsequently by Mosely and Flint. (See later discussion).

Since Müller obviously encountered what he identified as sieboldii in a number of localities more than one species may be involved; this problem will only be resolved when Müller's original material is located and examined. There has been no response so far to my requests for information regarding the whereabouts of this material.

Genus ANCHITRICHIA Flint (Tribe II. Group A)

Anchitrichia Flint, 1970: 14. Type-species, Anchitrichia spangleri Flint, by original designation.

Distribution: Central America (Mexico, Guatemala, Honduras, Costa Rica, Panama).

This genus contains only the type-species and is very closely related to Zumatrichia from which it is distinguished by a number of adult features including its relatively larger size (4-5mm forewing length), its habit of holding its wings roof-like over the body, the unmodified antennae, the presence of 2 ocelli in both sexes, and the general form of the male genitalia. The larva, described by Flint (1970), was not reared but associated 'by supposition' and is distinguished by the bilobed anterior margin and postero-medial process of the fronto-clypeus, the enlarged antero-lateral angles of the pronota, the arborescent baso-dorsal seta of the femur and the form of the abdominal tergites. The larval case is typical of the Leucotrichiini but has an enlarged, transversely oval, protective hood at one end and a flared collar at the other. The pupal case is unique in that it is quite unlke that of the larva being torpedo-shaped and attached at one end to the substrate by a silk strand 2-8mm long. In this way the case floats just below the surface of the water and may be an adaptation to prevent desiccation due to fluctuating water levels.

The true status of Anchitrichia has yet to be established; the examination of more species is required to define the limits of the genus. It may prove to be synonymous with one or more of the other Leucotrichiine genera.

Genus COSTATRICHIA Mosely (Tribe II. Group A)

Costatrichia Mosely, 1937: 166. Type-species, Costatrichia lodora Mosely, by original designation.

Distribution: Central America.

Costatrichia was erected for a single Mexican species and now contains three additional species from Panama (Flint, 1967a, 1970), one from Nicaragua and one from El Salvador (Flint, 1970). The immature stages are unknown.

Generic diagnosis

Adult. Forewing length 2.0-2.5mm; head unmodified; ocelli 3; basal antennal segments simple, middle segments sometimes broad and flat (fig. 5): metascutellum subtriangular: forewing often with basal costal 'bulla' (fig. 35): spur formula 1.3.4: ♂ genitalia with lateral processes often on sternite VIII; segment IX with setose postero-lateral processes; tergite X strongly sclerotised and fused with segment IX; subgenital appendages elongate, separate, often with baso-dorsal bracteoles; aedeagus with median complex and spinose membranous apex.

Species-groups

Flint (1970) splits the genus into two distinct species-groups on the basis of features of the male genitalia, head and wings:

1 the simplex-group (simplex, spinifera): unmodified antennae, no basal costal bulla.

2 the lodora-group (lodora, panamensis, tripartita, bipartita): modified antennae, basal costal bulla present.

Flint (1970) gives a key to separate the males of all six species. He distinguishes the genus from Zumatrichia by the presence of 3 ocelli and the unmodified basal segments, but sometimes modified middle segments, of the male antennae.

Genus ACOSTATRICHIA Mosely (Tribe II. Group A)

Acostatrichia Mosely, 1939d: 228. Type-species, *Acostatrichia plaumanni* by original designation.

Distribution: South America (Brazil, Surinam)

Mosely erected this genus for two south Brazilian species, *plaumanni* and *simulans*, and Flint (1974) later described three new species from Surinam. The immature stages are unknown.

Generic diagnosis

Adult. Forewing length 2.0-2.5mm: head unmodified; ocelli 3; antennae unmodified; forewing with basal costal pouch (c.f. fig. 34) filled with broadened hairs: spur formula 1.3.4: ♂ genitalia usually with two short ventral processes on segment VII; sternite VIII with postero-lateral processes; inferior appendages sometimes with bracteoles; aedeagus with median complex and spinose membranous apex.

Discussion

The three Surinamese species are said by Flint (1974) to resemble the two original Mosely species although the basic form of the male genitalia is slightly different (but not enough to warrant the erection of a new genus). According to Flint, *fimbriata* is closest to *brevipenis*, while *spinifera* resembles *simulans* and *plaumanni*. As Mosely (1939a) points out, the genus is closely relatedto *Costatrichia* Mosely, differing only in features of wing venation and in having unmodified antennae but, again as noted by Mosely, these may be specific rather than generic characteristics (see later discussion). The larvae will probably prove to be of the general *Leucotrichia* type, as will those of *Costatrichia*.

Genus BETRICHIA Mosely (Tribe II. Group A)

Betrichia Mosely, 1939d: 230. Type-species, Betrichia zilbra Mosely, by original designation.

Distribution: South America (Brazil, Argentina).

Erected for a single Brazilian species, this genus now also contains argentinica from north Argentina and surinamensis, bispinosa and occidentalis from Surinam (Flint, 1972c, 1974).

Mosely gives no precise reasons for erecting this genus but it may be assumed that it was mainly on account of venational and antennal features as well as the general form of the male genitalia; in the male type-specimen (BMNH) there are 2 ocelli, the antennae are 19-jointed with an elongate basal segment. Flint (1972c) places argentinica in this genus on genitalic features alone although there are 3 ocelli and the antennae are simple. Of Flint's (1974) Surinamese species only occidentalis resembles the type-species while in surinamensis the head is greatly modified and the genitalia are quite different; in bispinosa, although the genitalia resemble those of zilbra, the forewing has a basal costal pouch. Flint (1974) states that 'he would prefer to wait until the South American fauna is better known .....before erecting more genera' but I am of the opinion that all the small Leucotrichiine genera, such as Betrichia, Costatrichia and Acostatrichia for example, should be grouped together as the characters originally given as diagnostic generic features are now proving to be specific instead; this, however, will be discussed more fully later. As such no precise diagnosis of the genus Bredinia can be given; only the main features are listed below. The immature stages are unknown.

Generic diagnosis

Adult. Forewing length 2-4mm: head and antennae slightly modified or simple; ocelli 2 or 3: forewing with or without basal costal pouch: spur formula 1.3.4: ♂ genitalia with a process on sternite VII; sternite VIII usually without postero-lateral processes: segment IX with or without postero-lateral processes; inferior appendages fused medially; tergite X and subgenital plate variable; aedeagus with median complex and spinose membranous apex.

Discussion

As is evident from the above account this genus is very difficult to key out satisfactorily. As with a number of other genera in the Leucotrichiini all species descriptions must be referred to before a specimen suspected of belonging to *Betrichia* can be positively identified.

Genus ABTRICHIA Mosely (Tribe II. Group A)

Abtrichia Mosely, 1939a: 244. Type-species, *Abtrichia antennata* Mosely, by original designation.

Distribution: South America (Brazil, Argentina).

Abtrichia was erected for two very distinct species from southern Brazil, *antennata* and *squamosa*, of which the former has since been recorded, along with its immature stages, from northern Argentina by Flint (1972c). *Abtrichia* is characterised by the highly modified head of the male with the enlarged, process-bearing, basal antennal segment (fig. 4) and the large basal costal pouches of the male forewings which contain small scales or coarse hairs (fig. 34). According to Flint (1972c) the larvae bear most resemblance to those of *Zumatrichia* antilliensis, differing only in having a papillate dorsal head surface.

Generic diagnosis

Adult. Forewing length 4mm: head of male modified with dorsal and ventral anterior beak-like processes (fig. 4); ocelli 2 (both sexes); antennae 12-jointed in the male with an enlarged, process-bearing, basal segment (fig. 4): forewing with costal pouch along basal half (fig. 34): spur formula 1.3.4: ♂ genitalia with a short process on sternite VII; sternite VIII and segment IX without postero-lateral processes; subgenital appendages well developed; inferior appendages distinct, with or without bracteoles; aedeagus with median complex and spinose membranous apex.

Larva and case typical of the Leucotrichia-group.

Biology. According to Flint (1972c) the cases are tightly attached to rocks in riffles.

Genus CELAENOTRICHIA Mosely (Tribe II. Group A)

Celaenotrichia Mosely, 1934a: 158. Type-species Celaenotrichia edwardsi Mosely, by original designation.

Distribution: South America (Chile).

C. edwardsi was originally described from Chiloe Island and Flint and Barria have since collected additional specimens (USNM) of which I have examined a female example. From the adult features the genus appears to belong in the Leucotrichiini; it is characterised by the unmodified antennae and forewings and the distinctive genitalia of the male. The immaturecstages are unknown.

Generic diagnosis

Adult. Forewing length 3mm: head and antennae simple, latter

26-segmented; ocelli 3: forewings unmodified: mesoscutellum with transverse suture; metascutellum pentagonal: spur formula 1.3.4: ♂ genitalia relatively simple with a process on sternite VII; sternite VIII produced postero-ventrally, without postero-lateral processes; segment IX open ventrally with deep postero-dorsal V-shaped cleft enclosing the membranous Xth tergite which has two narrow longitudinal supporting sclerites; subgenital appendages heavily sclerotised and spinose; subgenital plate well developed; inferior appendages curved inwards, without bracteoles; aedeagus appears to have a median complex (microscope slide preparation of the type-specimen (BMNH) indistinct here), apex membranous and spinose.

Genus ALISOTRICHIA Flint (Tribe II. Group B)

Alisotrichia Flint, 1964: 46. Type-species, *Alisotrichia hirudopsis* Flint, by original designation.

Distribution: Central America (including the Antilles).

Alisotrichia contains thirteen species, three of which are also known in their larval stages, and is a member of the Leucotrichiini but forms a distinct subgroup according to both adult and larval features. The insects are very small and, although adult characters are somewhat variable, constant diagnostic features include the absence of a fore-tibial spur, the simplified aedeagus and modified VIIth tergite of the male and the simple internal apparatus of the female genitalia. The larvae are unique in that the Vth-instars remain free-living until pupation and thus retain the general appearance of the earlier instars of this and other Leucotrichiine genera. The following diagnosis is adapted from Flint (1970).

Generic diagnosis

Adult. Forewing length 1.2-2.5mm: basal antennal segment of male often enlarged; ocelli 2 or 3: metascutellum pentagonal to subtriangular: spur formula 0.2.4, 0.2.3 or 0.3.4: ♀ genitalia simple, tergite VII modified (no details or figures given), internal apparatus with a simple ring or sphere: ♂ genitalia with sternite VIII and segment IX often with postero-lateral processes; inferior appendages, tergite X, subgenital appendages and plate very variable and difficult to interpret; aedeagus simple with a median constriction and a simple to complex internal structure but never with a midlength complex (basal loop, 'windows', etc).

Larva (fig. 82). Abdomen not distended, tapering posteriorly; tergites I-VIII covering most of dorsum of each segment and each with three contiguous central pores, tergite IX shield-shaped without pores; anal prolegs long, projecting freely from segment X.

Pupal case (after Flint, 1964, for *hirudopsis*). This is built just prior to pupation and is similar to the typical Leucotrichiine larval and pupal case being silken, dorso-ventrally flattened, with an ovoid central region containing the pupa surrounded by an irregular flange which attaches the case to the substrate and has two to six small round openings (for water circulation ?(Flint, 1964))

Biology. The larvae of *hirudopsis* are found on rocks in fast-flowing water at various altitudes and occur abundantly on exposed boulders kept wet by the spray from nearby cascades. The adults are also abundant and run about in the sunlight on the dry exposed parts of the rocks on which the larvae live.

Species-groups

Flint (1970) splits the genus into several groups of species on the basis of adult characters such as the number of ocelli, spur formula and antennal modifications. However, as Flint does not define the groups clearly, I have not discussed them here.

Discussion

The Vth-instar larva of Alisotrichia conforms to the basic Leucotrichiine plan but retains the free-living adaptations of the earlier instars; on the basis of this and the characteristic adult features this genus would appear to be a specialised and distinct member of the Leucotrichiini and is placed here in its own subgroup.

DISCUSSION THE TRIBE LEUCOTRICHIINI (II)

As can be seen from the generic key (see Appendix, section VIIIB) in couplets 15 to 19, it has not been possible to define the genera of the Leucotrichiini satisfactorily; species from two or more genera often key out with one another (e.g. Abtrichia and Betrichia; Costatrichia partim., Betrichia partim., Leucotrichia partim. and Celaenotrichia). Flint (e.g. 1972c, 1974) appears to be very inconsistent in his choice of criteria when assigning new Neotropical species to genera, using features of the head, antennae and wings in some cases and genitalic features in others. Genera were originally erected on the basis of certain (then apparently distinctive) characters common to a group of species from a particular geographical area but, as new species have been discovered from other areas, the generic limits do not appear to be so clear-cut. The larval generic key (see Appendix, section VIIIB) is also very unsatisfactory at present since it is based on only a few species of each genus (only one in some cases and, in Anchitrichia, association with adults is purely assumptive). The tribe is thus in need of a thorough review which, however, would probably best be done by American workers due to the location of most of the material.

In general, however, the Leucotrichiini appears to form a distinct group within the Hydroptilinae and is characterised by a number of both adult and larval features. The origins of the tribe are speculative but the ancestral form appears to have given rise to a very diverse, but specialised, group with an essentially Central American distribution where, in general, the ecological conditions favour short generation cycles resulting in high speciation rates.

The tribe has greatest superficial affinities with the essentially Old World Stactobiini, particularly the Stactobia-group, with respect to the short antennae, the transverse mesoscutellar suture (c.f.figs 11, 14) and the simple basic form of the male genitalia (c.f. figs 43, 49) of the adults and the dorso-ventral-flattening, clinging legs, protective abdominal tergites, modified setae and fixed cases of the larvae (c.f. figs 77, 78, 81, 82, 83). However, the larval similarities between the Leucotrichiini and the Stactobia-group are probably due to their comparable madicolous habits since they are all functional and protective adaptations to living in this type of aquatic habitat and are also seen in a number of quite unrelated insect groups (see Hynes, 1970 and Vaillant, 1956). The larvae of the two tribes may be distinguished by certain fundamental differences in, for example, the form of the head, the complete fusion of all thoracic nota (i.e. medianly) and the characteristic enlargement of the abdomen in the Leucotrichiini; the cases of the Leucotrichiini do not have dorsal and ventral seams and are of a different shape. The adults differ in the shape of the metascutellum, the reduced spur formula of the Stactobiini and the different modifications of the male genitalia.

Nevertheless, the Leucotrichiini and the Stactobiini do appear to have more in common with one another than with any other group of Hydroptilids and may have arisen from a common ancestor very early in the evolutionary history of the Hydroptilinae. This common ancestor may have arisen in the Old World toperate region and given rise to two main lines, one of which colonised the cool, montane streams of the Palaearctic and Palaeotropical regions (the present day Stactobiini) and the other which penetrated the American continent (probably via the Bering connection) and passed down to the Central American region where the descendants of these early arrivals into the highly succesful Neotropical Leucotrichiini.

However, this hypothesis is very tentative and further evidence from new species and distribution records is required in order to present a more accurate picture of the evolutionary history of the Leucotrichiini. The tribe may prove to be more distantly related to the Stactobiini than indicated above, the morphological similarities being the result of convergent rather than parallel evolution. In conclusion the Leucotrichiini is a very specialised and successful member of the Hydroptilinae which has a predominantly Central American distribution and may share a common ancestry with the Stactobiini.

Tribe III OCHROTRICHIINI (trib. n.)

Type-genus, Ochrotrichia Mosely, 1934a.

Distribution: North and Central America.

The tribe Ochrotrichiini is proposed here for the small group of Nearctic and Neotropical Hydroptilids composed of Ochrotrichia (O. Ochrotrichia and O. Metrichia) and Rhyacopsyche. As will be discussed in more detail below, Metrichia was reduced to a subgenus of Ochrotrichia by Flint (1972b) on the basis of larval affinities, Flint (1971a) having previously indicated the relationships of the adults of Metrichia and Rhyacopsyche. Although I have not been able to investigate these relationships, I propose for the present to accept Flint's views and, as the group exhibits a number of characteristic adult features which distinguish it from the other Hydroptiline groups, to assign it the provisional status of tribe. However, I am not totally satisfied with this arrangement and the group may subsequently prove to be a subgroup of the tribe Hydroptilini (V). This will be discussed in more detail at the end of the Ochrotrichiini section.

Genus OCHROTRICHIA Mosely (Tribe III)

Polytrichia Sibley, 1926: 102. Type-species, Ithytrichia confusa Morton, by monotypy. (Preoccupied by Polytrichia Borg de St. Vincent, 1831 in Protozoa).

Ochrotrichia Mosely, 1934a: 162. Type-species, Ochrotrichia insularis Mosely, by original designation. (Synonymised by Mosely, 1937 and reinstated by Ross, 1944).

Distribution: Nearctic.

The genus Ochrotrichia has recently been reviewed by Denning &

Blickle (1972) who give a list of the 40 known species with descriptions of 15 additional new species from the western United States and Mexico. In the same year Flint (1972b) published a paper on 'The genus *Ochrotrichia* from Mexico and Central America (Trichoptera: Hydroptilidae)' in which he described a number of new species and proposed *Metrichia* as a subgenus of *Ochrotrichia* , and *Rhyacopsyche* Müller as a close, but distinct, relative. Flint (1968b) had already stated these views regarding the congenericity of *Metrichia* and *Ochrotrichia* but they were not accepted by Denning & Blickle (1972). As I have not been able to investigate this matter due to the paucity of representative material in the BMNH collections, I can only stress the need for a thorough review of the group to establish the true relationships of the genera concerned, not only with one another but also within the Hydroptilinae.

Generic diagnosis (*Ochrotrichia* sensu Flint, 1972b)

Adult. Forewing length 1.5-3.0mm: head unmodified (fig. 18); tentorium complete; antennae simple (c. 33-segmented in *insularis*); ocelli 3; post-occipital lobes small, subspherical: mesoscutellum (fig. 18) with transverse suture; metascutellum convexly subtriangular: spur formula 0.3.4 or 1.3.4: abdomen with typical Hydroptiline setate processes of segment V: ♀ genitalia a simple oviscapt; internal surface of sternite VIII often sclerotised and reticulate in *Ochrotrichia* (*Metrichia* not described): ♂ genitalia distinct (fig. 48) with segment VIII unmodified; segment IX fused, annular, deeply incised dorsally; tergite X often highly developed with numerous spines and processes; inferior appendages usually strongly developed, basically broad and elongate, usually with various processes and rows of spines; aedeagus simple, threadlike (*Ochrotrichia*) sometimes armed with strong spines (*Metrichia*).

Larva (fig. 85) after Flint (1972b). General appearance typical of basic, unspecialised Hydroptilid: head unmodified; labrum symmetrical, mandibles robust, broadly subtriangular, medial brush in left only: three pairs of thoracic nota, each with distinct median longitudinal line, meso- and metanota with pronounced antero-dorsal processes; prothorax with a pair of anal sternites (fig. 127, after Wiggins, in press); pleurites well developed (at least in prothorax): abdomen similar to that of Hydroptila (c.f. fig. 90) being slightly distended and laterally compressed; abdominal tergites absent except on segment IX; dorsal 'rings' present; anal prolegs fused to sides of segment X.

Case. Similar to that of Hydroptila; constructed of two laterally compressed silken valves, 'purse-type', covered in fine sand-grains and, occasionally, filamentous algae (Wiggins, in press); sometimes the case consists of a single dorsal convex valve carried 'tortoise-shell' like, the ventral valve being flat and of secretion only.

Pupa. No description available, but probably typically Hydroptiline with long, untoothed mandibles.

Biology. The larvae occur in a wide variety of running water habitats (rivers to warm streams and cold springs) and temporary streams according to Ross (1944); the specimens with cases carried 'tortoise-shell' like were from a spring stream on rocks in a thin film of water; the feeding habits are unknown but possibly the larvae are detriphagous.

Key to Subgenera (adults) - adapted from Flint (1972b)

1 Spur formula 0.3.4; male inferior appendages and Xth tergite complex, aedeagus simple and threadlike.....Ochrotrichia

- Spur formula 1.3.4; male inferior appendages and Xth tergite simple, aedeagus with well developed spines.....Metrichia

Subgenus OCHROTRICHIA Mosely (Tribe III)

This subgenus is distributed throughout North America, with a few species recorded from southern Canada, Panama and the Antilles, although the group appears to be predominant in the midwest and montane regions of the United States. There are about 70 species which Flint (1972b) splits into two distinct groups (for the Central American species only). The *xena*-group is characterised by the simple IXth segment, the relatively simple tergite X and the aedeagus which varies from a simple tube to one which bears various processes (not as well developed as in *Metrichia*); this appears to be the simpler of the two groups with respect to the structure of the male genitalia and seems to be intermediate between the next group and *Metrichia*; it contains *xena*, *unio*, *flagellata*, *pectinata*, *brayi*, *caligula*, *marica*, *spinosissima* and *verda*. The second group consists of all other Central American and Antillean species which Flint (1972b) further splits into six subgroups; the group is characterised by the fusion of tergites IX and X to form a complex structure bearing many spines and plates (fig. 48b, terminology after Ross, 1944) and the very simple, thread-like aedeagus. A key to the males of the Central American species is given by Flint (1972b).

Larvae have been associated with the following: *anisca*, *riesi*, *spinosa*, *tarsalis*, *unio* and *xena*, a key to which is given by Ross (1944).

According to Flint (1972b) the larvae of this subgenus are found in running water, usually in small to moderately sized streams, sometimes in very shallow water and often in streams that dry up during the dry season. Flint also remarks that the adults come readily to light.

Subgenus METRICHIA Ross (Tribe III)

Metrichia Ross, 1938: 9. Type-species, *Orthotrichia nigritta* Banks, by monotypy.

** *Metrichia* was reduced to a subgenus of *Ochrotrichia* by Flint (1972b) mainly on the basis of the inseparability of the larval stages. This subgenus has a more southerly distribution than *Ochrotrichia*, occuring in the south-west United States, throughout Central America and the Antilles, Peru, north-west Argentina, central Chile and Surinam. According to Flint (1972b) the area of greatest diversity occurs throughout Central America and the Antilles. There are 18 distinct species of which Flint (1972b) splits the Central American representatives into five groups on the basis of the presence and positioning of the internal abdominal sacs of the males (between IV-V, V-VI or VI-VII), the dorso-lateral hair brushes (segments V and VI) and the structure of the aedeagus. Flint also gives a key to the Central American species (males).

Larvae have been associated with *nigritta* by Edwards & Arnold (1961) and *juana* by Flint (1968a). According to Flint (1972b) the larvae build purse-type cases of silk and organic particles. On the basis of features of the two known species Flint concludes that the subgenus appears to be closely associated with springs, seeps, waterfalls and the like (rather than the larger, relativly more slowly-flowing streams preferred by *O. Ochrotrichia*). Flint also states that the adults are more frequently taken by sweeping vegetation than at light.

Flint, following Schmid (1958) considers *Metrichia* to be most closely related to the Palaearctic genus *Microptila* (sensu Schmid, *vide*

** *Argentitrichia* Jacquemart, 1963d. Type-species, *Argentitrichia bulbosa* Jacquemart, by monotypy. (Syn. n.).

Tribe V, Agraylea-group) on the basis of the form of the male genitalia and wing venation, and recognises the possibility that Microptila may eventually come to be considered as a third subgenus of Ochrotrichia. As will be seen in the account of Microptila (tribe V, group A) I consider Metrichia to be very distantly removed from Microptila, these conclusions being based on a comparative study of features of the head, thorax and male genitalia of the two groups.

Finally, Argentitrichia bulbosa, described by Jacquemart (1963d) from the Argentine, appears to me to be a species of Metrichia by the characteristic form of the male genitalia (material not examined).

Genus RHYACOPSYCHE Müller (Tribe III)

Rhyacopsyche Müller, 1879: 40. Type-species, Rhyacopsyche hagenii
Müller, by monotypy.

Distribution: Central America.

Müller (1879) erected Rhyacopsyche for a single Brazilian species, which he subsequently (1879b) named hagenii, on the basis of the larval cases only. Figures and full descriptions of the larval and pupal cases were not published until 1880 by Müller, the first descriptions of the adults and larvae being given by Thienemann (1905) and Müller (1921) who subsequently reproduced a previously unpublished figure (by Müller) of the general appearance of the larva.

Flint (1971a) describes why, following his discovery of immature and adult stages of Metrichia mexicana in Guatemala (first described from Mexico by Flint, 1967a), he considers this species to be congeneric with Rhyacopsyche hagenii (not hageni as in Flint, 1971a). Consequently Flint (1971a) described the genus Rhyacopsyche and gave a key to the males of mexicana and three new species.

Generic diagnosis (after Flint, 1971a)

Adult. Forewing length 2.5-3.5mm: head and antennae simple; ocelli 3: mesoscutellum with transverse suture (c.f. fig. 18); metascutellum pentagonal: spur formula 1.3.4: ♀ genitalia an oviscapt, tergite VIII with posterior lobes: ♂ genitalia with segment VIII unmodified; IX produced into dorso-lateral lobes; tergite X contracted inside lobes of IX; inferior appendages large and distinct, elongate and curved upwards; single, reduced, median subgenital sclerite; aedeagus with tubular basal half, apical half with central tube and thin spiral filament, apex with thickened spine.

Larva (fig. 86a). Typically Hydroptilid with thoracic nota present on all three segments, divided medially; sternites apparently absent; legs short, subequal, apex of fore-tibia with a distinct process-bearing several enlarged setae, tarsus short with one or two enlarged plate-like setae (fig. 86b): abdomen distended, slightly compressed, tergites absent, anal prolegs fused to segment X.

Case (fig. 86a). Larval case elongate, tubular, tapering anteriorly and posteriorly; silken, covered in sand-grains (mexicana); of secretion only (hagenii) and attached to substrate by a long silken thread. Pupal case of mexicana apparently split along posterior end according to the figure in Flint (1971a) but this may have been drawn after emergence of the adult; pupal cases of both mexicana and hagenii anchored by a short silken stalk.

Biology. The larvae and pupae of mexicana were found on an exposed boulder subjected to constant wetting from spray and a thin film of water r unning down from a nearby cascade. The pupal cases were attached at right angles to the boulder on the moist, but not submerged, surfaces. According to Flint (1971a) the larval cases of *mexicana*, unlike those of *hagenii*, are not attached by a thread to the substrate until just prior to pupation.

Discussion

According to Flint (1971a) the adults of *Rhyacopsyche* may be distinguished from those of *Metrichia* only by the form of the male and female genitalia (the lobes of segment IX and the relatively simple aedeagus of the male and the lobes of tergite VIII of the female in *Rhyacopsyche*) The larvae of *Rhyacopsyche* are, according to Flint (1971a), very similar to those of *Ochrotrichia* s.l. and *Hydroptila*, being distinguished by the plate-like setae of the fore-tibia and the hook-like tarsal claws. The larval and pupal cases are, however, so far unique to *Rhyacopsyche* and are probably adapted to torrenticolous conditions being fusiform in shape and anchored by a silk thread to the substrate.

The morphology of the larva has not been described in sufficient detail to allow a deeper investigation into the generic relationships of *Rhyacopsyche* but adult features suggest that the genus is closely allied to *Ochrotrichia* s.l. I do not agree with Schmid (1958) and Flint (1971a) that these genera are closely related to *Microptila*.

DISCUSSION THE TRIBE OCHROTRICHIINI (III)

The Ochrotrichiini constitutes a distinct, warm-adapted, New World group of the subfamily Hydroptilinae which may be distinguished from the Leucotrichiini, with which it shares the feature of a transverse meso-scutellar suture, by the distinctive and highly specialised male genitalia, and the basic Hydroptilid appearance of the larva. The tribe may later prove to be a subgroup of the Hydroptilini but is provisionally treated here as distinct on the basis of the presence of a transverse meso-scutellar suture and the characteristic male and female genitalia, including the absence of a spiral 'titillator' on the male aedeagus; and the associations of the larvae with running water habitats and their possibly detriphagous habits (c.f. the predominantly algal-feeding Hydroptilini). However, such features may be secondarily derived from the basic Hydroptilini condition, a thorough examination of representative adult and larval material being essential for the establishment of the true relationships of the group within the Hydroptilinae and of the genera with one another.

Tribe IV NEOTRICHIINI Ross

Neotrichiini Ross, 1956: 18. Type-genus, Neotrichia Morton.

Distribution: Nearctic, Neotropical.

Ross first used the name Neotrichiini in a phylogenetic diagram (Ross, 1956: 18, chart II) showing the coincidence of the primitive lines of Trichoptera with the 'cool-adapted habitat', the Neotrichiini representing a specialised 'warm-adapted' offshoot of the main Hydroptilini branch. Ross, however, did not then or subsequently define the tribe although he is still of the opinion that the group should be maintained as distinct from the rest of the Hydroptilidae, principally on account of the characteristic form of the larvae and their 'Limnephilid-like' cases (Ross, in litt.). Therefore, although I am modifying Ross's (1956) classificatory scheme somewhat by further subdividing what he terms the Hydroptilini into a number of tribes, I am maintaining the status of the Neotrichiini as originally proposed.

The Neotrichiini consists of two exclusively warm-adapted New World genera, Neotrichia and Mayatrichia, the combined distribution of which extends from Canada, through the United States and Central America (the regions of greatest species and individual numbers) down into Central Argentina. The genera share a number of unique adult and larval characters which distinguish them from all other Hydroptilinae, although they still retain the basic diagnostic features of this subfamily. As indicated above, the immature stages are what really set the Neotrichiini apart since the larvae construct cylindrical cases, with circular anterior and posterior openings, reminiscent of the higher Limnephiloid groups and quite unlike the basic 'purse-type' case of the Hydroptilidae. The larvae accordingly exhibit parallel Limnephiloid-like morphological features associated with the form of the case, for example the cylindrical abdomen and the free anal prolegs which may be extended through the wide posterior opening of the case, and in one species of Neotrichia a lateral line appears to be present.

The following diagnosis is based on Ross (1944) and examination of adult material in the BMNH collection and larvae of both genera (USNM loan).

Tribe diagnosis

Adult. Forewing length 1.5-2.0mm: head and antennae simple; tentorium complete; ocelli 3: mesoscutellum without transverse suture, anterior margin convex; metascutellum convexly subtriangular: fore-tibia without apical spur: abdomen with typical lateral setate processes on sternite V: ♀ genitalia a simple oviscapt: ♂ genitalia (fig. 52)- segment VIII unmodified; IX fused, annular, open postero-ventrally, well developed postero-lateral processes present; inferior appendages and subgenital plate well developed; bilobed process sometimes present and often may be fused to the underside of the subgenital plate in some species of Neotrichia; tergite X usually membranous with various lobes; subgenital appendages present (homologies uncertain).

Larva (figs 87, 88). Head conical, tapering anteriorly, antennae relatively long (c.f. other Hydroptilidae): thoracic nota paired: abdomen only slightly distended, cylindrical, abruptly enlarged from segment II, from there gradually tapering posteriorly; tergites VIII and IX present only, latter covering whole of dorsum; anal prolegs slender, long, projecting freely from segment X; lateral fringe of short setae ('lateral line') sometimes present along sides of abdomen: thoracic legs slender, tarsal claws long.

Case. Cylindrical, slightly tapering posteriorly, constructed of secretion only (surface strongly ridged) (fig. 88b) or with a covering of small sand-grains (fig. 87b); openings ovoid to circular, wider anteriorly.

Biology. Larvae occur on rocks in rapid sections of rivers and streams; details of feeding habits unknown, but probably detriphagous; according to Wiggins (in press) the guts of three specimens of Mayatrichia contained almost exclusively fine organic particles although, from the shape of the head, he suspects them to have specialised feeding habits.

Key to genera

Adults (modified after Ross, 1944)

- Spur formula 0.2.4: male genitalia- sternite VI with slender ventral process; inferior appendages with broad, setae-bearing apex and a small, digitate baso-dorsal projection; aedeagus without lateral processes or spines..Mayatrichia
- Spur formula 0.2.3: male genitalia- sternite VI without ventral process; inferior appendages not as above; aedeagus with spiral process and spines in apical half...................................Neotrichia

Larvae (after Wiggins, in press)

- Abdomen slightly depressed, intersegmental grooves prominent, lateral fringe of hairs sometimes present; case of silk and fine sand-grains (fig. 87)...Neotrichia
- Abdomen relatively more distended, not depressed, intersegmental grooves not prominent, lateral fringe of hairs absent; case of silk only, usually with transverse or longitudinal ridges (fig. 88)..... ....Mayatrichia

Genus NEOTRICHIA Morton (Tribe IV)

Cyllene Chambers, 1873: 124. Type-species, Cyllene minutisimella Chambers, by monotypy. (Preoccupied several times, vide Fischer, 1961)

Neotrichia Morton, 1905: 72. Type-species, Neotrichia collata Morton, by monotypy.

Exitrichia Mosely, 1937: 170. Type-species, Exitrichia anahua Mosely, by original designation. (Synonymised by Ross, 1944).

Dolotrichia Mosely, 1937: 177. Type-species, Dolotrichia canixa Mosely, by original designation. (Synonymised by Ross, 1944).

Guerrotrichia Mosely, 1937: 179. Type-species, Guerrotrichia caxima Mosely, by original designation. (Synonymised by Ross, 1944).

Lorotrichia Mosely, 1937: 181. Type-species, Lorotrichia hiaspa Mosely, by original designation. (Synonymised by Ross, 1944).

Distribution: Nearctic, Neotropical.

Neotrichia is exclusively a New World genus with representatives occurring most abundantly in the U.S.A. and Mexico, although a few species have been recorded from Canada, the Antilles, Surinam and Brazil. There are 46 species which fall into a number of distinct groups which are characterised by features of the male genitalia and which correspond with the genera described by Mosely (1937) subsequently synonymised by Ross (1944). The Surinameso species (Flint, 1974) appear to fall into two additional groups.

According to Ross (1944) the larvae of minutisimella, okopa, collata and riegeli are known but only those of the first named have been described. However, Flint (1964, 1968b, 1968c) has since described the larva of iridescens.

Generic diagnosis

Adult. Spur formula 0.2.3: ♂ genitalia (fig. 52) sometimes with ventral process on sternite VIII; IXth segment annular, generally complete dorsally and ventrally; tergite X variable but usually forming a well developed dorsal plate; inferior appendages distinct, somewhat elongate, usually with prominent, spatulate bracteole (br); subgenital plate well developed with a pair of apico-ventral setae lobes (representing fused bilobed process ?); a pair of narrow subgenital appendages sometimes present ('slender structure' of Flint, 1964; 'filiform appendage' of Ross, 1941); aedeagus elongate, generally with a wide tubular base narrowing to a median constriction or neck from which arises a stout spiral process, apical half more slender, divided at apex or bearing apical spines.

Larva (fig. 87a,c). Head cone-shaped, tapering anteriorly; labrum symmetrical; mandibles subsymmetrical, short, robust, not markedly dentate: thoracic nota covered in long sparse setae; legs long and slender (c.f. _Mayatrichia_): abdomen cylindrical but not as rotund as in _Mayatrichia_, intersegmental grooves distinct.

Case (fig. 87b). Cylindrical, tapering posteriorly, basically of silk and often covered in small sand-grains.

Biology. Larvae found in rapid sections of rivers and streams.

Genus MAYATRICHIA Mosely (Tribe IV)

Mayatrichia Mosely, 1937: 182. Type-species, _Mayatrichia_ _ayama_ Mosely, by original designation.

Distribution: Nearctic.

There are only four species in this genus; they are all of local occurrence but have an overall distribution ranging from Saskatchewan to Mexico and from Ontario to Maine. Ross (1944: 278) gives a key to the males of the three North American species (*ayama*, *ponta* and *acuna*) with *rualda* from Mexico being described by Mosely (1937: 183). The larvae and cases of *ayama* (including an early instar) and *ponta* have been described by Ross (1944) and Wiggins (in press) respectively.

Generic diagnosis

Adult. Spur formula 0.2.4: ♂ genitalia with sternite VI with a long, slender ventral process; segment IX annular, deeply incised along postero-ventral margin, accentuated by postero-lateral processes; tergite X membranous, hood-like; inferior appendages with broad, setae-bearing posterior margin and a small, digitate, dorso-lateral projection; sub-genital plate well developed with postero-medial, ventrally directed processes and produced dorso-laterally to meet tergite X; bilobed process absent; aedeagus simple, long, apex filiform or with three 'staggered tubercules'(ross, 1944).

Larva (fig. 88a,c). Head very attenuate anteriorly: thoracic nota covered in short, stout setae; legs relatively shorter and more robust than in *Neotrichia*: abdomen rotund, cylindrical, with faint intersegmental grooves; lateral setal fringe present only in *ayama*.

Case (fig. 88b). Cylindrical, tapering posteriorly, constructed of secretion only but with strengthening transverse or longitudinal ridges.

Biology. According to Wiggins (in press) the larvae occur on rocks in rapid sections of rivers and streams, generally in rather large bodies of water (running).

DISCUSSION THE TRIBE NEOTRICHIINI (IV)

The Neotrichiini is exclusively a New World group containing two very closely related genera which are distinguished from each other by features of the male genitalia, adult spur formula and the general form of the larva. The structure of the adult thorax and presence of the spiral aedeagal process in the males of Neotrichia indicate that the group may have arisen relatively recently from the main Hydroptilini branch and evolved its characteristic features in isolation on the American continent. The most notable feature, apart from their minute size, is the distinctive appearance of the larvae which seem to have developed characteristics similar to those of the Limnephiloid groups in association with the possession of cylindrical cases. As Ross (1956) points out, however, it is unlikely that the Neotrichiini gave rise to the Limnephiloid branch of the Trichoptera since this tribe is a very specialised member of the Hydroptilinae, the superficial similarities having arisen by parallel evolution. In addition, the larvae do not seem to have the habit of feeding on filamentous green algae, as is characteristic of the Hydroptilini, and are supposed to be detriphagous. From the form of the larval mandibles, which are robust and not markedly dentate or asymmetrical, the detriphagous habit would appear to be a primary characteristic and not secondarily derived from the algal-feeding condition (c.f. Ithytrichia, tribe VI). The position of the Neotrichiini within the Hydroptilidae will be discussed later.

Tribe V HYDROPTILINI Stephens (sens. n.)

Type-genus, Hydroptila Dalman, 1819.

Distribution: Cosmopolitan (excluding polar regions).

The Hydroptilini, as interpreted here, contains the most widely distributed and most recently successful genera of the subfamily Hydroptilinae grouped on the basis of features of the adult thorax and male genitalia and the association of the larval stages with green filamentous algae. The tribe is considered to contain three subgroups, distinguished by male and female genitalic characters and the general appearance and habits of the larvae, which variously exhibit both generalised and specialised adult and larval Hydroptilid features. These groups will be discussed in the order given below.

A The Agraylea-group. This contains some of the larger and more generalised Hydroptilids with respect to the overall external appearance of the adults while the male genitalia conform to a common basic pattern within the group; the larvae are essentially adapted for life in vegetation thickets in slow-moving to static bodies of water (at least in Agraylea).

B The Hydroptila-group. This essentially consists of the nominate genus Hydroptila with which a number of genera have here been synonymised. The adults exhibit generalised but distinctive patterns of genitalia which vary slightly between species-groups; the larvae are basically typical of the hypothetical generalised Hydroptilid but are adapted for feeding on filamentous algae on more or less exposed substrates in moderate to fast-flowing water. The genus is distinguished by the specialised cephalic (post-occipital) scent-caps of the males and the absence of ocelli in both sexes. Hydroptila contains the greatest number of species within the Hydroptilidae and has the widest geographical distribution; it therefore may be regarded as the most successful genus of the family.

C The Oxyethira-group. This is a more heterogeneous group with regard to adult features, each genus possessing a very distinct set of genitalia, but it is characterised by the relatively uniform appearance of the larvae. The latter are specialised filamentous algal feeders and are generally associated with vegetation thickets in slowly moving to static bodies of water. Within the group there is a definite trend towards the elongation of the mid- and hind-legs in the larvae which reaches its extreme condition in Tricholeiochiton fagesii. Oxyethira, like Hydroptila, has a continuous world-wide distribution (although represented by fewer species) while Stenoxyethira, Paroxyethira and Xuthotrichia are restricted toSE. Asia, New Zealand and Australia respectively, and Tricholeiochiton has one west Palaearctic and two SE. Asian representatives only.

Genus AGRAYLEA Curtis (Tribe V. Group A)

Agraylea Curtis, 1834: 217. Type-species, Agraylea sexmaculata Curtis, by subsequent designation by Westwood, 1840.

Agraules Agassiz, 1846: 32. (Unjustified emendation of Agraylea according to Fischer, 1961).

Hydrorchestria Kolenati, 1848: 103. Type-species, Agraylea sexmaculata Curtis, by subsequent designation by Kimmins, 1950. (Synonymised by Kimmins, 1950).

Distribution: Holarctic.

There are nine species in this small Holarctic genus although some of these are of doubtful status and are very restricted in occurence. The most successful species are sexmaculata, which has a wide western Palaearctic distribution, and multipunctata, which is reputedly Holarctic but which probably involves a species complex. In my opinion the Nearctic form of *multipunctata* , as figured in Ross (1944), is distinct from the Palaearctic form (the type) in features of both the male and female genitalia (notably the relative size and shape of the inferior appendages and ventral process of sternite VII of the male) and should be referred to by its original designation (*signata* Banks). However, Ross (*in litt.*) has Alaskan material of what may prove to be a third species and he agrees that a thorough study should be made of all records previously referrable to *multipunctata* from throughout the Holarctic region, including the records of the closely related European species, *cognatella*.

The following list summarises the status of the species at present comprising the genus *Agraylea*:

spathifera Ulmer: Baltic Amber; closely related to *multipunctata*.

insularis Hagen: known only from a single female specimen (now lost) from Madeira which, according to Nybom (1948), was probably a female of *Stactobia atra* (Hagen).

drosima Navás: Navás (1917) gives only a crude description and figure of this subsequently unrecorded species from Spain; its identity remains doubtful until the type-specimen can be located.

argyricola Kolenati: originally described from Sweden and subsequently from Finland, this species has been regarded of doubtful identity ever since Eaton (1873) considered it to be a possible synonym of *multipunctata*; Nybom (1960) regards it as an 'unintelligible species' and has withdrawn it from the Finnish list.

multipunctata Curtis: possibly represented by a species complex (see above) consisting of *multipunctata* Curtis (Palaearctic) and *multipunctata* Curtis sensu Morton (1905) (Nearctic) (= *signata* Banks ?).

sexmaculata Curtis: a distinct Palaearctic species.

cognatella McLachlan: in this species the abdomen of the type-specimen, which has been crudely figured by McLachlan (1880), has been lost; however, it appears to be most closely related to multipunctata; the larva has been described by Solem (1972), although he had no spare adult specimens available for examination.

saltesea Ross: Nearctic (Montana, California); according to Ross (1944) this bears most resemblance to multipunctata.

costello Ross: Nearctic (Ontario, Maine); Ross (1944) considers this to be most closely related to Allotrichia pallicornis (Eaton) (q.v.).

The larvae of the following species have been described: multipunctata (Nielsen, 1948; Lepneva, 1964; Hickin, 1967); sexmaculata (Lepneva, 1964; Barnard, 1971) and cognatella (Solem, 1972).

Agraylea is most closely allied morphologically to Allotrichia from which it was originally distinguished by the presence of fork 1 (R_2 and R_3) in the hindwing of Agraylea. This has not proved to be a consistent generic feature and the genera may later be found to be synonymous. They have been treated separately in this account, however, because the male genitalia of the Allotrichia group of species conform to a distinct pattern (which may, nevertheless, be derived from the basic Agraylea plan). Also, the form of the male genitalia appears to link Agraylea with Ugandatrichia (and Moselyella) and Dhatrichia, the relationships of which will be discussed later.

The following diagnosis is based on specifis descriptions and examination of adult and larval material in the BMNH collections. The general morphological features, apart from those of the genitalia, also apply to Allotrichia.

Generic diagnosis

Adult. Forewing length 4-5mm; wings (fig. 32) relatively broad, apices slightly tapered, venation fairly complete (c.f. figs 30 and 33): head (fig. 15) and antennae simple; ocelli 3; post-occipital lobes unmodified; tentorium distinct: mesoscutellum (fig. 15) narrow, diamond-shaped; metascutellum narrow, pentagonal, parallel-sided: spur formula 0.3.4: lateral setate processes of abdominal segment V present, typical: ♀ genitalia a simple ovisc~~a~~pt (figs 192, 193): ♂ genitalia (c.f. figs 50, 189, 190) generally with a long ventral process on segment VIII; segment IX forming an annulus, usually with a deep dorso-anal indentation; tergite X reduced to a short membranous lobe; inferior appendages generally well developed; subgenital plate triangular, tapering posteriorly (ventral view) and with a median, ventrally projecting process; aedeagus relatively short and stout with distinct proximal and distal halves (fig. 72), proximal broad ejaculatory duct giving rise to the slender distal intromittent organ from which arises the spiral 'titillator' (midway between the end of the ejaculatory duct and the constriction at the base of the intromittent organ).

Larva (fig. 89). Body slightly compressed laterally: dorsal ecdysial lines of head indistinct; labrum symmetrical, short and broad with convex sides, concave anterior margin and small, antero-lateral projections; mandibles asymmetrical, robust (left with apical tooth and projecting dorsal blade without teeth but with small apical denticles, median brush present; right mandible without teeth which are replaced distally by two tubercules, inner median margin with central membranous bladder-like structure);'postmental sclerites' entire in multipunctata, paired in sexmaculata (figs 104, 103); posterior ventral apotome absent: legs short, subequal; fore-femur short and broad, baso-ventrally produced into a short process with apico-ventral projection of trochanter; distal process of tibia with typical spinose setae: small oral sternite present on prothorax only (fig. 117): abdominal segment I larger than metathorax, abdomen widest at segment IV, intersegmental constrictions deep; dorsal 'rings' present on segments II-VIII; tergite present on segment IX; anal prolegs fused to X, anal claws relatively longer than in other Hydroptilids. The early instars are described by Nielsen (1948).

The larvae of multipunctata, sexmaculata and cognatella can be distinguished by the markings of the dorsal head capsule (Solem, 1972).

Case (fig. 89b). 'Purse-type', constructed of silk and filaments of algae. The case-building behaviour of multipunctata is described by Nielsen (1948).

Pupa. Typically Hydroptilid, mandibles long, without median teeth; case a sealed larval case attached at each corner by a short silken pad to the surrounding vegetation.

Biology. The larvae of Agraylea occur in plant thickets in lakes and slowly-flowing rivers in association with green filamentous algae. The larvae of multipunctata and sexmaculata have been observed to feed (Nielsen, 1948; Barnard, 1971) by grasping each algal filament with their modified chelate forelegs and passing it upwards between the mandibles with which they bite into each cell; the cell contents are then sucked out through this excision. According to Wiggins (in press) gut contents of multipunctata (Nearctic)included diatoms while Siltala (1907) records Fucus, algae and diatoms from the guts of Palaearctic specimens of this species.

Genus ALLOTRICHIA McLachlan (Tribe V. Group A)

Allotrichia McLachlan, 1880: 508. Type-species, *Agraylea pallicornis* Eaton, by monotypy.

Distribution: Palaearctic (including N. Africa).

This genus was erected for a single male specimen of what McLachlan regarded as a new species from Worcester, England but, just prior to publication, he discovered that it was identical to *Agraylea pallicornis* Eaton which thus became the type-species. McLachlan regarded the genus as distinct from *Agraylea* on the basis of the absence of fork 1 (R_2 and R_3) (*vide* fig. 32, arrowed) in the hindwing. As pointed out previously, this has not proved to be a constant diagnostic feature and the genera may later come to be regarded as synonyms. *Allotrichia* is retained here, however, as the male genitalia of the constituent species conform to a characteristic pattern and the female genitalia and larval habits of *pallicornis* are distinct from those of *Agraylea* (although it is not certain whether *pallicornis* is typical of the *Allotrichia* group in general).

Apart from *pallicornis*, which has a widespread western Palaearctic distribution, the other members of this genus are all very local in occurrence; the following list summarises the distribution and status of the species of *Allotrichia*.

ampullata Ulmer: Baltic Amber.

succinica Hagen: Baltic Amber.

heterocera Navás: based on a single female specimen from Spain with a vague description accompanied by a very nondescript figure and said by Navás to 'resemble *pallicornis*'; this species is therefore unrecognisable and must await the discovery and examination of the type.

pallicornis (Eaton): central and southern Europe, Algeria, Iran.

vilnensis Raciecka: refigured by Schmid (1959a) and known from the type-specimen from Poland and further material from Iran (Schmid leg.); this species is distinct but very closely related to *pallicornis*.

tauri Jacquemart: described from a single male specimen from Turkey; it may prove to be synonymous with *pallicornis*.

teldanica Botosaneanu: a distinct species from Israel, closely related to *vilnensis*.

africana Marlier & Vaillant: I believe this species from the Congo to be closely related to, if not synonymous with, *Ugandatrichia nigra* Mosely (q.v.).

laerma Malicky (in press): I have not been able to investigate the affinities of this species.

The members of the genus *Allotrichia* are morphologically very similar to those of *Agraylea* and the generic diagnosis given for the latter also applies to *Allotrichia* and therefore has not been repeated here. New species are allocated to either genus not according to the fusion of R_2 and R_3 in the hindwings, as was previously the practice, but by the general form of the male genitalia. However, Ross (1941) states that the genitalia of *Agraylea costello* Ross are more like those of *Allotrichia pallicornis*, thus implying that the two genera are synonymous. Before any definite conclusions can be drawn, however, a thorough study of the *Agraylea*-*Allotrichia* complex needs to be carried out, incorporating as many male, female and larval features as possible; only the larva of *pallicornis* has so far been described (Giudicelli & Vaillant, 1967).

The following generic diagnosis is based on original descriptions and examination of adult material (pallicornis) in the BMNH collections.

Generic diagnosis (see also Agraylea)

Adult. ♀ genitalia an oviscapt; segment VIII without a ventral sclerite but with a characteristic asymmetrical groove (fig. 194). ♂ genitalia (figs 50, 191) with concave inferior appendages, broad with concave posterior margins; the subgenital plate bears a pair of characteristic asymmetrical dorsal processes.

Larva (c.f. fig. 89a). Characterised by the lightness of the pigmentation of the sclerites and absence of dorsal markings (c.f. Agraylea): setae of head and labrum much shorter than in Agraylea; dorsal ecdysial lines of head appear to be more distinct than in Agraylea; mandibles similar to those of Agraylea although the apices are more dentate: foreleg with distinctive chelate form but devoid of the specialised distal process of the tibia: abdominal tergites absent, including tergite IX (unusual); anal prolegs simple, claws apparently short. (After Giudicelli& Vaillant, 1967).

Case. Identical with that of Agraylea.

Pupa. Typical; mandibles long with fine serrations along inner edge; case similar to that of larva but sealed, with two attachment pedicels (c.f. four in Agraylea) at either end of one long side by which the case is held vertical to the substrate.

Biology. The immature stages were found in a rapid stream at 750m altitude with little shelter or marginal vegetation. Larval gut contents revealed, according to Giudicelli & Vaillant (1967), that the larvae are secondary substrate feeders which have been derived from the basic filamentous algal-feeding Agraylea stock; they have retained certain features associated with algal-feeding such as the asymmetrical mandibles, chelate forelegs, lateral flattening of the body and case and the incorporation of algal filaments into the latter.

The larvae of *Allotrichia pallicornis* thus differ from those of the known species of *Agraylea* in the lack of pigmentation, absence of abdominal tergite IX, simplicity of the anal prolegs, shorter head and labral setae, dentate mandibles and the attachment of the pupal case by two (c.f. four) adhesive discs. These differences are apparently due to structural adaptations to living in fast-flowing water conditions and detriphagous feeding habits. As only the larva of *pallicornis* has so far been described, it is not known whether these features are diagnostic of *Allotrichia* species in general.

Genus MICROPTILA Ris (Tribe V. Group A)

Microptila Ris, 1879: 416. Type-species, *Microptila minutissima* Ris,
by monotypy.

Distribution: W. Palaearctic.

Microptila was erected for a new Swiss species, *minutissima* and *bejela* Mosely was subsequently described from Aden. Schmid (1960), as a result of studies on the Trichoptera fauna of Sri Lanka and Pakistan, synonymised the African genus *Ugandatrichia* Mosely and the SE. Asian genus *Moselyella* Kimmins with *Microptila* on the basis of features of the wing venation and the general form of the male genitalia. Schmid described a number of new species, mainly from Pakistan and adjacent areas, which he considered to exhibit male genitalic features intermediate between those of the *Ugandatrichia*-*Moselyella* complex, which contains some of the largest known Hydroptilids, and *Microptila*, which contains some of the smallest.

I have examined type-material of all three genera (BMNH collections) (including paratypes of three species described by Schmid (1960) and placed in *Microptila* sensu Schmid); only one specimen of the type-species, *minutissima*, of *Microptila* was available for study but this is mounted in Canada Balsam and is now in a very poor condition, the features of the genitalia (male) being indistinct and the thorax completely destroyed thus rendering a comparative study impossible. Nevertheless, I consider *Ugandatrichia* and *Moselyella* to be distinct from *Microptila* s.s., the two former genera comprising a distinct group which has more affinities, at least in the adult stages, with *Agraylea* and *Allotrichia*, whereas *Microptila* s.s. bears more resemblance to *Dhatrichia* Mosely. This, however, raises the problem of the correct generic identity of the species described by Schmid as *Microptila* s.l.; this will be dealt with below.

In this account, on the basis of adult features alone, I propose to reinstate the genus *Ugandatrichia*, with *Moselyella* as a junior synonym, and to interpret *Microptila* in its original sense. These views may need to be modified with the discovery of new species and the larval stages (as yet unknown for any genus).

Generic diagnosis (*Microptila* s.s.)

Adult. Forewing length 1.5-3.0mm; antennae 20- to 25-segmented; ocelli 3; mesoscutellum short, anterior margin convex; metascutellum trapezoidal: spur formula 0.3.4: ♀ genitalia an oviscapt: ♂ genitalia simple; segment IX large, fused, with a shallow excision along dorso-posterior margin; tergite X forming a short membranous dorsal lobe; subgenital appendages elongate, slender, apparently arising lateral to tergite X; inferior appendages elongate, apices slightly incurved;

subgenital plate elongate, semi-tubular; aedeagus simple, long and slender, tapering to a pointed apex in bejela (vide Mosely, 1948) and with a short spiral 'titillator' in indra and apsara.

M. indra is retained in this genus on the basis of the form of the thoracic nota; apsara is only doubtfully retained.

Genus UGANDATRICHIA Mosely (Tribe V. Group A)

Ugandatrichia Mosely, 1939b: 36. Type-species, Ugandatrichia minor Mosely, by original designation. (Gen. rev.).

Moselyella Kimmins, 1951: 195. Type-species, Ithytrichia violacea Morton, by original designation. (Synonymised by Schmid, 1960).

Distribution: Africa (Congo, Uganda, Kenya); SE. Asia (Burma, Assam, Pakistan, Sri Lanka).

Generic diagnosis

Adult. Forewing length variable, 2-6mm; wings relatively broad but still long and acuminate as typical of the Hydroptilinae; forewings with dense setal covering (dark) with an oval patch of creamy scale-like hairs arising centrally from the membrane in cyanotrichia (Kimmins) (fig. 31): tentorium complete (figs 16, 17); antennae usually long (32- 37 segments); ocelli 3: mesoscutellum diamond-shaped (figs 16, 17) as in Agraylea (fig. 15); metascutellum 'convexly subtriangular', narrow: spur formula 0.3.4: violacea, cyanotrichia and nikitaruwa (Schmid) each has a pair of long, membranous extrusible processes arising laterally between the tergite and sternite of segment II in the male: ♀ genitalia an oviscapt; sternite VII with diagnostic patch or row of setae in certain species; sternite VIII with process or some sort of marking: ♂ genitalia with segment IX well developed, variously with dorsal and ventral posterior and anterior excisions; tergite X a median lobe with well developed elongate lateral processes; inferior appendages large, broad and elongate; subgenital plate trilobed (or emarginate) with distinct proximal and distal regions, divided by a constriction adjacent to which arises a short, spiral 'titillator'.

The thoraces of *nikitaruwa* (Schmid) and *sourya* (Schmid) are almost identical to that of *Ugandatrichia* (as seen in species of *Moselyella*), while *roudra* (Schmid) is included here on the basis of size and male genitalic affinities with *Ugandatrichia* species as noted by Schmid (1960). *M. apsara* Schmid may also belong here (see *Microptila* s.s. section).

Discussion

According to the basic form of the male genitalia and the structure of the thoracic nota, especially with regard to the characteristic diamond-shaped mesoscutellum, I consider *Ugandatrichia* and *Moselyella* to be synonymous and closely related to *Agraylea* as apposed to *Microptila* in which the mesoscutellum is more 'kite-shaped' with a convex anterior margin. Only specimens of *nikitaruwa* (Schmid), *sourya* (Schmid) and *indra* (Schmid) were available for study (BMNH collection, paratypes) and, from their thoracic features, the last mentioned would appear to belong to *Microptila* s.s. while the other two strongly resemble *Ugandatrichia* species. The affinities of *apsara* (Schmid) and *roudra* (Schmid) are still doubtful.

Thoracic structure alone, however, cannot be used as an indication of generic affinity. As Schmid (1960) rightly states, the genitalia of the *Microptila-Ugandatrichia-Moselyella* complex do have a common basic form but, on the other hand, this is a very generalised form and has certain features in common with the genitalia of *Agraylea*, *Allotrichia* and *Dhatrichia*. Indeed, *Allotrichia africana* Marlier & Jacquemart appears to belong to *Ugandatrichia* and is very close to, if not synonymous with, *U. nigra* Mosely. I do not agree with Schmid (1960) in their being any possible relationship between *Microptila* s.l. and the Nearctic-Neotropical subgenus *Ochrotrichia Metrichia* since the genitalia of the two groups are quite distinct and the characteristic mesoscutellar suture of *Ochrotichia* is absent in *Microptila*.

Genus DHATRICHIA Mosely (Tribe V. Group A)

Dhatrichia Mosely, 1948: 78. Type-species, *Dhatrichia inasa* Mosely, by original designation.

Distribution: Yemen, Zaire.

This small African genus was first described for a single male specimen from the Yemen which is now mounted as a microscope slide preparation in the BMNH collection. A new species from Zaire (*bipunctata*) is being described by Statzner (in press, pers.comm.), paratypes of which have been donated to the BMNH. The immature stages are unknown.

The following generic diagnosis is based on examination of the above material.

Generic diagnosis

Adult. Forewing length 2mm; wings narrow, tapering: tentorium complete but very fine medially; ocelli 3; antennae 19-segmented (male *inasa*); post-occipital lobes ovoid: mesoscutellum with convex anterior margin; metascutellum pentagonal, sides convergent anteriorly; spur formula 0.3.4: typical lateral setate processes of abdominal segment V present: ♀ genitalia an oviscapt: ♂ genitalia with segment IX annular, dorsally reduced to a narrow chitinised band and with well developed postero-lateral sides (almost concealing genitalia in lateral view); tergite X ('upper penis cover', Mosely, 1948) broad, bilobed in inasa; inferior appendages short, apically broad, trilobed in inasa; subgenital plate an elongate flat process with a pair of apical setae and not extending beyond the sides of IX; aedeagus with a broad proximal ejaculatory duct and slender distal intromittent organ and with a spiral 'titillator' arising midlength adjacent to the median constriction.

Discussion

From the structure of the male aedeagus and the thoracic nota, Dhatrichia would appear to be a member of the Hydroptilini. The form of the male genitalia indicates an affinity with Agraylea, especially by the shape of segment IX and the form of the aedeagus; however, the thorax bears more resemblance to that of Microptila s.s. and these two genera (i.e. Microptila and Dhatrichia) can only be separated in the generic key (Appendix, section VIIIB) by the form of the male genitalia.

Genus HYDROPTILA Dalman (Tribe V. Group B)

Hydroptila Dalman, 1819: 125. Type-species, *Hydroptila tineoides* Dalman, by monotypy.

Phrixocoma Eaton, 1873: 132. Type-species, *Hydroptila sparsa* Curtis, by original designation.

Hydropneuma Enderlein, 1929: 232. Type-species, *Hydropneuma juba* Enderlein, by original designation. (Synonymised by Nybom, 1963).

Hydroptilina Martynov, 1934: 144. Type-species, *Hydroptilina angustipennis* Martynov, by monotypy. (Synonymised by Fischer, 1971).

Oxydroptila Martynov, 1935: 114. Type-species, *Oxydroptila furcata* Martynov, by original designation. (Syn. n.).

Oeceotrichia Ulmer, 1951: 85. Type-species, *Oeceotrichia elongata* Ulmer, by original designation. (Syn. n.).

Pasirotrichia Ulmer, 1951: 90. Type-species, *Pasirotrichia crenata* Ulmer, by original designation. (Syn. n.).

Sumatranotrichia Ulmer, 1951: 87. Type-species, *Sumatranotrichia trullata**, by original designation. (Syn. n.).(*Ulmer).

Distribution: Cosmopolitan (excluding polar regions).

Hydroptila is the most successful genus of the Hydroptilidae with over 150 species and with an almost world-wide distribution; species have been recorded from Lapland and the northern U.S.S.R. to S. Africa and Australia (including Tasmania)in the 'Old World' and throughout the Americas as far south as Nova Teutonia in Brazil. A number of more or less geographically distinct species-groups may be recognised by the forms of the male and female genitalia, and may eventually come to be considered as definite subgenera. However, the species all have the following features in common: basic genitalia patterns; thoracic nota;

absence of ocelli and presence of male dorsal occipital scent-organs in the adults and general larval and case forms. The immature stages are difficult to identify at the species level although Ross(1944) gives head and thoracic pigmentation patterns as rough guides to the identity of some Nearctic species although these tend to be very variable intra-specifically. My own observations indicate the possible use of features of the sculpturing and shape of the mandibles as specific guides but a full investigation was not carried out. The only satisfactory means of identification is by association with correctly identified pupae and adults.

There is no single comprehensive work on the genus as a whole, any one species-group or any particular faunal group nor is there a key to the species of Hydroptila, identification at present relying on faunal keys (of which there are few) and reference to original descriptions, some of which are unsatisfactory and in need of redefinition. A species key was beyond the scope of this project but I have attempted to indicate the main species-groups, these groupings being based on affinities suggested by the original authors and, in many instances, by my own observations.

Generic diagnosis

Adult (fig. 1). Forewing length 3-4mm: head (fig. 18) with tentorium reduced medially; ocelli 0; antennae c. 30-segmented: mesoscutellum (fig. 18) subtriangular with convex anterior margin; metascutellum pentagonal to triangular, anterior margin strongly convex: spur formula 0.2.4: setate processes present on abdominal segment V: ♀ genitalia a simple oviscapt (fig. 61); sternite VIII ('ventral plate', vp) and small sternite/s on IX ('dorsal plate/s', dp) sometimes present: ♂ genitalia (figs 53, 54, 55) distinctive for each species-group but basically as follows - sternite VII often with ventral process; segment VIII rarely with ventral process; segment IX fused, annular, sometimes with antero-lateral apodemes (fig. 55) and often with postero-lateral processes; inferior appendages distinct, usually simple, straight and elongate, sometimes modified (fig. 55); tergite X forming a variable 'dorsal plate'; subgenital appendages variable (= 'parameres', 'lateral penis sheaths', 'intermediate appendages'); subgenital plate simple, broad, slightly emarginate in the *sparsa*- and *consimilis*-groups but absent or inconspicuous in others; bilobed process apparently absent (but may be incorporated into subgenital plate); aedeagus (c.f. fig. 72) with distinct proximal and distal ejaculatory duct and intromittent organ respectively and a well developed spiral 'titillator'.

Larva (fig. 90a). The following species have been described. Palaearctic: Nielsen (1948)(*tineoides**); Lepneva (1964)(*tineoides*, *sparsa**, *pulchricornis*, *vectis**); Hickin (1967)(*tineoides*, *sparsa*).

acuta (Jacquemart & Coineau, 1962); *emarginata* (Lepneva, 1932); *forcipata** (Fahy, 1971); *occulta**(s.l.)(in BMNH only);*sparsa* (Hanna, 1961); *taurica* (Botoşaneanu & Sykora, 1963); *trilobata* (Jacquemart, 1965); *vectis* (Jacquemart & Coineau, 1962); *simulans**(BMNH only). S. Africa: *capensis* (Barnard, 1934).

Nearctic: Ross (1944) (*ajax*, *albicornis*, *angusta*, *armata*, *consimilis*, *grandiosa*, *hamata*, *spatulata*, *waubesiana*).

delineata (Sibley, 1926); *martorelli* (Flint, 1964d).

Head elongate with almost parallel sides, almost circular in cross-section; ecdysial lines indistinct; 'postmental' sclerites (fig. 108) fused, although a faint median line may be detected, crescentic, without

* indicates material available in BMNH collections

posterior process (c.f. Agraylea); labrum long, anterior margin deeply indented, lateral lobes slightly asymmetrical, row of setae anteriorly; mandibles asymmetrical (fig. 113), form variable between species, median brush in left only: thoracic pleurites as in Agraylea (c.f. fig. 117) but with pre-episternite free on prothorax only; single oral and paired anal sternites on prothorax only (fig. 122); legs short, subequal (fig. 115) with distal ventral process of fore-tibia well developed and armed with specialised setae (fig. 120) as in Agraylea: abdomen typically distended; dorsal 'rings' present on segments I-VIII; tergites absent except on IX; anal prolegs fused to X; three filamentous caudal gills present (fig. 130).

Case (fig. 90b). 'Purse-type', laterally compressed, constructed of silk and covered in fine sand-grains and other inorganic particles and occasionally with diatoms and algal filaments.

Pupa (fig. 143). Typically Hydroptilid, mandibles long, without teeth; pupal case simply a sealed larval case, attached to substrate by anterior and posterior adhesive discs on ventral edge, held vertically.

Biology. The larvae prefer running water in lakes, streams and rivers, usually on the bottom substrate in association with the green filamentous algae on which they feed. According to Nielsen (1948) the typical habitat of tineoides is that of 'stony brooks in shallow water of lakes' while others tend to prefer swifter flowing water. I agree with Nielsen's (1948) observation that this is probably due to true species preferences as distinct differences have benn observed in the habitats of the British species (vide section IV).

Life-cycles are very variable according to species and locality; both univoltine and bivoltine species have been observed. The larvae feed on filamentous green algae by grasping the filament with the modified chelate forelegs, biting into each cell and sucking out the fluid contents.

Species-groups (for species see checklist, section VIIIC, table 3)

1 the *sparsa*-group: a very large Palaearctic group recognised by the form of the male genitalia (fig. 53).

2 the *uncinata*-group: possibly related to groups 1 and 3, Palaearctic.

3 the *capensis*-group: a small African group, possibly close to 1.

4 the *consimilis*-group: a large Nearctic group, closely related to group 1.

5 the *occulta*-group: a distinct group of approximately 25 species with a distribution extending throughout Europe into Asia Minor, N. Africa, Africa and SE. Asia and with at least 4 Nearctic representatives; male genitalia (fig. 54).

6. the *tineoides*-group: *tineoides* is the only Palaearctic member of this predominantly Nearctic group (*moselyi* Ulmer from Peking may also belong here; male genitalia (fig. 55).

8* the *losida*-group: a small group of Australasian species (Australia, Tasmania, Solomon Islands, Guadalcanal, New Guinea) which may have some affinity with the SE. Asian members of the occulta-group such as *panchaoi*.

7* the *dikirilagoda*-group: a distinct group of 3 species from Sri Lanka; possibly related to group 6.

9 the *pulchricornis*-group: a small group of Palaearctic species with possibly one N. African representative.

10 the *forcipata*-group: of 3 Palaearctic species; Schmid considers *armathai* to belong here (Schmid, 1959a), but I do not agree.

11 the *vectis*-group: 2 Palaearctic species.

12 the *tigurina*-group: 3 distinctive European species.

* order changed to comply with checklist

13 the *waubesiana*-group: a very distinct Nearctic group of 7 species.

14 incertae sedis: a number of species have not been assigned to any group owing to the unavailability of material for study and the inadequacy of descriptions in the literature.

Generic synonyms

Oxydroptila is a small genus of only two species, *furcata* Martynov from India and *kirilawela* Schmid from Sri Lanka, which is distinguished from Hydroptila on minor venational differences and the form of the male genitalia which is said to resemble that of *Oxyethira*, especially with respect to segment VIII. As in *Hydroptila*, ocelli are absent and the spur formula is 0.2.4; examination of a male paratype of *kirilawela* (BMNH) has revealed the presence of post-occipital scent organs and a thoracic structure identical to that of *Hydroptila*. Contrary to Martynov (1935) and Schmid (1958), the male genitalia do not resemble those of *Oxyethira* and the female genitalia of *kirilawela*, as figured by Schmid (1958) , form a simple oviscapt and not the modified, specialised condition characteristic of *Oxyethira* (q.v.). The larvae are unknown. I therefore propose to sink *Oxydroptila* as a junior synonym of *Hydroptila*.

Oecsotrichia Ulmer, *Pasirotrichia* Ulmer and *Sumatranotrichia* Ulmer are three monotypic genera described by Ulmer (1951) from Indonesia (the Sunda Islands) and distinguished from *Hydroptila* solely on minor venational differences. Each has a spur formula of 0.2.4, ocelli absent, male genitalia of the *Hydroptila* pattern and, from examination of type-material (UHZM loan), post-occipital scent-organs (males) and a thorax identical with that of *Hydroptila*. According to the descriptions and figures of the larvae and cases given by Ulmer (1957), these are also almost identical with those of *Hydroptila* (notably with respect to the fore-tibial process and the three caudal filaments). It would thus appear that *Oecetrichia*, *Pasirotrichia* and *Sumatranotrichia* are all junior synonyms of *Hydroptila*, the species showing certain affinities, according to the forms of the male genitalia, to the SE. Asian members of the *occulta*-group (e.g. *panchaoi* Schmid) and the Australasian *losida*-group.

(As an additional point it was noted, during the examination of Ulmer's Suhda Island material, that two females in spirit labelled *Pasirotrichia* bore no resemblance to *Hydroptila* : sp. A had no ocelli but had a thorax resembling that of *Orthotrichia*, and sp. B had 3 ocelli and a thorax similar to that of *Oxyethira* or *Tricholeiochiton*. However, I was not able to identify the specimens positively owing to their fragile conditions .)

Genus OXYETHIRA Eaton (Tribe V. Group C)

Oxyethira Eaton, 1873: 143. Type-species, *Hydroptila costalis* Curtis, by original designation.

Lagenopsyche Müller, 1879: 39. Type-species, *Lagenopsyche spirogyrae* Müller, by subsequent designation by Fischer, 1961. (Synonymised by Fischer, 1961).

Argyrobothrus Barnard, 1934: 392. Type-species, *Argyrobothrus velocipes* Barnard, by monotypy. (Synonymised by Ross, 1948).

Loxotrichia Mosely, 1937: 165. Type-species, *Loxotrichia azteca* Mosely, by original designation. (Synonymised by Ross, 1944).

Dampfitrichia Mosely, 1937: 169. Type-species, *Dampfitrichia ulmeri* Mosely, by original designation. (Synonymised by Ross, 1944).

Oxytrichia Mosely, 1939: 289. Type-species, *Oxytrichia mirabilis* Mosely, by original designation. (Synonymised by Kimmins, 1966).

Distribution: Cosmopolitan (excluding polar regions).

Oxyethira is a very successful genus with a world-wide distribution and with very distinctive larvae which feed on green filamentous algae. The true identity of the type-species is still in dispute. Eaton originally proposed the genus for two species, *Hydroptila costalis* Curtis and *H. albiceps* McLachlan, the latter being an endemic New Zealand species. Eaton (1873) considered *costalis* (Curtis) to be a senior synonym of *H. tineoides* Stephens and, doubtfully, of *H. flavicornis* Pictet. However, subsequent dissection of Curtis's male type of *costalis* by Neboiss (1963) showed this to be conspecific with *Orthotrichia tetensii* Kolbe, the latter being placed as a junior synonym of *costalis* (Curtis) and congeneric with *angustella* (McLachlan), the type-species of *Orthotrichia*. The next available name for *costalis* (Curtis) sensu Eaton was *Oxyethira flavicornis* (Pictet).

This is still not an unequivocal solution to the problem, however, since Pictet's type-specimen of *flavicornis* has not yet been located (one female specimen in Geneva is labelled 'Zurich 9/81' and a second specimen has no abdomen according to Neboiss, 1963). Neboiss therefore merely proposes the synonymy as'one of the possible answers' but does not ignore the fact that *flavicornis* Pictet could be a synonym of *H. tineoides* Dalman sensu Stephens, thus leaving *costalis* (Curtis) sensu Eaton without a name. However, until the problem can be resolved (and this is unlikely since Pictet's type appears to be missing), the proposal of Neboiss (1963) must be accepted. Nevertheless there is no doubt as to the actual species referred to by Eaton since his figures of the distinctive male genitalia are clearly recognisable (he merely considered that *costalis* Curtis was the same species). The generic status of *Oxyethira* is thus valid as Eaton's species is typical of the group and is what all interpretations of the genus have been based on.

The larval stages of *Oxyethira* (discounting Pictet's (1834) figures of *H. flavicornis*) were first described by Müller (1879) as *Lagenopsyche spirogyrae* Müller from Brazilian material. The first description of British material was by Morton (1886) from specimens of *O. costalis* (Curtis) sensu Eaton sent to him by McLachlan and, in the same year, Hudson (1886) described larvae of an unidentified New Zealand Hydroptilid which subsequently proved to be *O. albiceps* McLachlan. The most detailed larval description is that of *O. costalis* (Curtis) sensu Eaton as given by Nielsen (1948) upon which the generic diagnosis given below is partly based. The following list summarises the published descriptions of species of *Oxyethira* larvae to date, (the type-species will now be called *flavicornis*).

Nielsen (1948) (*flavicornis*); Lepneva (1964) (*flavicornis*, *distinctella*, *ecornuta*, *frici*, *sagittifera*, *tristella*); Hickin (1967) (*flavicornis*, *simplex*).

albiceps (Mosely & Kimmins, 1953); *delcourti* (Jacquemart, 1973); *dualis* (Sibley, 1926); *hyalina*, *spirogyrae* (Müller, 1879); *incana* (Ulmer, 1957); *meridionalis* (= *unidentata*) (Jacquemart & Coineau, 1962); *puertoricensis* (Flint, 1964d); *serrata* (Ross, 1944); *simplex* (Macdonald, 1950); *velocipes* (Barnard, 1934).

Apart from Kimmins's (1958) paper on the British species of *Oxyethira* there has been no previous review of the genus as a whole. The following diagnosis and species-groupings have been based on published species descriptions and examination of adult and larval material in the BMNH collections. To date there are approximately 75 species which fall into more or less distinct species-groups each distinguished by the form of the male genitalia. The status of *Stenoxyethira* Kimmins will be discussed later but, according to Schmid (1958), it should be considered as a synonym of *Oxyethira*.

Generic diagnosis

Adult. Forewing length 2.5-3.5mm: head and antennae unmodified (fig. 20); anterior tentorial arms reduced medially; ocelli 3: thorax (fig. 20) - mesoscutellum with anterior margin convex and posterior margins slightly concave, metascutellum convexly subtriangular: spur formula 0.3.4: ♀ genitalia a modified oviscapt (fig. 62) (after Kimmins, 1958) with sternite VI with a short, acute ventral process; segment VII with tergite and sternite more or less fused, ventral apical margin sometimes excised; tergite VIII reduced to a narrow arched band, the centre of its apical margin produced as a spatulate lobe; sternite VIII forming a short 'subgenital plate'; tergite IX either free or fused to

VIII, short and hood-like; tergite X forming a short, broad plate carrying two short slender cerci; details of internal vaginal structures obscure but apparently with an upper and lower lobe, the latter with a conspicuous baso-ventral process directed caudad: ♂ genitalia (fig. 56) (after Kimmins, 1958) with sternite VII with short, acute ventral process; segment VIII with tergite and sternite more or less fused, apical margins dorsally and ventrally excised, that of tergite with dorsal or lateral processes, the latter sometimes armed with stout spines; segment IX mostly withdrawn into VIII, its upper half generally much shorter than lower, often reduced to a short transverse band, lateral apical margins of IX sometimes produced or with variously formed spiniform processes, ventral margin generally excised and from which arises a lobe; tergite X obscure, membranous; subgenital appendages represented by two sclerotised plates attached to the IXth segment, fused basally with their apices variously hooked downwards ('fused claspers' of Kimmins, 1958; 'lower penis cover' of Mosely, 1939; 'subgenital plate' of Ross, 1948); above and arising from them are two pairs of short, membranous 'bilobed' processes each terminating in a short apical seta; aedeagus long and slender with a spiniform 'titillator' arising at midlength.

Larva (fig. 91a). Head elongate, of uniform diameter, slightly laterally compressed; dorsal and ventral ecdysial lines distinct; postmental sclerites paired, anterior ventral apotome well developed, U-shaped with a distinct transverse ridge, posterior ventral apotome present (fig. 109); labrum with strongly convex lateral margins and deep median anterior indentation; mandibles asymmetrical - left with projecting blades bearing small teeth and with a median brush, right with blades poorly defined and distal only, teeth only near apices: thoracic pleurites of each segment fused except for the free anal epimeron of the prothorax; three sternites present on each thoracic segment (fig. 124); forelegs short with small baso-ventral setate lobe on femur and long distal process bearing a ventral row of short, spine-like setae on tibia (chelate); mid- and hindlegs twice as long as forelegs, tarsal claws long and slender: abdomen typically distended, intersegmental constrictions distinct; laterally compressed and usually held in characteristic comma-shaped attitude; dorsal 'rings' present on segments II-VII; tergites absent except on segment IX ; anal prolegs fused to side of segment X; caudal gills absent.

The early instars of flavicornis (Pictet), as costalis (Curtis), are described and figured in Nielsen (1948).

Case(fig. 91). Laterally compressed, semi-transparent, constructed of secretion only; 'jug-' or 'bottle-shaped; posterior end broad with slit-like opening, anterior end narrow, constricted to form a neck with a well defined rim around the opening. The pupal case (fig. 91c) is basically a sealed larval case attached horizontally to the substrate by four short ligaments, each with an adhesive disc and arising from each corner (in some species there are two ligaments from each of the anterior corners); the pupa lies with its head towards the broad (hence anterior)end (c.f. larva), with its dorsum towards the substrate; the case is closed anteriorly by a narrow curved membrane, the posterorior neck being filled with a plug of silk; the pupal cases usually occur on aquatic plants, rarely on submerged rocks or wood.

Pupa. Typically Hydroptilid; mandibles long with serrate inner blades.

Biology. the larvae are generally considered to occur in plant thickets in slow moving and static bodies of water in association with the green filamentous algae upon which they feed. This is true for *distinctella*, *ecornuta* and *sagittifera*, for example (Lepneva, 1964), and also *velocipes* (Barnard, 1934) and *spirogyrae* (Müller, 1879b) but a number of species are reputed to frequent faster-flowing streams where the larvae are found on the rocky substrate in areas covered with algae; these are *frici* and *tristella* (Lepneva, 1964), *azteca* (or *janella*)(Flint, 1968a) and *hyalina* (Müller, 1879b). *O. flavicornis* (Pictet) in the sense of *costalis* (Curtis) sensu Eaton is a pond dweller although, in Pictet's (1834) original description the larva of *flavicornis* is reputed to occur in fast-flowing streams with *Hydroptila pulchricornis* Pictet thus casting further doubts on the identity of *flavicornis* (see above). In Illinois, Ross (1944) records pupae of *serrata* from the underside of rocks in 2-3 ft of water along the open beaches of glacial lakes. Pupal cases of *albiceps* in New Zealand, according to Hudson (1886), were found attached to stones in streams, especially in the late summer when 'the rivers are generally very low .... and a luxurious growth of green slime weed is present'. Finally, *puertoricensis* is found in all types of streams and at all elevations in Jamaica (Flint, 1968b) and, on Puerto Rico (Flint, 1964d), the cases are found 'in tangles of filamentous green algae' and are fixed to irregularities in the rocks at pupation.

The larvae are highly specialised for feeding on filamentous algae and for living in masses of vegetation as indicated by their chelate forelegs, laterally compressed bodies and very long, slender mid- and hindlegs. According to Siltala (1907) gut contents of an *Oxyethira* species included diatoms and entire algal filaments and Jacquemart (1962) similarly records diatoms and desmids (the normal food source is reputed to be simply the fluid contents of algal cells.). Nielsen (1948) describes the case-building behaviour of *flavicornis* while Jacquemart (1962) describes the similar habits of an unidentified *Oxyethira* species.

Species-groups

At least ten species-groups may be recognised by the form of the male genitalia. The following groupings have been based on relationships suggested in original species descriptions and have been verified by me as far as the literature and available material would allow. The lists of species are given in the checklist (*vide* Appendix, section VIIIC, table 3).

1 the *falcata*-group: essentially a western Palaearctic group of seven species, three occurring only in the Atlantic Islands, and with possibly one Nearctic representative. Two species (*falcata* and *frici*) are British. The group is distinguished by the spinose postero-lateral processes of the male VIIIth segment. There is still some doubt as to the status of *fischeri* and *dentata* which both have very similar genitalia to those of *falcata*; as Higler (1974) points out in his paper on *fischeri*, falcata may exhibit 'eco-geographic' forms (after Jacquemart & Coineau, 1962) and he considers that *dentata* may belong to one of these forms. However, Higler believes that *fischeri* is distinct from *falcata*, mainly on account of features of the male aedeagus (based on the figures of *falcata* in Jacquemart & Coineau, 1962) although Mosely's (1939) figures of the aedeagus of *falcata* are very similar to Higler's figures of *fischeri* ! A thorough study of *falcata* and its reputed close relatives is obviously required in order to sort out this species-complex. *O.boreella* also seems close to *falcata* but would seem to be distinct according to both male and female genitalic characters (Svensonn & Tjeder, 1975).

2 the *flavicornis*-group: a Palaearctic group extending from Europe (and Egypt) to Korea with perhaps one species from Sri Lanka. It may be related to the Nearctic *rivicola*-group (3) and is distinguished by the absence of a median ventral lobe on the fused claspers and the broad, widely separated subgenital plates (in ventral view).

3 the *rivicola*-group: possibly related to group 2 and, although essentially Nearctic, may contain a number of Neotropical members (from Surinam, described by Flint, 1974).

4 the *simplex*-group: again possibly related to group 2; this group may require further investigation as, at present, it contains two geographically distinct elements:- *simplex* and *tristella* from northern Europe and NW. U.S.S.R, and *paramartha*, *ramosa*, *harpagella* and *galekoluma* (and, possibly, *Stenoxyethira excisa*) from SE. Asia.

5 the *distinctella*-group: a small Holarctic group distinguished by the prominent dorso-lateral posterior serrate processes of segment VIII (♂).

6 the *azteca*-group: (= *Loxotrichia* Mosely) a small group from Central America and the Antilles, characterised by the form of the male segment IX.

7 the *ulmeri*-group: (= *Dampfitrichia* Mosely) another small Nearctic group distinguished by the dorso-lateral tapering processes of segment IX.

8 the *zeronia*-group: essentially Central American and characterised by the anterior prolongation of the ventral margin of segment IX.

9 the *pallida*-group: a small but distinct Nearctic group of uncertain affinities.

10 the *bidentata*-group: a Nearctic-Neotropical group of three species.

11 the *mirabilis*-group: containing *mirabilis* (Palaearctic) and *flagellata* (Reunion Island); the latter has some affinity with *bidentata*

(group 10) which itself was once included with *mirabilis* in the genus *Oxytrichia*.

12 *incertae sedis*: of these, *albiceps* is endemic to New Zealand and *velocipes* to S. Africa; *spirogyrae* and *hyalina* (*Lagenopsyche*) from Brazil are known only in their larval stages; *incana* (Indonesia) was described from the female and larva only (Ulmer, 1951, 1957), while *angustella* is known from the wings alone. *O. anabola* and *berneri* are distinct Nearctic species while *mithi*, from Greece, has not yet been placed.

Genus STENOXYETHIRA Kimmins (Tribe V. Group C)

Stenoxyethira Kimmins, 1951: 207. Type-species, *Stenoxyethira minima* Kimmins, by original designation.

Gnathotrichia Ulmer, 1951: 59. Type-species, *Gnathotrichia isabellina* Ulmer, by original designation. (Syn. n.).

Distribution: SE. Asia (Burma, Indonesia).

Kimmins (1951) erected *Stenoxyethira* principally for the type-species, *minima*, but included, somewhat doubtfully, *excisa* Kimmins on the basis of the general similarity of the wing venation. The following generic diagnosis is based on Kimmins (1951). The immature stages are unknown.

Generic diagnosis

Adult. Forewing length 1.6mm: head and antennae unmodified; ocelli 3; spur formula 0.2.4* (0.3.4 in *G. isabellina*): ♂ genitalia (c.f. fig. 56) with segment VIII forming a ring concealing segment IX, latter narrow and lightly sclerotised dorsally, ventral margin produced as a rounded, bilobed plate (fused inferior appendages ?) above which is a triangular, trough-shaped subgenital plate; tergite X difficult to interpret; aedeagus

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* *minima*; 0.3.4 in *excisa*

rod-like, with a single spine or sheath.

S. excisa was included in this genus on the basis of venational features, being distinguished from *minima* by the presence of a small spine or microscopic spur on the mid-tibia, the form of the aedeagus and the produced spines of the VIIIth segment (male). Kimmins (1951) was in no way satisfied with this arrangement and noted on the card for *Stenoxyethira* in the BMNH index (Hydroptilidae) '? = *Gnathotrichia* Ulmer, 1951'. I noted indepedently of Kimmins the similarity between these two genera when examining type-material of *G. isabellina* Ulmer (UHZIM loan) and concluded that this species, from Java and Sumatra, was probably synonymous with *S. excisa* Kimmins. According to the dates of publication (Kimmins, March, 1951; Ulmer, April, 1951) *S. excisa* takes priority. However, as Schmid (1958) points out, *S. excisa* may truly belong in *Oxyethira*, being closely related by the form of the male genitalia and wing venation to *O. galekoluma* Schmid from Sri Lanka (the venation of the latter approaching that of *G. isabellina* and *O. angustella* Martynov). I agree that there is this similarity in form which is also supprted by the spur formula (0.3.4) and the structure of the thoracic nota, but I do not agree with Schmid that Kimmins's figures of the male genitalia of *S. excisa* are inverted in comparison with those of *O. galekoluma* (Schmid, 1958); on the contrary, it is Schmid who has misinterpreted their orientation.

It would thus seem that *Stenoxyethira* and *Gnathotrichia* should be regarded as synonyms of *Oxyethira*, at least with regard to *S. excisa*. The status of *S. minima* is not so easily resolved - as regards venational and male genitalic characters it could well be a specialised member of *Oxyethira*, although it is the only species so far recorded without a preapical spur on the mid-tibia. This may well prove to be simply a specific or even individual variation; as in most of these problems the solution must await the collection and examination of further material. In conclusion, therefore, it is proposed to retain the genus *Stenoxyethira* for the time being with *Gnathotrichia* as a junior synonym although the latter should probably more correctly be placed as a synonym of *Oxyethira* along with *Stenoxyethira excisa*. In this case the genus *Stenoxyethira* may need to be retained solely for the type-species, *minima*, although this may also prove to belong in *Oxyethira*.

Genus PAROXYETHIRA Mosely (Tribe V. Group C)

Paroxyethira Mosely, 1924: 670. Type-species, *Paroxyethira hendersoni* Mosely, by subsequent designation by Mosely & Kimmins, 1953.

Distribution: New Zealand.

This endemic New Zealand genus contains five species although I believe that further species are at present being described (Michaelis, pers. comm.). Mosely (1924) originally described *eatoni*, *tillyardi* and *hendersoni*; *hintoni* and *kimminsi* being subsequently described by Leader (1972) in which paper a key to all males and females was provided. Leader (1970) also discussed the function of the setal equipment of the early and Vth-instar larvae of *Paroxyethira*, giving very generalised figures of each but no detailed morphological descriptions. *Paroxyethira* is characterised by the unique forms of both the male and female genitalia, especially the elongate inferior appendages and ventral processes of the former, and the general appearance of the larva and its case, The following diagnosis is based on Leader (1972) and Mosely's original material (BMNH collections).

Generic diagnosis

Adult. Forewing length 2.5-3.5mm: anterior tentorial arms reduced to fine strands medially; antennae of approximately 25-40 segments; ocelli 3: thorax* as in Ithytrichia: spur formula 0.3.4: ♀ genitalia a modified oviscapt with sternite VI with a small ventral 'tooth'; posterior margin of sternite VII with a triangular ventral process; tergite VIII deeply excised dorsally and elongate postero-ventrally, almost meeting mid-ventrally; sternite VIII small, appearing as a small lobe just above the projection from VII; segment IX small, mostly concealed by VIII; segment X small, bilobed, each lobe with a short apical cercus: ♂ genitalia (fig. 57) with sternite VII with an elongate flattened ventral process extending beyond the posterior margin of segment IX; segment IX fused, with a deep postero-dorsal excision such that the segment is incomplete dorsally; tergite X absent; inferior appendages basically elongate, concave with apices directed inwards; aedeagus with a very characteristic basal, sleeve-like sheath with the posterior margin produced as a long spine extending almost to the apex of the aedeagus, latter long and slender with a short, broad proximal region which tapers anteriorly to a distinct constriction just before which arisese a spiral process or 'titillator'.

Larva (fig. 93). According to Leader (1972) the larva of Paroxyethira differs from that of Oxyethira only in the possession of a complex spine on the ventral process of the fore-tarsus which resembles the fan-like seta present on the fore-tarsus of Hydroptila (c.f. fig. 120). As in Oxyethira, the legs of Paroxyethira are longer and more slender than those of Hydroptila but apart from these general points no further

* head and thorax, Paroxyethira, fig. 21.

comparisons can be drawn. Leader (1972) states that the five species of Paroxyethira can only be distinguished by the fine sculpturing of the thoracic sternites which, however, tends to be rather an inconsistent feature and thus not a reliable taxonomic character.

Case (fig. 93). 'Purse-type', constructed of secretion only, oblong and sometimes with outward pointing anterior and posterior ventral spines as extensions of the ventral seam by which the case is attached to the substrate (pupal).

Biology. According to Pendergrast & Cowley (1966), the larvae of hendersoni are abundant in vegetation in lakes, ponds and streams where filamentous green algae occur. Leader (1972) briefly gives collecting data for each species.

Discussion

From features of the adult head and thorax and the basic form of the female genitalia, I consider Paroxyethira to be closely allied to the endemic Australian genus Xuthotrichia Mosely. The general morphology and habits of the larvae suggest that it may, along with Xuthotrichia, be an offshoot of the Oxyethira branch of the Hydroptilini.

Genus XUTHOTRICHIA Mosely (Tribe V. Group C)

Xuthotrichia Mosely, 1934a: 139. Type-species, Xuthotrichia ochracea Mosely, by original designation.

Distribution: Australia.

This endemic Australian genus is known from the four original species described by Mosely (1934a) - ochracea, simplex, fimbriata and eskensis; I believe that more species are being described (Alice Wells, in litt.)

and there are specimens of an unidentified (and possibly new) species from Western Australia in the BMNH collections.

The genus is characterised by the unique form of the male genitalia which show considerable specific variation; they are asymmetrical and often very complex and identification of species is very difficult from Mosely's original descriptions. The females have not been described but from examples in the unidentified material in the BMNH collections mentioned above the genitalia appear to bear some resemblance to those of Paroxyethira. The immature stages are unknown although a figure of an unidentified Australian Hydroptilid larva in Riek (1970) greatly resembles that of Paroxyethira in general appearance (c.f. fig. 93) and, if so, may be the larva of Xuthotrichia (see Paroxyethira account). The case of the larva figured in Riek (1970) is constructed of silk and sand grains although, according to Alice Wells (in litt.), the cases of larvae which she believes to be of Xuthotrichia (larvae not described however) are of secretion only but of a slightly different shape to those of Paroxyethira (also of secretion only). It would be necessary to compare specimens of the two genera, however, before any conclusions regarding affinities could be drawn.

The following diagnosis is based on a study of material in the BMNH collections (Mosely's types) and the original descriptions.

Generic diagnosis

Adult. Forewing length 2.5-3.0mm: anterior tentorial arms reduced to fine strands medially; antennae c. 40-segmented; ocelli 3: mesoscutellum similar to that of Hydroptila and Oxyethira (c.f. figs 18, 20); metascutellum pentagonal with slightly anteriorly convergent lateral sides: spur formula 0.3.4: ♂ genitalia (fig. 58) - sternite VII with a moderately long, slender ventral process; segment VIII unmodified; segment IX fused, usually obliquely truncate in lateral view, dorsal and ventral margins more of less excised; tergite X, inferior appendages, subgenital appendages, subgenital plate and bilobed process very variable; aedeagus long and slender, without a median constriction or spiral process but sometimes with additional short lateral processes arising just before apex.

Biology. According to Wells (*in litt.*), the larvae of *Xuthotrichia* occur in all types of still water in Australia such as lakes, billabongs, etc.

Discussion

Xuthotrichia may be closely related to *Paroxyethira* as indicated by adult head and thoracic features (and also, possibly, by the general form of the larva); these genera may in turn be allied to the cosmopolitan genus *Oxyethira*.

Genus TRICHOLEIOCHITON Kloet & Hincks (Tribe V. Group C)

Tricholeiochiton Kloet & Hincks, 1944: 97. Type-species, *Leiochiton fagesii*, Guinard, by monotypy. (Replacement name for *Leiochiton*).
Leiochiton Guinard, 1879: 139. Type-species, *Leiochiton fagesii* Guinard, by monotypy. (Preoccupied by *Leiochiton* Curtis, 1831 in Coleoptera).
Synagotrichia Ulmer, 1951: 81. Type-species, *Synagotrichia fortensis* Ulmer, by original designation. (Syn. n.).

Distribution: W. Palaearctic; SE. Asia (Burma, Indonesia).

The genus *Tricholeiochiton* contained originally only two species, *fagesii* (Guinard), which is known locally from Europe and the U.S.S.R., and *lacustris* Kimmins from Burma (S. Shan States). Examination of type-material of *Synagotrichia fortensis* Ulmer (UHZEM loan) reveals that this genus should be regarded as a junior synonym of *Tricholeichiton*.

The unique larva of *fagesii* was first noticed by Bremi in 1849 and for which he gave an extended description under the name of *Hydroptila flabellifera* in a letter to Hagen which was published by the latter in 1864. Hagen considered the species to belong to the genus *Agraylea* due, possibly, to the shape of the case which was covered with filaments of 'Confervae'(?). However, it is now known that the cases of *Tricholeiochiton* are constructed of secretion only and that Bremi's *H. flabellifera* consisted of a mixed series of *T. fagesii* and *Agraylea sexmaculata* Curtis.

The next reference to the larva was in 1867 when Dr Barker presented a series to the Dublin Microscopical Society as specimens of Diptera. Then, in 1878, Guinard published figures of the larva and, albeit rather crudely, the male genitalia, and named the species *Leiochiton fagesii*. The species has since been variously referred to as *Oxyethira fagesii* and *O. felina* Ris, and was first recorded on the British list by Mosely (1932) who subsequently recognised the synonymy with *L. fagesii* (Mosely, 1939). The generic name was changed to *Tricholeiochiton* by Kloet & Hincks (1944) when it was discovered that *Leiochiton* was preoccupied for a genus of beetles.

The larva of *fagesii* has been described a number of times but not in any great detail. The account given below is based on Lepneva (1964) and a study of material donated to the BMNH by Dr B. Higler (Netherlands) and Dr I.D. Wallace (MCM). A formal description has not been given since it is understood that Wallace (pers. comm.) proposes to publish a full account based on recently discovered British material.

Kimmins (1951) described a second species, *lacustris*, from Burma in which the genitalia (male) are almost identical with those of *fagesii* except for the presence of a long ventral process on the VIIth abdominal sternite. The immature stages of *lacustris* are unknown.

From the form of the male genitalia, wing venation and shape of the metascutellum, *Synagotrichia fortensis* Ulmer, from Indonesia (Sumatra), probably represents a third species of *Tricholeiochiton*. Discovery of the larval stages, however, would confirm this view.

Generic diagnosis

Adult. Forewing length 2.25-3.00mm: anterior tentorial arms reduced to fine strands medially; antennae of c. 37 segments in *lacustris*; ocelli 3: metascutellum pentagonal, lateral sides slightly divergent anteriorly: spur formula 0.3.4: lateral processes of abdominal sternite V absent, basal pit with characteristic sculpturing in *fagesii* (fig. 38): ♀ genitalia an oviscapt (*fagesii*, fig. 200): ♂ genitalia very distinct, but very similar in the three known species (figs 60,199)- sternite VII sometimes with a long, slender ventral process; segment VIII unmodified; segment IX fused, produced ventro-posteriorly (obliquely truncate in lateral view), dorsal and ventral posterior margins deeply incised; segment X forming a dorsal membranous lobe with a pair of postero-ventrally produced lateral processes which partly enclose the aedeagus; inferior appendages small, fused baso-medially, contained within ventral incision of IX and concealed by latero-ventral processes of IX; subgenital plate transverse with down-curved posterior 'lip' and produced antero-ventrally to join the inferior appendages, base of plate with a pair of small seta-bearing processes, junction of plate and inferior appendage produced anteriorly as a slender truncate process; aedeagus short and robust with a distinct median constriction, just before which arises a slender spiral 'titillator' which has a slightly dilated apex (homologies of genitalia uncertain).

Larva (fig. 92). Head long and slender with parallel sides; dorsal ecdysial lines indistinct anteriorly; tentorial pits distinct; 'postmental sclerites' crescent-shaped, undivided, with short blunt postero-median process (fig. 105); mandibles typically subtriangular with slender pointed apices, left with bluntly toothed dorsal blade: thoracic nota paired; three well developed sternites on prothorax only (fig. 129); pleurites with pre-episternite fused in all three segments (according to Lepneva, 1964); forelegs short, tibiae with distinct disto-ventral processes bearing apical spines and a row of short ventral setae; mid- and hindlegs characteristically very long and slender, achieved by elongation of trochanter, femur, tibia and tarsal claw: abdomen long, more slender than in other Hydroptilidae, characteristically curved; tergite on segment IX only; anal prolegs fused to X, anal claw short; dorsal 'rings' present on segments III-VIII.

Case (fig. 92). 'Purse-type', oblong, 'sac-shaped', sides slightly convex, constructed of secretion only.

Pupa. Undescribed but pupal case with two stalked attachment discs at each anterior corner and one at each posterior corner .

Biology. According to Lepneva (1964) the larvae of fagesii inhabit stagnant and slow-moving bodies of water in plant thickets, the pupal cases being attached to the undersides of aquatic plants.

Discussion.

The form of the male aedeagus and the algae-associated habits of the larval stages indicate that Tricholeiochiton is a member of the Hydroptilini. Although obviously very specialised with respect to both the male genitalia and the morphology and habits of the larvae, the general appearance of the latter and the form of the adult head and thorax are suggestive of the genus Oxyethira, of which branch of the

Hydroptilini Tricholeiochiton may be an early offshoot. The distribution of this genus is rather unusual with only two Oriental and one Palaearctic representatives.

DISCUSSION THE TRIBE HYDROPTLINI (V)

The Hydroptilini, as intergreted here, consists of three highly specialised and distinct generic groups which are united on the basis of the form of the male aedeagus and the associations of the larval stages with green filamentous algae. The three groups probably diverged relatively early in the evolution of the Hydroptilini branch although somewhat later than the Ochrotrichiini, Neotrichiini and Orthotrichiini split off from this main stem (vide Chart II). The hypothetical ancestral Hydroptilini larva probably differed little in appearance from that of the present day generalised condition as seen, for example, in Hydroptila, with the slightly laterally compressed abdomen, subequal legs and simple 'purse-type' case; such a condition is also seen in the unspecialised members of the other tribes such as the Ptilocolepinae, Stactobiella, Ochrotrichia and Dibusa. Within the Hydroptilini, however, the form of the larval case varies little from the generalised condition in Agraylea, Allotrichia, Hydroptila, Tricholeiochiton, Paroxyethira and, perhaps, Xuthotrichia, the only specialised genus in this respect being Oxyethira with its distinct 'jug-shaped' cases. The main differences in case-form appear to be associated with corresponding differences in larval morphology which reflect trends towards adaptation to life in vegetation thickets in slow-moving bodies of water. Thus the cases lose any extraneous particles which might weigh them down and the larvae tend to have longer mid- and hindlegs.

Within the Agraylea-group (A), Agraylea and Allotrichia have a temperate (to cool temperate) distribution, Dhatrichia and Microptila are more subtropical(to temperate) while Ugandatrichia is tropical. Hydroptila and Oxyethira are cosmopolitan genera and occur throughout the Americas and through SE. Asia and Indonesia to the Australian region. The endemic Australian and New Zealand genera, Xuthotrichia and Paroxyethira respectively, probably represent descendants of an early branch of the Oxyethira-line which occurred in the Australian region but which was cut off from the mainland leaving the two genera to evolve in isolation ever since. Tricholeiochiton is distinguished by its rather unusual distribution pattern with one western Palaearctic species and two SE. Asian species. The origins of this genus are obscure but, from the general form of the larva, it may again have been derived from an early offshoot of the Oxyethira-line.

The success of the Hydroptilini (in terms of its present day distribution and numbers) may be due partly to its larval associations with green filamentous algae and partly to its tolerance of a wider range of aquatic habitats in comparison with the more specialised Stactobiini and Leucotrichiini and the more restricted Ochrotrichiini and Neotrichiini. The utilisation of algal filaments (i.e. their cell fluid contents) may have opened the pathway from a life restricted to rocky and stony substrates, which is maintained to a certain extent in Hydroptila, to one in vegetation thickets. The latter may have at first been restricted to the banks of streams and larger, moderately flowing rivers but from thence radiated into the more slowly moving waters of backwaters, lakes and ponds culminating in artificial, almost static, bodies of water such as reservoirs etc. The distribution of vegetation-dwellers, or rather their dispersal, may also be enhanced by the accidental transport of the immature stages with the aquatic plants on which they dwell; here again the influence of man may play an important part in the success of these insects (vide the discussions on Agraylea and Tricholeiochiton species in section IV). Hydroptila shows great species variation as to habitat preference (as does Oxyethira to a certain extent); some, such as forcipata and angulata in Britain, favour the more stony fast-flowing streams of the north and west uplands while others, such as sparsa and simulans, occur more frequently in the slower and relatively more vegetated streams and canals of the lower regions of Britain. A complete review of the British Hydroptilid fauna is given in section IV.

In conclusion the Hydroptilini, although superficially seeming to be a somewhat heterogeneous tribe, can be seen to have a relatively recent point of origin along the main Hydroptilinae branch (although this was still geologically quite distant as indicated by the very modern looking fossil amber species of Agraylea and Allotrichia). The group has radiated out to fill a number of aquatic niches in association with green filamentous algae and larger and more slowly moving bodies of water. Early offshoots of the Hydroptilini-line may have given rise to the Ochrotrichiini and Neotrichiini in the Americas(and the unique, red-alga associated, Nearctic genus Dibusa) and the highly specialised Orthotrichiini (q.v.).

Tribe VI ORTHOTRICHIINI Nielsen (stat, n.)

Orthotrichiinae Nielsen, 1948. Type-genus, Orthotrichia Eaton.

Nielsen erected the subfamily Orthotrichiinae for two genera, Orthotrichia and Ithytrichia on the basis of larval morphological and behavioural affinities. Although the adults and larvae are very distinctive for each genus, the larvae do exhibit a number of fundamental similarities which distinguish them from other members of the Hydroptilinae. However, according to certain adult features, such as the structure of the head and thorax and the male aedeagus, the Orthotrichiini appears to have arisen from an early Hydroptilini-type ancestor. I therefore propose to accept Nielsen's original grouping but as a tribe of the subfamily Hydroptilinae and with the inclusion of Ithytrichia remaining open to further speculation; the latter may later be found to form a distinct unit on its own.

The characteristic features of the larvae of the Orthotrichiini are listed briefly below: labium broad and flat; mandibles flattened, tapering; general form of the ventral apotome and 'postmental sclerites'; the thoracic sternites; the comb-like setae of the fore-coxae; the circle of 'rings' on abdominal segment I and the single median caudal filament from segment X.

Genus ORTHOTRICHIA Eaton (Tribe VI)

Orthotrichia Eaton, 1873: 141. Type-species, *Hydroptila angustella* McLachlan, by original designation.

Clymene Chambers, 1873: 114. Type-species, *Clymene aegerfasciella* Chambers, by monotypy. (Synonymised by Flint, 1966).

Javanotrichia Ulmer, 1951: 75. Type-species, *Javanotrichia maeandrica* Ulmer, by original designation. (Syn. n.).

Orthotrichiella Ulmer, 1951: 79. Type-species, *Orthotrichiella ranauana* Ulmer, by original designation. (Syn. n.).

Baliotrichia Ulmer, 1951: 88. Type-species, *Baliotrichia litoralis* Ulmer, by original designation. (Syn.n.).

Distribution: Holarctic; Africa; SE. Asia (to New Guinea).

The genus *Orthotrichia* is a very successful genus with an almost continuous world-wide distribution, although it has not so far been recorded from Central or South America or the Australian region. The genus is well represented in the Palaeotropical regions of Africa and SE. Asia, through Indonesia (Sunda Islands) to New Guinea (Papua) and, possibly, Fiji. The adults are characterised by the uniquely developed asymmetrical male genitalia and the absence of ocelli (c.f. *Hydroptila* which may be distinguished by the presence of post-occipital scent organs in the males). The larvae are associated with aquatic vegetation in standing waters and are highly specialised for feeding on the cell contents of green filamentous algae.

The genus was eredted by Eaton (1873) for *angustella* (McLachlan) and *atra* (Hagen), the latter being transferred to *Stactobia* by McLachlan (1884). *O. tetensii* Kolbe was subsequently found by Neboiss (1963) to be a junior synonym of *Hydroptila costalis* Curtis (vide *Oxyethira* section, tribe V, group C) and Flint (1966) showed *Clymene aegerfasciella* to be a senior synonym of *Orthotrichia americana* Banks.

The larva of *costalis* (Curtis) was described in detail by Nielsen and that of *angustella* by Jacquemart (1962), although no distinguishing features were indicated in the latter work for separating the two species; it should be noted that Jacquemart's figure of the dorsal view of the head of *angustella* does not indicate that the anterior beak is an extension of the labrum and has been drawn pointing in the opposite direction to that as figured by Nielsen.

Regarding the genera described by Ulmer (1951) from the Sunda Islands, larvae are described by Ulmer (1957) for *Orthotrichiella ranauana* and *Baliotrichia litoralis*. The relationships of these two genera, as well as that of *Javanotrichia*, with *Orthotrichia* will be discussed later.

The following generic diagnosis is based on the literature and examination of adult and larval material in the BMNH collections.

Generic diagnosis

Adult. Forewing length 2-4mm; wings markedly attenuate, forewings with a row of black, flattened basal subcostal setae in males of the *angustella*-group;tentorium (fig. 25) complete; antennae of 30-40 segments; post-occipital lobes prominent, subspherical, but not modified as scent-organs; ocelli 0: thorax (fig. 25)- metascutellum characteristically rectangular: spur formula 0.3.4: ♀ genitalia a modified oviscapt (figs 63, 186, 187, 188), segment VIII fused and sclerotized, segments IX and X membranous, IX short: ♂ genitalia (figs 59, 183, 184, 185) characteristically asymmetrical; sternites VI and VII variously with ventral processes or tufts of setae; segment VIII unmodified; segment IX fused, often with asymmetrical, postero-lateral processes; inferior appendages usually small and fused medially, but well developed, porrect and strongly curved in costalis; subgenital appendages indistinct or absent; bilobed process present (bp); tergite X forming a large, asymmetrical dorsal plate, ventrally concave, often with laterally directed dorsal spines; beneath X is a variously shaped, slender, asymmetrical sclerite usually with two asymmetrical processes, one of which is long and slender and lies diagonally beneath X and alongside the aedeagus (according to Nielsen, 1970, a similar structure was described by Ulmer, 1951, for Javanotrichia, Orthotrichiella and Sumatranotrichia); aedeagus very long and slender with distinct proximal and distal halves near the junction of which arises a slender, spiral 'titillator'.

Larva (fig. 94a). Slightly depressed dorso-ventrally: dorsal ecdysial lines of head distinct; postmental sclerites and anterior ventral apotomes as in fig. 110; labrum asymmetrical with a beak-like median process (fig. 94c); mandibles slender, flat, asymmetrical (fig. 114): thoracic nota paired; mid- and hindlegs just slightly longer than forelegs; fore-tibia without a ventral process or modified setae; each tarsus with a distal, flattened, plate-like spur; fore-coxa with comb-like rows of setae; pre-episternite of prothorax free; paired anal sternites present on all three thoracic venters, fused in prothorax (fig. 127): abdomen cylindrical, slightly broader at midlength; segment II with a pair of lateral 'humps'; dorsal 'rings' present on segments III-VIII, segment I with a complete circle of 'rings' near anterior margin; tergite present on segment IX only; median caudal filament in early instars only.

Case (fig. 94b). Of the 'wheat-seed' type, almost circular in cross-section, tapering gradually towards slit-like anterior and posterior openings; convex dorsal surface characteristically ribbed, ventral surface flat.

Pupa. Typically Hydroptilid but mandibles short; pupal case attached by a single attachment disc at each end.

Biology. The larvae prefer slowly running and sometimes almost stagnant water in plant thickets. According to Nielsen (1948) the larva bites into each cell of a filament of green algae and enlarges the hole by inserting the labral beak; the cell contents are then sucked out. This is a more efficient mechanism than that found in *Agraylea*, *Hydroptila* and *Oxyethira*.

Species-groups (see checklist, Appendix, section VIIIC, table 3)

The 36 species may be split into four main groups on the basis of the form of the male genitalia.

1 the *angustella*-group: exclusively 'Old World' with the majority of representatives being recorded from the regions of Africa and SE. Asia (the latter region may include the species originally described by Ulmer, 1951, in *Javanotrichia*, *Baliotrichia* and *Orthotrichiella* from Indonesia); *angustella* is the only truly Palaearctic representative and has a very wide distribution extending from northern Europe (including the British Isles) to northern Africa and from Iberia to the Urals; the group is characterised by the development of the lateral processes of segment IX in the males and the row of subcostal scales on the forewings of the males of most species.

2 the *litoralis*-group: the species mentioned above from Indonesia originally described by Ulmer (1951, 1957) as *Javanotrichia*, *Baliotrichia* and *Orthotrichiella* may form a distinct group; it also includes species described by Schmid (1958) from Sri Lanka.

3 the *costalis*-group: a small 'Old World' group; *costalis* is the most common species and has a wide European distribution (including the British Isles) and has also been recorded from the Sudan, U.S.S.R. and Japan; the group is distinguished by the absence of lateral processes on segment IX and the small, more or less symmetrical inferior appendages in the males.

4 the *aegerfasciella*-group: principally Nearctic in distribution with one well established Palaearctic representative (*tragetti*); the group is characterised by the lateral development of the asymmetrical inferior appendages of the males.

A fifth group may also be recognised:

5 the *kokodana*-group; this consists of two distinct species from Papua, New Guinea characterised by the simplicity of the male genitalia.

Generic synonyms

The genera discussed below are here considered to be junior synonyms of *Orthotrichia*.

Javanotrichia Ulmer contains three species, *maeandrica* Ulmer and *curvata* Ulmer from Indonesia and *dampfi* Ulmer from Egypt. Ulmer (1951) distinguished the genus from *Orthotrichia* solely on venational characters but, as can be seen from other adult features such as the absence of ocelli, spur formula 0.3.4 and the distinctive asymmetrical form of the male genitalia in *Javanotrichia*, these two genera are probably synonymous. Examination of type-material (UHZIM loan) reveals that the structure of the thorax of *J. curvata* is typical of *Orthotrichia*; in addition the male genitalia are very similar to those of *O. avicularis* Kimmins from India. *J. dampfi* greatly resembles other African *Orthotrichia* species, such as *O. benguelensis*, especially with respect to the spinose lateral processes of segment IX in the male. The immature stages are unknown.

Baliotrichia Ulmer contains *litoralis* Ulmer from Indonesia (Bali) and four species from Sri Lanka (Schmid, 1958). As in *Javanotrichia* the genus is only distinguished on minor venational features. According to Schmid (1958) the male genitalia of *B. udawarama* bear a'curious similarity' to those of *O. extensa* Martynov from India while, in my opinion, the genitalia of *B. litoralis* are most like those of *O. avicularis* Kimmins. The larva and case of *B. litoralis*, as described by Ulmer (1957), are unmistakably those of *Orthotrichia* and thus, taking both adult and larval features into account, I propose that *Baliotrichia* be placed as a synonym of *Orthotrichia*.

Orthotrichiella Ulmer is a monotypic genus from Indonesia again distinguished from *Orthotrichia* on minor venational features only. Examination of type-material (UHZM loan) indicates that the two genera are synonymous and this is supported by the appearance of the immature stages as described by Ulmer (1957).

In conclusion, therefore, these three, small tropical genera provide a natural geographical link with the *Orthotrichia* species from the mainland and New Guinea, this genus being previously unrecorded from the Indonesian region.

Discussion

The genus *Orthotrichia* is a specialised and very successful recent member of the Hydroptilinae with a wide continuous present day distribution. It is the only Hydroptilid genus which has a truly tropical component (c.f. the Stactobiini which, although tropical, are confined to the relict cool montane areas of SE. Asia and Africa) and probably owes its success to its tolerance of still water conditions and its efficient larval feeding habits.

Genus ITHYTRICHIA Eaton (Tribe VI)

Ithytrichia Eaton, 1873: 139. Type-species, *Ithytrichia lamellaris* Eaton, by original designation.

Saranganotrichia Ulmer, 1951: 83. Type-species, *Saranganotrichia decussata* Ulmer, by original designation. (Syn. n.).

Distribution: Holarctic.

Ithytrichia is a small genus at present containing only four species. *I. lamellaris* is the most common Palaearctic species while *clavata* Morton, originally described from North America; was found by Tjeder (1930) to occur in Sweden and has since been recorded from France, Great Britain and Finland (Karelia) and may prove to be the only Hydroptilid with a truly Holarctic distribution (c.f. *Agraylea multipunctata* which may involve a species complex). *I. mazon* Ross from Illinois is known from the holotype male only while *bosniaca* Botosaneanu, a Jugoslavian species described from the immature stages only, is regarded as a doubtful species by Botosaneanu (1967).

The larva of *lamellaris* has been described several times, the most detailed account being given by Nielsen (1948). That of *clavata* has not positively been identified although the larva referred to by Needham (1902) and figured by Ross (1944) as well as that described by Wiggins (in press) is probably this species.

Saranganotrichia decussata Ulmer from Indonesia (Java) is known from both the adult and larval stages (Ulmer, 1951, 1957 respectively) of which the latter show distinct affinities with *Ithytrichia* in the form of the case, larval head shape and possession of abdominal 'buds'. However, the male genitalia of *Saranganotrichia* are atypical of *Ithytrichia* and thus cast doubts on the associations of the adults and larvae.

Examination of Ulmer's specimen of decussata (adult) failed to reveal any diagnostic characters as the microscopical preparation was in a very poor condition. Nevertheless, on the basis of the affinities of the larval stages, it is proposed here that Saranganotrichia be placed as a synonym of Ithytrichia until the true identity of the adults are discovered.

The following generic diagnosis is based on the literature and on examination of material in the BMNH collections.

Generic diagnosis

Adult. Forewing length 3mm: tentorium complete (fig. 24); antennae with 20-25 segments; ocelli 3: thorax (fig. 24) with mesoscutellum with anterior margin convex, posterior edge separated from posterior margin of mesonotum by a narrow strip; metascutellum with a strongly convex anterior margin: spur formula 0.3.4: abdominal sternite V with typical setate processes, although shorter than usual and in a faintly sculptured pit (fig. 39): ♀ genitalia an oviscapt, segment VIII with median ventral sclerite: ♂ genitalia distinct (fig. 51); sternite VI sometimes with a short ventral spine; segments VI and VII unmodified; IX and X membranous dorsally, former incomplete ventrally but with lateral sides tapering posteriorly ('side-pieces' of Tjeder, 1930) and with a hook-like structure arising ventrally near the apex; in lamellaris tergite X bears two characteristic parallel rod-like sclerites; inferior appendages slender, arising from antero-ventral margin of segment IX and extending to its lateral apex; subgenital plate with short postero-medial processes bearing short setae and attached basally to the apical hooks of IX; aedeagus long, well developed, with distinct proximal and distal halves divided by a median constriction by which arises the spiral 'titillator'.

Larva (fig. 95). Head broad with slight median lateral bulges in region of 'eyes', flattened, tapering anteriorly both dorso-ventrally and laterally: dorsal ecdysial lines distinct; posmental sclerite semi-spherical, ventral apotome V-shaped, prominent (fig. 106); labrum long and narrow, curved sides tapering anteriorly, anterior margin of sclerite with three shallow indentations, narrow anterior membranous portion with straight anterior margin; mandibles very flat (even more so than in Orthotrichia, c.f. fig. 114), left with short lower blade, serrated upper blade and median brush, apices of both mandibles pointed with a small basal tooth on upper blade: pleurites of prothorax only with three distinct sclerites; prothoracic venter with unpaired anal sclerite (as in Orthotrichia) with lateral ends fused with posterior corners of nota (fig. 125); median oral sternites present on meso- and metathoracic venters only: legs short, subequal, forelegs without trochanteral, femoral or tibial processes; fore-coxae with comb-like rows of setae: abdomen greatly compressed laterally, segment I very small, II with large lateral processes, III-VI with characteristic dorsal and ventral 'bud-like' processes, VII with dorsal process only, VIII with postero-ventral projection; segment I with complete circle of dorsal 'rings'; IX with tergite which projects 'roof-like' above anal prolegs (fused to X) and covering the base of the single median caudal filament;

Case (fig. 95b). This consists of secretion only and resembles a 'pumpkin seed'; narrow anteriorly with an oval ridged opening flanked by the lateral valves, 'slit' only open medially. The thorax of the larva may be extended through the narrow anterior opening and , due to the ability of the thorax and first abdominal segment to rotate on the rest of the abdomen, the case is usually carried horizontally (c.f. the lateral compression of the abdomen). Consequently the ventral surface of the case is slightly more convex while the anterior ventral margin is slightly indented so that the hindlegs may be held free of the case.

Pupa. Typical; mandibles long, without teeth. The pupal case is sealed and held, with the ventral side towards the substrate, by a single median posterior filament with a broad attachment disc, and an anterior cylindrical plug which also broadens into a single attachment disc.

Biology. According to Lepneva (1964) the larvae of lamellaris prefer running water, brooks and rivulets in plant thickets while Nielsen (1948) records them as being distinctly rheophilous, occurring in the strong current on exposed parts of submerged vegetation and smooth, current-swept stones, the cases being held flat against the substrate. Wallace (pers. comm.) has collected Ithytrichia larvae (probably lamellaris) from amongst willow roots in fine silt along with larvae of an Orthotrichia species. According to Ulmer (1957) the larvae and pupae of S. decussata occur in flowing water amongst moss and leaves, in waterfalls, spring-channels and mountain brooks.

Although Nielsen (1948) did not observe the feeding behaviour of lamellaris larvae, he considers them to be detriphagous unlike the specialised algal-feeding larvae of Orthotrichia to which Ithytrichia is supposed to be allied. The flattened labial lobe may be adapted to serve as a shovel for scooping up diatoms and other detritus from the substrate, the food then being conveyed to a groove on the ventral surface of the labrum along which it passes to the pharynx. Nielsen considers the anterior tapering of the head to be associated with such feeding habits while the flattened pointed mandibles, although apparently not adapted for scraping or scooping, may be derived from the Orthotrichia-like condition (c.f. fig. 114), their function being taken over by the labium.

DISCUSSION THE TRIBE ORTHOTRICHIINI (VI)

According to Nielsen (1948) Ithytrichia and Orthotrichia may be derived from a common ancestor which probably was associated with filamentous green algae; this, in my opinion, probably occurred early in the evolution of the Hydroptilini. Orthotrichia became a highly efficient algal feeder living in plant thickets in sluggish to still water while Ithytrichia, possibly in association with the colonisation of rheophilous and semi-exposed habitats, secondarily adopted the detriphagous habit but retained a number of morphological features derivable from algal-feeding ancestors. Such features which are shared by Ithytrichia and Orthotrichia larvae are the broad, flat labium; the flattened mandibles; the form of the ventral apotomes and postmental sclerites (c.f. figs 106, 110) and the thoracic sternites (figs 125, 127); the comb-like setae of the fore-coxae; the complete circle of abdominal 'rings' on segment I and the possession of a single median caudal filament which, according to Nielsen (1948), is present in the early instars of Orthotrichia.

On the basis of these larval affinities, Nielsen proposed the subfamily Orthotrichiinae for Orthotrichia and Ithytrichia and, although the larvae and adults of these two genera have evolved along different lines, I am retaining Nielsen's grouping but as a tribe of the Hydroptilinae. The Orthotrichiini is thus, on the basis of the form of the adult thorax, male aedeagus and fundamental larval associations with filamentous algae, a highly specialised and , probably early, offshoot of the Hydroptilini line. Orthotrichia is a very successful genus which has a wide present day distribution although no species have yet been recorded from the

Neotropical and Australian regions. Ithytrichia is less well represented with only three recognised Holarctic species and possibly one Indonesian and, until the genus is better known, its origins and evolutionary history must remain speculative.

INCERTAE SEDIS

The following group of essentially monotypic and geographically distinct genera have not been assigned to any particular tribe due to the inadequacy of the existing data, the insufficiency or unavailability of well-preserved material or , as in the case of Caledonotrichia and Dibusa, the unique morphological features which cannot be likened to those of any other Hydroptilid genus. All would, however, appear to be members of the subfamily Hydroptilinae; Caledonotrichia and Dibusa have typically Hydroptilid larvae while all have Hydroptilid adult features except Diceminus which is known from the larval cases only. Electrotrichia is only known from Baltic Amber and appears to be a distinct but now extinct genus.

Genus MACROSTACTOBIA Schmid

Macrostactobia Schmid, 1958: 46. Type-species, Macrostactobia elawalikanda Schmid, by original designation.

Distribution: Sri Lanka.

This monotypic genus is known only from the original series from Sri Lanka, of which there is a single paratype male in the BMNH collections. The adult diagnosis given below is based on Schmid (1958), the main characteristic being the unique form of the male genitalia. The larvae are unknown.

Generic diagnosis

Adult. Forewing length 2.5-3.0mm; head without large post-occipital lobes; antennae 18-segmented; ocelli 3: mesoscutellum subtriangular (BMNH specimen): ♂ genitalia with sternites VII and VIII very narrow; [illegible] sternite IX enlarged ventrally but not invaginated into the preceding segments; segment X of two distinct halves; inferior appendages complex and fused along their midlength; aedeagus a long narrow tube.

Biology. The species is reported to inhabit 'rivers at moderate altitudes'.

Discussion

Schmid places *Macrostactobia* at the base of the *Macrostactobia-Parastactobia-Plethus-Chrysotrichia* branch, its primitiveness being indicated by its 'complex' (i.e. more generalised) wing venation and its relatively larger size. The genitalia are stated to exhibit the typical (Stactobiine) characters of the group, the line of evolution resembling that of *Parastactobia* as suggested by the great development of the IXth segment at the expense of those preceding, and the long and rigid appendages.

The male genitalia are very unique but while the antennae are of 18-segments only, as is typical of the Stactobiini, the metathorax does not have the characteristic rectangular form of this tribe. Consequently I can give no positive indications as to the true affinities of this very specialised monotypic, and as yet endemic, genus but can merely stress the need for the examination of additional material.

Genus DIBUSA Ross

Dibusa Ross, 1939: 66. Type-species, *Dibusa angata* Ross, by original designation.

Distribution: Nearctic (N. Carolina, Tennessee, Arkansas, Kentucky, Oklahoma).

This North American genus is known only from the very local type-species. Ross (1939) first described the male and the larva has since been described by Wiggins (in press). The form of the male genitalia is unique within the Hydroptilidae but the associated larvae show unequivocally that Dibusa is a true member of the family. The following generic diagnosis is based on Ross (1939, 1944) and Wiggins (in press) and examination of larvae (USNM loan).

Generic diagnosis

Adult. Forewing length 5.5mm: head and antennae unmodified; ocelli 0; wing venation relatively complete, wings elliptical, ovate; spur formula 1.3.4: ♂ genitalia with IXth segment retracted into VIIIth, with sclerotised sides and a membranous dorsum; Xth tergite fused with IXth, divided into a pair of lateral sclerotised plates separated on the meson by membranous folds and curved downward at the apex to form a short hook; the 'cerci' arise as a small lobe in the middle of the lateral margin at the base of tergite X; inferior appendages biramous, ventral lobe slightly enlarged and upturned at apex, dorsal lobe more slender, out-curved and widest at middle; aedeagus with a filiform basal portion, markedly enlarged near base, and a semimembranous irregularly tapering pointed apex.

Larva (fig. 96), after Wiggins (in press). Head ovoid in lateral view (i.e. not compressed): distinctly paired thoracic nota on all segments; pleurites fused on all thoracic segments; legs short, subequal, robust; tarsal claws distinct (within Hydroptilidae) being stout and strongly curved with a thick, blunt spur basally on each (But smaller than that of Stactobiella, c.f. figs 96c and 97b): abdomen moderately distended, not markedly depressed or compressed, intersegmental grooves distinct; abdominal tergites present only on segment IX; dorsal 'rings' present on segments I-VIII; anal prolegs fused to segment X.

Case.(fig. 96b). Typically 'purse-like', of two adpressed silken valves covered with pieces of the red freshwater alga Lemanea.

Biology. The larvae collected by Neff and Resh (Wiggins, in press) were associated with the red freshwater alga Lemanea, the pupal cases being attached to the base of the algal thallus.

Discussion.

The relationships of Dibusa are not clear because no material was available for an examination of the diagnostic features of the adult head and thorax. However, from the general featurs of the adults, larvae and cases, Dibusa would appear to be a very specialised early offshoot of the tribe Hydroptilini. The relatively complete adult wing venation and the generalised form of the larva with its 'purse-type' case are very primitive features whereas the absence of ocelli, the unique male genitalia and the larval associations with Lemanea (and not the usual, more common green filamentous algae as in the Hydroptilini) indicate specialisation. The more primitive features are suggestive of affinities with Agraylea (Hydroptilini, group A) and Nothotrichia (incertae sedis) (vide Flint, 1967e).

Genus NOTHOTRICHIA Flint

Nothotrichia Flint, 1967e: 56. Type-species, Nothotrichia illiesi Flint, by original designation.

Distribution: South America (Chile).

This monotypic genus has so far only been recorded from Chile, the type being collected in the Cautin Province in 1957 by Professor J. Illies with further specimens being taken by Flint and Cekalovic in 1966.

Flint (1967e) provides the basis of the generic diagnosis given below which is supplemented by observations on the head and thoracic structure as seen in a female specimen of illiesi (USNM loan). The larval stages are unknown.

Generic diagnosis

Adult. Forewing length 3.5mm: head and antennae unmodified; ocelli 3; wings not markedly narrowed but with pointed apices; venation relatively complete; spur formula 1.3.4: thorax (fig. 23); mesoscutellum without transverse suture, anterior margin strongly convex; metascutellum deep, sub-quadrate, but with strongly convex anterior angles: ♂ genitalia (after Flint, 1967e) with segment IX incomplete dorsally, with a broad flap from dorsal angles; Xth tergite membranous, posterior margin trilobate; inferior appendages broad, large, 'mitten-like', with a small baso-dorsal 'thumb'; aedeagus with slightly expanded apex and apico-lateral process arising at midlength and contiguous with the central aedeagal duct, non-spiral 'titillator' present.

Discussion

This unique endemic Chilean genus may represent a descendant of an early offshoot of the Hydroptilini branch which evolved in isolation in this Neotropical region. This is indicated by the relatively complete venation, presence of 3 ocelli, presence of a fore-tibial spur, an undivided mesoscutellum and the non-spiral 'titillator' of the aedeagus. The male genitalia appear to be derived from the basic Hydroptilid form but are specialised in that they are greatly simplified. Discovery of further species and the immature stages may give some insight into the true relationships of this genus.

Genus DICAMINUS Müller

Dicaminus Müller, 1879: 39. Type-species, *Disulus ladislavii* Müller, by subsequent monotypy.

Disulus Müller, 1879b: 142. Type-species, *Disulus ladislavii* Müller, by monotypy. (Synonymised by Fischer, 1961).

Distribution: South America (Brazil).

Müller (1879) described a number of caddis cases from Brazil amongst which were some very distinct cases with two dorsal 'chimneys' and coverd in diatoms. Müller considered them to belong to Hydroptilid larvae and provisionally named the genus *Dicaminus* (no specific name given, however). In all subsequent papers concerning these cases (e.g. Müller 1879b, 1880) he refers to them as being of *Disulus ladislavii*, deriving the name *Disulus* from the Greek meaning 'of two chimneys' (*Dicaminus* being the Latin equivalent); however, according to Fischer (1961) the name *Dicaminus*, being the first published, takes priority over *Disulus* and consequently receives its type-species.

The following description is from the first account in which the species was named (Müller, 1879b) since this was in English.

Description

The strongly laterally compressed oval cases have slit-like anterior and posterior openings and are covered in diatoms. On the dorsal margin they bear two (rarely three) cylindrical chimneys which facilitate the passage of water through the case without, according to Müller, the incessant exertions of the larva as seen in other Hydroptilids where the case simply has slits at either end. The pupal cases are fixed vertically along their whole ventral margin to the upper side of stones 'and often these little houses form large villages of a rather picturesque aspect'.

The larval case is reprted to be 2.5mm long by 0.75mm broad.

Discussion

The relationships and validity of this genus are not known since only the cases of the immature stages have been described. Müller's original material, which has not yet been traced, may contain larvae and pharate adults which will permit a more positive identification.

Genus ORPHNINOTRICHIA Mosely

Orphninotrichia Mosely, 1934a: 138. Type-species, *Orphninotrichia maculata* Mosely, by original designation.

Distribution: Australia (New South Wales).

The holotype of this endemic Australian genus is the only known specimen and it is in such a poor condition (BMNH collection, slide mount) that details of the genitalia and thorax cannot be interpreted clearly.

Mosely erected the genus on the basis of the unique wing venation while the male genitalia also appear to be unlike those of any other Hydroptilid genus. Since the thoracic structure, female genitalia and larval stages are unknown, the genus cannot be placed with any certainty at present. However, from the simplicity of the male genitalia and the form of the aedeagus, with its distinctive spiral 'titillator', the genus may have affinities with the Hydroptilini, differing from *Hydroptila* in the possession of ocelli, the absence of cephalic scent-organs and venation, and from *Oxyethira* in venation and spur formula.

Generic diagnosis

Adult. Forewing length 2.75mm: tentorium incomplete; antennae 32-segmented; ocelli 3: spur formula 0.2.4: ♂ genitalia with sternite VII bearing a short spinous process; segment VIII unmodified; segment IX fused, deeply excised dorsally, appearing bifurcate from above and containing the membranous Xth tergite which tapers posteriorly to a pointed apex; subgenital plate not distinguishable unless it is fused with or replaces the 'inferior appendages'; 'inferior appendages short but slender, fused along almost entire mid-line except for a short distance apically (this structure may represent the subgenital plate, the inferior appendages being absent or vestigial as the two small medio-ventral processes of segment IX); aedeagus with a broad proximal region separated from the longer more slender distal region by a median constriction just anterior to which arises the spiral process or 'titillator'.

Genus CALEDONOTRICHIA Sykora

Caledonotrichia Sykora, 1967: 585. Type-species, Caledonotrichia illiesi Sykora, by original designation.

Distribution: New Caledonia.

This small endemic New Caledonian genus contains two species, illiesi and minor, both described by Sykora (1967) from material collected in 1966 by Professor J. Illies. I have been able to examine adult, larval and pupal material of unidentified and undescribed species of Caledonotrichia kindly loaned to me by Professor H.H. Ross of Athens, Georgia.

The genus is unique within the Hydroptilidae with respect to the very distinctive male genitalia, the corresponding parts of which, as noted by Sykora, are difficult to homologise with those of any other genus. The following diagnosis is based on Sykora (1967) and examination of Ross's material (the larvae have not previously been described).

Generic diagnosis

Adult. Forewing length 2.5-3.0mm: head unmodified; tentorium complete; antennae c. 30-segmented: wings elongate, tapering to narrow apex; base of forewing with costal area thickened with a dense fringe of black androconia, oval patch of androconia between Cu_1 and Rs in centre of wing (males): mesoscutellum without transvers suture: spur formula 0.3.4: ♀ genitalia an oviscapt: ♂ genitalia characterised by the inferior appendages ('claspers' of Sykora, 1967) which are 'bean-shaped' with dorsal and ventral lobes; 'subgenital plate' of Sykora with two long rods; tergite X short, membranous; aedeagus simple, long, rod-like.

Larva (fig. 98). Head relatively short, wide posteriorly, narrowing anteriorly; 'postmental sclerites' difficult to interpret, but apparently U-shaped: body somewhat compressed dorso-ventrally: thorax widest at segment III; mid- and hind-legs held out more to side than in, for example, Hydroptila; legs short, subequal; tibia of each leg with a short apico-ventral process bearing two stout, blunt spines; tarsal claw very small, hook-like; pre-episternite free on all segments, epimeron of each apparently fused; single pair of anal sternites present on prothoracic venter only: abdomen not greatly distended, tapering slightly back from metathorax; intersegmental grooves distinct; dorsal 'rings' present on segments II-VIII; in dorsal view the Malpighian tubules can be seen just under the abdominal cuticle, one pair passes along the abdomen laterally and has a distinct loop in each of segments II-VII (possibly having some special osmoregulatory or excretory function ?); tergite IX present; anal prolegs fused to sides of segment X.

Case (fig. 98b). This consists of secretion only and is dorso-ventrally compressed with a central tubular section (in which the larva lives) surrounded by a folded lateral fringe with which the case is probably fixed to the substrate. The central region has two small dorsal holes (possibly to aid water circulation) and the whole case characteristically 'rolls up', at least in fluid-preserved specimens.

Biology. There is no data available on this subject but, from the general appearance of the larva and its case, the genus would seem to be associated with fast-running water habitats (case fixed, flattened).

Discussion

Caledonotrichia is a very distinct Hydroptilid genus both with respect to the adult and immature stages, neither of which provide any clues as to the relationships of the group. It would appear to have evolved in complete isolation on the island of New Caledonia to which it is endemic.

Genus ELECTROTRICHIA Ulmer

Electrotrichia Ulmer, 1912a: 42. Type-species, Electrotrichia subtilis Ulmer, by monotypy.

Distribution: Baltic Amber (therefore possibly Eocene, of western Palaearctic origin).

This genus is known from specimens of the type-species in Baltic Amber only; no material was available for examination. From Ulmer's original description (ocelli present; spur formula 0.3.4; forewing length 2.0-2.6mm; male genitalia figured) it is impossible to place the genus with any certainty within the Hydroptilidae, although the narrow tapering wings and spur formula suggest that it may have affinities with the Hydroptilinae.

SECTION III C THE PHYLOGENY OF THE HYDROPTILIDAE

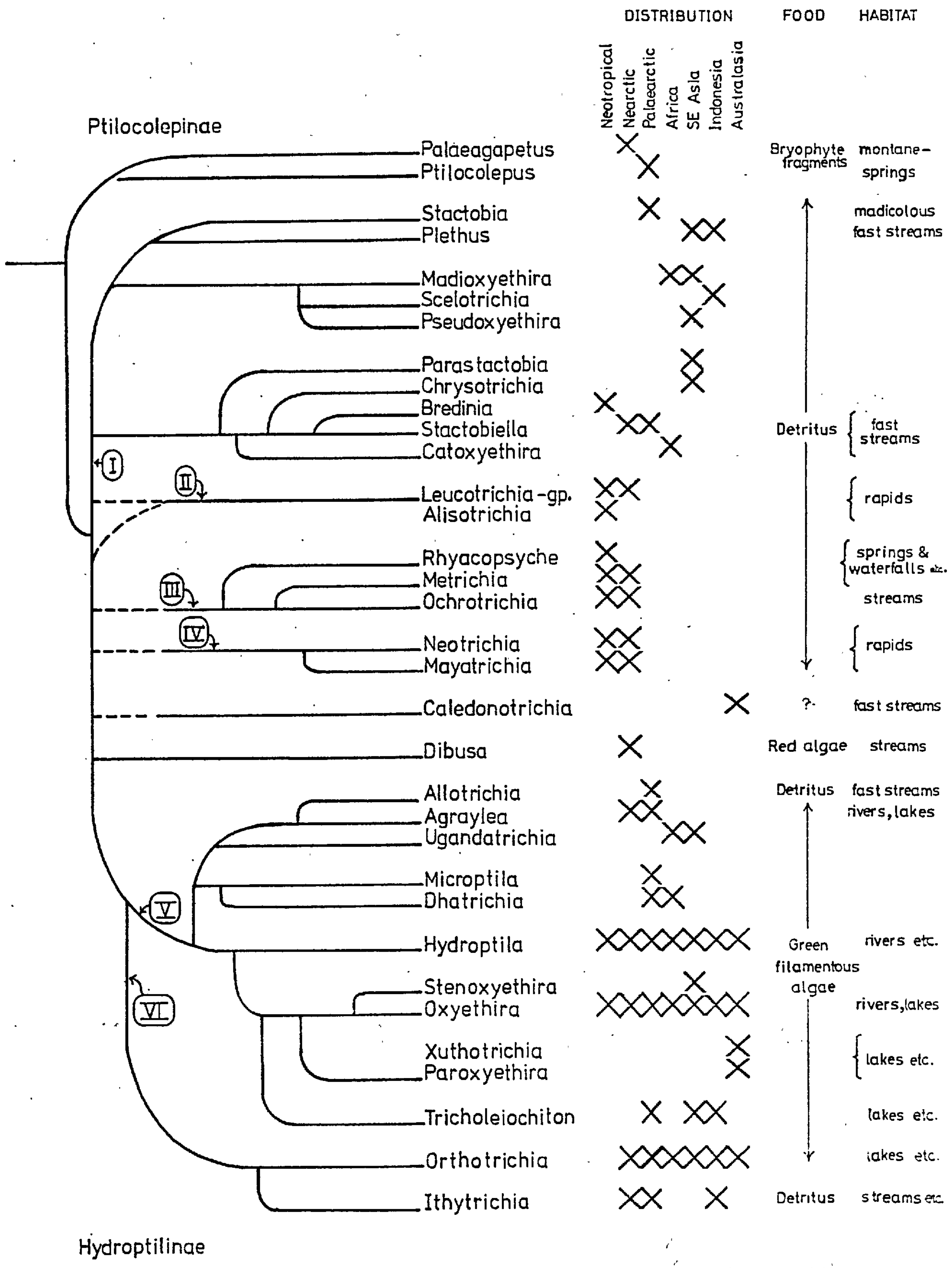
The family Hydroptilidae appears to have arisen early in the evolutionary history of the Trichoptera from a primitive Glossosomatid-like ancestor which adopted the simple 'purse-type' form of larval case. This ancestor soon gave rise to two main lines which resulted in the present day subfamilies Ptilocolepinae and Hydroptilinae of which the former retained the primitive adult features similar to those of the other Rhyacophiloid groups, while the latter adopted the typical adult form generally associated with the Hydroptilidae. The larvae of the Ptilocolepinae also appear to have retained the basic form of the hypothetical generalised Hydroptilid as well as the primitive, cool motane habitat preferences such that the present day representatives are now restricted to cool springs in shaded forest regions in the mountainous areas of western Europe and North America. In the Hydroptilinae, on the other hand, the larvae have radiated into a wide variety of aquatic habitats ranging from the primitive environment of cool montane springs and seeps to the larger moderately-flowing rivers and streams; however, certain groups have become structurally , behaviourally and, probably also, physiologically adapted for life in specialised environments such as the thin surface films of water on rocks and boulders in the splash zones of waterfalls and rapids, rocks in the more rapid sections of rivers and streams and, at the other extreme, vegetation thickets in slowly-moving to large, almost static, bodies of water.

An early member of the Hydroptilinae branch possibly gave rise to two, or perhaps three, subsidiary evolutionary lines, the first leading to the Stactobiini, the second (which may otherwise have been an early offshoot of the Stactobiini branch) to the Leucotrichiini and the third to the Ochrotrichiini, Neotrichiini, Hydroptilini and Orthotrichini. These four tribes seem to have diverged relatively more recently but have each undergone such remarkable larval morphological modifications (as adaptations to specialised ecological conditions) that they superficially appear quite distinct, at least in the larval stages. However, a study of both larval and adult features has revealed a number of basic relationships which, although they have not satisfactorily been fully resolved, are suggestive of the following evolutionary pathways.

The early ancestors of what ultimately led to the group recognised here as the Hydroptilini gave rise independently to two distinct Nearctic-Neotropical tribes, the Ochrotrichiini and the Neotrichiini, perhaps before the larvae adopted associations with green filamentous algae (however, the habits of the larvae of these two tribes are still not very well known; they may have associations with algae or they may be secondarily derived from algal-associated stock). The Orthotrichiini, however, probably arose at a slightly later stage since the larvae, at least those of Orthotrichia, are highly specialised algal feeders and can sometimes even tolerate almost stagnant and polluted aquatic conditions.

The relationships of the genera and generic-groups within each tribe have been discussed in the relevant sections of this systematic account. These and the above major evolutionary steps have been summarised in chart II below.

Chart II. The Phylogeny of the Hydroptilidae - Generic Relationships



I. Stactobiini. II. Leucotrichiini. III. Ochrotrichiini. IV. Neotrichiini. V. Hydroptilinae

VI. Orthotrichiini.

SECTION IIID GENERA TO BE TRANSFERRED TO OTHER FAMILIES OF TRICHOPTERA

As a result of a study of all genera belonging to the Hydroptilidae the following three small geographically restricted groups are considered to rightly belong to other Trichopteran families as indicated:

Padunia Martynov, 1910 (= *Uenotrichia* Tsuda, 1942);to PROTOPTILINAE: GLOSSOSOMATIDAE.

Tsukushitrichia Koboyashi, 1964; possibly a synonym of *Kibuneopsychomyia* Tsuda, 1942; PSYCHOMYIIDAE.

Petrotrichia Ulmer, 1910; possibly related to the primitive, unplaced African genera *Petrothrincus* Barnard and *Hydrosalpinx* Barnard.

Material examined: *Padunia* spp. (loaned from the Lepneva collection by courtesy of Dr L. Zhiltzova, Leningrad); *Petrotrichia palpalis* Ulmer, paratypes, BMNH; the transfer of *Tsukushitrichia* is based on a study of the original description and figures, material being unavailable for study.

Genus PADUNIA Martynov (Protoptilinae: Glossosomatidae)

Padunia Martynov, 1910: 425. Type-species, *Padunia adelungi* Martynov,
by monotypy.

Uenotrichia Tsuda, 1942: 228. Type-species, *Uenotrichia fasciata* Tsuda,
by monotypy.

Distribution: Asia (central and eastern U.S.S.R.; Korea).

This small Asian genus contains four species described by Martynov from the U.S.S.R. (*adelungi*, *forcipata*, *lepnevae* and *bikinensis*) and one from Korea originally described as *Uenotrichia fasciata* Tsuda. Fischer (1971) synonymised these two genera but wrongly gave preference to *Uenotrichia* since *Padunia* clearly should have date priority.

Examination of adult features indicates that *Padunia* , especially with respect to the structure of the thorax, the male genitalia and the shape and venation of the wings, is closely related to *Matrioptila* Ross and *Nepaloptila* Kimmins, primitive members of the Protoptilinae (Glossosomatidae) from the SE. United States and SE. Asia respectively. Figures 26 and 27 show the resemblance of the head and thorax of *Padunia* to those of *Nepaloptila*.

In 1954, Mosely transferred *Mortoniella* Ulmer, *Protoptila* Banks, *Mexitrichia* Mosely, *Canoptila* Mosely and *Anoptila* Mosely, which are essentially Neotropical genera, from the Hydroptilidae to the Glossosomatinae, then a subfamily of the Rhyacophilidae. Subsequently Ross (1956) elevated the group, with the inclusion of *Culoptila* Mosely, to the subfamily Protoptilinae within the Glossosomatidae, at the same time erecting the genus *Matrioptila* for a single primitive species originally described in *Protoptila*.

Representatives of the Protoptilinae occur from southern Canada to central Chile and the subfamily now contains the following new genera: *Campsiophora* Flint, *Cariboptila* Flint, *Mastigoptila* Schmid, *Merionoptila* Schmid and *Tolhuaca* Schmid. The description of *Nepaloptila* Kimmins (1964) from a single Nepalese species furnished the first Palaearctic record of this subfamily and this may now be supported by this discovery of the true identity of *Padunia* Martynov.

Ulmer (*in litt.* to Mosely, *vide* Mosely, 1954) suggested that *Padunia* might also belong with the *Protoptila*-group but, possibly due to not having any material to study, Mosely did not transfer it with the others. He did, however, remark upon its more primitive venation (and its resemblance to *Antoptila*) which is now substantiated if this character is compared with those of *Matrioptila* and *Nepaloptila* which are both considered to be the the more primitive members of the Protoptilinae. Ross (1956) considered the subfamily to have originated in the New World due to the occurrence here of *Matrioptila*, but this theory may now need to be modified on account of the discovery of the equally primitive genera *Nepaloptila* and *Padunia* in the Old World. The possibility that *Matrioptila* and *Padunia* were derived from New World ancestors which passed into Asia, however, cannot be ruled out. The immature stages of *Padunia* are unknown.

Genus TSUKUSHITRICHIA Koboyashi (Psychomyiidae)

Kibuneopsychomyia Tsuda, 1942: 275. Type-species, *Kibuneopsychomyia kibuneana* Tsuda, by monotypy.

Tsukushitrichia Kobayashi, 1964: 211. Type-species, *Tsukushitrichia forficula* Koboyashi, by monotypy.

Distribution: Japan.

Koboyashi originally described this monotypic genus in the Hydroptilidae but stated that it was unique within the family on account of its atypical spur formula (2.4.3), the structure of the Vth abdominal segment and the wing venation. In addition ocelli are absent, the Vth segment of the maxillary palp is long and flexible and the male genitalia are quite unlike those of any other Hydroptilid.

If the spur formula is considered to be derived from the combination 2.4.4, the species keys out in Ross (1944) to the family Psychomyiidae, very close to the genus Psychomyia especially with respect to the wing venation and the distinctive elongate Vth segment of the maxillary palp, the latter always being proportionately shorter in the Hydroptilidae. Of the known species of Japanese Psychomyiids, *Kibuneopsychomyia kibuneana*

Tsuda bears most resemblence to *T. forficula*, both in the venation, which is almost identical, and the general aspect of the male genitalia. It is thus proposed that the genus *Tsukushitrichia* be transferred from the Hydroptilidae to the Psychomyiidae where it may be synonymous with the genus *Kibuneopsychomyia* Tsuda. Examination of material would be necessary to confirm these propositions. Neither the immature stages of *Tsukushitrichia* nor *Kibuneopsychomyia* are known.

Genus PETROTRICHIA Ulmer

Petrotrichia Ulmer, 1910: 43. Type-species, *Petrotrichia palpalis* Ulmer, by monotypy.

Distribution: the Seychelles.

This isolated monotypic genus is known only from the original series of males and females from the Seychelles, the immature stages being unknown. Examination of paratype material in the BMNH indicates that this genus is definitely not a member of the Hydroptilidae, in which it was originally placed, although difficulty has been encountered in assigning it to its proper family.

The adult features are as follows: head without ocelli or post-occipital warts; basal antennal segment elongate; maxillary palpi (male and female) 5-segmented (c.f. Ulmer, 1910); spur formula originally stated to be 0.2.4 but a minute spur has been detected on the fore-tibia; mesothorax elongate (c.f. Hydroptilidae), mesoscutellum ovoid, with a short distance between posterior margins of mesoscutellum and notum; metascutellum elongate, subtriangular; wings with rounded apices (slightly tapered); abdominal sternite V without lateral setate processes or sternal ridge; ♂ IXth segment fused, with a pair of parallel, tapering, ventro-lateral processes (= fused inferior appendages), dorsal cerci each with a short median process and longer lateral baso-ventral processes, aedeagus 'fan-like'.

Following Scott's (1967) key to South African caddis-flies, *Petrotrichia* keys out with *Hydrosalpinx* Barnard and *Petrothrincus* Barnard which have been placed in the Beraeidae and Molannidae respectively. The head and thorax of *Petrotrichia* accord well with those of *Molanna flavicornis* as figured by Wiggins (1968, p. 11, fig. 12). Ross (pers. comm.) is at present studying the relationships of *Hydrosalpinx* and *Petrothrincus* which may prove, at least in the case of the latter, to be primitive relict Trichoptera so far found only in the southern African continent. Ross agrees (pers. comm.) that it is possible that *Petrotrichia* might be a Beraeid or a small Molannid, especially with respect to the 'weird dorsal processes (cerci)' and the venation. Discovery of the immature stages would greatly aid in establishing the relationships of these genera.

Although such a conclusion is very unsatisfactory, it is proposed that *Petrotrichia* should be removed from the Hydroptilidae,on the basis of the great differences in the structures of the head, antennae, thorax, abdominal segment V and the male genitalia, and that it should be grouped, for the time being, with *Hydrosalpinx* and *Petrothrincus*.

SECTION IIIB INDEX TO GENERA (Section III)

The following index is a guide to the generic descriptions given in the Systematics section (III). Names in brackets indicate synonymies, those with asterisks denoting new synonymies. Names are accompanied by tribe, group and page numbers.

Genus	Tr. Gr.	Page	Genus	Tr. Gr.	Page
Ochrotrichia	III	208	Rhyacopsyche	III	213
(Oeceotrichia)*	V B	239			
Orphninotrichia	Inc.S.	286	(Saranganotrichia)*	VI	274
Orthotrichia	VI	268	(Scelotrichia	I C	181
(Orthotrichiella)*	VI	268	Stactobia	I A	162
(Oxydroptila)*	V B	239	Stactobiella	I B	170
Oxyethira	V C	246	Stenoxyethira	V C	254
(Oxytrichia)	V C	246	(Sumatranotrichia)*	VI	239
			(Synagotrichia)*	V C	260
Padunia	+	293			
Palaeagapetus	Ptil.	153	(Tascobia)	I B	170
Parastactobia	I B	178	Tricholeiochiton	V C	260
=(Pasirotrichia)*	V B	239	Tsukushitrichia	+	295
Peltopsyche	II A	194			
Petrotrichia	+	296	Ugandatrichia	V A	235
(Plethotrichia)*	I A	167	(Uenotrichia)	+	293
Plethus	I A	167	Xuthotrichia	V C	258
(Polytrichia)	III	208			
Pseudoxyethira	I C	180	Zumatrichia	II A	192
Ptilocolepus	Ptil.	152			
= Paroxyethira	V C	256			

\+ denotes genus transferred to another family of Trichoptera

STUDIES ON THE HYDROPTILIDAE (TRICHOPTERA): MORPHOLOGY, Phylogeny TAXONOMY AND DISTRIBUTION

Volume 2

By

Jane Elizabeth Marshall, B.Sc.(London), A.R.C.S.

SECTION IV. THE BRITISH HYDROPTILIDAE

Introduction

The last major review of the British Hydroptilidae was made by Mosely (1939) who described the males and nine females of the 27 species known at that time. Since then two species have been added to the list, *Hydroptila lotensis* Mosely and *Ithytrichia clavata* Morton, and Kimmins (1958a) reviewed the British species of the genus *Oxyethira* (excluding *mirabilis* Morton) refiguring the male genitalia and describing the females of all but *distinctella* McLachlan for the first time. Therefore, apart from Kimmins's (1966) checklist and Macan's (1973) key to British Trichoptera, which merely reproduces Mosely's and Kimmins's original figures, very little has been published recently on adult Hydroptilidae. In the following account two species are added to the British list, both having been previously confused with *Hydroptila occulta* (Eaton); *H. martini* sp.n. is the species figured by Mosely (1939) as *occulta* (Eaton) but which, after examination of the genitalia of the male lectotype, has since proved to be distinct, and *H. valesiaca* Schmid which was originally described from the Swiss Alps and of which two specimens from Scotland have recently been discovered in the BMNH and RSM (Edinburgh) collections. The total number of British Hydroptilide now stands, therefore, at 31.

In this review the genitalia of both sexes of all British species, with the sole exception of the female of *H. tigurina*, have been refigured or described for the first time. In a few cases where very little British material was available the figures were drawn from continental specimens except that of the male of *I. clavata* Morton which was adapted from Tjeder (1930). For each species the following information has been given where possible: type data (including the location of the type material); diagnoses of male and female genitalic characters with references to previous illustrated descriptions; references to known larval descriptions; brief biological data (larval and adult) including habitat preferences and flight periods (and life-cycle where known); British distribution, accompanied by a Biological Records Centre map; general distribution and, finally, a discussion. Personal observations regarding collecting data have also been included where available and of interest.

Larval descriptions have not been included here because, although the genera are easily recognised by the general appearance of the larvae and their cases, no reliable specific characters have yet been found except in *Agraylea* where markings of the head and thorax appear to be constant for each of the two British species. References have been given to descriptions given in the literature, the principal works being those of Nielsen (1948), Lepneva (1964) and Hickin (1967), but these vary so much in content, detail and standard that they are of little comparative value. Nevertheless the following species have been described at some time: *Agraylea multipunctata**, *A. sexmaculata**, *Allotrichia pallicornis*, *Hydroptila forcipata*, *H. pulchricornis**, *H. sparsa**, *H. tineoides**, *Orthotrichia angustella**, *O. costalis**, *Ithytrichia lamellaris**, *Oxyethira distinctella*, *O. flavicornis**, *O. frici*, *O. sagittifera*, *O. simplex**, *O. tristella*, *Tricholeiochiton fagesii**. Material is available (in my collection which is now part of the BMNH collection) of those species above marked with an asterisk plus the previously undescribed *Hydroptila occulta* and *H. vectis*. Examples of *Oxyethira distinctella*, *O. frici*, *O. sagittifera* and *O. tristella* may be available from the Lepneva collection in Leningrad (of which I have examined specimens of *O. distinctella* loaned by the courtesy of Dr. L. Zhiltzova) and larvae of *Hydroptila lotensis* may be in the possession of Dr. O.L. Kachalova of Riga, Latvia (crude figures of this species being given in Kachalova, 1972, although requests for loans of material have not yet been answered).

A key is given to the British genera of Hydroptilid larvae but the only reliable way to identify species is to collect associated pupae or, if these have not yet developed, to try and rear the larvae through to this or the adult stage. Fully developed pupae are preferable, however, if larval characters are to be investigated because the pupae at this stage have clearly recognisable genitalia, can be extracted from the pupal case in which the associated larval exuviae remain and which can themselves be removed if care is taken in doing so (see later paragraph on materials and techniques).

This thesis grew out of the original intention of describing the larvae of all the British Hydroptilid species but attempts to locate adequate material and identify associated pupae, which usually proved to be undescribed females, led to a thorough review of the British fauna and the family as a whole; with this foundation, it is hoped that further studies may now proceed so that knowledge of this previously relatively neglected group may be brought up to the same level as that of the other families of Trichoptera.

Collecting techniques and methods of examination.

The most effective method of collecting adult Hydroptilids is by m.v. light in a trap strategically positioned close to water although, contrary to what might be expected from their small size, the imagines can fly distances of a few hundred yards. Once in the trap the adults scuttle about and often seek out small cracks and crevices to hide in and are very difficult to spot but once an 'eye' for them has been developed they can easily be picked out from the rest of the trap material using small individual tubes or, as I have found most effective, a pooter. The latter is not to be recommended, however, in the middle of torrential downpours during violent thunderstorms for sucking up bedraggled insects stuck to completely saturated sheets. During the daytime the adults can be seen, if sought carefully, in the crevices of the bark of tree-trunks and on the walls of bridges or other objects close to the water's edge; they can then be collected with the aid of a pooter. This is, however, a rather tedious process with little return in the way of numbers taken although this may be enhanced by using a sweep-net to sample from the nearby vegetation.

Once collected the insects should then be preserved in alcohol (70%) since it is easier to examine the genitalia, tibial spurs, ocelli and thoracic structures in such material rather than in pinned specimens which are small, delicate and difficult to manipulate. When dealing with pinned material from collections, however, it is usually preferable to potash either the whole insect, or just the abdomen, examine the specimen in glycerol or alcohol and return it to the pin in a small phial of glycerol; if necessary a permanent microscope slide mount can be made, staining usually being unnecessary except, perhaps, with females and pupae which have not developed fully sclerotised genitalia. The usual mounting medium as used in the BMNH is Euparal with chlorazol black or acid fuchsin as stains.

Collecting larvae is relatively simple but involves searching submerged objects such as stones and the undersides of the leaves of aquatic plants, especially water lilies and also thickets of water-weeds. To avoid wasting valuable collecting time searching for these small, inconspicuous larvae in the field it is often advisable simply to collect masses of vegetation in plastic bags which may be sorted through at leisure in the laboratory. Wallace (pers. comm.) has collected a number of larvae of *Ithytrichia* and *Orthotrichia* spp. from among submerged willow roots in silt.

Again the larvae (and pupae) are best preserved in alcohol and extraction of larval exuviae from pupal cases may proceed as follows, although it is likely that a better method can be devised when the need arises: dehydrate whole case through alcohols; final soak in Euparal; transfer to Euparal on slide; open case and carefully extract exuviae adding Euparal essence when necessary; retain or discard case as required and arrange exuviae on slide and position coverslip.

Abbreviations used in the text.

The abbreviations used in this section refer to the following collectors or museums as indicated: B.R.B. (B.R. Baker); G.S.R. (G.S. Robinson); I.D.W. (I.D. Wallace); J.D.B. (J.D. Bradley); J.D.H. (J.D. Holloway); J.E.M. (Jane E. Marshall); J.P.O'C. (J.P. O'Connor); K.J.M. (K.J. Morton); M.C.M. (Merseyside County Museum); M.J.S. (Mary J. Sutherland); P.C.B. (P.C. Barnard); R.A.J. (R.A. Jenkins); R.J.S. (R.J. Spittle).

Checklist of British Hydroptilidae (and index to IV)

Agraylea	Page
multipunctata Curtis	62
sexmaculata Curtis	67
Allotrichia	
pallicornis (Eaton)	71
Hydroptila	
angulata Mosely	44
cornuta Mosely	39
forcipata (Eaton)	30
lotensis Mosely	45
martini Marshall	47
occulta (Eaton)	49
pulchricornis Pictet	32
simulans Mosely	42
sparsa Curtis	36
sylvestris Morton	34
tigurina Ris	28
tineoides Dalman	24
valesiaca Schmid	53
vectis Curtis	26

Orthotrichia	Page
angustella (McLachlan)	55
costalis (Curtis)	58
tragetti Mosely	60
Ithytrichia	
clavata Morton	76
lamellaris Eaton	74
Oxyethira	
distinctella McLachlan	84
falcata Morton	99
flavicornis (Pictet)	91
frici Klapálek	97
mirabilis Morton	81
sagittifera Ris	86
simplex Ris	90
tristella Klapálek	88
Tricholeiochiton	
fagesii (Guinard)	79

Key to the British species of Hydroptilidae (♂♂ and ♀♀)

1 Spur formula 0.2.4., ocelli absent .... Hydroptila 6

\- Spur formula 0.3.4., ocelli present or absent 2

2\. Ocelli absent .... Orthotrichia 32

\- Ocelli present 3

3 Forewing length over 4mm, forewings relatively broad, apices not markedly attenuate ... Agraylea and Allotrichia 37

\- Forewing length 3.0 - 3.5mm, forewings narrow, attenuate 4

4 Segment IX of ♂ genitalia tapering posteriorly, inferior appendages elongate, lying almost entirely ventral to segment IX; ♀ genitalia an oviscapt, segment IX narrow and elongate .... Ithytrichia 42

\- ♂ and ♀ genitalia not as above 5

5 ♂ genital appendages concealed by segment IX, latter oblique in lateral view, aedeagus very large with broad apex (fig. 199); ♀ genitalia an oviscapt but with segment IX short, ventro-posterior margin of segment VIII with median lobe (fig. 200).. Tricholeiochiton fagesii

\- ♂ genitalia concealed within segment VIII; ♀ genitalia an oviscapt but with segment IX reduced, often fused with VIII, totally membranous, internal apparatus highly sclerotised and complex .... Oxyethira 45

6 Males 7

Females 20

7 Fore-femora covered in black hairs; tergite X narrow, constricted at base, tapering to a round apex; inferior appendages small, baso-dorsal process with long apical seta; ventral process of VII long and stout (fig. 145) ....*tineoides*

\- Fore-femora without black hairs; genitalia not as above 8

8 A pair of long black sinuous spines projecting from beneath tergite X; subgenital appendages short, broad in lateral view; inferior appendages short, bifurcate, pointed; ventral process of VII long, pointed (fig. 146) .... *vectis*

\- Genitalia not as above 9

9 Postero-lateral margins of segment IX truncate, strongly ridged with dorsal black hook; inferior appendages fused basally (U-shaped in ventral view), slender, long and slightly up-turned apically (fig. 147) .... *tigurina*

\- Genitalia not as above 10

10 Tergite X short, membranous, quadrate; inferior appendages elongate, slender, up-turned apically; 'superior appendages' elongate, slender, down-curved apically giving an overall 'forcipate' appearance in lateral view (figs. 148, 149) .... *forcipata*

\- Genitalia not as above 11

11 Genitalia appearing very compressed in lateral view; tergite X elongate, slender; subgenital plate broad basally (two-thirds), apical third narrow, tapering to point; inferior appendages elongate, narrow, apices slightly up-turned (figs. 150, 151) .... *pulchricornis*

\- Genitalia not as above 12

12 Tergite X well developed, broad; lateral processes of IX elongate, slender; inferior appendages straight, usually dilated at apex ..... (*sparsa*-group) 13

\- Tergite X membranous, elongate, narrow; lateral processes of IX short, broad; inferior appendages elongate, slightly dilated and down-turned apically with upper apical margin darkly sclerotised; long, slender 'parameres' present alongside aedeagus, sharply up-turned apically .... (*occulta*-group) 18

13 Lateral processes of IX elongate, projecting as far as tergite X, broad basally, oblique in lateral view, concealing the genital appendages; tergite X relatively narrow, apex rounded with slight median excision (figs. 152, 154) .... *sylvestris*

\- Lateral processes of IX relatively short; tergite X broad 14

14 Posterior margin of tergite X sinuous, lateral angles pointed, angles of median excision rounded 15

\- Tergite X not as above 16

15 Inferior appendages with pointed apices (figs. 153, 155) .... sparsa

\- Inferior appendages with dilated apices (figs. 156, 158) .... cornuta

16 Posterior margin of tergite X with shallow V-shaped median cleft, lateral angles pointed; inferior appendages dilated at apex, truncate in lateral view with distinct spot in ventral corner (figs. 157, 159) .... simulans

\- Lateral angles of posterior margin of tergite X rounded; dilated apices of inferior appendages acutely up- and out-turned 17

17 Posterior margin of tergite X with shallow u-shaped median excision; inferior appendages with bluntly produced dorsal corners (figs. 160, 162) ...... angulata

\- Posterior margin of tergite X with a slight median 'nick'; apices of inferior appendages each with a strong up-turned pointed claw and a small dark spot in the ventral corner (figs. 161, 163) ... lotensis

18 Posterior margin of tergite X with deep quadrate median excision; 'parameres' with simple pointed apices; dorso-apical sclerotisation of inferior appendages from approximately the medio-dorsal setae to the dorso-apical angle (figs. 166, 169) .... valesiaca

\- Posterior margin of tergite X with median lobe; apices of 'parameres' variously sculptured; sclerotisation of inferior appendages restricted to apical third 19

19 Median lobe of posterior margin of tergite X well developed, extending beyond lateral angles; apical sculpturing of 'parameres' relatively short, rugose; dorsal arm of lateral process of IX slightly longer than ventral arm; sclerotisation of inferior appendages extending towards ventro-apical angle (figs. 164, 167) .... martini

\- Median process of posterior margin of tergite X small and inconspicuous or absent; ventral arm of lateral process of IX slightly longer than dorsal; apical sculpturing of 'parameres' relatively longer, mosaic-like; apical sclerotisation of inferior appendages not extending around tip (figs. 165, 168) .... occulta

20 Ventro-posterior margin of VIII with two prominent rounded setate lobes, dorsal margin with dark-edged, deep, narrow, anteriorly tapering V-shaped excision (fig. 170) .... tineoides

\- Genitalia not as above 21

21 Ventro-posterior margin of VIII with sub-quadrate excision, the base of which leads to a short median dark line (fig. 171) .... vectis

\- Segment VIII not as above 22

22 Ventro-posterior margin of VIII with short median bifurcate process (fig. 173) .... forcipata

\- Genitalia not as above 23

23 Ventro-posterior margin of VIII with a pair of short setate lobes separated by a slight median excision, dorso-posterior margin extending hood-like beyond ventral (fig. 172) .... *pulchricornis*

\- Genitalia not as above 24

24 Ventro-posterior margin of VIII with short, narrow, rounded lobe; dorso-posterior margin variously excised; sternum VIII with 'mushroom'-shaped sclerite .... *sparsa*-group 25

\- Semi-circular sternite between segments VIII and IX; T- to Y-shaped sclerite on sternum VIII .... *occulta*-group 30

25 Dorsal excision of VIII narrow, deep (fig. 179) .... *sylvestris*

\- Dorsal excision of VIII not as above 26

26 Dorsal excision of VIII shallow, inconspicuous, slightly quadrate (fig. 176) .... *simulans*

\- Dorsal excision of VIII not as above 27

27 Dorsal margin of VIII with two lateral shallow convex excisions (fig. 178) .... *cornuta*

\- Dorsal excision of VIII deep and wide 28

28 Dorsal excision of VIII with marginal ridge, pointed at lateral angles, widening posteriorly to a broad transverse base (fig. 177) .... *angulata*

\- Dorsal excision quadrate, without marginal thickening 29

29 Ventral lobe of VIII short, lateral arms of internal apparatus not extending beyond median process, cross-piece of 'mushroom' with rounded basal angles (fig. 174) .... *sparsa*

\- Ventral lobe of VIII relatively long and slender; lateral arms of internal apparatus extending just beyond median process, cross-piece of 'mushroom' with almost right-angled basal corners (fig. 175) .... *lotensis*

30 Sternite between VIII and IX with small posterior median lobe and 4 long setae; Y-shaped sternite VIII large, with slight apical swellings on lateral arms; internal anterior ridges of segment VIII absent (fig. 182) .... *valesiaca*

\- Sternite between VII and IX without median lobe and with 6 long setae; sternite VIII not as above; internal anterior ridges present on segment VIII ... 21

31 Sternite between VIII and IX broad, ovoid; sternite VIII Y-shaped, relatively narrow; two anterior internal ridges present on segment VIII (fig. 180) ..... *martini*

\- Sternite between VIII and IX semi-circular, narrow; sternite VIII T-shaped, broad, apical angles of cross-piece with short posterior processes; single anterior internal ridge on segment VIII (fig. 181) .. .. *occulta*

32 Males 33

Females 39

33 Forewing with a row of black scale-like setae along base of sub-costa; lateral processes of IX long and slender, almost symmetrical; two slender lateral spines present, left elongate, right short; inferior appendages small, inconspicuous, slightly asymmetrical (fig. 183) .... *angustella*

\- Forewing without row of black sub-costal setae 34

34 Lateral processes of IX absent or inconspicuous; inferior appendages small, heart-shaped, inconspicuous; tergite X relatively broad (fig. 185) .... *tragetti*

\- Lateral process of IX on left only; inferior appendages large, elongate, strongly curved inwards asymmetrical; tergite X relatively narrow (fig. 184) .... *costalis*

35 Segment VIII with short but slender ventro-median membranous process (fig. 188) .... *tragetti*

\- Ventral process of VIII absent 36

36 Dorso-posterior margin of VIII straight, membranous venter with a pair of dark subtriangular patches (fig. 187) .... *angustella*

\- Tergite and sternite of VIII fused; dorso-posterior margin of VIII with small median ovoid excision, sternite with oblique groove (fig. 186) .... *costalis*

37 Males 38

\- Females 40

38 Inferior appendages small, L-shaped with broad bases and slender median and parallel apical processes (fig. 189) .... *Agraylea multipunctata*

\- Inferior appendages large, broad, plate-like 39

39 Apical margins of inferior appendages convex, dark-edged; subgenital plate without asymmetrical processes (fig. 190) .... *Agraylea sexmaculata*

\- Apical margins of inferior appendages concave, slightly more elongate medially, median angles with small, dark, asymmetrical, sclerotised processes; subgenital plate with asymmetrical processes (fig. 191) .... *Allotrichia pallicornis*

40 Segment VIII narrow with ventral, elongate, asymmetrical, slightly oblique groove (fig. 194) ... . *Allotrichia pallicornis*

\- Segment VIII broad with small median ventral sclerite .. 41

41 Ventral sclerite of VIII relatively large, anterior margin convex, posterior margin bilobed; internal apparatus elongate (fig. 192) .... *Agraylea multipunctata*

\- Ventral sclerite of VIII inconspicuous, merely represented by a very narrow, U-shaped, sclerotised ridge; internal apparatus very short with median crown-like ring (fig. 193) .... *Agraylea sexmaculata*

42 Males 43

\- Females 44

43 Pair of dark parallel dorsal rods; inferior appendages broad, parallel, apices truncate with dark spot on outer corner; apex of subgenital plate bilobed (fig. 195) .... lamellaris

\- Dorsal rods absent; inferior appendages sinuous, apices pointed; apex of subgenital plate produced as a single short process (fig. 196, after Tjeder, 1930) .... clavata

44 Sternite VIII with trilobed posterior margin (fig. 197) .... lamellaris

\- Sternite VIII with convex anterior margin, anterior margin with wide brim (fig. 198) .... clavata

45 Males 46

\- Females 53

46 Segment IX reduced essentially to its marginal framework of which the two dorsal arms project as a pair of slender spines alongside the apex of the aedeagus; subgenital plate broad, slightly bilobed with a pair of subapical ventral patches of concentric sclerotised rings; inferior appendages short, fused basally, rounded apically, each with a short apical seta and a slender seta-bearing baso-dorsal process; apex of aedeagus dilated with concentric inner lines (figs. 201, 202) .... mirabilis

\- Segment IX well sclerotised, annular 47

47 Posterior margin of segment VIII with a pair of dorso-lateral slender digitate processes, apices bi- or trifurcate 48

\- Dorso-lateral processes of VIII absent 49

48 Segment VIII elongate, longer than IX; lateral processes of IX produced as long slender spines; subgenital appendages slender, tapering apically; inferior appendages truncate with finely serrate (or setate) edges (fig. 203) .... *distinctella*

\- Segment VIII shorter than IX; lateral processes of IX thin and rounded apically, each giving rise internally to a strong sinuous spine; subgenital appendages broad basally with strongly in-curved, short medio-apical processes; inferior appendages with short up-turned processes (fig. 204) .. *sagittifera*

49 Lateral processes of segment IX sharply curved inwards (fig. 205) .... *tristella*

\- Lateral processes of IX completely absent 50

50 Lateral apical margins of segment VIII rounded and neither hooked inwards nor armed with stout black spines (fig. 206) .... *simplex*

\- Lateral apical margins of VIII hooked inwards or with stout spines 51

51 Lateral margins of VIII strongly hooked inwards, dorsal margin with a pair of short, blunt setae-bearing processes (fig. 207) .... *flavicornis*

\- Lateral margins of VIII armed with stout black spines .. 52

52 Lateral spines of VIII (3) relatively long; small ventral plate with a bilobed apex; subgenital appendages with short out- and down-turned hooks (fig. 208) .... *frici*

\- Lateral spines of VIII (2 or 3) short; ventral plate trilobed; median ventral process with acute, up-turned apex; apices of subgenital appendages blunt (fig. 209) .... *falcata*

53 Internal apparatus extremely elongate, narrow, projecting anteriorly well into segment VI (fig. 210) .... *mirabilis*

\- Internal apparatus comparatively short 54

54 Tergites VIII and IX distinct, internal apparatus elongate 55

\- Tergites VIII and IX fused, internal apparatus broad, quadrate 56

55 Postero-ventral margin of VIII with broad V-shaped median excision, internal apodemes of IX (?) short, strongly curved outwards (fig. 212) .. *sagittifera*

\- Postero-ventral V-shaped excision of VIII relatively narrow and deep; internal apodemes of IX (?) comparatively longer and less strongly curved (fig. 211) .... *distinctella*

56 Sternum VIII with a small, dark, median sclerotised patch (fig. 213) .... *tristella*

\- Sternum VIII without such a patch 57

57 Lateral margins of tergites VIII and IX (fused) strongly concave (fig. 215) .... *flavicornis*

\- Lateral margins of tergites VIII and IX not concave 58

58 Posterior sclerites of internal apparatus slender and convergent apically (fig. 214) .... *simplex*

\- Posterior sclerites of internal apparatus broad and plate-like 59

59 Posterior lobes relatively faint, subtriangular, almost convergent apically; internal apparatus narrow (fig. 216) .... *frici*

\- Posterior lobes dark, distinct, comma-shaped, divergent basally and apically (fig. 217) .... *falcata*

Key to the British genera of Hydroptilidae larvae (7th-instar)

1 Abdominal segments II-VIII with dorsal and ventral median sucker-shaped processes; case constructed of secretion, sac-shaped, oval ('pumpkin'-seed) (fig. 95) .... *Ithytrichia*

- Abdominal segments without median processes; case of different shape 2

2 Labrum asymmetrical; abdominal segment II with lateral processes; case with deep grooves and ridges on the convex dorsal surface and a flat ventral surface (fig. 94) .... *Orthotrichia*

- Labrum symmetrical or slightly asymmetrical in membranous part only; no lateral processes on abdominal segment II, case laterally compressed 3

3 Abdomen straight or almost straight, with transverse folds on the middle segments; case constructed of secretion and algae or minute sand grains 4

- Abdomen curved; segments without transverse folds; case of secretion only 6

4 Smaller, 3.1 - 4.1 mm; case bean-shaped with slightly concave ventral sides, constructed of secretion and sand-grains, diatoms or silt-particles (fig. 90) .... *Hydroptila*

- Larger, 4.5 - 5.5 mm; case oval, broader in the middle and at the ends (fig. 89) 5

5 Sclerites of head and thorax very pale (light ochreous), barely discernible and devoid of markings .... *Allotrichia*

\- Sclerites pale yellow with brown markings .... *Agraylea**

6 Mid and hind legs moderately long, 2-3 x fore legs; case jug-shaped (fig. 91) .... *Oxyethira*

\- Mid and hind legs very long, 4-5 x fore legs; case sac-shaped (fig. 92) .... *Tricholeiochiton*

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*The two species of *Agraylea* may be readily distinguished by the line of four dark brown spots on the dorsal surface of the head capsule in *A. sexmaculata* which is absent in *A. multipunctata* (Barnard, 1971).

Hydroptila tineoides Dalman

Hydroptila tineoides Dalman, 1819, *K. svenska VetenskAkad. Handl.* 40: 126-127, pl. 6, figs. 1-4.

Phrixocoma femoralis Eaton, 1873, *Trans. ent. Soc. Lond.* 1873: 136, pl. 2, fig. 1a, pl. 3, figs. 5-5b.

Hydroptila longispina McLachlan, 1884, *Rev. Syn. Add. Suppl.* 1884: 71, pl. 7, figs. 1-3.

Type data. Sweden; "Habitat in monte Kinnekulle ad littora lacus Wenneri". Original type lost, neotype from type-locality ('topotype') collected by Prof. Boheman (no date given) and designated by Forsslund (1955). Neotype of *H. tineoides* in Riksmuseum, Stockholm.

Lectotype ♂ and lectoallotype ♀ of *Phrixocoma femoralis* Eaton, lectotype ♂ and lectotype ♀ of *Hydroptila longispina* McLachlan all designated by Kimmins (1957) and in BMNH collections.

Diagnosis. ♂ characterised by distinct black hairs on the fore-femora. ♂ genitalia, fig. 145 (Eaton, 1873; McLachlan, 1880, as *femoralis* and *longispina*; Martynov, 1924, 1934; Mosely, 1939; Macan, 1973); tergite X narrow, spatulate, with convex lateral sides tapering posteriorly; segment IX with elongate slender lateral apodemes each continuing dorso-posteriorly as a strongly developed lateral ridge; inferior appendages short, 'down-hooked', each with a seta-bearing baso-dorsal process; stout, elongate, ventral process of sternite VIII with serrate apex truncate in lateral view.

♀ genitalia, fig. 170 (Mosely, 1939; Macan, 1973): segment VIII elongate and narrow; ventro-posterior margin (VIII) with two lobes, each bearing three apical setae; dorso-posterior margin (VIII) with a deep, narrow median cleft, the median angles of which are strongly pointed apically.

Larva: (Silfvenius, 1904; Nielsen, 1948; Lepneva, 1964; Hickin, 1967).

Biology. Lakes and running water (Mosely, 1939). Shallow water on stony banks of lakes, large stagnant waters and also (although in fewer numbers and possibly of a different species) fairly swift-flowing waters (Nielsen, 1948). Stony shores of lakes, rivers and brooks (Forsslund, 1955). Lakes, streams and brooks (Nybom, 1960). Lakes, rivers, rivulets, on stones, sometimes on plants (Lepneva, 1964).

British distribution (map 1). Widely distributed and abundant; perhaps the commonest British species of *Hydroptila*.

General distribution. British Isles; northern and central Europe (including the Faroes); Italy, Yugoslavia and Bulgaria; Algeria.

Discussion. Although widely distributed and abundant, *tineoides* is the only western Palaearctic representative of the *tineoides*-group, all other members of which (except, perhaps, *moselyi* Ulmer from Peking, China) are exclusively Nearctic. The group is characterised by the distinctive form of the male genitalia (fig. 55), the male of *tineoides* being further distinguished by the dense, black, hairy fringes of the fore-femora.

The observation that this is, perhaps, the commonest British species of the genus *Hydroptila* is supported by the fact that most of the material of this genus sent to me for identification has proved to be of *tineoides*. Locality data indicate that this species prefers natural bodies of water to the more artificial ponds, canals and streams; its occurrence thus reflects its true pattern of distribution which has been relatively unaffected by the activities of man.

Hydroptila vectis Curtis

Hydroptila vectis Curtis, 1834, *Phil. Mag.* 4: 217.
Hydroptila maclachlani Klapálek, 1891, *Sber. K. böhm. Ges. Wiss. Math.-nat. Kl.* 1890: 177-181, 186, 190, pl. 7, figs. 1-4, pl. 8, figs. 1-8.

Type data. England; Isle of Wight; "15 Aug. on the wet moss covering a spring in Ventnor." Lectotype ♂ designated by Neboiss (1963), abdomen mounted on microscope slide T-122 and in the Curtis Collection, National Museum of Victoria, Australia.
Diagnosis. ♂ genitalia, fig. 146 (Klapálek, 1891; Morton, 1893; Martynov, 1924, 1934; Mosely, 1939; Jacquemart & Coineau, 1962; Neboiss, 1963; Macan, 1973): tergite X narrow, short, quadrate and membranous; segment IX with short, slender, pointed ventro-lateral processes; inferior appendages short, bifurcate; 'subgenital appendages' short and broad in lateral view, slightly curved outwardly and ventrally; characteristic pair of slender black up-curved spines arising dorso-laterally

from segment IX (or X?); sternite VII with slender, apically pointed median process; aedeagus short, truncate.

♀ genitalia, fig. 171 (Mosely, 1939; Jacquemart & Coineau, 1962; Macan, 1973): ventro-posterior margin of segment VIII with a pair of small lateral processes, each bearing four to five stout bristles; short, longitudinal median slit on venter VIII.

Larva: (Klapálek, 1893; Silfvenius, 1904; Jacquemart & Coineau, 1962; Lepneva, 1964).

Biology. 'Limnimadicolous' and 'bryomadicolous' (Vaillant, 1955). Brooks and rivulets, mainly in calm places among vegetation or on stones (Lepneva, 1964). Larvae plentiful under stones and among masses of *Fontinalis* (Philipson, 1955). Attached to substrate in moderate flow, stony bottom with *Ranunculus* clumps, 2" - 2' deep; attached to *Cladophora*-covered stones in fast flow; moderate flow, 1' - 2' deep, large boulders and gravel (Severn - Trent, 1974, P. Woodiwiss, *in litt.*). In the British Isles the adults occur mainly between July and October, although some records have been taken in June and even May.

British distribution. (map 2). Widely distributed throughout Great Britain from central Scotland to Land's End, Cornwall; not so far recorded from East Anglia, north and central Wales or Ireland.

General distribution. Throughout Europe (except Norway, Denmark, Poland, Rumania and Sicily), Atlantic Islands, Iran, Israel, Pakistan. *H. vectis* v. *corsicanus* Mosely occurs in Corsica.

Discussion. *H. vectis* is characterised by the unique form of the male genitalia, especially by the black dorsal spines, the 'subgenital appendages' and the bifurcate inferior appendages. The only closely related species is *viganoi* Botosaneanu from Israel.

The southerly distribution of this species in Great Britain, and the Palaearctic region in general, may be associated with its preference for living amongst moss and other aquatic vegetation growing in slowly moving brooks and streams, such habitats often occurring in lowland regions. *H. vectis* may therefore be adapted to milder climates and hence may tolerate latitudes relatively nearer the Equator but at slightly higher altitudes.

Hydroptila tigurina Ris

Hydroptila tigurina Ris, 1894, *Mitt. schweiz. ent. Ges.* 9: 133-134, 3 figs.

Type data. Switzerland; Zürich; August, 1888; "by the pillars of the railway bridge in Zürich" ("an den Pfeilern der Bahnofbrücke in Zürich"). Type in the Ris Collection, Zürich; six paratypes in the BMNH collections.

Diagnosis. ♂ genitalia, fig. 147 (Ris, 1894; Mosely, 1937*a*, 1939): characterised by the unique lateral processes of segment IX which are sinuous in dorso-ventral view and have broad, truncate apices which are produced dorsally, as short, but strongly down-curved, spines and have strongly ridged posterior margins; segment IX deeply excised dorsally and ventrally, the former surrounding the short, quadrate membranous Xth tergum and the latter bearing the U-shaped inferior appendages (dorso-ventral view), each being elongate and narrow with an up-curved apex; aedeagus with a distinct sub-apical spiral process.

♀ genitalia: undescribed but examples may be in Zürich and in the King Collection, Glasgow University.

Larva: unknown.

Biology. Unknown. Swiss and British imagines taken in August.

British distribution. (map 3). Ambleside, Westmorland.

General distribution. Known only from the type-locality, Zürich (Switzerland) and from Ambleside (England).

Discussion. The males of *tigurina* are easily recognised by the distinct form of the genitalia characterised by the postero-lateral processes of segment IX. The females are unknown, the only specimen of this sex present in the BMNH collections (paratype) having genitalia identical to those of *tineoides* and therefore not described here. Correctly associated examples may be present in the Ris Collection in Zürich and the King Collection in Scotland (according to Mosely, 1937*a*, specimens from the latter are present in Glasgow University).

The only British examples of *tigurina* were taken by King in August, 1881 from Ambleside (King, 1895; Morton, 1904), five specimens of which are in the BMNH collections. This is the material referred to by Mosely (1939) who, however, erroneously states that it is from 'Northern Scotland' - this should read 'Northern England'.

The distribution of *tigurina* suggests that it is a relict species surviving in isolated colonies in the higher regions of northern Europe. Although it has not been recorded since the end of the last century, the species may still occur in remote montane regions of northern Europe as yet unexplored entomologically.

Hydroptila forcipata (Eaton)

Phrixocoma forcipata Eaton, 1873, *Trans. ent. Soc. Lond.* 1873: 135, pl. 3, figs. 3-3c.

Hydroptila forcipata (Eaton) McLachlan, 1880, *Rev. Syn.* 1880: 513, 514, pl. 58, figs. 1-4.

Type data. England; Mappleton, near Ashbourne, Derbyshire; 9-10.vi.1871; A.E. Eaton. Lectotype ♂ and lectoallotype ♀ designated by Kimmins (1957) and in the BMNH collections (both pinned, entire and with abdomens not dissected).

Diagnosis. ♂ genitalia, figs. 148, 149. (Eaton, 1873; McLachlan, 1880; Martynov, 1913, 1924, 1934; Mosely, 1939; Macan, 1973): tergite X small, quadrate, membranous to either side of which arise strongly chitinised elongate, slender, downwardly curved, forcipate appendages, each with small baso-ventral process, inferior appendages elongate, moderately stout, apices directed inwardly and dorsally between forcipate appendages.

♀ genitalia, fig. 173 (Mosely, 1939); segment VIII with slight median ventral excision containing a pair of short, slender, setae-bearing, divergent processes.

Larva: (Fahy, 1971).

Biology. Rapids (Nybom, 1960). British records indicate an association with fast flowing water in streams and rivers in hilly or montane regions; this species has twice been found with Allotrichia pallicornis which is also considered to be an inhabitant of similar aquatic environments.

Adults have been recorded in Britain between May and September, peak numbers occurring in June, tailing off slightly in July and August and with a few specimens taken in April and October.

British distribution. (map 4). H. forcipata is widespread and abundant throughout the British Isles, especially Scotland and central England, although the species has not yet been recorded from East Anglia. It appears to be very common throughout Ireland.

General distribution. British Isles, Scandinavia, central Europe, the Balkans, Spain, Italy, European U.S.S.R.. According to Nybom (1960), forcipata is rare in Finland.

Discussion. This species may be readily distinguished by the characteristic forms of both male and female genitalia. The association of forcipata with faster-moving bodies of water is reflected in its British distribution pattern; like Allotrichia pallicornis, it occurs mainly in the north and west and in the higher regions where swifter-moving streams flow in the south of England such as at Forest Row (Sussex) and on the River Mole at Fetcham (Surrey). There are many recent records of forcipata which thus indicate that it is a very successful and well established species.

Hydroptila pulchricornis Pictet

Hydroptila pulchricornis Pictet, 1834, *Recherches Phryganides* 1834: 224-225, pl. 20, figs. 10a-e.

Phrixocoma pulchricornis (Pictet) Eaton, 1873, *Trans. ent. Soc. Lond.* 1873: 134, pl. 3, figs. 2-2b.

Type data. Pictet merely states that the species "lives on stones in running water in our neighbourhood" and therefore the type-locality is probably in the environs of Geneva, Switzerland. The location of the type-material is unknown, but it is possibly in the Pictet Collection in the Muséum d'Histoire Naturelle, Geneva (see discussion below).

Diagnosis. ♂ genitalia, figs. 150, 151 (Eaton, 1873; McLachlan, 1880; Martynov, 1924, 1934; Mosely, 1939; Macan, 1973): tergite X elongate, slender, membranous; inferior appendages elongate, narrow with slightly up-curved apices, slightly divergent in dorso-ventral view; subgenital plate elongate, proximally relatively wide but tapering abruptly to a narrow pointed slightly down-curved apex for distal third of length.

♀ genitalia, fig. 172 (Mosely, 1939): dorsal margin of segment VIII projects hood-like beyond ventral margin, former with slight, concave median indentation, latter sinuous with two distinct convex setae-bearing lobes; ventral sclerite absent.

Larva: (Pictet, 1834; Silfvenius, 1904; Lepneva, 1964).

Biology. Lakes (Mosely, 1939). Rivulets and lakes, among riparian vegetation (Lepneva, 1964). Lakes, ponds, rivulets and brooks (Nybom, 1960).

In Britain the adults emerge between May and September with most records from June to August and with one odd record from the R. Darenth, Kent, in April 1867.

British distribution. (Map 5). Widely distributed throughout the British Isles, this species has recently been recorded for the first time from Ireland by O'Connor (*in litt.*, data to be published later). *H. pulchricornis* is by no means a common British species and I have only one recent record of a single specimen from Kinrara Marsh, Alvie, Inverness-shire, 1968 (RJS). Although not indicated on the map, *pulchricornis* has been recorded from W. Kent, R. Darenth (1867), London and Hertfordshire (1859) but has not so far been taken in north Wales or south-west England. Locality data indicate that this species prefers larger natural or semi-artificial lakes and slowly moving rivers such as are found in the Lake District, Yorkshire Dales, Scottish lochs, Fenland and south-east England (e.g. Windsor Park and Hillbarn Pond, Berkshire and Virginia Water, Surrey).

General distribution. British Isles; throughout north and central Europe, Italy and Israel; common in south and central Finland (Nybom, 1960).

Discussion. *H. pulchricornis* is a very distinct member of the British species of *Hydroptila* with respect to the form of the male and female genitalia. It appears to be a local but widespread north to central western Palaearctic species, preferring larger and more slowly moving bodies of water.

As implied above, the type of Pictet's *pulchricornis* has not yet been located and the species is not listed in Botosaneanu & Schmid's (1973) paper on the Trichoptera in the Pictet collection in the Muséum d'Histoire Naturelle, Geneva. The true identity of this species is thus in some doubt and, according to McLachlan (1880), the present interpretation of *pulchricornis* originated with Hagen (1859) who may have based his views on those of Kolenati (1848), McLachlan only having seen specimens examined by Hagen and Eaton. However, unless the discovery of Pictet's type should prove otherwise, the present accepted identity of this species must remain unchanged.

Hydroptila sylvestris Morton

Hydroptila sylvestris Morton, 1898, *Entomologist's mon. Mag.* 34: 107-108, figs. 1-3.

Type data. Scotland: "Taken in July by beating pine trees on the shores of Loch Morlich, Glen More, Inverness-shire, 1046 feet (Morton & King), a large and beautiful lake surrounded by extensive pine forests" (Morton, 1898). The location of the type is unknown, but it is possibly one of the two male specimens in the Royal Scottish Museum, Edinburgh, in the Morton Collection. 1♂ paratype in BMNH collection (ex McLachlan Collection) labelled "Rothiemurchus, July 1896".

Diagnosis. ♂ genitalia, figs. 152, 154 (Morton, 1898; Mosely, 1939; Macan, 1973): tergite X long and narrow with deep V-shaped median cleft and strongly convex lateral angles;

inferior appendages narrow, slightly broader medially with short, curved apical claw, small median ventral spot; very characteristic lateral processes of segment IX projecting beyond tergite X, with elongate dorsal arm and short ventral arm in lateral view.

♀ genitalia, fig. 179 (Mosely, 1930; Macan, 1973): ventral sclerite of segment VIII characteristically fan-shaped; dorsal excision of posterior margin of VIII deep but narrow.

Larva: unknown.

Biology. Unknown. Adults recorded from Britain in July and August.

British distribution. (map 6). Known from only five records, three from Inverness-shire (Aviemore, Rothiemurchus and L. Morlich, 1896) and two from the Lake District (Ambleside, 1881 and R. Braythay, nr. Ambleside, 1943). The species has not been recorded since although, according to Mr. D. Jacques (*in litt.*), a single ♂ specimen was taken inside a car near the R. Avon, Hampshire in May, 1968 (material not examined, therefore record not shown on map).

General distribution. Great Britain and France, the latest record being from the Pyrenees (Décamps, 1967).

Discussion. *H. sylvestris* is distinguished from all other British *Hydroptila* species by the lateral processes of segment IX of the male genitalia. The female is characterised by the shape of the ventral sclerite and the shape of the dorso-posterior margin of segment VIII although I am not wholly satisfied with my interpretation of the latter as the drawing was made from the single female specimen in the BMNH collection which was mounted on a microscope slide by Mosely, the details of which were very difficult to discern accurately.

H. sylvestris is a very rare and local species which probably once had a widespread north European distribution but is now restricted to the higher regions of Scotland and northern England and the French Pyrenees. The species has not been recorded in Great Britain since 1943, despite recent collecting trips to the type-locality and environs by both R.J. Spittle (1966, 1967, 1968) and myself (1975).

Hydroptila sparsa Curtis

Hydroptila sparsa Curtis, 1834, Phil. Mag. 4: 217.

Phrixocoma sparsa (Curtis) Eaton, 1873, *Trans. ent. Soc. Lond.* 1873: 133, pl. 2, figs. 1-1b, pl. 3, figs. 1-1b.

Hydroptila brunneicornis Stephens, 1836, *Ill. Brit. Ent.* (Mandibulata) 6: 152.

Type data. ♀ lectotype labelled "July Scotland", designated by Neboiss (1963); the paralectotype ♂ labelled "6 Aug. Dublin" is *Hydroptila angulata* Mosely according to Neboiss (1963). The type material is in the National Museum of Victoria; lectotype ♀ abdomen, microscope slide T-124; paralectotype ♂ (*angulata*), microscope slide T-123.

Diagnosis. ♂ genitalia, figs. 153, 155 (Eaton, 1873; McLachlan 1880; Mosely, 1939; Macan, 1973): posterior margin of tergite X sinuous with pointed corners and slight median incision; inferior appendages narrow, tapering posteriorly. ♀ genitalia, fig. 174, (Mosely, 1939; Neboiss, 1963; Macan, 1973): dorsal excision of posterior margin of segment VIII rectangular, deep and broad, lateral sides parallel.

Larva. (Pictet, 1834; Klapálek, 1897; Silfvenius, 1904. Hanna, 1961; Lepneva, 1964; Hickin, 1967).

Biology. Running water (Mosely, 1939). Slowly flowing brooks and rivulets (Lepneva, 1964). Rivulets and brooks (Nybom, 1960). Rivers and lakes (Schmid, 1959a).

I have recently collected sparsa from small slowly flowing rivers with sandy or gravelly beds such as the Wey, Eden and Eden Brook (Surrey) and at Hartfield (Sussex). I have taken a single ♂ at m.v. light in my garden at Croydon, Surrey, the specimen probably originating from a nearby ornamental pond, and the species also occurs in the grounds of Buckingham Palace Gardens, London (J.D.B.), suggesting that transport with aquatic vegetation or stones, for example, may contribute to its distribution. The larvae occur in numbers near the water's edge on submerged stones and the adults run about in the daytime on adjacent tree trunks, vegetation and especially on the upper sides of bridges in the sunlight. The adults occur in Britain from May to October with peak numbers in June and August with just a slight fall-off in July.

British distribution. (map 7). Widespread and abundant throughout south and central England and Wales but apparently more local in the north of England and Scotland (although the species has been recorded from the Shetlands, the Outer Hebrides, and Moray); also widespread throughout Ireland.

General distribution. British Isles, throughout Europe (rarer in the Scandinavian countries) and west and north-west European U.S.S.R., Iran, Israel, Algeria. *H. sparsa* appears to have a relatively more southerly distribution than *simulans.*

Discussion. The form of the male genitalia most closely resembles that of *cornuta*, especially with respect to the shape of the posterior margin of the Xth tergite, but from which species *sparsa* may be distinguished by the uniquely narrow, posteriorly tapered inferior appendages. The female genitalia are very similar to those of *lotensis* but may be distinguished by the less quadrate ventral sclerite of segment VIII and the shorter lateral arms of the internal apparatus in *sparsa* (the shape of the dorso-posterior excision of segment VIII is almost identical in the two species).

As noted by Mosely, *sparsa* often occurs with *simulans* and I have records of large numbers of both species taken from m.v. light-trap material at Woolhampton, R. Kennet, Berkshire (B.R.B.). However, *sparsa* appears to have a more southerly general and British distribution than *simulans*, being rare in the north of England and Scotland, although even these records may subsequently prove to be of a different species (material not examined). I suspect that a number of species belonging to the *sparsa*-group have been erroneously identified in the past as *sparsa* so that the map (7) may not give a true representation of the British distribution of this species;

all past records should therefore be checked where possible, especially those from Scotland and the north of England where *simulans* and *angulata* may be relatively more common than *sparsa*.

The identity of the type of *sparsa* is also somewhat questionable since, of the two specimens labelled as this species in the Curtis Collection, the male is *angulata* while the female, according to Neboiss (1963) from the figure in Mosely (1939) is *sparsa* in the sense generally accepted subsequent to Curtis's original description. The female specimen has therefore been designated by Neboiss (1963) as the lectotype of *sparsa* although the genitalia of the latter, as figured by Neboiss, differ slightly from those figured by Mosely (1939) especially in the form of the ventral sclerite and the internal apparatus; unfortunately, Neboiss did not illustrate the dorso-posterior margin of segment VIII. Examination of the lectotype is thus required to establish its true identity and hence that of *sparsa* in its original sense.

Hydroptila cornuta Mosely

Hydroptila cornuta Mosely, 1922, *Trans. ent. Soc. Lond.* 1922: 178, 179, pl. 2, figs. 1-3.

Type data. England; R. Test, Hampshire, 17.v.1916. The holotype ♂ and a long ♂ and ♀ paratype series are in the BMNH collections.

Diagnosis. ♂ genitalia, figs. 156, 158 (Mosely, 1922, 1939; Martynov, 1924, 1934; Nielsen, 1948a; Kimmins, 1961; Macan, 1973): posterior margin of segment X sinuous, lateral corners produced, pointed; inferior appendages (in lateral view) slightly widening posteriorly but tapering abruptly dorsally to form a short upcurved apical claw and with a small dark sub-apical ventral spot.

♀ genitalia, fig. 178 (Tjeder, 1941; Kimmins, 1961): dorso-posterior margin of segment VIII deeply and widely excised, lateral edges sinuous, base with distinctive median convex process, edges with strengthening ridge.

Larva. Unknown.

Biology. Running water (Mosely, 1939). Rheophilous (Kachalova, 1972). Rivulets and brooks (Nybom, 1960).

Adults recorded in Britain between mid-May and early September although data are insufficient to indicate peak emergence periods.

British distribution. (map 8). Local; the Shetlands, Hampshire and Suffolk with new records from Ireland (J.P.O'C. *in litt.*). *H. cornuta* has not been recorded from the mainland of Scotland; north, central or south-west England or Wales.

General distribution. British Isles, Norway, Sweden, Finland, Denmark, Netherlands, Germany, Poland, European USSR and Italy.

Discussion. By the form of the male genitalia *cornuta* is most closely related to *lotensis* within the sparsa-group from which it may be distinguished by the more acute lateral angles of the posterior margin of the Xth tergite and the shorter apical 'claw' of the inferior appendage. According to Kimmins (1961) the female genitalia of cornuta differ from those of lotensis by the longer and narrower ventral apical lobe of segment VIII, the less quadrate ventral sclerite and the shorter lateral arms of the internal apparatus in addition to which, as also figured by Tjeder (1941), the shape of the dorso-posterior excision of segment VIII is quite distinctive in cornuta.

As there are so few records available for cornuta little can be said of its origin and British distribution pattern. From its continental distribution it would appear to be more adapted to cooler climates as it is common in the northern Scandinavian countries and at higher altitudes in central and southern Europe (the most southerly record being from Tuscany, Italy). The British distribution is rather unusual in this respect, being concentrated in south-east and eastern England, but may represent local populations surviving in small areas maintaining favourable conditions that were once more widespread (which is almost certainly the case with respect to the Shetland record) or a result of a more recent introduction to the south-east. The recent records from Ireland establish it as a true British species and may again represent survivors of once more widely distributed British populations. However, as more Hydroptilids are collected and correctly identified, the true origin and distribution pattern of this species may be revealed.

Hydroptila simulans Mosely

Hydroptila simulans Mosely, 1920, *Trans. ent. Soc. Lond.* 1919: 391-392.

Type data. England; Mottisfont, R.Test, Hampshire; 14.ix.1913. The holotype ♂ and a long mixed paratype series are in the BMNH collections.

Diagnosis. ♂ genitalia, figs. 157, 159. (Mosely, 1920; 1939; Schmid, 1959a; Macan, 1973): posterior margin of tergite X with V-shaped median incision, corners rounded and not produced as points; inferior appendages widening posteriorly in lateral view to broad, truncate apex, dorsal corner not produced and with a characteristic dark subapical spot on the ventral margin.

♀ genitalia, fig. 176 (Mosely, 1939; Macan, 1973): dorso-posterior margin of segment VIII with a very short, parallel-sided median excision.

Larva: unknown.

Biology. Frequents running water (Mosely, 1939). Rivers at medium altitudes, 2000'-8000', and rivulets running through forests (Schmid, 1959a). Rivulets and brooks (Forsslund & Tjeder, 1942). In Britain the adults occur from May to October, with relatively more records for these two months than for *sparsa* and with peak numbers occurring in June.

British distribution. (map 9). More widespread but less common than *sparsa* with which it often occurs; new records establish it as a true Scottish species (Sutherland, C.S.E.; Inverness-shire, R.J.S., 1968 and J.E.M., 1975) and O'Connor (*in. litt.*) has data for new

Irish localities. The species has not yet been recorded from northern England, East Anglia or south Wales.

General distribution. British Isles; throughout Europe (excluding the Netherlands, Switzerland and Spain); Israel, Iran, Afghanistan.

Discussion. This species is distinguished within the *sparsa*-group by the form of the male Xth tergite and inferior appendages(the latter differing from those of *cornuta* , *angulata* and *lotensis* by the non-produced dorso-posterior apex), and the inconspicuous dorsal excision of the posterior margin of segment VIII of the female.

This species has a more northerly general distribution in comparison with *sparsa* and is common in the Scandinavian countries where the latter is rare (Finland, Nybom, 1960 and Sweden, Tobias, 1969) or totally absent (Norway). In Britain also, *simulans* tends to be more common in the north of Scotland while *sparsa* occurs more in the south of England although, in this region, the two species often occur together in numbers. It may be that *simulans* prefers slightly cooler conditions, higher altitudes and slightly faster running water than *sparsa*, the latter possibly being more tolerant of slower moving lowland water courses.

Hydroptila angulata Mosely

Hydroptila angulata Mosely, 1922, *Trans. ent. Soc. Lond.* 1922: 178, 179-180, pl. 2, figs. 4-6.

Type data. England; R. Lambourn, 31.viii.1913. The holotype ♂ and a ♀ paratype series are in the BMNH collections.

Diagnosis. ♂ genitalia, figs. 160, 162 (Mosely, 1922, 1939; Martynov, 1934; Schmid, 1960; Macan, 1973): posterior margin of tergite X with a slight U-shaped median indentation, lateral corners rounded; inferior appendages in lateral view slightly widening posteriorly, posterior ridge produced slightly apico-dorsally but not forming a strongly sclerotised or incurved apical claw.

♀ genitalia, fig. 177 (Mosely, 1939; Macan, 1973): dorso-posterior margin of segment VIII deeply and widely excised, sides S-shaped with anteriorly broadening strengthening ridges.

Larva. Unknown.

Biology. Lakes and seashore (Nybom, 1960). Large rivers (Schmid, 1960). Still and tranquil water (Moretti, 1952). The adults occur in Britain from mid-June to the end of August, with one record in the end of October from Malham Tarn, Yorkshire, 1953 (Holmes, 1963).

British distribution. (map 10). Local; the Shetlands, north and south-west England, South Wales and Ireland. New records indicate that this species may be more common in this country than previously thought.

General distribution. British Isles, Sweden, Finland, Germany, France, Spain, Italy, Yugoslavia, Greece, European U.S.S.R., Iran, Pakistan.

Discussion. *H. angulata* is distinguished within the *sparsa*-group by features of the male Xth tergite and inferior appendages and segment VIII of the female genitalia.

From the literature *angulata* would appear to prefer larger and more slowly moving water bodies but its northern and western distribution pattern in Britain and its association with *H. forcipata* suggest a possible tolerance of faster-moving water.

Hydroptila lotensis Mosely

Hydroptila lotensis Mosely, 1930*c*, *Trans. ent. Soc. Lond.* 78: 245, pl. 14, fig. 1.

Type data. France; Cahors, R. Lot, 29-30.vi.1924; M.E. Mosely. The holotype ♂ and four ♂ and two ♀ paratypes are in the BMNH collections.

Diagnosis. ♂ genitalia, figs. 161, 163 (Mosely, 1930*c*; Martynov, 1934; Kimmins, 1961; Macan, 1973): posterior margin of tergite X with a slight median excision and somewhat convex lateral angles; inferior appendages in lateral view gradually widening posteriorly, then abruptly tapering to an elongate dorsal apical claw, a small dark sub-apical spot present on the ventral margin.

♀ genitalia, fig. 175 (Kimmins, 1961): ventro-apical process of segment VIII short and broad; ventral sclerite quadrate; lateral arms of internal apparatus long; dorsal excision of posterior margin deep and wide, quadrate with lateral parallel sides and straight base.

Larva: a crude general figure is given by Kachalova (1972) but no detailed description is available.

Biology. Rivers, June-August (Kachalova, 1972). Rivers and streams, July (Nybom, 1960). Rivers (Schmid, 1959a).

British distribution. (map 11). *H. lotensis* is known in Britain from the single record of a short series collected at m.v. light by C.H. Harrisson at Hampton Bishop, R. Wye, Herefordshire, 12.viii.1959, the species being added to the British list by Kimmins (1961).

General distribution. England, Finland (rare, Nybom, 1960), Poland, France (type); Rumania, European U.S.S.R., Iran.

Discussion. The form of the male genitalia most closely resembles that of *cornuta* from which *lotensis* may be distinguished by the more convex lateral angles of the posterior margin of tergite X and the longer apical claw. The female genitalia are almost identical with those of *sparsa*, differing only in the more quadrate ventral sclerite of segment VIII and the longer lateral arms of the internal apparatus.

This species appears to be generally very local and rare but has quite a widespread overall western Palaearctic distribution ranging from central Finland through central Europe (where it is best represented) to Iran. It thus seems to prefer moderate climates, avoiding the extreme northern regions and warmer Mediterranean countries. Little can be said of its occurrence in Britain, the single record suggesting a chance introduction and, until further records can show it to be established here, its status as a true British species must remain questionable.

Hydroptila martini Marshall

Hydroptila martini Marshall, 1977, *Entomologist's Gaz.* 28 (2).
Hydroptila occulta (Eaton); Mosely, 1939, *British Caddis flies*: 265, figs. 572, 573.

Type data. Holotype ♂ and mixed ♂ and ♀ paratype series designated here. Holotype data: England; R. Test, 10.viii.1913, M.E. Mosely. Holotype and paratypes in BMNH collections.

Diagnosis. ♂ genitalia, figs. 164, 167 (Mosely, 1939; Schmid, 1947; Macan, 1973): tergite X narrow, elongate, posterior margin distinctly trilobed, median lobe as long as or longer than lateral lobes; dorso-lateral process of segment IX projects beyond broader ventro-lateral process; 'subgenital appendages' (parameres) elongate, broad, right-angled, dilated considerably before tapering abruptly to short, narrow, rugose, dorsally-directed apex; inferior appendages typically club-shaped but apparently more truncate apically in lateral view with sclerotisation of apico-dorsal third extending to ventral margin of appendage.

♀ genitalia, fig. 180 (Mosely, 1939; Macan, 1973): segment VIII with a single anterior internal ridge; ventral sclerite of VIII ('ventral plate' of Nielsen, 1951) Y-shaped with posterior 'cross-piece' shallowly concave; ventral sclerite between VIII and IX ('dorsal plate' of Nielsen, 1951) relatively broad and ovoid with six posteriorly directed bristles.

Larva: unknown.

Biology. Unknown. Verified British records indicate a preference for larger rivers; the adults occur in June and July.

British distribution. (map 12). The map conveys the impression that the species is restricted to central and southern England, including East Anglia and Wales with a single record from Ireland. However, the records from the Shetlands (Unst) and Wigtownshire should not be overlooked.

General distribution. Specimens of martini have only so far been positively identified from Yugoslavia (Mostar, 1897, Klapálek) and France (Olette, 1923, Mosely) from material erroneously determined as occulta (Eaton) in the BMNH collections. Schmid (1947) records this species as occulta (Eaton) from Switzerland.

Discussion. Pelham-Clinton first drew my attention to the fact that the genitalia figured and described by Mosely (1939) did not agree with those of the male lectotype which had not previously been dissected. Comparison of the latter with specimens determined by Mosely as occulta (Eaton) in the BMNH slide collection (from which Mosely drew his figures) revealed distinct differences in the male genitalia, especially with regard to the apex of tergite X, the lateral processes of segment IX and the apices of the parameres and the inferior appendages. Further differences in the shape of the ventral sclerites of the genitalia of females associated with Mosely's and Eaton's occulta led me to regard Mosely's species as distinct, although very closely related to the true occulta. I therefore propose to name this species Hydroptila martini sp.n. after Martin E. Mosely, the eminent British trichopterist.

For the holotype I have selected a male from the series of slides prepared by Mosely and from which it would seem likely (from their dates of preparation) that his descriptions and figures of occulta sensu Mosely were made. The lateral figure of the male genitalia appears to be a diagrammatic composite but the specimen from which the ventral figure was drawn can be easily recognised and is mounted with a number of other abdomens on a single slide. For this reason it was thought best not to designate this as the lectotype but to select a slide with just a single abdomen in which the diagnostic features of the genitalia could be clearly seen. The data are given above.

Of the previous records of occulta s.l. from the British Isles and the Continent, I have not been able to examine sufficient material to establish the distribution of each species concerned in the complex. I cannot therefore comment on the distribution or biology of the new species.

Hydroptila occulta (Eaton)

Phrixocoma occulta Eaton, 1873, Trans. ent. Soc. Lond. 1873: 135, pl. 3, figs. 4-4b.

Hydroptila occulta (Eaton) McLachlan, 1880, Rev. Syn. 1880: 512, pl. 58, figs. 1-2.

Hydroptila insignis Martynov, 1927, Ezheg. zool. Muz. 28: 176, pl. 19, figs. 28-29, synonymised by Botosaneanu, 1967.

Hydroptila kimminsi Mosely, 1930*c*, *Trans. ent. Soc. Lond.* 78: 245, figs. 19-20, pl. 14, fig. 1 (syn. n.).

Hydroptila parthava Schmid, 1959*a*, *Beitr. Ent.* 9: 686. Synonymised by Botosaneanu, 1967.

Type data. England; Mappleton, nr. Ashbourne, Derbyshire; "between the bridge and the weir, June". Lectotype ♂ designated by Kimmins (1957) from a series of four specimens collected by Eaton (England, no locality labels) and labelled '*occulta* Eaton, det. McLachlan' (see discussion). Lectotype ♂ and three paralectotypes (not paratypes as termed by Kimmins, 1957; two with abdomens missing) in BMNH collections.

Diagnosis. ♂ genitalia, figs. 165, 168 (Eaton, 1873; McLachlan, 1880; Martynov, 1927, 1934 as *insignis*; Mosely, 1930*c* as *kimminsi*; Nielsen, 1951, 1956, 1957, 1970; Schmid, 1959*a* as *parthava*); tergite X elongate, narrow, membranous, posterior margin slightly convex with median lobe absent or very small and not projecting beyond lateral angles; small dorso-lateral process of segment IX not projecting beyond the broader ventral process; 'subgenital appendages' (parameres) elongate, ribbon-like, curved upwards dorsally, each terminating in a relatively elongate, tapering, apical process with a 'mosaic-like' sculptured surface (just before apex the appendage is distinctly dilated); inferior appendages elongate, truncate in lateral view, dorsal sclerotisation not extending around posterior margin.

♀ genitalia, fig. 181 (Nielsen, 1951, 1956, 1970); internal tube of segment VIII with two distinct sets of 'concertina-like' ridges anteriorly; ventral sclerite of VIII basically T-shaped with anteriorly tapering median stalk and an almost horizontal cross-piece, the lateral ends of which are produced as short, posteriorly directed arms; posterior ventral sclerite (between VIII and IX) subcircular with six posteriorly directed setae.

Larva: unknown.

Biology. Unknown. Verified British records indicate that the larvae prefer fast-flowing streams and rivers and that the adults occur from July through to October; there is insufficient data, however, to comment on peak emergence periods.

British distribution. (map 13). This map shows all records of occulta (Eaton) which I have been able to confirm. The species appears to be widely distributed throughout England, Wales and Scotland although I have not seen any material from East Anglia or Ireland. Map 14 shows the overall distribution of the occulta-complex (i.e. occulta (Eaton), martini sp.n. and valesiaca Schmid) in the British Isles compiled from all available sources.

General distribution. The overall distribution of occulta s.l. extends throughout Great Britain, Scandinavia, central Europe, Italy, the Balkans, Portugal, Iran and SinKiang (Chinese Turkestan). I have confirmed the identity of specimens of occulta (Eaton) from Norway (ex Trond Andersen) while this species is recorded as kimminsi from Sweden, Finland, France and Switzerland; as insignis from SinKiang and as parthava from Iran.

Discussion. As mentioned in the discussion on the previous species, martini sp.n., the true occulta (Eaton) may be distinguished from the former by features of both the male and female genitalia. The species figured and described by Nielsen (1951, 1956, 1957, 1970) is the true occulta but, although he noticed differences between his and Mosely's descriptions, Nielsen did not consider the possibility that they might be distinct species. I believe kimminsi Mosely to be synonymous with occulta (Eaton) since Mosely, not having examined the genitalia of Eaton's type, considered his specimens (as figured in 1939) to be of the latter species.

In his original description Eaton (1873) refers only to the type-series from England but McLachlan (1880) mentions specimens collected by Eaton from Switzerland which, as will be shown in the discussion on the following species, have proved to be valesiaca Schmid and not occulta (Eaton) as originally determined.

It has not been possible to examine sufficient material to comment on the distribution, biology and ecology of the true occulta as distinct from martini sp.n. with which all past records have been confused.

Hydroptila valesiaca Schmid

Hydroptila valesiaca Schmid, 1947, *Mitt. schweiz. ent. Ges.* 20: 530, figs. 76, 77.

Hydroptila occulta (Eaton) sensu McLachlan, 1880, *Rev. Syn.* 1880: 512 (partim).

Type data. Switzerland; Praz-de-Fort (Val Ferret, Valais), 11.vii.1944, F. Schmid. Holotype ♂, allotype ♀, mixed ♂ and ♀ paratype series in Schmid Collection ? (location unknown); paratypes (♂ and ♀) in BMNH collections.

Diagnosis. ♂ genitalia, figs. 166, 169 (Schmid, 1947): tergite X elongate, narrow, posterior margin with deep median excision of which the base is straight and the lateral sides divergent and convex; dorso-lateral process of segment X elongate, slender, tapering, projecting well beyond the more truncate ventro-lateral process; 'subgenital appendages' relatively wide, strongly right-angled, base gradually widening to angle then tapering to short, dorsal, unsculptured point; inferior appendages characteristically club-shaped, dorsal ridge of sclerotisation strongly developed extending from almost mid-length (beyond midlength seta) to halfway along rounded apex.

♀ genitalia, fig. 182 (not previously described): internal tube of segment VIII short, without ridged bands anteriorly; ventral sclerite of VIII large, V-shaped, lateral arms with slight sub-apical swellings; anterior sternite between VIII and IX small, ovoid, with a small postero-median process and four posteriorly directed setae.

Larva: unknown.

Biology. Unknown. Imagines taken by the banks of clear, cool streams in a damp and mossy meadow at 1200m, Praz-de-Fort, and in a peat-bog (tourbière) at 1421m, Crans sur Sierre (Swiss Alps; Schmid, 1947).

British distribution. (map 15). I have discovered one specimen of *valesiaca* in the BMNH collection, previously identified as *occulta* (Eaton) from Loch Awe, Portsonachan, Scotland, 28.vi.1935 (M.E. Mosely). There is one specimen in the Royal Scottish Museum (Edinburgh), according to Pelham-Clinton (*in litt.*), which is labelled 'Wigtownshire, July, 1899' and which was collected by K.J. Morton. No other specimens have been recorded or located in other collections.

General distribution. Schmid (1947) described *valesiaca* originally from Praz-de-Fort (Valais, Switzerland) and Crans sur Sierre and suggests that Eaton's specimens of *occulta* (Eaton) from nearby Champéry, Val d'Illiez (Valais) taken at similar altitudes and habitats are also of this species. I have examined Eaton's specimens in the BMNH collections and agree with Schmid's suggested synonymy. In addition to these, specimens from the French Alps at Chamonix (close to the type-locality) and from Bourg d'Oisans (a little further in from the border), all collected by Mosely and identified by him as *occulta* (Eaton), have also proved to be *valesiaca*. The species is therefore known only from the type-locality (and its environs) and Scotland.

Discussion. This species is readily distinguished from *occulta* (Eaton) and *martini* sp.n. by features of the male and female genitalia as described above. From the very local distribution of *valesiaca*, both here and on the continent, it would appear to be a rare species which prefers higher altitudes and which once had a widespread distribution but is now restricted to a few isolated regions in the mountain ranges of northernand central Europe. The species may still survive in some of the remoter regions of the Scottish Highlands and there may be specimens, previously misidentified as *occulta* (Eaton), in various collections from such regions and, perhaps, also northern England.

Orthotrichia angustella (McLachlan)

Hydroptila brunneicornis Pictet, 1834, *Recherches Phryganides* 226, partim.

Hydroptila angustella McLachlan, 1865, *Trans. ent. Soc. Lond.* 5: 95-96, pl. 1, fig. 5.

Orthotrichia angustella (McLachlan); Eaton, 1873, *Trans. ent. Soc. Lond.* 1873: 142, pl. 2, figs. 4-4a, pl. 3, figs. 4-4c.

Type data. England; R. Thames, nr. Hampton, 12.vii.1865, R. McLachlan. The lectotype ♀, designated by Kimmins (1957) as the only traceable specimen of the original three referred to by McLachlan (1865), has lost the metathorax and abdomen; it is now in the BMNH collections.

Diagnosis. ♂ with a row of black scale-like setae along base of sub-costa of forewing. ♂ genitalia, fig. 183 (Eaton, 1873; McLachlan, 1880; Martynov, 1924, 1934; Ulmer, 1929; Mosely, 1939; Macan, 1973): tergite X narrow, posterior margin convex, with a right-directed dorsal process arising sub-apically from the left margin and with the right margin produced basally as an outwardly directed, broad but pointed process; lateral processes of segment IX prominent, not markedly asymmetrical, narrow, obliquely directed dorso-posteriorly in lateral view, posterior margin with a row of bristle-like setae; inferior appendages small and inconspicuous, not projecting beyond tergite X, truncate with small inwardly directed apico-medial processes; bilobed process distinctly Y-shaped; left spine long, slender, elongate, extending from anterior edge of IX almost to apex of X; right spine shorter, approximately from base to apex of right lateral process; short ventral processes on segments VII and VIII, latter with tuft of coarse hairs.

♀ genitalia, fig. 186 (not previously described: dorso-posterior margin of segment VIII with a small median ovoid excision, ventral surface with what appears to be a somewhat broad oblique approximately median groove, which is extended posteriorly as a small rounded projection of the ventral margin; venter IX with a pair of elongate apical lobes which project just beyond the small cerci-bearing, apically convex segment X.

Larva: (Jacquemart, 1962a).

Biology. Near standing water (McLachlan, 1865). Standing water and slow streams (Eaton, 1873). Running water (Mosely, 1939). Wallace (pers. comm.) has reared this species from larvae found in a fine particulate substrate amongst willow roots, along with larvae of Ithytrichia sp. from the Thame, Dorchester, Oxford, vi.1972. The adults occur in England between June and August (one record from Tadnoll, Dorset, April, 1922).

British distribution. (map 16). A local species recorded so far only from England (Westmorland to south and south-east counties) and Co. Kerry, Ireland. O'Connor (*in litt.*) has recently collected this species in Ireland (no data); *angustella* has yet to be found in Scotland and Wales.

General distribution. England, Ireland, Norway, Sweden, central Europe, European U.S.S.R., Spain and Italy.

Discussion. *O. angustella* is the most widely distributed of the *angustella*-group, the overall distribution of which extends throughout the Palaearctic, Africa and S.E. Asia. The group may be distinguished from the *costalis*- and *tragetti*-groups by the reduced inferior appendages and produced lateral processes of segment IX of the male genitalia and, in most species, by the row of black scale-like setae along the base of the subcosta of the male forewing.

The overall distribution of *angustella* suggests that it prefers the more slowly flowing, larger lowland rivers (and sometimes also lakes) and is tolerant of the milder climatic conditions of the south of England, Ireland and Europe in general. It is a rare species in the north of Europe and in the northern, more hilly and mountainous regions of the British Isles (Scotland and Wales) where the rivers are, in general, fast-flowing. However, *angustella* may occur locally in small numbers in these areas where there are larger bodies of water.

Orthotrichia costalis (Curtis)

Hydroptila costalis Curtis, 1834, Phil. Mag. 4: 218.

Hydroptila tineoides Dalman sensu Mühlen, 1880, *Arch. naturk. Liv.-Est. u. Kurlands* 9: 231.

Orthotrichia tetensii Kolbe, 1887, *Ent. Nachr.* 13: 356-359.

Orthotrichia angustella (McLachlan) sensu Ris, 1889, *Mitt. schweiz. ent. Ges.* 8: 142-145.

Orthotrichia costalis (Curtis); Neboiss, 1963, *Beitr. Ent.* 13: 594, fig. 4.

Type data. 'Aug.'; no locality given in Curtis's notebook. Single ♂ specimen labelled *costalis* in Curtis Collection (National Museum Victoria, Australia) designated as (lecto)holotype by Neboiss (1963); genitalia mounted on microscope slide T-125.

Diagnosis. ♂ genitalia, fig. 184 (Martynov, 1924, 1934; Mosely, 1939; Nielsen, 1957; Macan, 1973): tergite X narrow, elongate, truncate with an asymmetrical, right-directed, stout pointed process arising dorsally and sub-apically from both right and left sides; lateral margin of segment IX with a narrow, posteriorly tapering, slightly upturned process on left side only; inferior appendages well developed, projecting just beyond tergite X, slight asymmetrical, elongate, upturned and strongly inwardly curved; bilobed process with apical arms fused to form a dilated truncate apex bearing a pair of short setae; short slender spine present on right side only, approximately medial and ventral to tergite X; tufts of coarse hairs on venter VIII and the ventral process of VII, the ventral process of VI short and without setae.

♀ genitalia, fig. 187 (not previously described); segment VIII with straight dorso-posterior margin, venter totally membranous; venter IX with characteristic pair of dark patches; segment X typically small, apex truncate.

Larva: (Nielsen, 1948; Lepneva, 1964; Hickin, 1967).

Biology. Ponds and lakes (Mosely, 1939). On reeds in outer part of reed swamps, still to slow-moving water (Nielsen, 1948). Lakes (Nybom, 1960). Lakes and slowly running rivers in the plains, in plant thickets (Lepneva, 1964). In Denmark, according to Nielsen (1948) costalis is univoltine; the adults swarm in July and August and the Vth-instar larvae appear by the end of September, development ceasing towards the end of October to begin again in the following May. In Britain the imagines are encountered from June to September, although there is insufficient data to comment on peak emergent periods.

British distribution. (map 17). Throughout England and Scotland from Hampshire in the south to Argyllshire in the north; there are no records from Wales or south-west England and the species has only recently been recorded from Ireland (O'Connor, pers. comm., no data).

General distribution. British Isles, north and central Europe (except Norway, Belgium, Switzerland and Austria), Italy, Yugoslavia, Iran, Afghanistan, U.S.S.R., Ethiopia.

Discussion. O. costalis is readily distinguished by the large, incurved inferior appendages and reduced lateral processes of segment IX in the male genitalia and the dark patches of venter IX in the female. This species, like *angustella*, is absent from the faster flowing rivers in the west and south-west regions of Britain but it tends to be relatively more northerly in distribution due, possibly, to its apparent preference for lakes and ponds and resultant occurrence in some Scottish lochs. All present British records appear to come from lakes and ponds, some of which are partly or wholly ornamental (e.g. Buckingham Palace Gardens, London, J.D.B.; Croydon, Surrey, J.E.M.), thus indicating that the distribution of *costalis* may be influenced by the transport of aquatic vegetation by man.

Orthotrichia tragetti Mosely

Orthotrichia tragetti Mosely, 1930*c*, *Trans. ent. Soc. Lond.* 78: 247-249, figs. 25, 26.

Type data. England; Tragget's Lake, Mottisfont, Awbridge Danes, Romsey, Hampshire, 31.vii.1915, M.E. Mosely. Two ♂ specimens mounted on a single microscope slide labelled 'Type' in the BMNH collections. Paratype ♂: St. Paul-de-Varax, Ain, France, 6.vii.1925, M.E. Mosely (BMNH).

Diagnosis. ♂ genitalia, fig. 185 (Mosely, 1930*c*, 1939; Martynov, 1934; Macan, 1973): tergite X relatively broad and elongate, apices pointed and lateral margins slightly curved ventrally; lateral margins of segment IX not greatly produced, represented only by short ventrally and inwardly directed processes; inferior appendages very small and inconspicuous, but symmetrical and somewhat heart-shaped; single elongate curved spine relatively stout, extending from right anterior margin of IX almost to posterior margin of X, lying slightly to left of median line; bilobed process with dilated apex bearing two stout setae.

♀ genitalia, fig. 188 (not previously described): segment VIII with straight dorso-posterior margin, venter membranous with a short, median, posteriorly directed VII without dark patches; posterior margin of segment X with a slight median 'nick'.

Larva: unknown.

Biology. Unknown. Both English and French imagines were captured in July.

British distribution. (map 18). Hampshire, nr. Romsey (private lake).

General distribution. England, Sweden, Finland, France, Switzerland, Italy, European U.S.S.R.

Discussion. *O. tragetti* is a very rare western Palaearctic species of which only the two male 'types' have been taken in England; these were probably introduced into the private fishing lake at Mottisfont, Hampshire. This is the only Palaearctic member of the predominantly Nearctic *aegerfasciella*-group.

Agraylea multipunctata Curtis

Phryganea sexpunctata Fourcroy, 1785, *Entomologia Parisiensis* : 356.

Agraylea multipunctata Curtis, 1834, *Phil. Mag.* 4: 217.

Hydrorchestria multipunctata (Curtis) Kolenati, 1859, *Nouv.* mem *mem. Soc. imp. Nat. Mosc.* 17(11): 163, 181, 192.

Agraylea multiguttata Uljanin, 1869, *Nachr. Ges. Fr. naturw. Moskau* 6, 2: 37, 100.

Allotrichia signata Banks, 1904*b*, *Proc. ent. Soc. Wash.* 6: 215, pl. 2, figs. 8, 17.

Allotrichia flavida Banks, 1907, *Jl N.Y. ent. Soc.* 15: 164.

Agraylea fraterna Banks, 1907, *Jl N.Y. ent. Soc.* 15: 164.

Type data. England; "29 July Thatford River. 3^{d} abundant on rushes by side of river by Guildford". Lectotype ♂ abdomen mounted on microscope slide T-121, Curtis Collection, National Museum of Victoria, Australia (Neboiss, 1963).

Diagnosis. Forewing length 4-5 mm. ♂ genitalia, fig. 189 (McLachlan, 1880; Martynov, 1924; Mosely, 1939; Nielsen, 1957; Macan, 1973): sternite VII with elongate broad truncate process; inferior appendages (fig. 189, arrowed) narrow, each with wide proximal base and narrow tapering median process.

♀ genitalia, fig. 192 (not previously figured): ventral sclerite of segment VIII prominent, anterior margin U-shaped, posterior margin bilobed, extending just beyond edge of segment; internal apparatus (fig. 192, inset) without medial 'crown'.

Larva: (Silfvenius, 1904; Nielsen, 1948; Lepneva, 1964; Hickin, 1967; Solem, 1972): head yellow with two dark dorsal spots (sometimes absent) between eyes; thoracic nota without dark spots.

Biology. Lakes, ponds and large rivers (Mosely, 1939). In lakes in submerged vegetation near surface and frequently on stony but sheltered banks, always in association with abundant filamentous algae (Nielsen, 1948). Stagnant and running water in plant thickets, avoiding small and shallow bodies of water (especially estuarine parts of lakes); also in slowly flowing rivers or rivulets overgrown with plants or in similar bodies of water in river floodplains; all zones of plant thickets but rarer in the *Potamogeton* zone; pupae often found on leaves of water lilies (Lepneva, 1964). Lakes and seashore, Finland (Nybom, 1960). Tarn shores, larvae abundant under stones within first two feet of edge (Holmes, 1963).

In Denmark, according to Nielsen (1948), the Vth-instar larvae are fully grown by the end of October and fasten (but do not close) their cases in which they remain active, but do not feed, during the winter; observed vertical migrations could have been due to fluctuating O_2-tensions and experiments showed that the larvae could tolerate freezing conditions for a few days; pupation occurred at the end of May, without prior feeding, and the adults emerged from June onwards. Both Nielsen (1948) and Holmes (1963) consider the species to be bivoltine in Denmark and England respectively, the first generation flying in June (sometimes end of May) and the second, after having undergone a rapid larval developmental period, emerging in August.

I have collected multipunctata mainly from large lakes and ponds associated in some way with man either as fishing sites or boating lakes, for example (Dungeness, Kent; East Grinstead and Virginia Water, Surrey); ornamental ponds in parks and the grounds of large houses (Buckingham Palace Gardens, London, J.D.B.; Menabilly, Cornwall); small private residential gardens (Wootton, Surrey, J.D.B.) and small, slowly flowing rivers and backwaters (R. Wey, Surrey). The larvae were found by searching the submerged vegetation by the banks of the bodies of water while adults were collected from tree-trunks and vegetation by the waterside during the day (although they do not have the 'scuttling' habits of Hydroptila) and in m.v. light-traps at night, often some distance away from the water. Indeed, at Dungeness the adults must have flown approximately 200-300 yards and overcome an intervening barrier of high shrubs between the pond and the trap. British records indicate that adults occur throughout May to September with peak numbers in July and August, while odd specimens have been taken in March (1972, Westmorland, I.D.W.) and October (1936, Oxfordshire, A.D.G.). Larval records are mainly from February through to June.

British distribution. (map 19). Abundant and widespread throughout the British Isles avoiding the higher mountainous regions such as the Pennines, the Scottish and Welsh ranges and the higher areas of Ireland. Most records are from the more natural Scottish, Welsh and Irish lakes, Yorkshire tarns and English Lake District and some artificial waters such as fishing sites, boating lakes, reservoirs, fenlands, parks, canals, coastal marshes and ponds on shingle beaches. New records have extended the known distribution of *multipunctata* to E. Cornwall (J.E.M.) and Carmarthenshire (R.A.J.), south-east to E. Kent (J.E.M.) and north to Sutherland and Caithness (M.J.S.).

General distribution. *A. multipunctata* is reputedly Holarctic but I believe the Nearctic form to be a distinct species (see discussion). The Palaearctic distribution extends throughout Scandinavia, central Europe and north European U.S.S.R. but not the Mediterranean countries, the most southern records being from Rumania. This species has a relatively more northerly distribution than *Agraylea sexmaculata*.

Discussion. This genus and *Allotrichia* may both be recognised by the relatively larger size and somewhat Psychomyiid appearance, having broader and more obtuse wings and a fuller complement of veins than is usual of the more typical Hydroptilid genera such as *Hydroptila* and *Oxyethira*. *Agraylea* may also be recognised by the more golden-yellowish pubescence of the wings often arranged in distinct markings especially, according to Mosely (1939), in *multipunctata*. This species is readily distinguished from *sexmaculata* even in unprepared specimens by the form of the male genitalia, notably in the form of the broad spatulate ventral process and the inconspicuous inferior appendages. The females require closer examination, involving clearing the abdomen in potash (but not necessarily staining) on which the presence of a distinct lip-shaped sternite on segment VIII reveals the species to be *multipunctata*. The larvae of *multipunctata* and *sexmaculata* are easily distinguished by the markings of the head and thoracic nota which can clearly be seen in fluid-preserved material under low magnification.

As stated above, I believe the Nearctic form of *multipunctata* to be a distinct species as indicated by discrete features of both the male and female genitalia. Comparison of British and North American material (New York, N.J.M.) in the BMNH collection (compare also figs. 189, 192 with Ross, 1944, figs. 454, 455) reveals differences in the relative proportions of the ventral process, inferior appendages and subgenital plate of the males and the ventral plate of the females. Ross (pers. comm.) agrees with these findings and suggests that a ring of species may be involved around the Holarctic region as he has specimens of what appears to be a third species from Alaska. Examination of material from as wide a range as possible, especially the eastern Palaearctic zone, and including the closely related Scandinavian species *cognatella* McLachlan is therefore necessary to resolve this problem. If the Nearctic form does prove to be distinct it should be known by its first designated name *signata* Banks, with *flavida* Banks and *fraterna* Banks probably as junior synonyms (examination of type-material required).

Finally, the principal works containing further morphological, ecological and behavioural information on this species are those of Nielsen (1957) on the male genitalia, Nielsen (1948) on the immature stages and Watts (1976) on pupation.

Agraylea sexmaculata Curtis

Agraylea sexmaculata Curtis, 1834, *Phil. Mag.* 4: 217.

Hydrorchestria sexmaculata (Curtis); Kolenati, 1848, *Abh. K. böhm. Ges. Wiss.* 1851, 5(6): 103.

Hydroptila flabellifera Bremi *in* Hagen, 1864, *Stettin ent. Ztg.* 25: 115-116, partim.

Agraylea pallidula McLachlan, 1875, *Fedtschenko's Reise Turkest.* : 46.

Agraylea multipunctata Curtis sensu Morton, 1886, *Entomologist's mon. Mag.* 22: 269-278.

Type data. England; "Sept. Lisson Grove". According to Kimmins (*in litt.* to Neboiss, 1963) this is a street near Marylebone Station, London, of which the north end crosses the Grand Union Canal and which, in the early nineteenth century, was right on the fringe of London.

Location of type. Holotype ♂, abdomen mounted on microscope slide T-120, Curtis Collection, National Museum of Victoria, Australia) (Neboiss, 1963).

Diagnosis. Forewing length 4.0 - 4.5 mm. ♂ genitalia, fig. 190 (McLachlan, 1880; Martynov, 1924; Mosely, 1939; Tjeder, 1941; Neboiss, 1963; Macan, 1973): ventral process of segment VII elongate, narrow, tapering apically; inferior appendages (arrowed) prominent, elongate concave plates with distinctive dark-rimmed rounded posterior margins.

♀ genitalia, fig. 193 (not previously figured): sternite of segment VIII inconspicuous, merely represented by a U-shaped, narrow, slightly sclerotised ridge; internal apparatus (fig. 193 inset) short with broad, 'crown-like' median ring.

Larva: (Lepneva, 1964; Barnard, 1971; Solem, 1972): head pale yellow, sometimes greyish-brown posteriorly, with characteristic row of four dorso-posterior dark spots and two additional spots anteriorly between the eyes; thoracic nota each with dark anterior border and two (prothorax) or one (meso- and metathorax) dark posterior marks.

Biology. Slowly running water in plant thickets; characteristic of small rivers and rivulets overgrown with plants in the plains (U.S.S.R.), and of the bodies of water of flood-plains of these rivers; occurs in estuarine parts of lakes (Lepneva, 1964). In the lake at Silwood Park, Berkshire, the larvae were restricted to a single small growth of filamentous algae, the cases being found attached to the leaf stems of water lilies (*Nymphea alba* and *Nuphar lutea*) near the edge of the lake in 1-2 feet of water (Barnard, 1971). I have recently collected *sexmaculata* from a number of localities often from the same sites as *multipunctata* (although at different times) and it appears to be more widespread and abundant than was originally thought in this country (cf. Barnard, 1971). Ornamental ponds, fens and other such bodies of water appear to be favourable habitats and I suspect the transport of aquatic vegetation by man to be the major factor in the distribution of this species. I was surprised at first to find large numbers of *sexmaculata* in an m.v. light-trap in my small garden in a moderately built-up area of Croydon, Surrey until I discovered that, to either side of me, live keen anglers who regularly restock their garden ponds with vegetation collected on fishing trips from all over the country. Indeed the type specimen may have been derived from continental material originally brought in on vegetation introduced into the Grand Union Canal. The life-cycle of *sexmaculata* is unknown but British records indicate that the adults occur from the end of May through to September (both single records) with the majority being taken during June and July.

Dissection of specimens collected from Croydon over a two week period revealed that the females emerged with undeveloped ovaries which took less than two weeks to develop to coincide with the emergence of the males (26.vi- 8.vii.1975).

British distribution. (map 20). Originally only recorded from London, Berkshire, Cambridgeshire, Hertfordshire, Wiltshire, the Lake District and Yorkshire, *sexmaculata* has, since 1974, been taken in Buckingham Palace Gardens, London (J.D.B.), Wootton and Croydon, Surrey (J.D.H. and J.E.M.), Dungeness, Kent (J.E.M.), Gussets Wood, Buckinghamshire (J.E.M.), Chippenham Fen, Cambridgeshire (J.E.M.), Rainham, Essex (G.S.R.), Carmarthenshire (R.A.J.), north Wales and Northumberland (I.D.W.) and Shropshire (M.C.M., collected 1939). The species has not been recorded from south-west England, Scotland or Ireland.

General distribution. Southern Scandinavia, central and southern Europe (including Italy and Spain), European U.S.S.R., Turkestan (U.S.S.R.) and Iran.

Discussion. This species is distinguished from Agraylea multipunctata and Allotrichia pallicornis by the form of the male ventral process, inferior appendages and subgenital plate and the female venter VIII and internal apparatus. The larvae are distinguished by the dorsal markings of the head and thoracic nota.

Evidence such as its more southerly continental range, its more local distribution and its absence from the larger natural British lakes seems to indicate that sexmaculata prefers warmer climates than those favoured by multipunctata and is a more recent introduction to the British fauna. The increasing number of more recent records also suggests that the species is now well established in this country and is gradually extending its range. It is more typical of small and artificial bodies of slowly moving to almost stagnant bodies of water, its distribution probably being largely dependent on the transfer of aquatic plants, to which the cases are attached, rather than by natural methods of dispersal.

Allotrichia pallicornis (Eaton)

Agraylea pallicornis Eaton, 1873, *Trans. ent. Soc. Lond.* 1873: 148, pl. 3, figs. 10, 10a.

Allotrichia pallicornis McLachlan, 1880, *Rev. Syn.*: 284, pl. 58, figs. 1-5.

Allotrichia tauri Jacquemart, 1965, *Inst. r. Sci. nat. Belg.* 41(33): 5. *Syn.n.*

Type data. Italy; Turin (Torino). Four ♂ specimens of *pallicornis* in BMNH collections; lectotype designated by Kimmins (1957).

Diagnosis. Forewing length 5mm. ♂ genitalia, fig. 191 (Eaton, 1873; McLachlan, 1880; Mosely, 1939; Schmid, 1959*a*; Jacquemart, 1965; Macan, 1973): ventral process of segment VII long, stout with blunt corners bearing two stout setae and slightly produced median corners (dorso-ventral view), a pair of small, dark asymmetrical processes dorsally near postero-medial edge; subgenital plate with a pair of characteristic asymmetrical processes, the right elongate with a dilated apex, one elongate curved spine arising basally and one short medial spine, and the left process short, subquadrate with an elongate narrow, slightly curved spine and a short, stout, abruptly bent spine both arising basally.

♀ genitalia, fig. 194 (not previously figured): segment VIII narrow (cf. *Agraylea multipunctata* and *sexmaculata*), without ventro-medial sclerite but with what appears to be a single, slightly oblique, asymmetrical groove which bifurcates posteriorly; internal apparatus narrow, elongate, without median 'crown' (fig. 194, inset).

Larva: (Giudicelli & Vaillant, 1967): head and thoracic tergites very pale, completely devoid of markings; tergite of abdominal segment IX absent (probably present but inconspicuous, J.E.M.).

Biology. The larvae described from Corsica by Giudicelli & Vaillant (1967) were collected from a rapid stream, poor in aquatic vegetation and with little shelter. Unlike the larvae of *Agraylea* which those of *Allotrichia pallicornis* most closely resemble, the latter are secondarily adapted for detritus-feeding and for life in fast-flowing water, the pupal cases being attached at two corners only and held vertical to the substrate. Schmid (1959*a*) records *pallicornis* from torrents at high altitudes (up to 8000 ft.) and 'agitated waters' in small rivers with very stony beds. The life cycle is unknown but adults have been collected in the British Isles throughout June and July.

British distribution. (map 21). Previously known from only a few localities in Lanarkshire, Wigtownshire, Monmouthshire, Hampshire, Worcestershire, Yorkshire and Berkshire, *pallicornis* has recently been recorded from Gloucestershire (1961, J.D.B.), Yorkshire, Northumberland and North Wales (1963, 1972, 1975, I.D.W.), Dorset and Devon (1975, R.J.S.). O'Connor (*in litt.*) has recently taken this species in Ireland (no data). *A. pallicornis*, as may be expected from its habitat preferences, is found in the more mountainous regions of north and west Britain and fast-flowing streams in the southern lowland regions.

General distribution. British Isles, central and southern Europe, European U.S.S.R., Iran, Algeria.

Discussion. *Allotrichia pallicornis* is distinguished from the two *Agraylea* species, with which it has the most affinities, by the distinctive forms of the male and female genitalia and the pale, unicolorous and rheophilous larvae. Although *pallicornis* has an overall similar (but slightly more southerly) distribution to *sexmaculata* it occurs at higher altitudes and is therefore probably not truly adapted to the warmer climatic conditions. Records indicate that it is probably an established British species but, due to its special habitat requirements, is very local in occurrence and not at all abundant. The early records would seem to indicate a northerly introduction, the species having since moved west and south as indicated by the most recent records from Wales and south-west England. However, the most northerly adjacent continental record so far is from Belgium, *pallicornis* being absent from the Scandinavian countries and the Netherlands, thus implying a more southerly route of introduction by way of France. The present distribution of *pallicornis* may possibly reflect a past continuous distribution over central Europe through Britain along the mountain and hill ranges, colonies being subsequently isolated by the Ice Ages and the sea leaving small numbers in the higher regions of the British Isles where fast running water habitats persist. The early Scottish records may reflect the distribution of collectors at that time.

Ithytrichia lamellaris Eaton

Hydroptila brunneicornis Pictet, 1834, *Recherches Phryganides*: 226, partim.

Ithytrichia lamellaris Eaton, 1873, *Trans. ent. Soc. Lond.* 1873: 140, pl. 2, fig. 3, pl. 3, figs. 6-6b.

Hydroptila costalis Curtis sensu Meyer-Dür, 1875, *Mitt. schweiz. ent. Ges.* 4: 406.

Type data. England; 'Derbyshire, Sandybrook, Nr. Hanging Bridge, 14.vi.1871, A.E. Eaton'. Lectotype ♂ designated by Kimmins (1957), thorax and one pair of wings only; paralectotype (not 'paratype' as stated by Kimmins, 1957) 'similarly affected by pests'; BMNH collections.

Diagnosis. ♂ genitalia, fig. 195 (Eaton, 1873; McLachlan, 1880; Martynov, 1924, 1934; Tjeder, 1930; Mosely, 1939; Macan, 1973): segment IX elongate, tapering posteriorly in both lateral and dorso-ventral views, incomplete dorsally; tergite X (dorsal plate of Tjeder) arising from and projecting beyond antero-dorsal margins of IX, giving rise posteriorly to a pair of parallel dark rods; inferior appendages broad, straight, with truncate apices lying parallel close to one another at base of IX, dark spot on outer apical angle of each; aedeagus with markedly truncate apex; apex of subgenital plate bilobed in dorso-ventral view, each lobe with a single, short apical seta (for fuller description see Tjeder, 1930).

♀ genitalia (not previously figured): oviscapt; ventral sclerite of segment VIII elongate, narrow, posterior margin trilobed (fig. 197).

Larva: (Lauterborn and Rimsky-Korsakow, 1903; Silfvenius, 1904; Nielsen, 1948; Lepneva, 1964; Hickin, 1967).

Biology. Running water, brooks and rivulets in plant thickets (Lepneva, 1964). Rheophilous; rivers, creeks and brooks in places where the current is strong, mostly staying in submerged vegetation where the velocity of the water is reduced but also occurring in the outer parts of the vegetation exposed to the current and on the smooth, current-swept stones on the bottom. The adults have a very short swarming season in June (two to three weeks); Vth-instar larvae occur from the end of August or the beginning of September, development ceasing towards the end of October to begin again at the end of April (Nielsen, 1948). In willow roots (Wallace, pers. comm.).

Adults have been observed in Britain throughout June to September, numbers being too few and records too far apart for any conclusions to be drawn regarding the life-cycle in this country.

British distribution. (map 22). Widely distributed throughout the British Isles, although not abundant, usually only one or two specimens being taken at a time (c.f. species which occur in light-traps in great numbers). New records have increased the known range of this species to N. Scotland in the Aviemore district, Inverness-shire (J.E.M., 1975). I. lamellaris has not so far been recorded from East Anglia.

General distribution. Throughout north and central Europe, Spain, European U.S.S.R. and Israel.

Discussion. The most distinctive feature of this species is the pair of dark dorsal rods of the male genitalia. This is the commonest of the western Palaearctic *Ithytrichia* species, being widespread throughout this region.

Ithytrichia clavata Morton

Ithytrichia clavata Morton, 1905, *Bull. N.Y. St. Mus.* 86: 67-68, pl. 14, figs. 14-15, pl. 15, fig. 35.

Type data. N. America; Ithaca, New York, 1901? (see discussion). There are six microscope slide preparations of *clavata* in the Morton Collection (Royal Scottish Museum, Edinburgh) without data and of which there is 1♂ labelled 'lectotype' and 5♂ specimens labelled 'paratypes'.

Diagnosis. ♂ genitalia, fig. 196 (Morton, 1905; Tjeder, 1930; Betten, 1934; Marshall, 1939; Kimmins, 1943; Ross, 1944; Macan, 1973): segment IX elongate, tapering posteriorly as in *lamellaris*; tergite X not projecting anteriorly beyond IX and without dark parallel rods; inferior appendages relatively slender with pointed apices, slightly divergent and dorsally directed apically; subgenital plate Y-shaped, posteriorly directed median process with a pair of short apical setae; aedeagus slender, apex slightly broader, truncate.

♀ genitalia, fig. 198, (Ross, 1944): oviscapt, ventral sclerite of segment VIII elongate, slender, posterior margin with a broad rim.

Larva: unknown but possibly the species figured by Needham (1902) and reproduced in Ross (1944).

Biology. Small rivers (Nybom, 1960, Rivulet, adult flying over water at a rapid, bottom stony (Tjeder, 1930). The adults have been recorded in Britain on 23.viii.1939, 30.vi.1941 and 30.vii.1943.

British distribution. (map 23). I. clavata was first recorded in Britain from Merioneth in 1939 and was subsequently discovered in Lancashire (1941) and Westmorland (1943). In the BMNH collections there is a female labelled Orthotrichia tetensii from Hampshire (Traggetts Lake) which may be I. clavata.

General distribution. England, Wales, Sweden, France, Finland (Karelia), North America.

Discussion. I. clavata was first described by Morton, 1905, from a collection of Hydroptilids preserved in alcohol, collected at Ithaca, New York, 1901, by Betten. However, Morton did not indicate in his original description whether he had designated a holotype, where the material was deposited, how many specimens were examined, whether females were present, nor did he give the precise locality and date of collection. In Betten's (1934) subsequent account of the Trichoptera of New York State he merely referred to 'a specimen collected at Ithaca in 1901' and did not give any indication of numbers examined, presence of females or the existence of a 'type'. The only clue comes from Tjeder (1930) who referred to three preparations (i.e. microscope slides) of *clavata* loaned to him by Morton in Edinburgh, thus implying that Morton had retained some, if not all, of the original material, and possibly also the 'type'. These may, therefore, now be in the Morton collection in the Royal Scottish Museum, Edinburgh, and, if there is no holotype so labelled amongst these, a lectotype, and possibly a lectoallotype, should be selected. It should be noted here that Ross (1944) designated an *Ithytrichia* female from British Columbia which was possibly of this species (although not positively correlated with male specimens) as the allotype of *clavata*. This raises two objections, firstly that the specimen may not be of this species and secondly that the use of the term allotype is erroneous, the specimen should correctly be referred to as a neallotype (there is no female present in the Morton Collection, Edinburgh; Barnard, pers. comm.).

This species was originally recorded in the Palaearctic region by Tjeder (1930) from Sweden and was subsequently discovered in England and Wales, Finland, European U.S.S.R. and the French Pyrenees. As the occurrence of *clavata* in the east Palaearctic region is unknown, this being a very under-collected area, little can be said of its apparently Holarctic distribution. *I. clavata* may be a true Holarctic species confined to northern Palaearctic regions, the link with North America being provided by the Bering connection, but on the other hand it may be an introduced species, although it is not easy to recognise the region of origin or date of introduction. More records of *clavata* are required to establish it as a true British species since the past records may have been due to separate chance introductions.

Tricholeiochiton fagesii (Guinard)

Hydroptila flabellifera Bremi *in* Hagen, 1864, *Stettin. ent. Ztg.* 25: 116, partim.

Leiochiton fagesii Guinard, 1879, *Mém. Acad. Sci. Lett. Montpellier* 9, 2: 139-143, pl. 5, figs. 1-15.

Oxyethira felina Ris, 1897, *Mitt. schweiz. ent. Ges.* 9: 422-423, 442, fig. 5.

Oxyethira fagesii (Guinard) Lauterborn, 1905, *Zool. Anz.* 29: 212.

Tricholeiochiton fagesii (Guinard) Kloet & Hincks, 1944, *Entomologist* 77: 97.

Type data. The location of the type is unknown. The species was first described from four or five larvae, collected by Guinard 'a few years previously' (i.e. to 1879) in March in or near Prés d'Arènes, which were reared through to adults although the latter were not described or figured in detail.

Diagnosis. ♂ genitalia, fig. 199 (Martynov, 1934; Mosely, 1939; Macan, 1973); (these are very difficult to homologise with those of any other Hydroptilid genus): segment IX forms a strongly sclerotised genital capsule produced postero-ventrally so that it appears oblique in lateral view and conceals the genital appendages; tergite X membranous basally, apex strongly sclerotised with a ventral transverse ridge; a pair of ventrally directed lateral appendages, apparently originating near the base of tergite X and with rounded apices terminating just above 'inferior appendages' (q.v.); inferior appendages apparently fused basally and produced anteriorly as a curious funnel-shaped structure, inf. apps. widely divergent posteriorly apices rounded, bearing a number of short, stout setae; aedeagus very broad and relatively large with respect to segment IX in comparison with other Hydroptilids.

♀ genitalia, fig. 200 (not previously described: modified oviscapt; segment IX short, not telescopic; postero-ventral margin of VIII with rounded median lobe.

Larva: (Guinard, 1879; Lepneva, 1964): the larva of *fagesii* is very distinctive and can easily be recognised by its rectangular silken transparent case and its extremely long mid and hind-legs.

Biology. Stagnant water and water with a slow current in plant thickets (Lepneva, 1964). On the underside of *Scirpus* leaves (Guinard, 1879).

British distribution. (map 24). Traggett's Lake, Mottisfont, Hampshire (17.vii.1932, Mosely) and the Wirral, Cheshire (Wallace, pers. comm.). Possibly also Carrick Mt. near Wicklow, Ireland but not Scotland (c.f. Fisher, 1961).

General distribution. England and Ireland, Sweden, Netherlands, Germany, Poland, Czechoslovakia, France, Switzerland, Italy, Spain, European U.S.S.R.

Discussion. *T. fagesii* may be distinguished from all other British Hydroptilids by the very characteristic form of the male and female genitalia and the general appearance of the larva and its case. Indeed the genus as a whole is quite unusual, at present containing two species (possibly three with the inclusion of *Synagotrichia fortensis* Ulmer, see Section III, Systematics) of which *fagesii* has a western Palaearctic distribution and *lacustris* Kimmins is known only from a single male specimen from Burma, S.E. Asia (*fortensis* Ulmer was described from Sumatra, Indonesia).

T. fagesii appears to be quite a common species on the continent, especially in north and central Europe, but is very rarely encountered in this country. The first possible record is from Ireland (Carrick Mt. near Wicklow), Barker (1867) exhibiting what he thought to be a dipterous larva from here and which Guinard (1879) considered to be the same as his new species. The first positively identified British specimen was collected by Mosely from a private fishing lake at Mottisfont, Hampshire, 17.vii.1932 and may have been introduced with ornamental vegetation from the continent. Wallace's recent discovery of this species from the Wirral, Cheshire, may also have resulted from a chance introduction.

Oxyethira mirabilis Morton

Oxyethira mirabilis Morton, 1904, *Trans. ent. Soc. Lond.* 1904: 327, pl. 21, figs. 5, 6.

Oxytrichia mirabilis (Morton); Mosely, 1939, *British Caddis flies*: 289, figs. 625-627.

Type data. Scotland: Loch Eigheach, Rannoch, Perthshire; single (holotype) ♂; no date given in original description.

There is a single slide in the Morton Collection, Royal Scottish Museum, Edinburgh, labelled *mirabilis* which is probably the ♂ holotype (although not designated as such) and bears the data "Rannoch, July, '03".

Diagnosis. ♂ genitalia, figs. 201, 202 (Morton, 1904; Mosely, 1939): segment VIII fused, concealing the elongate segment IX; IX appears to be reduced to just its marginal framework of which the two dorsal arms project posteriorly as a pair of slender spines lying alongside the apex of the aedeagus; subgenital plate broad, apex slightly bilobed, and with a pair of rings on the ventral surface; inferior appendages short, fused basally, rounded apically, each with a short apical seta and a slender baso-dorsal seta-bearing process; apex of aedeagus dilated, 'titillator' straight, slender, not extending beyond apex of aedeagus.

♀ genitalia, fig. 210 (previously undescribed): internal apparatus extremely elongate, narrow, parallel-sided, extending anteriorly well into segment VI.

Larva: unknown.

Biology. Unknown. Occurs in lakes (Nybom, 1960).

British distribution. (map 25). *O. mirabilis* is only known in Britain from the type-locality where just the single male holotype was taken. The species has not since been recorded.

General distribution. Scotland, Norway, Sweden, Finland, N.W. European U.S.S.R.

Discussion. The genitalia of both sexes of this species, although basically conforming to those of *Oxyethira*, are quite distinct from any other member of that genus so much so that Mosely (1939) erected the genus *Oxyetrichia* to contain it and a single South American species *bidentata* Mosely, also originally in *Oxyethira*. Kimmins, 1958*a*, did not include *mirabilis* in his paper on the British species of *Oxyethira* but in his subsequent checklist (1966) transferred the species back into this genus. Until the larvae are discovered I propose, therefore, to maintain this present arrangement, although it may prove necessary to reinstate the genus *Oxytrichia*.

From the little information available regarding the habitat preferences of this species it seems likely that it prefers lakes and larger static bodies of water. As stated by Morton (1904) the type locality (Loch Eighoach) was an expansion of the River Gaur on the Moor of Rannoch from which he also collected *O. sagittifera*, *flavicornis* and *tristella*. The only L. Eigheach which I was able to trace was a small stretch of water just west of and running into L. Rannoch but when I visited this in August 1975 it appeared to have been converted into some form of reservoir associated with a small electricity station. The banks on one side had been concreted and the other side was very shallow, leading straight from a marsh whose main inhabitants were small black flies which smothered us and caused immense irritation resulting in a rather premature departure and the abandonment of a plan to run a light trap there. No Hydroptilids at all were taken by sweeping vegetation (low marshland grasses) by the banks of the loch which, in any case, appeared to be devoid of any marginal aquatic vegetation or algae.

O. mirabilis appears to be a rare Scandinavian species preferring the larger bodies of water in the cooler climates of northern Europe and, possibly, Asia. The single British record may represent an isolated colony which had survived in the higher regions of Scotland and it may be possible that other colonies still exist in the more remote regions here and perhaps, also, in the north of England and Ireland.

Oxyethira distinctella McLachlan

Oxyethira distinctella McLachlan, 1880. *Rev. syn.* 1880: 521, pl. 59, figs. 1, 2.

Type data. "Finland; Fagervik, Nylandia, July. Palmén, 3♂."; no dates given either in description or with specimens. 'Type in Helsinki ?' (as noted in BMNH index). One paratype ♂ in BMNH collections labelled 'Finland'.

Diagnosis. ♂ genitalia, fig. 203 (McLachlan, 1880; Morton, 1893; Martynov, 1934; Mosely, 1939; Kimmins, 1958*a*; Macan, 1973): segment VIII elongate, deeply excised dorso-anteriorly and posteriorly, apical angles of latter produced as slender, elongate, outwardly curved, apically bifid or trifid processes; lateral processes of VIII large, concealing IX; postero-lateral processes of IX produced as long slender spines; ventral plate (fused inferior appendages?) broad, lateral margins convex, apex with U-shaped median excision, apical margins finely serrate or setate; subgenital appendages forming a pair of slightly down-turned hooks.

♀ genitalia, fig. 211 (not previously figured): very similar to those of *sagittifera* although the V-shaped excision of the postero-ventral margin of VIII is narrower, the apodemes of tergite VIII are relatively longer and slightly less curved outwardly. (Both male and female descriptions made from Finnish material loaned by Dr. O. Nybom, Helsinki).

Larva: (Lepneva, 1964).

Biology. Lakes, very rare (Nybom, 1960). Plant thickets in stagnant and running water with a slow current, preferring calm parts of thickets of water-lilies and broad-leaved *Potamogeton* in lakes, and avoiding the open littoral with reeds and *Scirpus*; pupae from June to August (Lepneva, 1964). The single British specimen was taken in July.

British distribution. (map 26). The single male specimen was taken at a private fishing lake at Mottisfont, Awbridge Danes, Hampshire by Mosely, 3.vii.1919.

General distribution. England, Norway, Sweden, Finland and N.W. European U.S.S.R..

Discussion. *O. distinctella* is most closely related to *sagittifera* from which it may be distinguished by the relatively longer VIIIth segment and the form of the appendages of the male genitalia and the narrower ventral excision of the posterior margin of the VIIth segment of the female. It should be noted, however, that only a single female specimen was examined and therefore further material should be studied to verify the above description. The single English record of distinctella suggests that this is not a true British species but a chance introduction which has not become established. Its general distribution indicates that it is a Scandinavian species preferring cooler climates in the north-west Palaearctic region; its occurrence in the east Palaearctic region has yet to be established.

Oxyethira sagittifera Ris

Oxyethira sagittifera Ris, 1897, Mitt. schweiz. ent. Ges. 9: 421-422, 434, fig. 4.

Type data. Switzerland; "Hausersee bei Ossingen, Ct. Zürich, 1 (holotype?) ♂ am 12.v. (18)95". Ris Collection (Zurich ?).

Diagnosis. ♂ genitalia, fig. 204 (Ris, 1897; Mosely, 1939; Kimmins, 1958a; Macan, 1973): segment VIII short and broad, deeply excised dorso-posteriorly as a pair of long, slender, inwardly curved processes, each with a trifid apex; lateral processes of VIII broad, concealing IX; lateral processes of IX short, rounded, each with a strong sinuous spine; ventral plate (fused inferior appendages) quadrate with median U-shaped excision; subgenital appendages fused and broad basally, apical processes strongly down-curved.

♀ genitalia, fig. 212 (Kimmins, 1958a; Macan, 1973): postero-ventral margin of segment VII forming a wide V-shaped excision, margin and lateral subapical regions of sternite VII relatively more sclerotised than rest of segment; apodemes of tergite VIII short, strongly curved outwards (cf. *distinctella*); internal apparatus elongate, narrow, anterior margin ovoid.

Larva: (Silfvenius, 1904; Lepneva, 1964).

Biology. Ponds, slow reaches of rivers (Kimmins, 1958*a*). Lakes and streams (Nybom, 1960). Rivulets in plant thickets (Lepneva, 1964). In Britain imagines have been collected in June and August and there is one Irish record in May (O'Connor, *in litt.*).

British distribution. (map 27). This species has only been recorded from Scotland (Perth and the Isle of Lewis), the English Lake District and Ireland (Co. Galway) with two new records from Co. Kerry (O'Connor, *in litt.*).

General distribution. British Isles, Norway, Sweden, Finland, Denmark, Switzerland, Austria, Hungary, N.W. European U.S.S.R..

Discussion. *C. sagittifera* is most closely related to *distinctella* from which it may be distinguished by features of the male and female genitalia. Unlike *distinctella*, *sagittifera* appears to be an established British species although uncommon and local in occurrence. It is interesting to note that Mosely (1939), when there were only records from Scotland, the Lake District and Co. Galway, predicted that this species was "perhaps more common in Ireland"; the only records since then have been from Co. Kerry.

Oxyethira tristella Klapálek

Oxyethira tristella Klapálek, 1895, *Entomologist's mon. Mag.* 31: 168-169, figs. A-C.

Type data. Czechoslovakia; "In May (1895), very common on the 'Zlata Stoka' in Trebon, Bohemia". Paratypes in the Klapálek Collection, Prague; no reference has been found to a holotype or a lectotype. Five specimens are in the BMNH collections, all with McLachlan 'type' labels, of which two (labelled 27.v.1895) have been further designated as 'cotypes' (authority unknown); of the remaining three specimens, two are dated v.1895 while the third is labelled viii.1895 and hence cannot be a paratype as it was collected after the original description was made (July, 1895).

Diagnosis. ♂ genitalia, fig. 205 (Klapálek, 1895; Martynov, 1924, 1934; Mosely, 1939; Kimmins, 1958*a*; Macan, 1973): segment IX elongate ventrally, reduced to a narrow transverse band dorsally; postero-lateral processes of IX short, rounded, with stout, incurved, subapical hooks; postero-ventral lobe (fused inferior appendages) spatulate medio-apically, above which lie two black up-turned hooks; subgenital appendages forming two strongly down-curved blackened hooks.

♀ genitalia, fig. 213 (Kimmins, 1958*a*; Macan, 1973): sternite VII widely excised; tergites VIII and IX fused, VIII not produced as a spatulate lobe; sternite VIII with a small central sclerotised U-shaped 'pocket' (fig. 213, arrowed); internal apparatus broad, quadrate.

Larva: (Klapálek, 1897; Lepneva, 1964).

Biology. Running water in the rapid current of small rivulets (Lepneva, 1964). Rivers and lakes (Kimmins, 1958a). Brooks (Nybom, 1960). In the British Isles the adults have been collected from May to September.

British distribution. (map 28). O. tristella has not been recorded in the British Isles since 1940 (Combe, Oxford, A.D. Grensted), the first specimens being taken at Insh (Inverness-shire ?) 1885 by J.J. King. The species is widely distributed throughout the British Isles with records from north and south-west Scotland, north Wales, southern England and the west of Ireland.

General distribution. British Isles, Norway, Finland, Sweden, Netherlands, Poland, Czechoslovakia, France, European U.S.S.R.

Discussion. O. tristella is distinguished by the incurved processes of segment IX and the inwardly pointing darkened median subgenital appendages of the male genitalia, and the small dark median ventral sclerite of segment VIII of the female. The species appears to be established in the British Isles, although local in distribution, but there have been no records of it since 1940. Its continental distribution suggests that it favours cooler climates as found in the northern parts of Europe and at higher altitudes in the more southerly regions where fast-running water occurs in hill and mountain streams and rivers.

Oxyethira simplex Ris

Oxyethira frici Klapálek sensu Ris, 1894, *Mitt. schweiz. ent. Ges.* 9: 131.

Oxyethira simplex Ris, 1897, *Mitt. schweiz. ent. Ges.* 9: 420-421, 442, fig. 3.

Type data. Switzerland; "Pfynwald in Wallis, Marz und April, 1889 u 90 (M. Paul). Oerlikon 13.v.93 in Mehrzahl an einem Sumpfbache" Ris Collection (Zürich?); there is no reference to either a holotype or a lectotype.

Diagnosis. ♂ genitalia, fig. 206 (Ris, 1897; Mosely, 1939; Kimmins, 1958*a*; Macan, 1973): segment VIII simple; segment IX longer than VIII, postero-lateral processes short, rounded, ventral plate produced posteriorly convergent, apices simple; aedeagus with apex of 'titillator' obtusely angled.

♀ genitalia, fig. 214,(Kimmins, 1958*a*; Macan, 1973: internal apparatus narrow, subquadrate, adjoined posteriorly by a pair of posteriorly convergent 'rods'.

Larva: (Macdonald, 1950; Hickin, 1967).

Biology. Different parts of Scotland, about springs, sometimes where there is no surface water in summer, the moisture being all absorbed by the sphagnum or moss (Morton, 1904). In Loch Lomond (Auchentullich Bay), larvae on a substratum of sand and gravel with *Isoetes*, pupae attached to algae-covered stones at mouth of Cross Burn and around shore of Bay (Macdonald, 1950). Larvae confined to areas with macrophytic vegetation (Weerekoon, 1956). Rivers and lakes (Kimmins, 1958*a*). Brooks and rivulets (Nybom, 1960). In the British Isles the adults occur mainly between May and August but there are a few records from October.

British distribution. (map 29). Local but widely distributed throughout the British Isles, most records being from Scotland and the west coast of Wales, the most recent being from Inverness-shire (1966, 1968; R.J.S.) and the Lambourn, Berkshire (1973: P.C.B.).

General distribution. British Isles, Norway, Sweden, Finland, Netherlands, Switzerland, European U.S.S.R..

Discussion. This is characterised, as its name suggests, by the simplicity of both the male and female genitalia. Its Scandinavian distribution suggests that it prefers the cooler and higher regions of the British Isles, although its habitat preferences do not show any tendency towards the faster-flowing streams of the hills and mountains. The species appears to be well established in this country, possibly becoming more widely distributed, although still rather local in occurrence.

Oxyethira flavicornis (Pictet)

Hydroptila flavicornis Pictet, 1834, *Recherches Phryganides*, 1834: 225, pl. 20, figs. 11a-d.

Hydroptila sparsa Curtis sensu Stephens, 1836, *Ill. Brit. Entom.* (Mandibulata) 6: 152.

Oxyethira costalis (Curtis) Eaton, 1873, *Phil. Mag.* 4: 218.

Oxyethira flavicornis (Pictet) Neboiss, 1963, *Beitr. Ent.* 13: 595.

Type data. Original description: "H. A. ANTENNES FAUVES. (Pl. XX, fig. 11). *H. flavicornis* Mihi. Noires; antennes fauves; ailes supérieures grises, à base blanchâtre et à points blancs formant deux bandes; pattes fauves. Longeur 1.1/4 lignes.

DESCRIPTION. Cette espèce diffère de la précédente (*H. pulchricornis* Pictet) par ses antennes qui sont d'un fauve uniforme et par l'absence d'une tache blanche entre leurs bases. Les ailes supérieures sont de même grisâtres et ont des points blancs, mais ils ne font que deux bandes; la base de l'aile est blanchâtre. Le larve (Pl. XX, fig. 11b) a le thorax et la tête plus larges que dans l'espèce précédente, et d'un fauve clair ainsi que les pattes. Les anneaux de l'abdomen n'ont pas de pièces écailleuses en dessus. Elles se font des étuis analogues aux précédens, c'est-à-dire aplatis et ouverts par une fente; mais à leur partie postérieure ils sont retrécis et terminés par une point émoussée (fig. 11a). Ces larves vivent avec les précédentes, mais sont moins communes." (i.e. with *pulchricornis* on stones in running water in the environs of Geneva, Switzerland).

The location of the type is unknown. However, according to Botosaneanu & Schmid (1973) there is a single male specimen of *Oxyethira flavicornis* from the Vaud canton, with possibly two females and two examples without abdomens, in the Muséum d'Histoire naturelle de Genève. Botosaneanu & Schmid do not state whether these were labelled as *flavicornis* by Pictet, neither do they give any collection dates or indication of the

possible type status of these specimens (see discussion).
Diagnosis. ♂ genitalia, fig. 207 (Eaton, 1873; McLachlan, 1880; Martynov, 1924; 1934; Mosely, 1939; Kimmins, 1958*a*; Macan, 1973): tergite VIII slightly excised posteriorly forming a pair of blunt, somewhat downcurved lobes each bearing a row of short spines; sternite VIII widely excised posteriorly and produced laterally to form a pair of short but strongly incurved hooks; segment IX as long as VIII, lateral processes short, bluntly rounded; inferior appendages apparently fused forming a distinct apico-ventral plate, slightly excised medially along posterior margin; subgenital appendages darkly pigmented, strongly developed, downcurved, not meeting medially; 'titillator' of aedeagus flat, ribbon-like, broad basally, tapering posteriorly, bifurcate.

♀ genitalia, fig. 215 (Kimmins, 1958*a*; Macan, 1973): small dorso-medial, spatulate, setate lobe (VIII) present above segment IX; sternite VIII with short concave lateral margins; segment X with somewhat convex lateral margins; internal apparatus short and broad.

Larva: (Nielsen, 1948; Lepneva, 1964; Hickin, 1967).
Biology. Rivers, lakes (Kimmins, 1958*a*). Lakes, large ponds and smaller bodies of water, rarely on stony banks of lakes not too much exposed to wave action (perhaps another species? - J.E.M.), sometimes found in slightly acid waters (unlike *Agraylea*, *Hydroptila* and *Orthotrichia*), always associated with filamentous algae (Nielsen, 1948). Lakes and large ponds (Mosely, 1939). Lakes (Nybom, 1960). In plant thickets in

stagnant water or water with slow current (Lepneva, 1964). I have taken *flavicornis* at Dungeness, Kent (viii.1974; vii.1975) in vast numbers in an m.v. light trap some distance from the pond. This species was also the most frequently encountered Hydroptilid in the Aviemore district during the first two weeks of August, 1975 (J.E.M.), being collected in vast numbers by sweeping the heather and marginal vegetation of lochs during the daytime and at m.v. and actinic light-traps at night by lochs and streams. Indeed this was the only species to be taken by the stream at the top of 'White Ladies' (c.3,000ft. altitude) in the Cairngorms by the start of the ski-lift. In general, from the available British records, *flavicornis* appears to frequent all forms of natural and artificial static to slowly moving bodies of water such as lochs, llyns, tarns, lakes, ponds, fens and small rivers and streams, always with marginal aquatic vegetation along their banks.

In Denmark the Vth-instar larvae are not fully grown by winter but cease developing in November and recommence in late April with the first generation flying in May - June and the second in August (Nielsen, 1948). In the British Isles the adults occur between May and September, with most records being taken in June and August, thus suggesting a similar bivoltine life-cycle.

British distribution. (map 30). Widely distributed and very abundant throughout the whole of the British Isles, including the Shetlands (Unst) and the whole of Ireland. The species has not so far been recorded from the extreme south-west of England.

General distribution. North and central Europe (including the Faroes), Italy, Yugoslavia, European U.S.S.R., Egypt.

Discussion. *O. flavicornis* is readily distinguished by the form of the male and female genitalia.

The identity of the type of this species is still in some doubt. Neboiss (1963) proposed *flavicornis* Pictet as the type-species of the genus *Oxyethira* to replace *costalis* Curtis since the latter proved to be a senior synonym of *Orthotrichia tetensii* Kolbe, and *flavicornis* was the first available suggested synonym of *costalis* Curtis sensu Eaton. There is no doubt as to the species chosen by Eaton as the type for *Oxyethira* as his figures of the male genitalia are perfectly recognisable, it was just that he erroneously considered it to be conspecific with *Hydroptila costalis* Curtis. The synonymy of Pictet's *flavicornis* with *costalis* sensu Eaton is still very doubtful as the type of the former has not been traced and the idea seems to have originated with Eaton 1873 (perhaps earlier) who gives no reasons for his views. Pictet's original description of *flavicornis* is quoted above and, from this and the original figures of the general appearance of the adult, larva and its case, I do not consider this species to be an *Oxyethira*. The species at present referred to as *Oxyethira flavicornis* has a distinct tuft of white setae between the bases of the antennae which are yellowish brown with darker brown tips; the forewings have a yellowish hue with more distinct spots and bands than as illustrated by Pictet. The larval case of *Oxyethira* is quite unlike that illustrated, being always of the typical 'jug' or 'bottle'-shape while those of *flavicornis*, from Pictet's figure, bears more resemblance to the pupal case of *Ithytrichia*. It is interesting to note that the general appearance of pinned specimens of *Ithytrichia lamellaris* Eaton is very similar to Pictet's description of *flavicornis* in that the antennae are often uniformly yellow, the tuft of white setae between the bases of the antennae is inconspicuous or absent and the forewings are black to greyish with just very faint transverse bands of white (cf. also *Hydroptila* and *Orthotrichia* which have white setae on the head, banded antennae and distinctly spotted or striped forewings). The suggestion that Pictet's *flavicornis* may be a species of *Ithytrichia* is yet another possibility to be considered in this already confused and complex problem, but should nevertheless be borne in mind. The only objection to this proposal, however, is that Pictet makes no reference to any dorsal and ventral abdominal papillae on the larvae as he might have been expected to if *flavicornis* was an *Ithytrichia* since this is a very characteristic feature of this genus.

Perhaps the only way this problem can be resolved once and for all, is to consider Pictet's type-species as lost but to maintain the name flavicornis due to its accepted usage and to select a neotype, possibly from the series of *Oxyethira costalis* (Curtis) *sensu* Eaton (1873) from which Eaton drew his figures of the male genitalia on which all subsequent identifications of this species have been based. From Eaton's original account this may have been one of a number of specimens collected by Eaton from Woburn and Battlesden Parks, Bedfordshire, of which there are, in the BMNH collections, four from the latter locality already labelled as syntypes of *costalis* Eaton. This, if acceptable, would appear to be the most reasonable solution as, on the one hand, the present sense of *flavicornis* would remain unchanged as would that of the species (possibly common such as *Ithytrichia lamellaris* Eaton) of which Pictet's *flavicornis* might prove to be the senior synonym.

In conclusion, *Oxyethira flavicornis* (in the present accepted sense) appears to be one of the most widespread and abundant western Palaearctic *Oxyethira* species and Hydroptilid species in general. This is probably due to its tolerance of a wide range of aquatic habitats from larger lowland standing bodies of water to upland streams which in turn may be due to the protection afforded by the vegetation thickets in which the larvae dwell.

Oxyethira frici Klapálek

Oxyethira frici Klapálek, 1891, *Sber. K. böhm. Ges. Wiss. Math.-nat. Kl.* 1890: 177, 182, 186, pl. 7, figs. 5-7.

Type data. Czechoslovakia; 'Jablone', T. Orlice, 14.15.vii. 1890'. The type is probably in the Klapálek Collection, Prague. In the BMNH collections there is a specimen designated as a 'cotype' and labelled 'Cernovice, 3.ix.1891. Type, Klapálek', and a second specimen labelled 'T. Orlice, 2.ix.91' (both from the McLachlan Collection).

Diagnosis. ♂ genitalia, fig. 208 (Klapálek, 1890; Morton, 1893; Martynov, 1924, 1934; Mosely, 1939; Kimmins, 1958*a*; Macan, 1973): postero-lateral margin of segment VIII armed with three stout spines; segment IX short, ventral margin produced as a median apical bilobed process; subgenital appendages broad and fused basally, produced medially as short slender processes with slightly out- and down-turned short apical hooks; aedeagus with short, slender lateral process sub-apically.

♀ genitalia, fig. 216 (Kimmins, 1958*a*; Macan, 1973): internal apparatus quadrate, adjoining the broad, subtriangular, anteriorly divergent posterior lobes; segment X with lateral sides markedly concave.

Larva: (Silfvenius, 1904; Lepneva, 1964).

Biology. Rivers (Kimmins, 1958*a*). Larger and smaller rapids (Nybom, 1960). Running water on bottom, pupae on stones (Lepneva, 1964). In the British Isles the adults occur between May and September.

British distribution. (map 31). Scotland, north-west and south-west England, Wales and Ireland.

General distribution. British Isles, Norway, Sweden, Finland, Germany, Poland, north-west and central European U.S.S.R.

Discussion. *O. frici* is most closely related to *falcata* from which it may be distinguished by the number and form of the spines of segment VIII, the ventral lobe and the subgenital appendages of the male genitalia and the relatively inconspicuous posterior internal lobes of the female. Although it is not a common or abundant species, *frici* has a wide British distribution with a slightly more northerly occurrence and higher altitude tendencies in comparison with *falcata* (possibly due to a preference for faster running water?). Recent records of *frici* show it to be an established component of the British fauna.

Oxyethira falcata Morton

Oxyethira falcata Morton, 1893, *Trans. ent. Soc. Lond.* 1893: 80-81, pl. 5, figs. 1-7.

Type data. The type specimen was probably taken in Scotland (Redmyre Loch, near Carluke, Lanarkshire, 1893) although Morton (1893) also listed specimens from Devon (see below) and Ireland in the original description. The type is in the Morton Collection (Royal Scottish Museum, Edinburgh); five paratypes in the BMNH collection, three from near Woodbury, Devon, 15.vii.1891, and two from Ottery Hill, Devon, 7.vii.1891.

Diagnosis. ♂ genitalia, fig. 209 (Morton, 1893; Klapálek, 1894; Martynov, 1934; Mosely, 1939; Kimmins, 1958*a*; Macan, 1973); postero-lateral margin of segment VIII armed with two or three short, stout spines; segment IX ventrally as long as VIII, dorsally reduced to a narrow, transverse, sclerotised band with a trilobed ventral margin and an elongate, apically rounded, median process; subgenital appendages broad, median apices simple, blunt to slightly produced; aedeagus without subapical process.

♀ genitalia, fig. 217 (Kimmins, 1958*a*; Macan, 1973): internal apparatus wide, subquadrate, apparently adjoined posteriorly by a pair of dark, strongly sclerotised, comma-shaped lobes.

Larva: unknown.

Biology. Rivers, lakes (Kimmins, 1958*a*). Brooks (Nybom, 1960). "Small streams flowing from springs into (Malham) Tarn ...." (Holmes, 1963). The adults occur in the British Isles mainly from June to September although a few odd records have been taken in May and October.

British distribution. (map 32). Widely distributed and abundant throughout the British Isles from the North Ebudes, Scotland, north-west, southern and south-west England, Wales, East Anglia and western Ireland.

General distribution. British Isles, Netherlands, Germany, Hungary, Rumania, Yugoslavia, Bulgaria, Greece, Iran, Pakistan, Israel, Algeria, Morocco.

Discussion. *O. falcata* is most closely related to *frici* from which it may be distinguished by details of the male and female genitalia (see discussion on *frici*). *O. falcata* has, in general, a more southerly distribution than *frici* and is a well established component of the British fauna. On the continent there appears to be a species complex centred around *falcata*; a number of the species involved may subsequently prove to be geographical races or subspecies.

THE ORIGIN OF THE BRITISH HYDROPTILID FAUNA

The British Hydroptilid fauna appears to be made up of three main elements: (i) those species with a present day widespread British and continental distribution; (ii) those which probably had a widespread distribution in the past but now, due to the possible influence of the ice ages, are restricted to the northern Scandinavian countries and isolated parts of higher ground in Scotland, the north of England and European mountain ranges such as the Alps and the Pyrenees and, finally, (iii) those species represented by single isolated records or, at most, a few sporadic records and which may be the result of chance introductions into this country. In the two last named categories, however, a few species once isolated or introduced into one small region may now have become firmly established and are gradually becoming more widely distributed throughout the British Isles (asterisked* below). The species belonging to the last two categories are:

(ii) *Hydroptila cornuta**, *H. sylvestris*, *H. tigurina*,
H. valesiaca, *Oxyethira mirabilis*, *O. sagittifera**,
O. tristella, *O. simplex**, *O. frici**.

(iii) *Hydroptila lotensis*, *Orthotrichia tragetti*,
*Ithytrichia clavata**, *Tricholeiochiton fagesii**.

Agraylea sexmaculata and *Allotrichia pallicornis* also seem to have once been very local but are now proving to be more frequently encountered and more widely distributed.

The British Hydroptilid fauna is made up of what are considered to be the more advanced genera of this family belonging to what are here referred to as the tribes Hydroptilini (*Agraylea*, *Allotrichia*, *Hydroptila*, *Oxyethira* and *Tricholeiochiton*) and Orthotrichiini (*Orthotrichia* and *Ithytrichia*) which have world-wide or, at least, Holarctic distributions and which have larvae primarily associated with filamentous green algae. The more primitive Palaearctic groups such as *Ptilocolepus* (Ptilocolepinae) and *Stactobia* (Stactobiini) are completely absent from this country even though some species of the latter genus are found in France (the Alps and the Pyrenees) and it would appear that habitat and climatic conditions are not suitable for these groups in this country. They may have been at some time in the past when Britain was joined to the continent but with the present change in climate, isolation from the mainland and inability to compete with the more advanced genera, these groups have disappeared completely from this country.

Although the British Hydroptilidae are poorly recorded in comparison with other families of larger Trichoptera, the distribution maps produced in conjunction with the Biological Records Centre do show in many cases the indications of various forms of distributional patterns correlated, as may be expected, with the topography of the land - the highlands and the lowlands and their associated bodies of water. These patterns have been discussed for each individual species but a division can be seen between those species which prefer the faster-flowing rivers and streams such as are found in the higher regions of the north and west and those which inhabit more static and slowly flowing bodies of water typical of the south and east. It is hoped that these studies will stimulate new interest in this ecologically and biologically quite diverse and fascinating group so that more (and correctly determined) records can be made to further the knowledge of the British fauna; a more accurate picture could then emerge of the distribution and origins of the constituent species.

MATERIAL EXAMINED (IMAGINES) OF THE BRITISH HYDROPTILIDAE

Agraylea multipunctata	c. 70, BMNH
A. sexmaculata	c. 30, BMNH
Allotrichia pallicornis	c. 70, BMNH (including type)
Hydroptila angulata	c. 40, BMNH (type); B.; N.
H. cornuta	c. 40, BMNH (type); B.
H. forcipata	c. 100+, BMNH (type); B.
H. lotensis	c. 10, BMNH (type); B.; M.
H. martini	c. 40, BMNH (type)
H. occulta	c. 20, BMNH (type); B.; M.; A.
H. pulchricornis	c. 70, BMNH; B.
H. simulans	c. 30, BMNH (type)
H. sparsa	c. 100+, BMNH
H. sylvestris	c. 12, BMNH
H. tigurina	c. 11, BMNH
H. tineoides	c. 100+, BMNH; B.
H. valesiaca	c. 20, BMNH (paratypes)
H. vectis	c. 100, BMNH
Orthotrichia angustella	c. 50, BMNH (type)
O. costalis	c. 60, BMNH; B.
O. tragetti	c. 3, BMNH (type); N.
Ithytrichia clavata	c. 7, BMNH (all ♂, possibly also 1 ♀)
I. lamellaris	c. 50, BMNH (type)
Oxyethira distinctella	c. 1, BMNH (♂); N.
O. falcata	c. 50, BMNH (type)
O. flavicornis	c. 100+, BMNH; B.
O. frici	c. 60, BMNH
O. mirabilis	c. 5, BMNH; N.
O. sagittifera	c. 7, BMNH
O. simplex	c. 30, BMNH
O. tristella	c. 15, BMNH (type); N.
Tricholeiochiton fagesii	c. 30, BMNH

Both male and female specimens were examined except where stated. Loaned material came from the following sources as indicated: A. Andersen, Norway: B. Botosaneanu, Europe: M. Malicky, Europe: N. Nybom, Finland.

SECTION V SUMMARY

In this thesis an attempt has been made to give a concise account of the morphology, taxonomy (to the species-group level), biology and distribution of the Hydroptilidae to bring the knowledge of the group into line with that of the other, relatively better studied families of Trichoptera. A section has been devoted to the British fauna.

The first section describes the general features of the family and includes a preliminary discourse on the history of its study and the principal contributors to this knowledge. The general appearance, life-cycle (with its unique larval hypermetamorphosis), larval feeding habits, habitat preferences (and associated larval structural adaptations) and methods of dispersal are described. Brief mention is made of the economic importance of the group and the section concludes with hints on methods of collecting, preserving, rearing and examining these minute caddisflies.

The morphological section, which is based on dissections and examination of transverse and longitudinal serial sections , surveys the external and internal (microanatomical) features of the adult and final instar larval stages with emphasis on those structures which are, or may be, of taxonomic and phylogenetic importance.

In the imagines, head and thoracic structures have proved (following Ross, 1944, etc) to be useful generic characters; spur formula is still of some importance but venation in this group has been found to be quite useless due to the reduced size of the wings and subsequent loss of veins. Emphasis has been laid on the morphological differences between the adults of the two subfamilies, the primitive Ptilocolepinae bearing more resemblance to small Rhyacophilids and Glossosomatids than to the more typical Hydroptilinae. Notable contributions to adult morphology include discussions on the thoracic pre-episternum and the terminology of the thoracic pleurites as well as a special section on the external structures of abdominal segment V which have been found to be associated with small sac-like glands in both sexes of the Hydroptilinae. The internal micro-anatomy of Agraylea sexmaculata Curtis (males and females) was investigated and was found to be typical of Trichoptera in general except in minor features, usually associated with reduced size and short adult life.

The larvae are first classified (non-phylogenetically) according to aquatic environment, food source and case-form. The main structural features are then described and includes discussions on the terminology of the regions of the head capsule, ecdysial lines, the 'gular controversy' and the maxillo-labial hypopharyngeal complex; here the system of Hinton (1963) has been followed although the views of Nielsen (1948) and Badcock (1961) have been compared and criticised. The section on internal morphology describes the main organ systems and includes discussions on the salivary and silk glands(and the possible homologue of 'Lyonet's gland' of Lepidoptera) and the possible function of the abdominal dorsal 'rings' as regions of chloride epithelia.

Finally, in section II, there are two short accounts of the main external features of the planktonic, free-living, early instar larvae and the relatively homogeneous pupae, including brief descriptions of pupation and adult emergence.

The major part of this study is concerned with the systematics of the Hydroptilidae and its phylogeny and position within the Trichoptera; this is principally based on material in the collections of the BMNH. The subfamily division into the primitive Ptilocolepinae and the more typical Hydroptilinae has been retained but, primarily for the sake of convenience in dealing with such a large group, the latter has been split into six tribes: the Stactobiini, Leucotrichiini, Ochrotrichiini, Neotrichiini, Hydroptilini and Orthotrichiini (with seven genera remaining of doubtful status and/or relationships). Twelve new generic synonymies have been proposed, while a few more doubtful ones have been indicated, one genus has been reinstated and three genera have been transferred to other families of Trichoptera. For each genus the taxonomy, distribution, diagnostic features (adults, larvae and pupae where known) and biology have been described and discussed. In the Appendix (section VIII) keys are given to distinguish 1. the adults, larvae and pupae of the Ptilocolepinae from those of the Rhyacophilidae and Glossosomatidae and 2. the adults and larvae (where known) of the genera of the Hydroptilidae; there is also a full species checklist of the family and a generic index to the Systematics section.

The fourth main section of the text deals exclusively with the

31 British species of the Hydroptilidae which are represented by seven genera, all of which belong to the more successful and widely distributed Hydroptilini and Orthotrichiini tribes : *Agraylea*, *Allotrichia*, *Hydroptila*, *Oxyethira*, *Tricholeiochiton*, *Ithytrichia* and *Orthotrichia*. The taxonomy, distribution (British and Continental), adult diagnostic features and biology of all species are discussed and there are accompanying distribution maps (produced in conjunction with the Biological Records Centre) and male and female genitalia figures (the female of *H. tigurina* is still unknown). Only the generic features of the larvae have been indicated since insufficient material was available for study and the species show very little interspecific variation within each genus. A key to the males and females of all British species has been included and two species, *H. martini* Marshall and *H. valesiaca* Schmid (both previously confused with *H. occulta* (Eaton)) have been added to the British list.

It is concluded that the Hydroptilidae, although containing the smallest members of the Order Trichoptera, is perhaps the most biologically and morphologically diverse family of caddisflies in both the adult and, particularly, the larval stages.

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SECTION VIII.

APPENDIX

VIIIA. KEYS TO DIFFERENTIATE THE PTILOCOLEPINAE FROM THE GLOSSOSOMATIDAE AND RHYACOPHILIDAE

At first sight the adults of the Ptilocolepinae may easily be mistaken for small Rhyacophilids or Glossosomatids due to their broad rounded wings, relatively complete venation, similar head and thoracic structures, spur formula and sternal ridge of abdominal segment V. The following key is therefore included to supplement the main generic key to the Hydroptilidae and aims to facilitate the identification of the Ptilocolepinae when presented with what appears to be a rather anomalous Rhyacophilid or Glossosomatid. The main diagnostic features have also been summarised in Chart I; the principal Hydroptilid key, in which the Ptilocolepinae may be differentiated from the Hydroptilinae, is given later, at the beginning of the systematic account after the family diagnosis. For completeness keys to differentiate the pupal and larval stages of the Ptilocolepinae, Hydroptilinae, Rhyacophilidae and Glossosomatidae have also been included here.

VIIIA.1. ADULTS

1 Discoidal cell of forewing open; spur formula 3.4.4 .... Rhyacophilidae

\- Discoidal cell of forewing closed; spur formula 2.4.4 or 1.3.4 2

2 Spur formula 2.4.4 3

\- Spur formula 1.3.4 .... Ptilocolepus

3 Lateral ocelli set immediately posterior to antennae, not close to eyes; posterior dorsal head warts small, oval or round, widely separated; pronotal warts widely separated .... Glossosomatidae

\- Lateral ocelli widely separated from antennae, set close to eyes; head warts large almost meeting medianly; pronotal warts closely set .... Palaeagapetus

VIIIA.2. LARVAE (partly after Ross, 1944)

1 A pair of well developed nota present on all three thoracic segments; larvae usually inhabiting 'purse'-type cases of silk only or with small particles of organic or inorganic material .... Hydroptilidae

- Pronotum only sclerotised; larvae without case or with small 'saddle-like' case (flat ventrally, vaulted dorsally) covered in small stones or large sand grains 2

2 Anal prolegs with large elongate hooks; abdominal tracheal gills present or absent; free-living without cases .... Rhyacophilidae

- Anal prolegs with very small retractile hooks; tracheal gills absent; living in small 'saddle-like' cases constructed of small stones .... Glossosomatidae

VIIIA.3. PUPAE

1 Presegmental and postsegmental dorsal hook plates on abdominal segments III-VII and III-V respectively 2

- Pre- and post-segmental hook plates not with full complement as above 4

2 Pupal mandibles without teeth .... Hydroptilinae

- Pupal mandibles with one or two teeth .. (Ptilocolepinae). 3

3. Pupal mandibles with 2 teeth .... *Palaeagapetus*

- Pupal mandibles with 1 tooth .... *Ptilocolepus*

4 Presegmental hook plates absent on Ab. III only (IV-VII; III-V); spur formula 3.4.4 ..... Rhyacophilidae

- Postsegmental hook plates absent from Ab. III, sometimes also from Ab. V; presegmental plates sometimes absent from Ab. III; spur formula 2.4.4 . Glossosomatidae

(Hook plates III-VII: IV-V Glossosomatinae
Hook plates IV-VII: IV Agapetinae)

VIIIB. KEYS TO THE WORLD GENERA OF HYDROPTILIDAE

VIIIB.1. ADULTS: KEY TO WORLD GENERA

1 Forewings broad with rounded apices, sparsely pubescent, fringes relatively short; venation well developed, Cu$_1$ forked in forewing; mesonotum convex, prescutum distinct, scutellum subtriangular with a straight posterior margin and a large oval wart; mesokatepisternal suture ('k') present; latero-ventral ridge of abdominal sternite V present with a pair of antero-dorsal filaments (PTILOCOLEPINAE) 2

- Forewings narrow, usually acuminate, densely pubescent, fringes long; venation exhibiting various degrees of reduction, forewing with Cu$_1$ unbranched; mesonotum flat, prescutum absent, scutellum with posterior portion forming a flat triangular area with steep sides and with a warty texture only along edges; mesokatepisternal suture absent; sternite of abdominal segment V with a pair of shallow antero-dorsal pits each with a short, setae-bearing digitate process (HYDROPTILINAE) 3

2 Veins R_2, R_3, M_1, M_2 free in the hindwing; spur formula 2.4.4; North America, Baltic Amber .... *Palaeagapetus*

- Veins $R_2 + R_3$, $M_1 + M_2$ fused in hindwing; spur formula 1.3.4 .... *Ptilocolepus*

3 Transverse suture present on mesoscutellum 4

- Transverse suture absent on mesoscutellum 20

4 Metascutellum sub-pentagonal to triangular (Nearctic) ... 10

- Metascutellum rectangular to short pentagonal (Palaearctic) or as wide as scutum, very short and rectangular (Holarctic) (STACTOBIINI) 5

5 Metascutellum as wide as scutum, short and rectangular .. 6

- Metascutellum not as wide as scutum 8

6 Spur formula 1.3.4 7

- Spur formula 0.2.4 .... (Oriental) *Chrysotrichia*

(Neotropical: Antilles) *Bredinia*

7 ♂ genitalia simple, segment VIII unmodified (Holarctic) .... *Stactobiella*

\- ♂ genitalia greatly modified, sternite VIII elongate with posterior dorso-lateral spines, segment IX much reduced and withdrawn into VIII (Africa) .. *Catoxyethira*

8 Spur formula 1.2.4 9

\- Spur formula 0.2.3 (S.E. Asia) .... *Plethus*

9 Fore-tibial spur reduced to small process; postoccipital lobes narrow, elongate; metascutellum wide, short, rectangular to pentagonal; ♂ genitalia greatly modified; ♀ internal apparatus with distinct loop in anterior duct (Africa, S.E. Asia) .... *Madioxyethira* (possibly including *Pseudoxyethira* and *Scelotrichia*)

\- Fore-tibial spur unmodified; postoccipital lobes broad, semispherical; metascutellum narrow, long, rectangular; ♂ genitalia relatively simple, sternite VIII produced posteroventrally, IXth reduced, VIIth with elongate process; ♀ internal apparatus without anterior loop (Palaearctic).................. *Stactobia*

10 ♂ inferior appendages large and distinct, projecting well beyond segment IX, often armed with various spines and processes; head and antennae always simple (OCHROTRICHIINI) 11

\- ♂ inferior appendages usually short, hardly projecting beyond segment IX but if narrow and elongate with elaborate baso-dorsal processes then head and antennae (♂) modified (LEUCOTRICHIINI) 13

11 Fore-tibia with apical spur 12

\- Fore-tibia without apical spur . *Ochrotrichia Ochrotrichia*

12 ♂ segment IX produced posteriorly as broad dorso-lateral lobes; inferior appendages narrow, elongate, projecting ventrally just beyond lobes of IX .... *Rhyacopsyche*

\- ♂ segment IX without lateral lobes, inferior appendages broad and elongate, projecting well beyond IX .... *Ochrotrichia Metrichia*

13 Spur formula 1.3.4; ♂ aedeagus with midlength complex; ♀ tergite VII unmodified, internal apparatus well developed (*Leucotrichia*-group) 14

\- Spur formula 0.3.4; 0.2.4; 0.2.3; ♂ aedeagus with median constriction only; ♀ tergite VII modified, internal apparatus simple, ring-like .... *Alisotrichia*

14 Basal costal pouch present on ♂ forewing 15

\- Basal costal pouch absent on ♂ forewing 17

15 Basal costal pouch large, almost ~~x~~½ forewing length; head and basal antennal segment (♂) greatly modified; ocelli 2 (♂) .... *Abtrichia* *Betrichia bispinosa*

\- Basal costal 'bulla' small; head and basal antennal segment (♂) unmodified; ocelli 3 16

16 Middle antennal segments (♂) wide and flat .... *Costatrichia* (*lodora*-group)

\- Middle antennal segments (♂) unmodified .... *Acostatrichia*

17 Basal segment of ♂ antenna enlarged .... *Peltopsyche*, *Zumatrichia*

\- Basal segment of ♂ antenna unmodified 18

18 Ocelli 3 (♂, ♀) .... *Costatrichia* (*simplex*-group); *Betrichia argentinica*; *Leucotrichia* (*melleopicta*-group); and *Celaenotrichia*

\- Ocelli 2 (♂) 19

19 ♂ abdominal sternite VIII with postero-lateral processes .... *Anchitrichia*

\- ♂ abdominal sternite VIII unmodified .... *Leucotrichia* (*pictipes*-group); *Betrichia* (except *argentinica* and *bispinosa*)

20 Ocelli absent 21

\- Ocelli present 23

21 Fore-tibia with apical spur; wings elliptical, ovate; insect large (forewing 5.5mm.); Nearctic .... *Dibusa*

\- Fore-tibia without apical spur;. wings acuminate 22

22 Metascutellum rectangular; spur formula 0.3.4; ♂ genitalia markedly asymmetrical; ♀ genitalia with segment IX relatively short .... *Orthotrichia*

- Metascutellum pentagonal to triangular; spur formula 0.2.4; ♂ genitalia symmetrical; IXth segment of ♀ long forming oviscapt; postoccipital lobes of ♂ modified as hinged caps concealing eversible scent organs .... *Hydroptila*

23 Mid tibia with no preapical spur (formula 0.2.3, 0.2.4) 24

- Mid tibia with preapical spur (formula 1.3.4, 0.3.4) .. 27

24 Spur formula 0.2.4 25

- Spur formula 0.2.3 (Nearctic) .... *Neotrichia*

25 ♂ segment VIII fused, annular; IXth segment almost entirely concealed within VIII; forewing length 1.6mm (S.E. Asia) .... *Stenoxyethira*

- ♂ genitalia not as above 26

26 ♂ segment IX with prominent postero-lateral processes and broad apices; inferior appendages with broad setae-bearing posterior margin and small digitate dorso-lateral basal projection (Nearctic; Neotropical) .... *Mayatrichia*

- ♂ segment IX without processes, inferior appendages apparently absent (Australia) .... *Orphninotrichia*

27 Fore-tibia with apical spur (Neotropical; Chile) ... . *Nothotrichia*

- Fore-tibia without apical spur 28

28 Mesoscutellum diamond shaped, narrow 29

- Mesoscutellum with anterior margin evenly convex, wide 32

29 ♂ ventral process of sternite VII short, laterally compressed, triangular; inferior appendages large, elongate, often broad 30

- ♂ ventral process of sternite VII usually long and spatulate; inferior appendages short and broad, sometimes with short postero-median processes 31

30 Lateral filaments of abdominal segment II present in ♂ (India, S.E. Asia) ..... *Ugandatrichia* (*violacea*-group)

- Lateral filaments absent (Africa) .... *Ugandatrichia* (*nigra*-group)

31 ♂ inferior appendages with concave posterior margins; subgenital plate with a pair of asymmetrical processes bearing asymmetrical spines or filamentous appendages .... *Allotrichia*

- ♂ inferior appendages with convex posterior margins (*sexmaculata*-group) or very short with posteromedian processes (multipunctata-group); processes of subgenital plate absent .... *Agraylea*

32 ♂ VIIIth abdominal segment fused, annular; IXth segment mostly concealed within VIII; ♀ genitalia not oviscapt, IXth segment reduced, tergite usually fused with that of VIII ....*Oxyethira*

- ♂ VIIIth segment with tergite and sternite distinct; segment IX distinct; ♀ genitalia usually oviscapt ... 33

33 ♂ genitalia very distinct - sclerites VII and VIII reduced to thin strips, sternite IX enlarged, tergite X forming an elongate narrow plate, inferior appendages short, slender with incurved apices (Sri Lanka) .... *Macrostactobia*

- ♂ genitalia not as above 34

34 ♂ segment IX with deep dorsal U-shaped incision revealing aedeagus in distinct sheath usually with subapical processes; inferior appendages elongate, concave, broad; ventral processes on segments VII and VIII, latter long and spatulate; (New Zealand) ... . *Paroxyethira*

- ♂ genitalia not as above 35

35 ♂ segment IX produced postero-ventrally (obliquely truncate in lateral view); genital appendages concealed within IX, difficult to homologise; (N.W. Palaearctic, S.W. Asia) .... *Tricholeiochiton*

- ♂ genitalia not as above 36

36 ♂ sternite VI with ventral process; sides of segment IX tapering postero-medially; inferior appendages elongate, parallel, arising near antero-ventral margin of IX, scarcely projecting posteriorly beyond IX .... *Ithytrichia*

\- ♂ genitalia not as above 37

37 ♂ inferior appendages apparently arising dorso-posteriorly from segment IX, 'bean-shaped' with distinct ventrally directed processes; aedeagus slender, tapering (New Caledonia) .... *Caledonotrichia*

\- ♂ genitalia not as above 38

38 ♂ sternite VII with long slender process; segment IX with broad postero-lateral truncate side-pieces; aedeagus with distinct apical or sub-apical hook; (Australia) .... *Xuthotrichia*

\- ♂ genitalia not as above 39

39 ♂ segment IX with postero-lateral side-pieces produced as broad truncate lobes, segment reduced dorsally to thin median transverse strip; aedeagus truncate with well developed spiral 'titillator' (Africa - Yemen, Zaïre) .... *Dhatrichia*

\- ♂ segment IX relatively complete dorsally; aedeagus slender with pointed apex or short spiral 'titillator' (Europe, Pakistan, Aden) .... *Microptila*

VIIIB.2. LARVAE: KEY TO KNOWN GENERA

1 Small tergites present on abdominal segments I-VIII; larval case dorso-ventrally flattened, fixed to substrate 2

- Segments I-VIII without distinct tergites; larval case variable but usually not fixed to substrate 8

2 Median sutures of meso- and meta- thoracic nota indistinct; Nearctic, Neotropical (LEUCOTRICHIINI) ... 5

- Median sutures of all three thoracic nota distinct; Palaearctic (STACTOBIINI) 3

3 Posterior margin of IXth tergite appearing crenellated; case dorso-ventrally flattened, barrel-shaped with mid dorsal and ventral longitudinal seams ..... *Stactobia*

- IXth tergite of larva and case not as above, latter usually with lateral 'wings' 4

4 Case rectangular in dorsal view with mid-dorsal and ventral longitudinal seams; S.E. Asia .... *Plethus*

- Case tapering anteriorly and posteriorly, without dorsal and ventral longitudinal seams; Africa .... *Catoxyethira*

5 Vth instar larva free-living until just prior to pupation; abdomen slender, tapering posteriorly; anal prolegs projecting from sides of abdominal segment X .... *Alisotrichia*

- Vth instar in a fixed, flattened ovoid-circular case abdomen enlarged, abruptly widened from segments V-VII; anal prolegs fused to sides of Xth segment 6

6 Anterolateral angle of pronotum produced anteriorly; femora with arborescent seta .... *Alisotrichia*

- Anterolateral angle of pronotum not produced; arborescent setae absent 7

7 IXth tergite with scattered short stout setae .... *Zumatrichia*, *Abtrichia* and *Peltopsyche*

- IXth tergite usually without short, stout setae, if present then in transverse band .... *Leucotrichia*

8 Mid and hind legs slender, much longer than forelegs 9

\- Thoracic legs short, subequal in length 11

9 Long edges of case almost parallel 10

\- Case 'bottle' or 'jug' shaped .... Oxyethira

10 Mid and hind legs greater than 4 x forelegs .... Tricholeiochiton

\- Mid and hind legs approximately 2½ x forelegs; New Zealand .... Paroxyethira

11 Abdominal segments with dorsal and ventral 'bud-like' processes; single filamentous caudal gill present .... Ithytrichia

\- Abdominal segments not as above, caudal filament absent .. 12

12 Abdomen more or less cylindrical; anal prolegs not fused to sides of Xth segment; case cylindrical, tapering posteriorly; Nearctic 13

\- Abdomen flattened dorso-ventrally or laterally, anal prolegs fused to sides of IX; case flattened with slit-like anterior and posterior openings 14

13 Abdomen slightly depressed, intersegmental grooves prominent; case of secretion and fine sand grains .... Neotrichia Morton

\- Abdomen more inflated, not depressed, intersegmental grooves not prominent, case of secretion only, usually with transverse or longitudinal ridges .... Mayatrichia Ross

14 Labrum with asymmetrical 'beak'; (abdominal segment 11 with lateral humps?); case fusiform, of secretion only with longitudinal ridges .... Orthotrichia

\- Labrum, abdomen and case not as above 15

15 Tibia of forelegs with pronounced baso-ventral process 16

\- Tibia of forelegs without pronounced baso-ventral process 19

16 Abdomen with three filamentous caudal gills; case laterally compressed of two silken valves covered in fine sand grains and sometimes diatoms .... *Hydroptila*

\- Caudal gills absent 17

17 Ventral intersegmental grooves of abdomen very pronounced; case of two silken valves covered in radially arranged algal filaments .... *Agraylea* (*Allotrichia* ?)

\- Abdomen and case not as above, exclusively 'New World' . 18

18 Tarsus with large plate-like seta and hook claw, antero-lateral expansion of metanotum absent; case fusiform of secretion only; Central America .... *Rhyacopsyche* Müller

\- Tarsal seta not plate-like, metanotum with antero-lateral expansion; case usually laterally compressed of two silken valves covered in fine sand grains, sometimes of one valve only carried horizontally .... *Ochrotrichia*

19 Abdomen and case compressed dorso-ventrally 20

\- Abdomen and case not compressed dorso-ventrally; tarsal claws stout, abruptly curved with thick blunt spur at base 22

20 Case of secretion only, with a central tubular section surrounded by lateral fringe, former with a pair or small dorsal pores; New Caledonia ...... *Caledonotrichia*

\- Case of two silken valves covered in fragments of moss and liverwort; Holarctic, montane regions 21

21 Abdomen with a pair of lateral tubercles on each segment; Ab. I without small tergite; Holarctic ... . *Palaeagapetus*

\- Abdomen without lateral tubercles; Ab. I with small dorsal tergite; Palaearctic .... *Ptilocolepus*

22 Dorsal abdominal setae stout, dorsal rings of abdominal segments distinct; larvae on red algae which is incorporated into silken valves of purse-like case; tarsal claw spurs short, thick and blunt; Eastern U.S. .... Dibusa

- Abdominal setae slender, dorsal rings indistinct; case of two symmetrical valves of silk; tarsal claw spurs elongate, thick, blunt; Holarctic .... Stactobiella (only Nearctic specimens known)

SECTION VIIIC CHECKLIST OF WORLD HYDROPTILIDAE TABLE 3

(The following genera have been transferred from the Hydroptilidae: Padunia Martynov (Uenotrichia Tsuda), Tsukushitrichia Koboyashi and Petrotrichia Ulmer.)

Family HYDROPTILIDAE Stephens, 1896

Subfamily PTILOCOLEPINAE Martynov, 1913

- PTILOCOLEPUS Kolenati, 1848
  - colchicus Martynov, 1913
  - extensus McLachlan, 1884
  - granulatus (Pictet, 1834)
    - dilatatus Martynov, 1913
    - funereus (Fourcroy, 1785) sensu Kolenati, 1859
    - turbidus Kolenati, 1848
  - villosus Navas, 1916
- PALAEAGAPETUS Ulmer, 1912a
  - ce[redacted]s Ross, 1938b
  - guppyi Schmid, 1951
  - nearcticus Banks, 1936
  - rotundatus Ulmer, 1912a

Subfamily HYDROPTILINAE Stephens, 1896

Tribe I STACTOBIINI Botosaneanu, 1956

A Stactobia-group

- STACTOBIA McLachlan, 1880
  - AFRITRICHIA Mosely, 1939b
  - ARATRICHIA Mosely, 1948
  - LAMONGANOTRICHIA Ulmer, 1951 (syn. n.)

1 furcata-group

- algira Vaillant, 1951a
- atra (Hagen, 1865)
- beatensis Mosely, 1934
- caspersi Ulmer, 1950
- decoosterai Jacquemart, 1965
- eatoniella McLachlan, 1880
  - oredonensis Mosely, 1934
- eretziana Botosaneanu & Gasith, 1971
- freyi Nybom, 1948
- furcata Mosely, 1930
  - fuscicornis sensu McLachlan, 1884, partim.
- fuscicornis (Schneider, 1845)
  - obscura (Kolenati, 1848)
- kimminsi Schmid, 1959a
- maculata Vaillant, 1951a
- malacantosa Schmid, 1952
- ma[redacted]alitana Botosaneanu, 1974
- mclachlani Kimmins, 1949b
  - botosaneanui Schmid, 1959
  - delamarei Coineau & Jacquemart, 1961
  - fuscicornis sensu McLachlan, 1884 partim.
- monnioti Jacquemart, 1963c
- moselyi Kimmins, 1949b
  - eatoniella sensu Mosely, 1933
  - fuscicornis sensu McLachlan, 1880
- nybomi Schmid, 1959
  - atra sensu Morton, 1893
  - atra sensu Nybom, 1948
  - atra sensu Schmid, 1952
- storai Nybom, 1948

2 martynovi-group

- dohleri Schmid, 1959
- fischeri Schmid, 1959
- forsslundi Schmid, 1959a
- klapaleki Schmid, 1959
- marlieri Schmid, 1959a
- martynovi Schmid, 1959
- mayeri Schmid, 1959a
- olgae Martynov, 1927
- quadrispina Kimmins, 19[illegible]
- schmidi Kimmins, 1964
- tjederi Schmid, 1959
- ulmeriana Schmid, 1959

3 nielseni-group

- bolzei Jacquemart, 1965
- crassa (Ulmer, 1951)(syn.n.)
- fahjia (Mosely, 1948)
- moretti Schmid, 1959
- nielseni Schmid, 1959a
- radovanovici Schmid, 1959
- risiana Schmid, 1959

4 vaillanti-group

- aurea (Mosely, 1939b)
- vaillanti, Schmid, 1959

incertae sedis

- japonica Iwata, 1930
- mallorcensis Vaillant, 1965 (nomen nudum)
- megalatlantica Vaillant, 1956 (nomen nudum)

PLETHUS Hagen, 1887
PLETHOTRICHIA Ulmer, 1951
(syn. n.)
acutus Ulmer, 1951
amogawarsa Schmid, 1958
baliana (Ulmer, 1951)
bodikatuwa Schmid, 1958
cilamegha Schmid, 1958
cruciatus Ulmer, 1951
cursitans (Hagen, 1859)
kala Schmid, 1958
usawasaderma Schmid, 1958
vajirobodhi Schmid, 1958

B Stactobiella-group

STACTOBIELLA Martynov, 1924
TASCOBIA Ross, 1948

1 biramosa-group
biramosa Martynov, 1929
palmata (Ross, 1938b)
2 ulmeri-group
delira (Ross, 1938b)
ulmeri (Siltala, 1908)
risi (Felber, 1908)
3 brustia-group
brustia (Ross, 1938b)

BREDINIA Flint, 1968c
dominicensis Flint, 1968c

CHRYSOTRICHIA Schmid, 1958
araruwa Schmid, 1958
badhami Schmid, 1960
dotalugola Schmid , 1958
hapitigola Schmid, 1958
hatnagola Schmid, 1958

CATOXYETHIRA Ulmer, 1912b
fasciata Ulmer, 1912b
improcera Statzner, in press
ocellata Statzner, in press
pinheyi Kimmins, 1958
veruta Morse, 1974
formosae (Iwata, 1928)

PARASTACTOBIA Schmid, 1958
talakalahena Schmid, 1958

C Madioxyethira-group

MADIOXYETHIRA Schmid, 1960
marshalli Statzner, in press
milinda Schmid, 1960
nepalensis Kimmins, 1964
trifurcata (Jacquemart, 1962)
(syn. n.)

PSEUDOXYETHIRA Schmid, 1958
asgiriskanda Schmid, 1958

SCELOTRICHIA Ulmer, 1951
saranganica Ulmer, 1951

Tribe II LEUCOTRICHIINI Flint, 1970

A Leucotrichia-group

LEUCOTRICHIA Mosely, 1934a

1 melleopicta-group
chiriquiensis Flint, 1970
gomezi Flint, 1970
limpia Ross, 1944
melleopicta Mosely, 1934a
tubifex Flint, 1964
viridis Flint, 1967a
2 pictipes-group
fairchildi Flint, 1970
imitator Flint, 1970
pictipes (Banks, 1911)
sarita Ross, 1944

ZUMATRICHIA Mosely, 1937

1 multisetosa-group
multisetosa Flint, 1970
2 galtena-group
antilliensis Flint, 1968a
attenuata Flint, 1970
bifida Flint, 1970
chiriquiensis Flint, 1970
diamphidia Flint, 1970
echinata Flint, 1967a
galtena Mosely, 1937
notosa (Ross, 1944)
saluda Flint, 1970
strobilina Flint, 1970
vieja Flint, 1970
3 filosa-group
caudifera Flint, 1970
filosa Mosely, 1937
rhamphoides Flint, 1970
teana Flint, 1970
4 palmara-group
anomaloptera Flint, 1968a
palmara Flint, 1970

PELTOPSYCHE Müller, 1879b
maclachlani Müller, 1879b
sieboldii Müller, 1879b

ANCHITRICHIA Flint, 1970
spangleri Flint, 1970

COSTATRICHIA Mosely, 1937

1 simplex-group
simplex Flint, 1970
spinifera Flint, 1970
2 lodora-group
bipartita Flint, 1970

lodora Mosely, 1937
panamensis Flint, 1967a
tripartita Flint, 1970

ACOSTATRICHIA Mosely, 1939d
brevipenis Flint, 1974
fimbriata Flint, 1974
plaumanni Mosely, 1939d
simulans Mosely, 1939d
spinifera Flint, 1970

BETRICHIA Mosely, 1939d
argentinica Flint, 1972c
bispinosa Flint, 1974
occidentalis Flint, 1974
surinamensis Flint, 1974
zilbra Mosely, 1939d

ABTRICHIA Mosely, 1939d
antennata Mosely, 1939d
squamosa Mosely, 1939d

CELAENOTRICHIA Mosely, 1934a
edwardsi Mosely, 1934a

B Alisotrichia-group

ALISOTRICHIA Flint, 1964
argentilinea Flint, 1968b
blantoni Flint, 1970
chorra Flint, 1970
dominicensis Flint, 1968c
hirudopsis Flint, 1964
lobata Flint, 1968c
orophila Flint, 1968c
quemada Flint, 1970
septempunctata Flint, 1968c
tamana Flint, 1970
trifida Flint, 1970
wirthi Flint, 1968c

Tribe III OCHROTRICHIINI

OCHROTRICHIA Mosely, 1934a
POLYTRICHIA Sibley, 1926
Subgenus OCHROTRICHIA
aldama (Mosely, 1937)
alexanderi Denning & Blickle, 1972
alsea Denning & Blickle, 1972
anisca (Ross, 1941b)
argentea Flint & Blickle, 1972
arizonica Denning & Blickle, 1972
arranca (Mosely, 1937)
arva (Ross, 1941b)
attenuata Flint, 1972b
brayi Flint, 1968c
buccata Denning & Blickle, 1972
caimita Flint, 1972b
caligula Flint, 1968b
capitana Ross, 1944
chiapa Denning & Blickle, 1972
confusa (Morton, 1905)
contorta (Ross, 1941b)
cruces Flint, 1967
dactylophora Flint, 1965
denningi Blickle & Morse, 1957
eliaga (Ross, 1941b)
escoba Flint, 1972b
felipe Ross, 1944
filiforma Flint, 1972b
flagellata Flint, 1972b
gurneyi Flint, 1964
hadria Denning & Blickle, 1972
ildria Denning & Blickle, 1972
insularis Mosely, 1934a
intermedia Flint, 1972b
lobifera Flint, 1968b
logana (Ross, 1941b)
lometa (Ross, 1941b)
lucia Denning & Blickle, 1972
marica Flint, 1964
mono (Ross, 1941b)
moselyi Flint, 1972
nacora Denning & Blickle, 1972
okanaganensis Flint, 1965
oregona (Ross, 1938b)
pacifica Flint, 1972b
palitla Flint, 1972b
panamensis Flint, 1972b
pectinata Flint, 1972b
pectinifera Flint, 1972b
phenosa Ross, 1947
ponta Flint, 1968c
potomus Denning, 1947c
provosti Blickle, 1961
quadrispina Denning & Blickle, 1972
riesi Ross, 1944
rothi Denning & Blickle, 1972
shawnee (Ross, 1938b)
spinosa (Ross, 1938b)
spinosissima Flint, 1964
spinulata Denning & Blickle, 1972
stylata (Ross, 1938b)
tagala Flint, 1972b
tarsalis (Hagen, 1861)
tenanga (Mosely, 1937)
trapoiza Ross, 1947

unio (Ross, 1941b)
verda Flint, 1968a
vertreesi Denning & Blickle, 1972
weddlesa Ross, 1944
wojcickyi Blickle, 1963
xena (Ross, 1938b)
zioni Denning & Blickle, 1972

Subgenus *METRICHIA* Ross, 1938c
ARGENTITRICHIA Jacquemart, 1963d (syn. n.)
aberrans Flint, 1972b
argentinica Schmid, 1958a
arizonensis Flint, 1972b
biungulata Flint, 1972b
bulbosa (Jacquemart, 1963d)
campana Flint, 1968c
continentalis Flint, 1972b
dietzi Flint, 1974
exclamationis Flint, 1968c
juana Flint, 1964
lemniscata Flint, 1972b
neotropicalis Schmid, 1958a
nigritta Banks, 1907
penicillata Flint, 1972b
quadrata Flint, 1972b
similis Flint, 1968c
trigonella Flint, 1972b
warema Flint, 1974
yalla Flint, 1968b

RHYACOPSYCHE Muller, 1879
hagenii Muller, 1879b
mexicana (Flint, 1967a)
obliqua Flint, 1971a
torulosa Flint, 1971a
turrialbae Flint, 1971a

Tribe IV NEOTRICHIINI Ross, 1956

NEOTRICHIA Morton, 1905
CYLLENE Chambers, 1873
EXITRICHIA Mosely, 1937
DOLOTRICHIA Mosely, 1937
GUERROTRICHIA Mosely, 1937
LOROTRICHIA Mosely, 1937
1 *Exitrichia*-group
alata Flint, 1968b
anahua (Mosely, 1937)
collata Morton, 1905
digitata (Mosely, 1937)
elerobi Blickle, 1961
eroga (Mosely, 1937)
ersitis Denning, 1947c
esmalda (Mosely, 1937)
exicona (Mosely, 1937)
falca Ross, 1938b
heleios Flint, 1968b
interrupta Flint, 1974
iridescens Flint, 1964
minutisimella (Chambers, 1873)
notuena (Mosely, 1939d)
novara (Mosely, 1939d)
mumii Ross, 1948
okopa Ross, 1939a
olorina (Mosely, 1937)
osmena Ross, 1944
ovona (Mosely, 1939d)
oxina (Mosely, 1937)
panneus Denning, 1947c
riegeli Ross, 1941b
sonora Ross, 1944
tertia (Mosely, 1939d)
vibrans Ross, 1938b
ranea Denning, 1947d
2 *Dolotrichia*-group
canixa (Mosely, 1937)
corniculans Flint, 1968c
dubitans (Mosely, 1939d)
xicana (Mosely, 1937)
3 *Guerrotrichia*-group
cameria (Mosely, 1937)
caxima (Mosely, 1937)
costaricensis Flint, 1967a
edalis Ross, 1941b
rotundata Flint, 1974
4 *Lorotrichia*-group
halia Denning, 1947c
hiaspa (Mosely, 1937)
kitae Ross, 1941b
5 *biuncifera*-group
biuncifera Flint, 1974
bullata Flint, 1974
falcifera Flint, 1974
proboscidea Flint, 1974
unispina Flint, 1974
6 *bifida*-group
bifida Flint, 1974
lobata Flint, 1974

Tribe V HYDROPTILINI Stephens, 1836

A Agraylea-group

AGRAYLEA Curtis, 1834
  argyricola Kolenati, 1848
  cognatella McLachlan, 1880
  costello Ross, 1941a
  drosima Navás, 1917
  insularis (Hagen, 1865)
  multipunctata Curtis, 1834
    multiguttata Uljanin, 1869
    signata Banks, 1904b
    flavida (Banks, 1907)
    fraterna Banks, 1907
  saltesea Ross, 1938b
  sexmaculata Curtis, 1834
    pallidula McLachlan, 1875
    flabellifera (Bremi, 1864)
      partim.
  spathifera Ulmer, 1912a

ALLOTRICHIA McLachlan, 1880
  ampullata Ulmer, 1912a
  heterocera Navás, 1917
  laerma Malicky, in press
  pallicornis (Eaton, 1873)
  succinica Hagen, 1856
  tauri Jacquemart, 1965
  teldanica Botosaneanu, 1974
  vilnensis Raciecka, 1937

MICROPTILA Ris, 1897
  ansara Schmid, 1960
  bejela Mosely, 1948
  indra Schmid, 1960
  minutissima Ris, 1897

UGANDATRICHIA Mosely, 1939b
  MOSELYELLA Kimmins, 1951
1 nigra-group
  acuta Mosely, 1939b
  africana (Marlier & Vaillant,
    1967) (syn. n.)
  minor Mosely, 1939b
  nigra Mosely, 1939b
2 violacea-group
  cyanotrichia (Kimmins, 1951)
  nikataruwa (Schmid, 1958)
  roudra (Schmid, 1960)
  sourya (Schmid, 1960)
  violacea (Morton, 1902)

DHATRICHIA Mosely, 1948
  bipunctata Statzner, in press
  ipasa Mosely, 1948

B Hydroptila-group

HYDROPTILA Dalman, 1819
  PHRIXOCOMA Eaton, 1873
  HYDROPNEUMA Enderlein, 1929
  HYDROPTILINA Martynov, 1934
  OXYDROPTILA Martynov, 1935
    (syn. n.)
  OECEOTRICHIA Ulmer, 1951
    (syn. n.)
  PASIROTRICHIA Ulmer, 1951
    (syn. n.)
  SUMATRANOTRICHIA Ulmer, 1951
    (syn. n.)
1 sparsa-group
  acuta Mosely, 1930
  africana Kimmins, 1958
  angulata Mosely, 1922
  angustata Mosely, 1939
  campanulata Morton, 1896
  cintrana Morton, 1904
  cornuta Mosely, 1922
  emarginata Martynov, 1927
  friedeli Malicky, 1972
  fuentaldeala Schmid, 1952
  hochyangba Schmid, 1959a
  lotensis Mosely, 1930c
  simulans Mosely, 1920
  sparsa Curtis, 1834
    brunneicornis Pictet, 1834
      sensu Stephens, 1836
2 uncinata-group
  angulifera Kumanski, 1974
  fortunata Morton, 1893
    juba Enderlein, 1929
  insubrica Ris, 1903
  kalonichtis Malicky, 1972
    bureschi Kumanski, 1972
  stellifera Morton, 1893
  sylvestris Morton, 1898
  uncinata Morton, 1893
  vichtaspa Schmid, 1959a
3 capensis-group
  calundoensis Marlier, 1965
  capensis Barnard, 1934
4 consimilis-group
  ajax Ross, 1938b
  albicornis Hagen, 1861
    maculata (Banks, 1904a)
    transversa Banks, 1907
  ancistrion Flint, 1968b
  angusta Ross, 1938b

- *antilliarum* Flint, 1968c
- *arctia* Ross, 1938b
- *berneri* Ross, 1941b
- *broweri* Blickle, 1963
- *consimilis* Morton, 1905
- *densa* Ross, 1948
- *ditalea* Flint, 1968b
- *grenadensis* Flint, 1968c
- *icona* Mosely, 1937
- *latosa* Ross, 1947
- *lloganae* Blickle, 1961
- *martorelli* Flint, 1964
- *medinai* Flint, 1964
- *melia* Ross, 1938b
- *meralda* Mosely, 1937
- *mexicana* Mosely, 1937
- *novicola* Blickle & Morse, 1954
- *paschia* Mosely, 1937
- *pecos* Ross, 1941b
- *perdita* Morton, 1905
- *producta* Mosely, 1939
- *pullatus* Denning, 1947c
- *quinola* Ross, 1947
- *scolops* Ross, 1947
- *strepha* Ross, 1938b
- *surinamensis* Flint, 1974
- *tusculum* Ross, 1947
- *valhalla* Denning, 1947b
- *veracr uzensis* Flint, 1967a
- 5 *occulta*-group
  - *adana* Mosely, 1948
  - *armata* Ross, 1938b
  - *cognata* Mosely, 1930c
  - *cruciata* Ulmer, 1912b
  - *gandhara* Schmid, 1960
  - *hirra* Mosely, 1948
  - *occulta* (Eaton, 1873)
    - *insignis* Martynov, 1927
    - *kimminsi* Mosely, 1930c (syn. n.)
    - *parthava* Schmid, 1959a
  - *martini* sp. n.
    - *occulta* (Eaton) sensu Mosely, 1939
  - *palestinae* Botosaneanu & Gasith, 1971
  - *panchaoi* Schmid, 1960
  - *rhodica* Jacquemart, 1973
    - *kumanskii* Malicky, 1974
  - *sanghala* Schmid, 1960
  - *spatulata* Morton, 1905
  - *taurica* Martynov, 1934
  - *vala* Ross, 1944
  - *valesiaca* Schmid, 1947
  - *waskesia* Ross, 1944
- 6 *tineoides*-group
  - *amoena* Ross, 1938b
  - *ampoda* Ross, 1941a
  - *callia* Denning, 1947c
  - *fiskei* Blickle, 1963
  - *hamata* Morton, 1905
    - *perplexa* Mosely, 1924
  - *lennoxi* Blickle, 1969
  - *metoeca* Blickle & Morse, 1954
  - *modica* Mosely, 1937
  - *moselyi* Ulmer, 1932
  - *remita* Blickle & Morse, 1954
  - *rono* Ross, 1941b
  - *spinata* Blickle & Morse, 1954
  - *tineoides* Dalman, 1819
    - *femoralis* (Eaton, 1873)
    - *longispina* McLachlan, 1884
  - *tortosa* Ross, 1938b
  - *wyomia* Denning, 1947c
- 7 *dikirilagoda*-group
  - *dikirilagoda* Schmid, 1958
  - *kurukenitiya* Schmid, 1958
  - *mitirigalla* Schmid, 1958
- 8 *losida*-group
  - *bispina* Kimmins, 1962
  - *incertula* Mosely, 1934a
  - *losida* Mosely, 1953
  - *tasmanica* Mosely, 1934a
  - *triloba* Kimmins, 1957
- 9 *pulchricornis*-group
  - *aegyptia* Ulmer, 1963
  - *dampfi* Ulmer, 1929
  - *kurnas* Malicky, 1974
  - *phenianica* Botosaneanu, 1970
  - *pulchricornis* Pictet, 1834
- 10 *forcipata*-group
  - *bifurcata* Mosely, 1930
  - *forcipata* (Eaton, 1873)
  - *ivisa* Malicky, 1972
- 11 *vectis*-group
  - *vectis* Curtis, 1834
    - *corsicanus* Mosely, 1939
    - *maclachlani* Klapálek, 1890
  - *viganoi* Botosaneanu, 1974
- 12 *tigurina*-group
  - *cortensis* Mosely, 1937a
    - *tigurina* Ris sensu Mosely, 1932
  - *rheni* Ris, 1896
  - *tigurina* Ris, 1894
- 13 *waubesiana*-group
  - *acadia* Ross, 1941b
  - *delineata* Morton, 1905
  - *nicoli* Ross, 1941b
  - *salmo* Ross, 1941b

- wakulla Denning, 1947d
- waubesiana Betten, 1934
- xoncla Ross, 1941a

14 incertae sedis
- acoma Denning, 1947b
- angustipennis (Martynov, 1934)
- annulicornis Matsumura, 1931
- argosa Ross, 1938b
- brincki Jacquemart, 1963a
- crenata (Ulmer, 1951)
- decia Etnier & Way, 1973
- dentata Ross, 1938b
- dodgei Denning, 1947d
- elongata (Ulmer, 1951)
- eramosa Harper, 1973
- fuentelarbola Schmid, 1952
- grandiosa Ross, 1938b
- gunda Milne, 1936
- jackmanni Blickle, 1963
- lonchera Blickle & Morse, 1954
- molsonae Blickle, 1961
- pectinifera Schmid, 1970a
- phaon Malicky, in press
- phileos Cockerell, 1920
- protera Ross, 1938b
- sengavi Schmid, 1960
- serrata Morton, 1898
- simplex Nielsen, 1948a (doubtful sp. acc. Nielsen, *in litt.*)
- touroumaya Schmid, 1960
- trilobata Jacquemart, 1965
- trullata (Ulmer, 1951)
- usurigenis Matsumura, 1931
- virgata Ross, 1938b
- xella Ross, 1941b
- xera Ross, 1938b

6 Oxyethira-group

- OXYETHIRA Eaton, 1873
  - LAGENOPSYCHE Müller, 1879a
  - ARGYROBOTHRUS Barnard, 1934
  - LOXOTRICHIA Mosely, 1937a
  - DAMPFITRICHIA Mosely, 1937a
  - OXYTRICHIA Mosely, 1939

1 falcata-group
- boreella Svensonn & Tjeder, 1975
- delcourti Jacquemart, 1973
- dentata Nybom, 1954
  - bidentata Nybom, 1948
- falcata Morton, 1893
  - rhodani Schmid, 1947
- fischeri Higler, 1974
- frici Klapálek, 1891
- spinosella McLachlan, 1884

2 flavicornis-group
- bogambara Schmid, 1958
- campanula Botosaneanu, 1970
- ecornuta Morton, 1893
- flavicornis (Pictet, 1834)
  - costalis (Curtis, 1834) sensu Eaton, 1893
- sida Blickle & Morse, 1954
- tenuella Martynov, 1924
- unidentata McLachlan, 1884
  - fuentejalona Schmid, 1952
  - meridionalis Jacquemart & Coineau, 1962

3 rivicola-group
- allagashensis Blickle, 1963
- dualis Morton, 1943
- forcipata Mosely, 1934b
- grisea Betten, 1934
- lumosa Ross, 1948
- michiganensis Mosely, 1934b
- novasota Ross, 1944
- obscura Flint, 1974
- obtatus Denning, 1947b
- rivicola Blickle & Morse, 1954
- rossi Blickle & Morse, 1957
- setosa Denning, 1947d
- sodalis Ross & Spencer, 1952
- unispina Flint, 1974

4 simplex-group
- galekoluma Schmid, 1958
- harpagella Kimmins, 1951
- paramartha Schmid, 1960
- ramosa Martynov, 1938
  - angustella Martynov, 1935
- simplex Ris, 1897
- tristella Klapálek, 1895

5 distinctella-group
- araya Ross, 1941a
- distinctella McLachlan, 1880
- sagittifera Ris, 1897
- serrata Ross, 1938b

6 azteca-group (Loxotrichia)
- azteca (Mosely, 1937a)
- dalmeria (Mosely, 1937a)
- glasa (Ross, 1941b)
- janella Denning, 1948d
- neglecta Flint, 1964
- puertoricensis Flint, 1964
- zilaba (Mosely, 1939d)

7 *ulmeri*-group (*Dampfitrichia*)
- *aculea* Ross, 1941b
- *arizona* Ross, 1948
- *cirrifera* Flint, 1964
- *taga* Flint, 1968b
- *ulmeri* (Mosely, 1937)

8 *zeronia*-group
- *jamaicensis* Flint, 1968b
- *longissima* Flint, 1974
- *macrosterna* Flint, 1974
- *simulatrix* Flint, 1968b
- *verna* Ross, 1938b
- *walteri* Denning, 1947d
- *zeronia* Ross, 1941a

9 *pallida*-group
- *florida* Denning 1947d
- *maya* Denning, 1947d
- *pallida* (Banks, 1904b)
  - *cibola* Denning, 1947d
  - *viminalis* Morton, 1905

10 *bidentata*-group
- *abacatia* Denning, 1947d
- *secla* Ross, 1938b
- *bidentata* Mosely, 1934b

11 *mirabilis*-group
- *flagellata* Jacquemart, 1965b
- *mirabilis* Morton, 1904

12 *incertae sedis*
- *albiceps* (McLachlan, 1862)
- *anabola* Blickle, 1966
- *angustella* Martynov, 1933
- *berneri* Etnier & Way, 1965
- *coercens* Morton, 1905
- *hyalina* (Müller, 1879a
- *incana* Ulmer, 1906
- *mithi* Malicky, 1974
- *spirogyrae* (Müller, 1880)
- *velocipes* (Barnard, 1934)

STENOXYETHIRA Kimmins, 1951
- *GNATHOTRICHIA* Ulmer, 1951 (syn. n.)
- *excisa* Kimmins, 1951
  - *isabellina* (Ulmer, 1951) (syn. n.)
- *minima* Kimmins, 1951

PAROXYETHIRA Mosely, 1924
- *eatoni* Mosely, 1924
- *hendersoni* Mosely, 1924
- *hintoni* Leader, 1972
- *kimminsi* Leader, 1972
- *tillyardi* Mosely, 1924

XUTHOTRICHIA Mosely, 1934a
- *askensis* Mosely, 1934a
- *fimbriata* Mosely, 1934a
- *ochracea* Mosely, 1934a
- *simplex* Mosely, 1934a

TRICHOLEIOCHITON Kloet & Hincks, 1944
- *LEIOCHITON* Guinard, 1879
- *SYNAGOTRICHIA* Ulmer, 1951 (syn. n.)
- *fagesii* (Guinard, 1879)
  - *felina* (Ris, 1897)
  - *flabellifera* (Bremi, 1864) partim.
- *fortensis* (Ulmer, 1951)
- *lacustris* Kimmins, 1951

Tribe VI ORTHOTRICHIINI Nielsen, 1948

ORTHOTRICHIA Eaton, 1873
- *CLYMENE* Chambers, 1873
- *JAVANOTRICHIA* Ulmer, 1951 (syn. n.)
- *ORTHOTRICHIELLA* Ulmer, 1951 (syn. n.)
- *BALIOTRICHIA* Ulmer, 1951 (syn. n.)

1 *angustella*-group
- *angustella* (McLachlan, 1865)
  - *brunneicornis* (Pictet, 1834) partim.
- *avicularis* Kimmins, 1951
- *barnardi* Scott, 1963
- *benguelensis* Marlier, 1965
- *damasi* Marlier, 1943
- *dampfi* (Ulmer, 1963)
- *flagellum* Marlier, 1965
- *indica* Martynov, 1935
- *kivuensis* Jacquemart, 1956
- *moselyi* Tjeder, 1946
- *sarva* Mosely, 1948
- *spinicauda* Kimmins, 1958
- *straeleni* Jacquemart, 1956
- *verbeki* Jacquemart, 1958

2 *litoralis*-group
- *curvata* (Ulmer, 1951)
- *guruluhela* (Schmid, 1958)
- *hinipitigola* (Schmid, 1958)
- *litoralis* (Ulmer, 1951)
- *maeandrica* (Ulmer, 1951)
- *medinitigola* (Schmid, 1958)
- *ranauana* (Ulmer, 1951)
- *udawarama* (Schmid, 1958)

3 costalis-group
aequatoriana Kimmins, 1957
alboguttata Jacquemart, 1956
costalis (Curtis, 1834)
tetensii Kolbe, 1887
extensa Martynov, 1935
4 aegerfasciella-group
aegerfasciella (Chambers, 1873)
americana Banks, 1904a
dorsalis Banks, 1904b
brachiata Morton, 1905
baldufi Kingsolver & Ross, 1961
cristata Morton, 1905
americana Betten, 1934
curta Kingsolver & Ross, 1961
instabilis Denning, 1948d
tragetti Mosely, 1930c
5 kokodana-group
kokodana Kimmins, 1962
obscura Kimmins, 1962
6 incertae sedis
dentata Kingsolver & Ross, 1961
petiti Jacquemart, 1962
trilineata Jacquemart, 1963a

ITHYTRICHIA Eaton, 1873
SARANGANOTRICHIA Ulmer, 1951 (syn. n.)
bosniaca Botosaneanu, 1948
clavata Morton, 1905
decussata (Ulmer, 1951)
lamellaris Eaton, 1873
brunneicornis (Pictet, 1834) partim.
mazon Ross, 1944

INCERTAE SEDIS

MACROSTACTOBIA Schmid, 1958
alawalikanda Schmid, 1958

DIBUSA Ross, 1939
angata Ross, 1939

NOTHOTRICHIA Flint, 1967e
illiesi Flint, 1967e

DICAMINUS Müller 1879a
DIAULUS Müller, 1879b
ladislavii (Müller, 1879b)

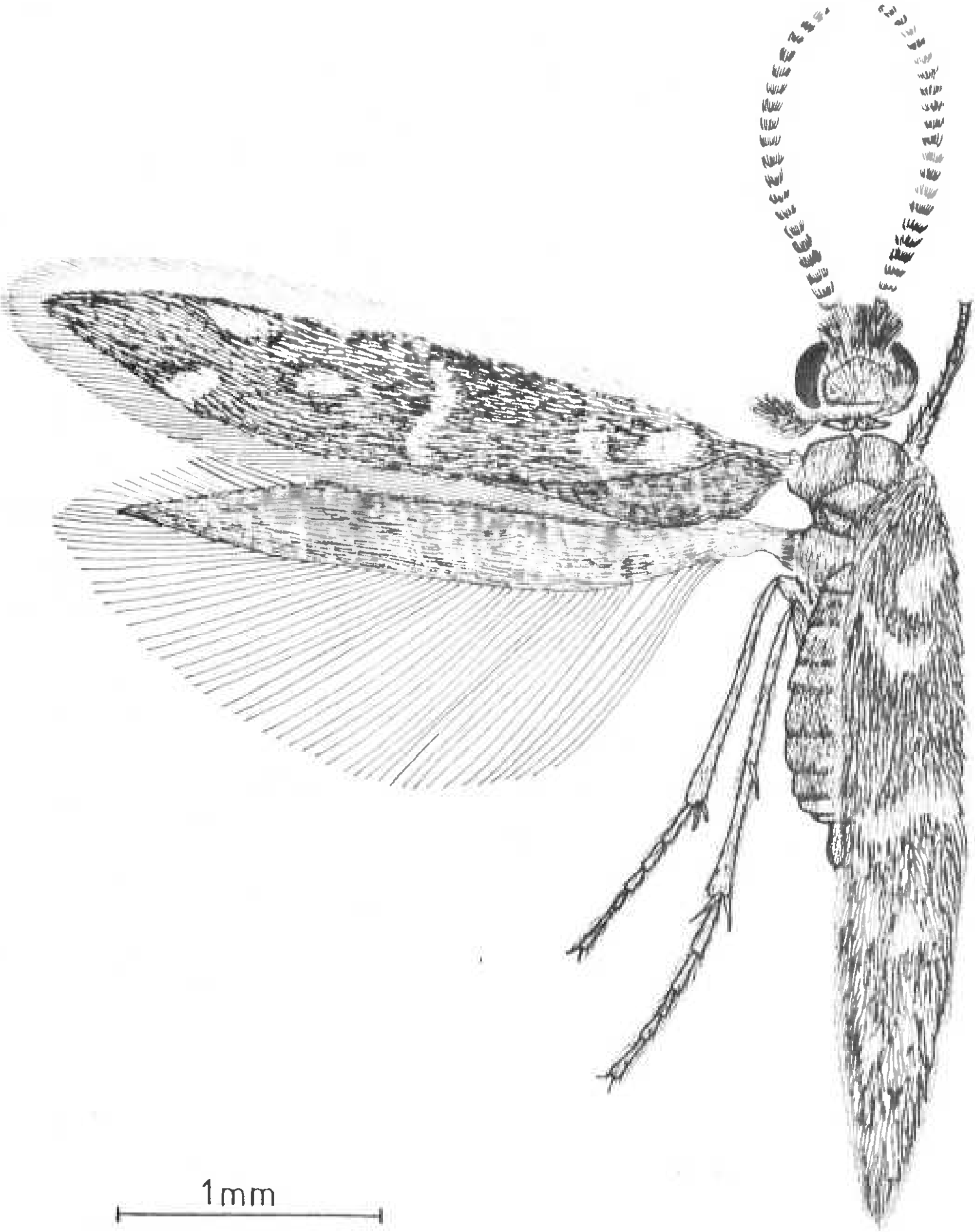
ORPHNINOTRICHIA Mosely, 1934a
maculata Mosely, 1934a

CALEDONOTRICHIA Sykora, 1967
illiesi Sykora, 1967
minor, Sykora, 1967

ELECTROTRICHIA Ulmer, 1912a
subtilis Ulmer, 1912a

FIGURES

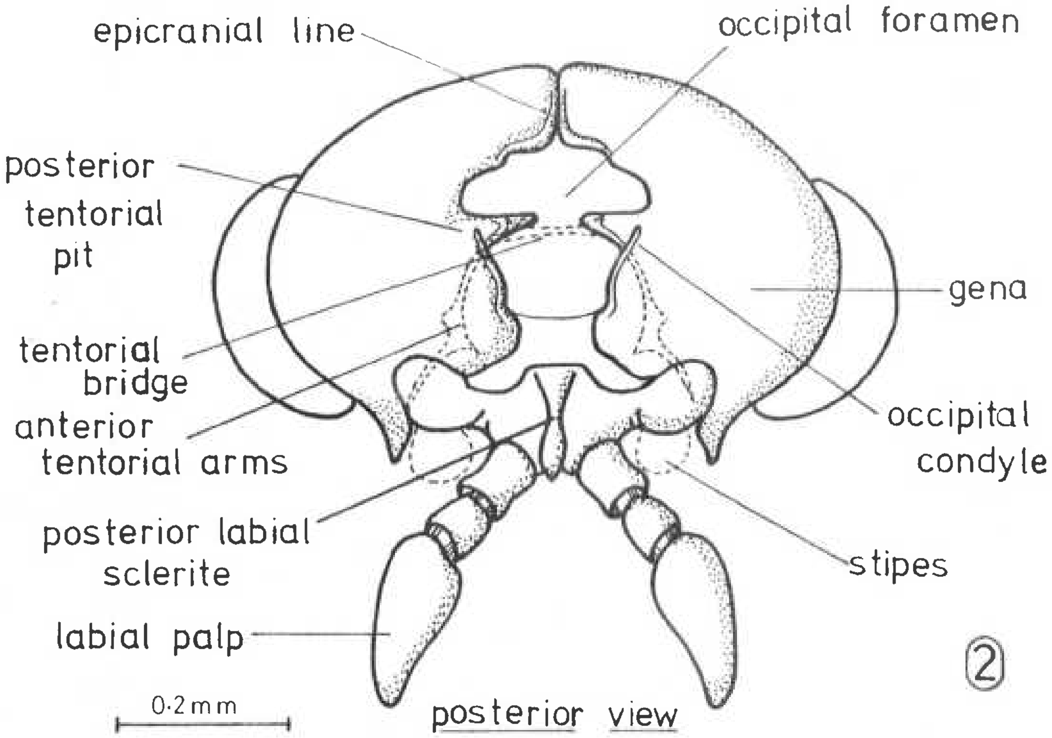
(1 - 217)



(1)

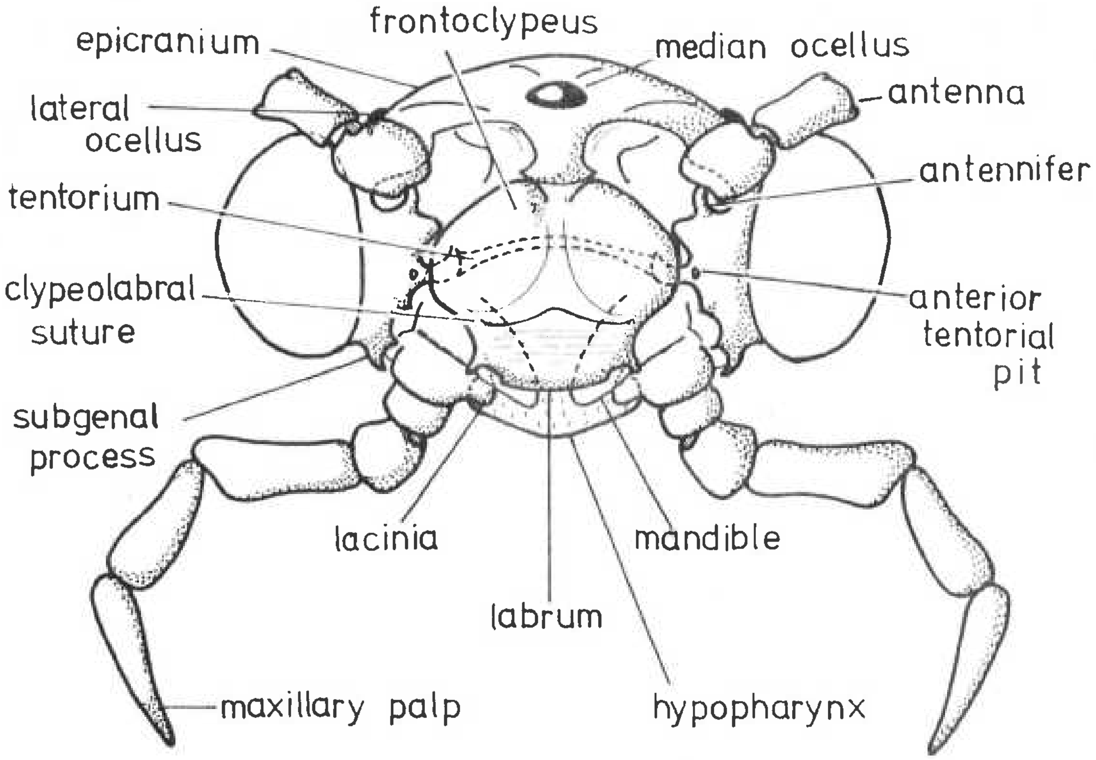
Adult, dorsal view

Hydroptila tineoides Dalman ♂



posterior view

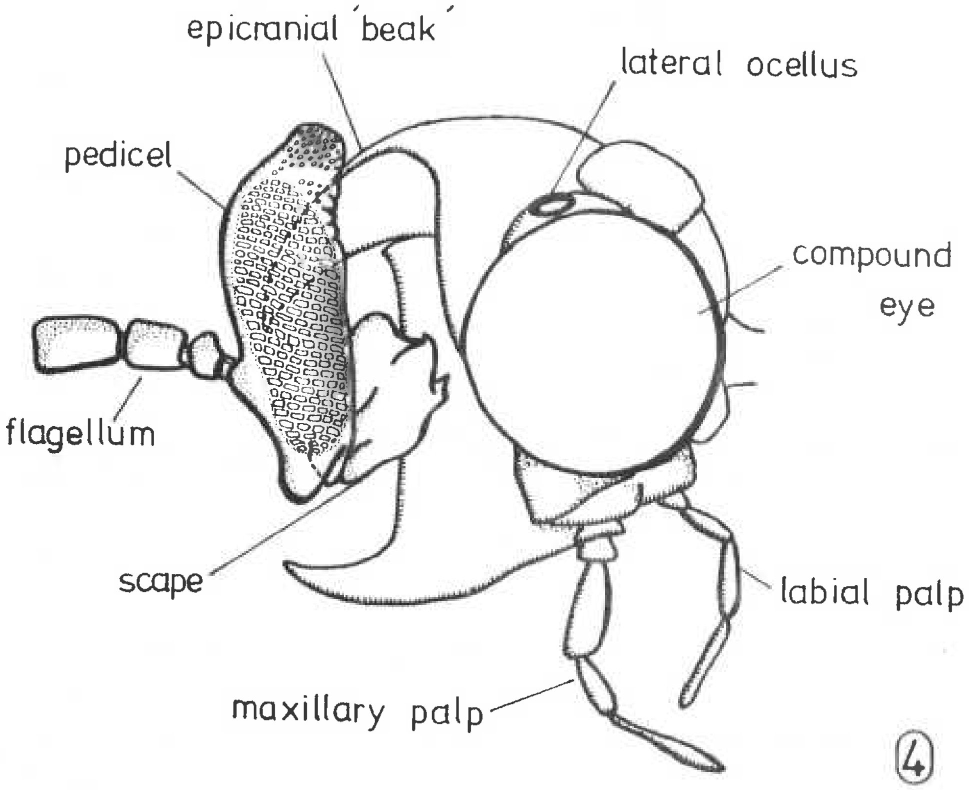
②



anterior view

③

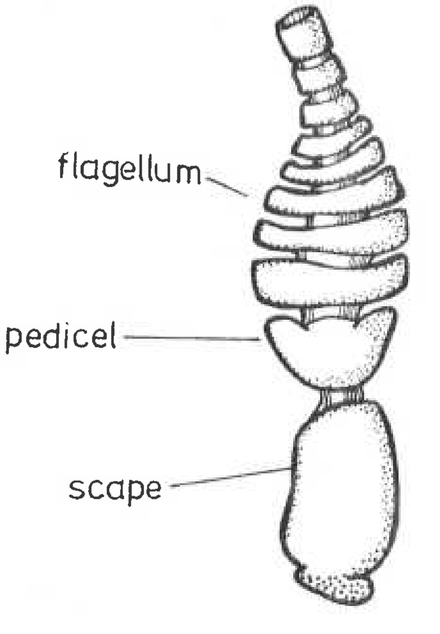
Adult head – Agraylea sexmaculata Curtis



④

Abtrichia squamosa Mosely - ♂

Adult head – lateral view (after Mosely, 1939)



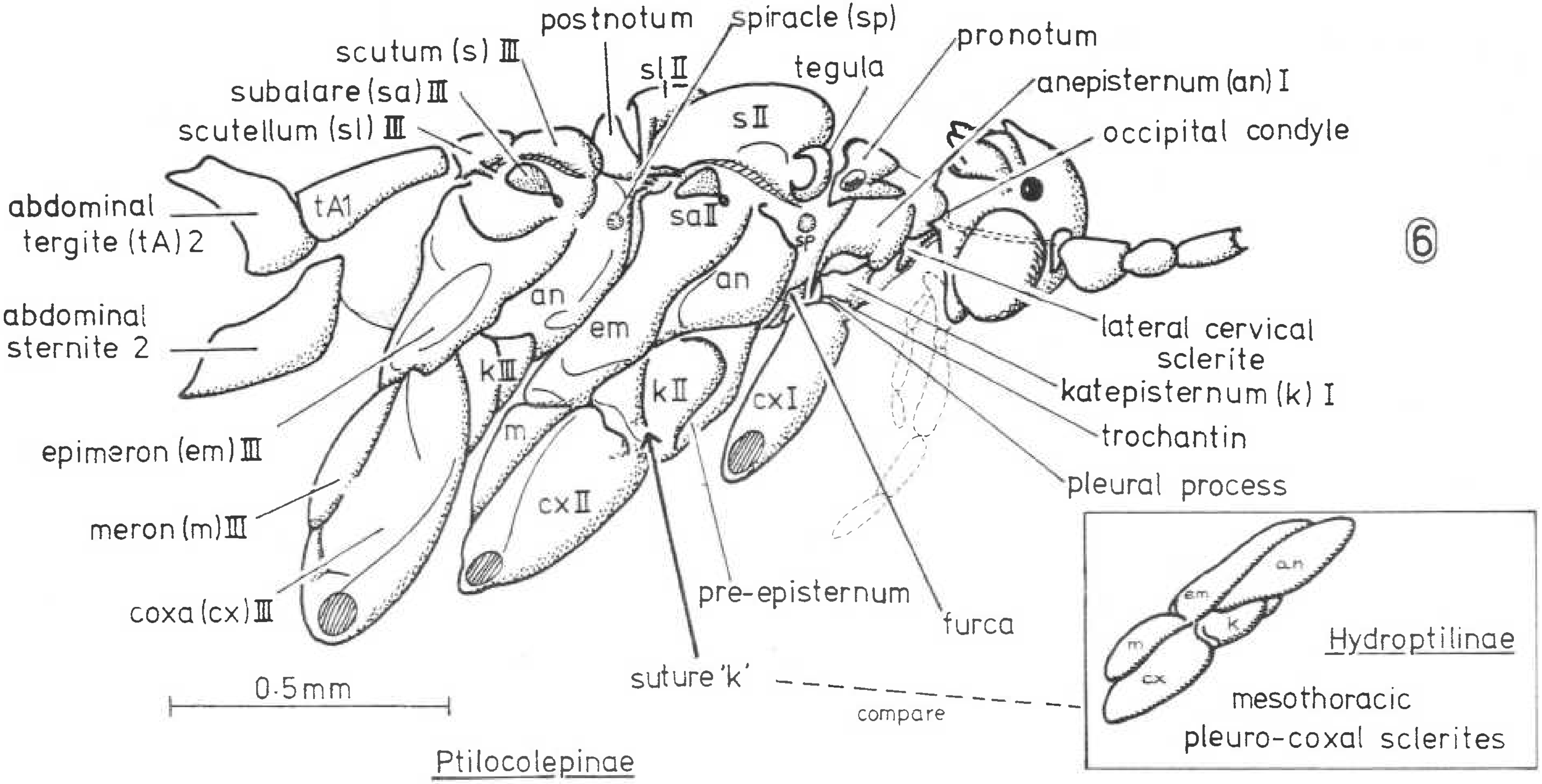
Costatrichia lodora Mosely - ♂

(BMNH Collection)

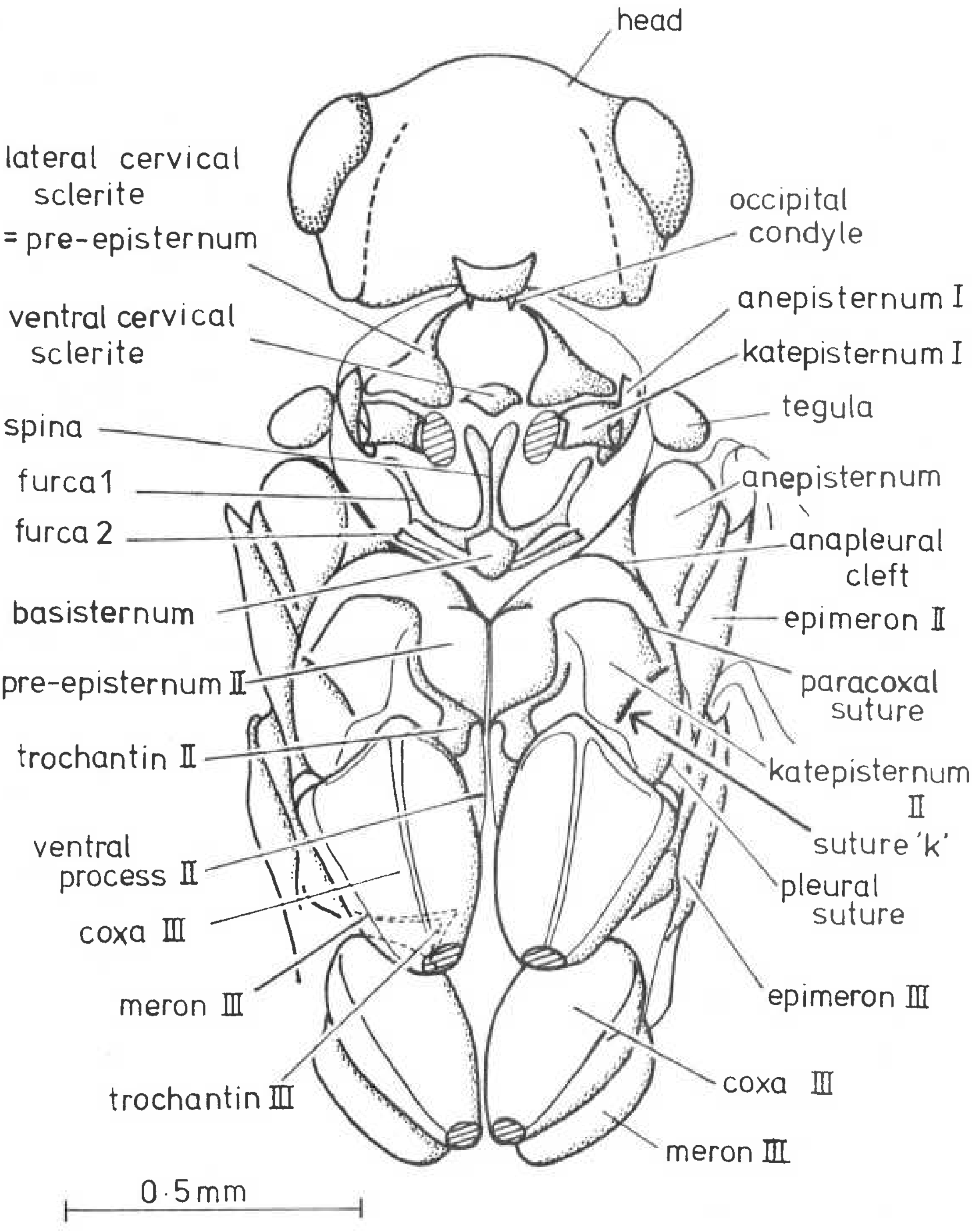
⑤

Basal antennal segments

⑥



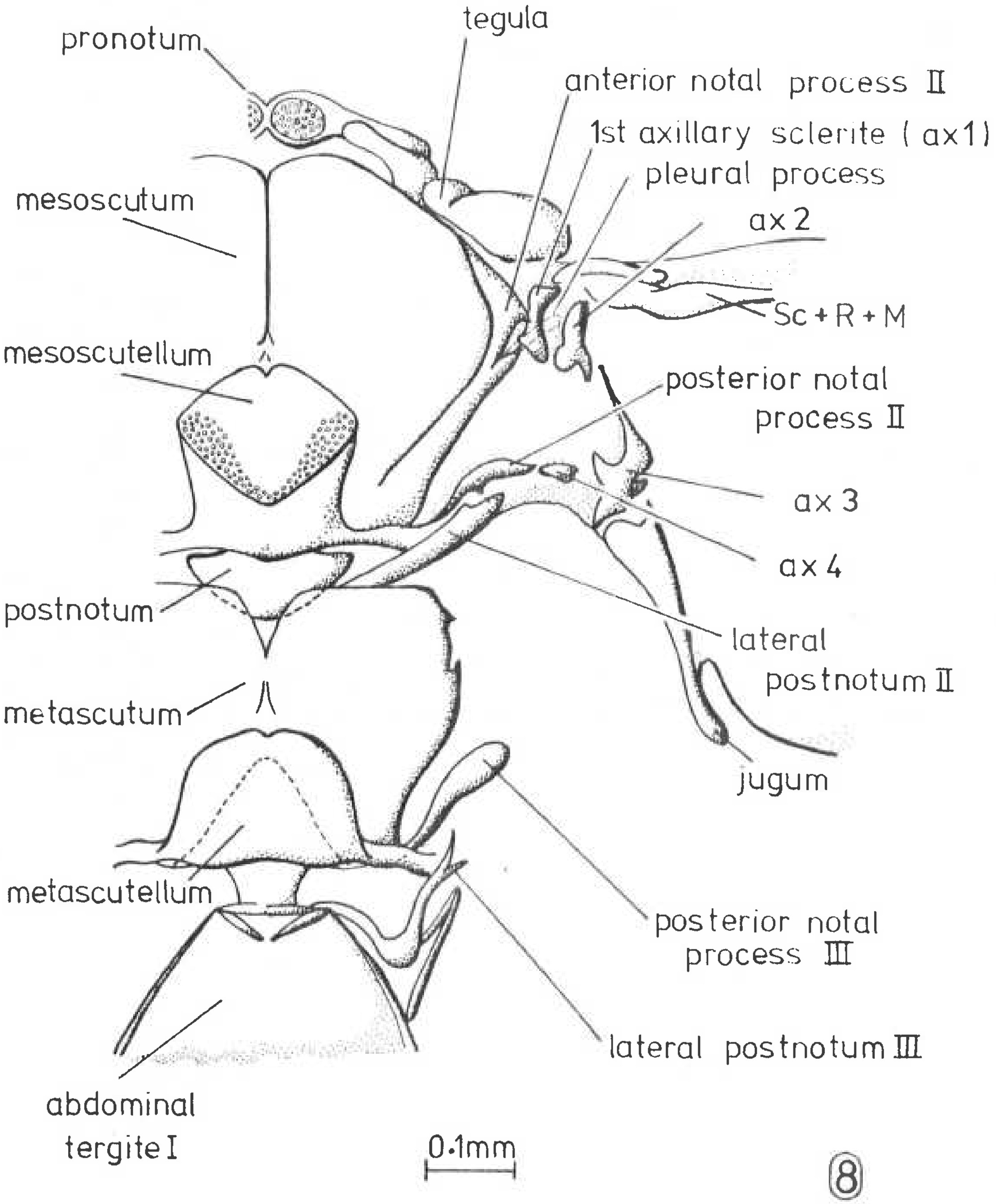
Adult thorax - lateral view



⑦

Ptilocolepinae

Adult thorax - ventral view

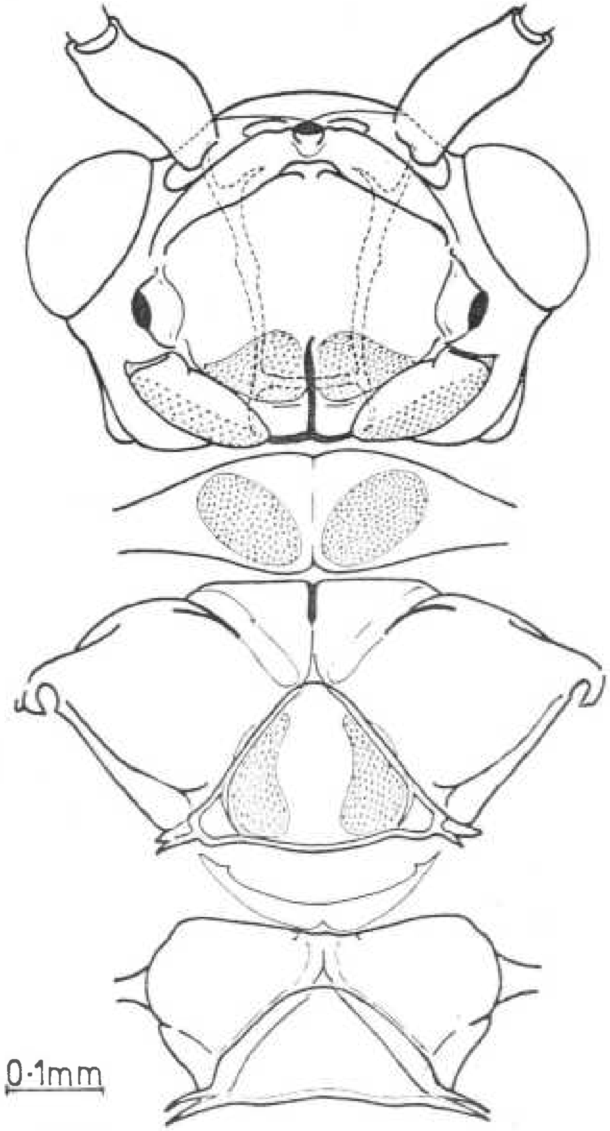


⑧

Adult thorax – dorsal view (right)

Agraylea

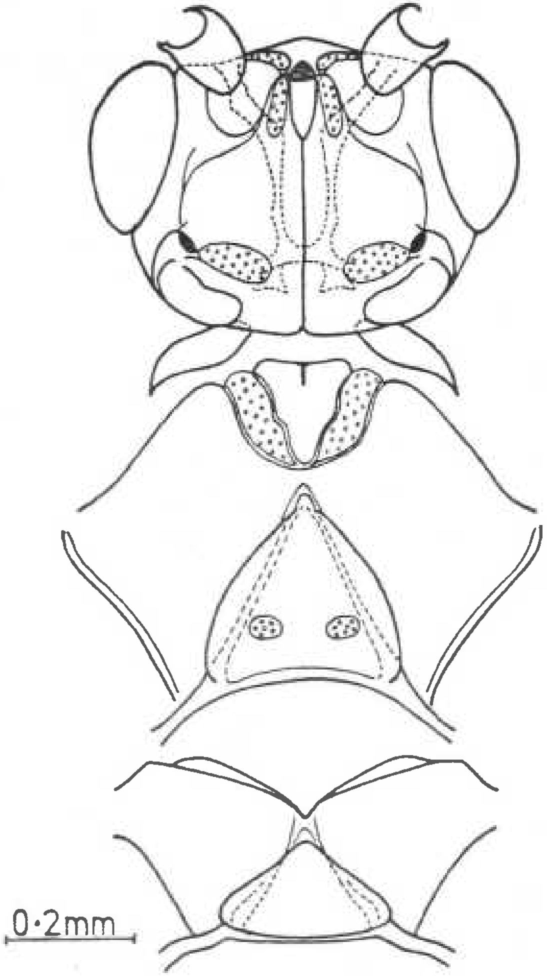
ax - axillary sclerite



9

Ptilocolepus

[Ptilocolepinae]



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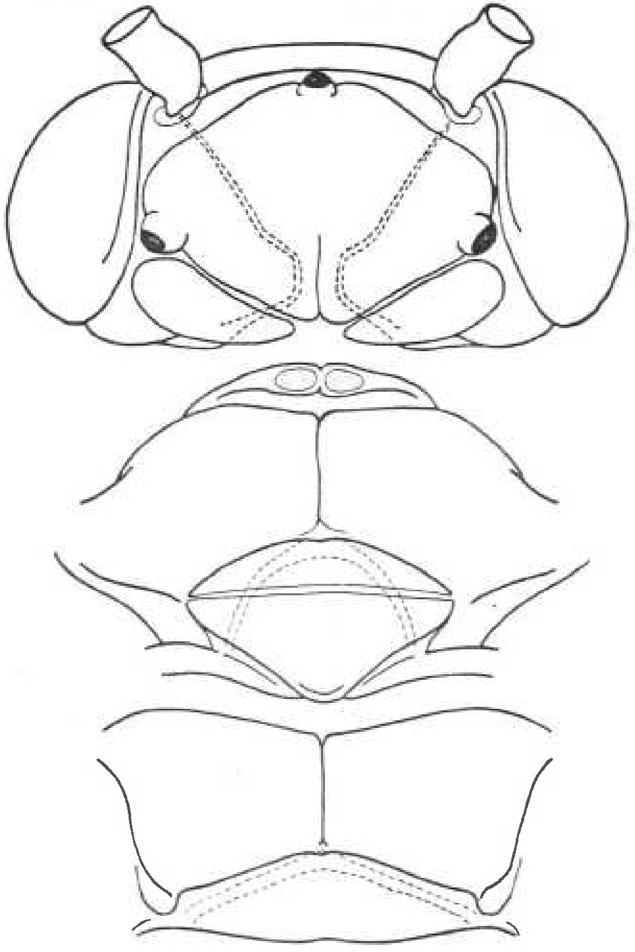
Agapetus

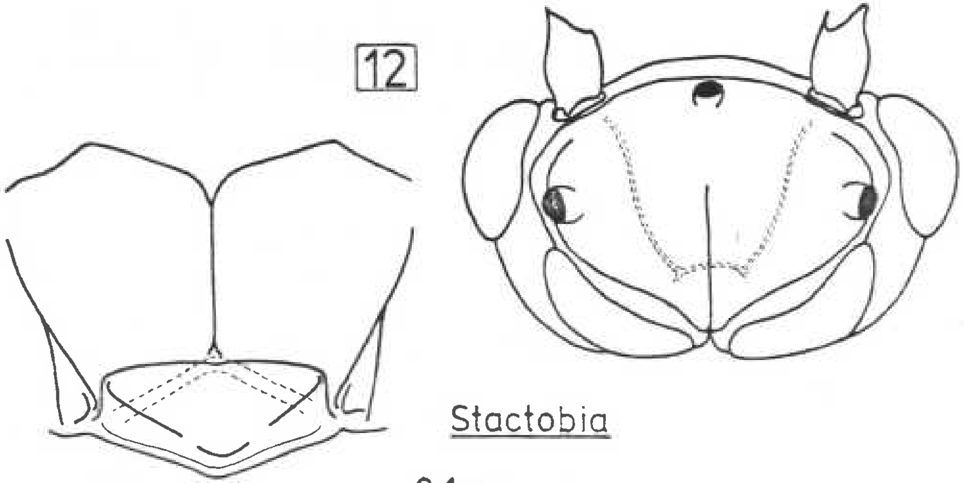
[Glossosomatidae]



11

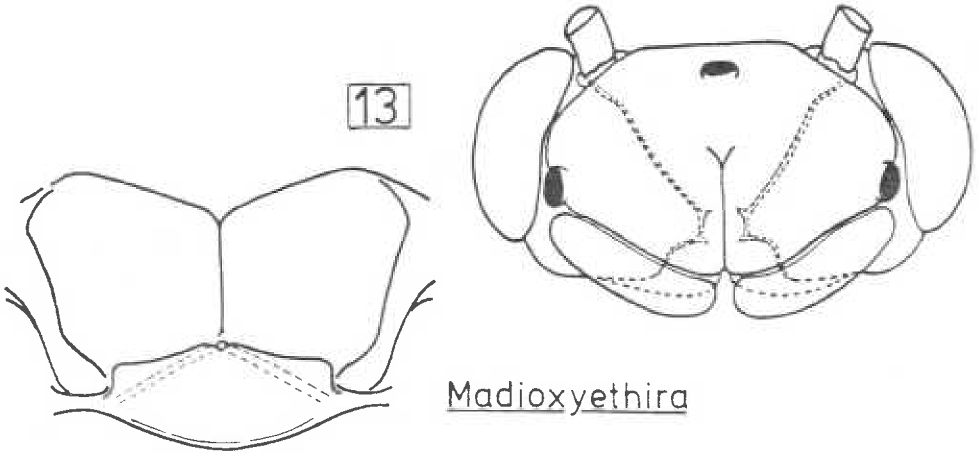
Catoxyethira

12

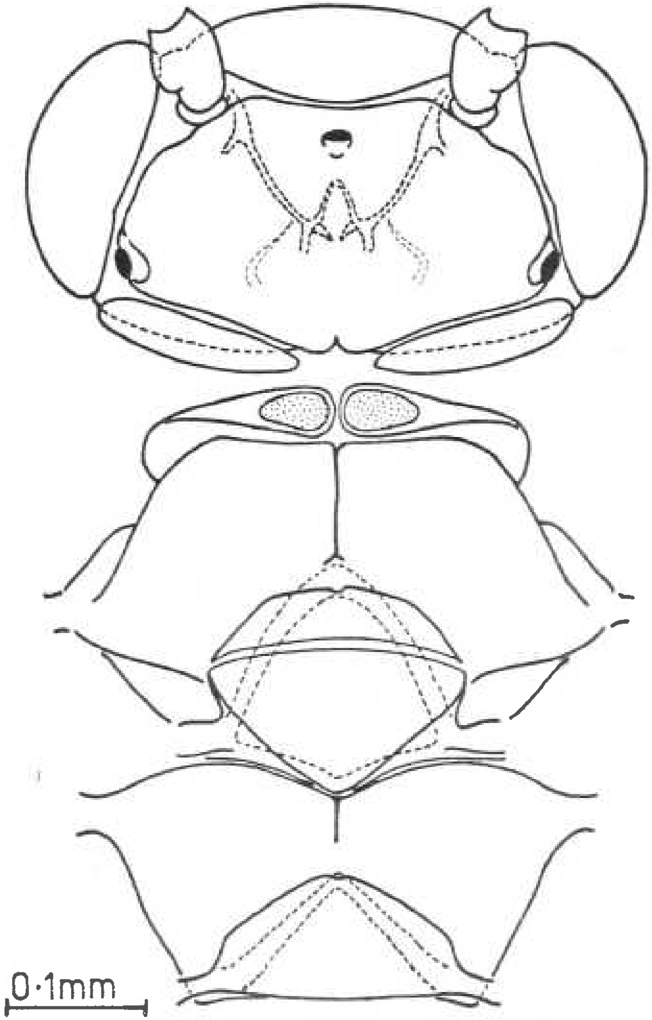


Stactobia

13



Madioxyethira



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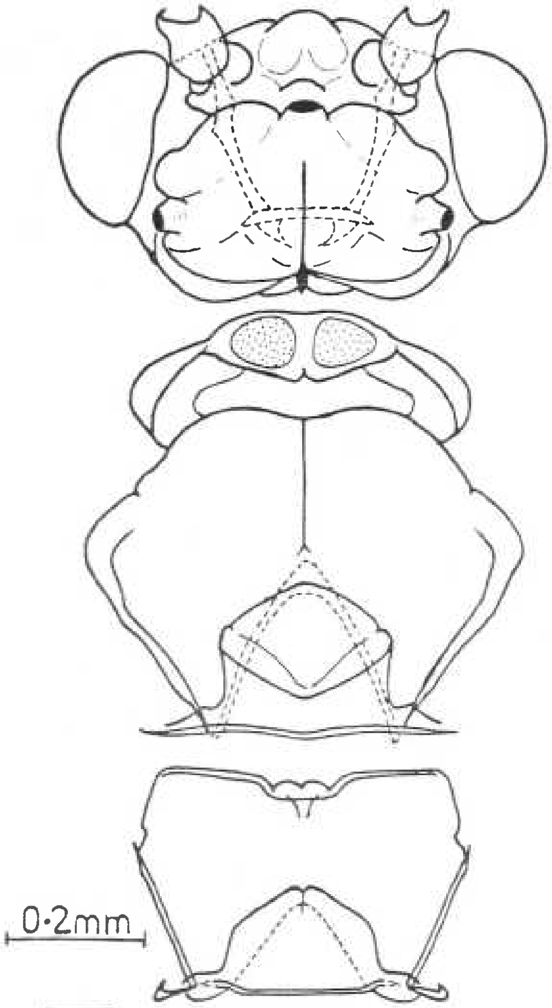
Leucotrichia



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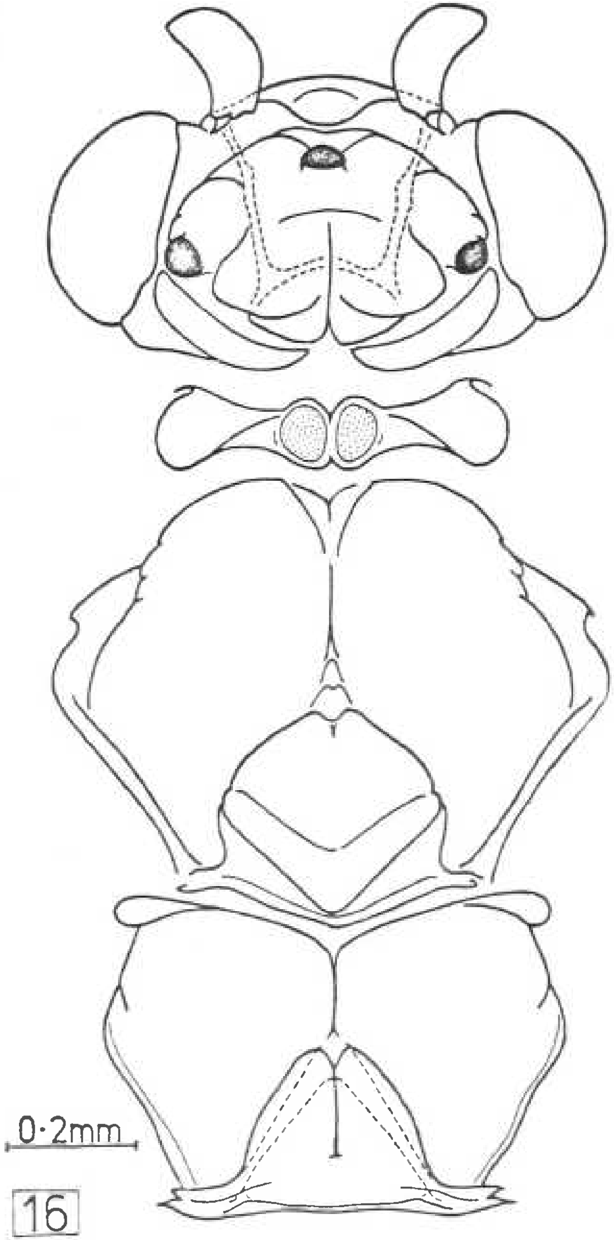
Agraylea



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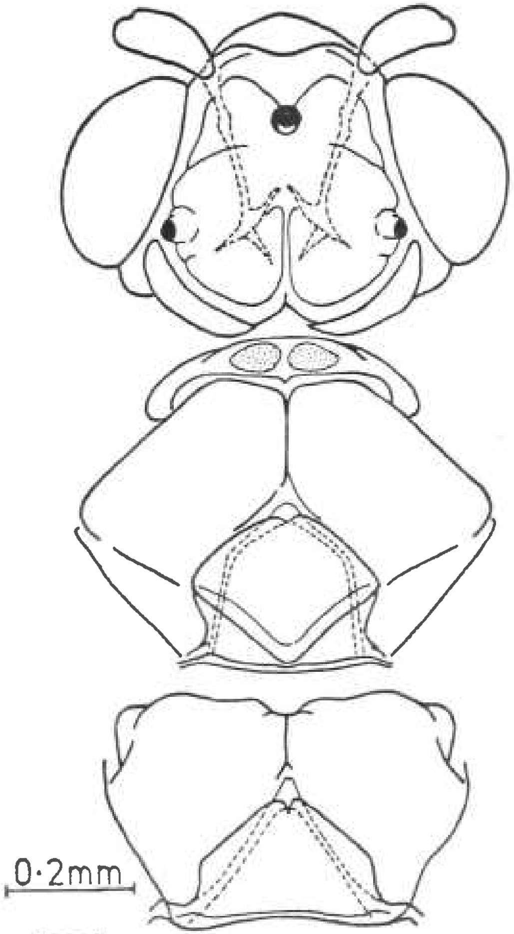
Ugandatrichia (Moselyella)



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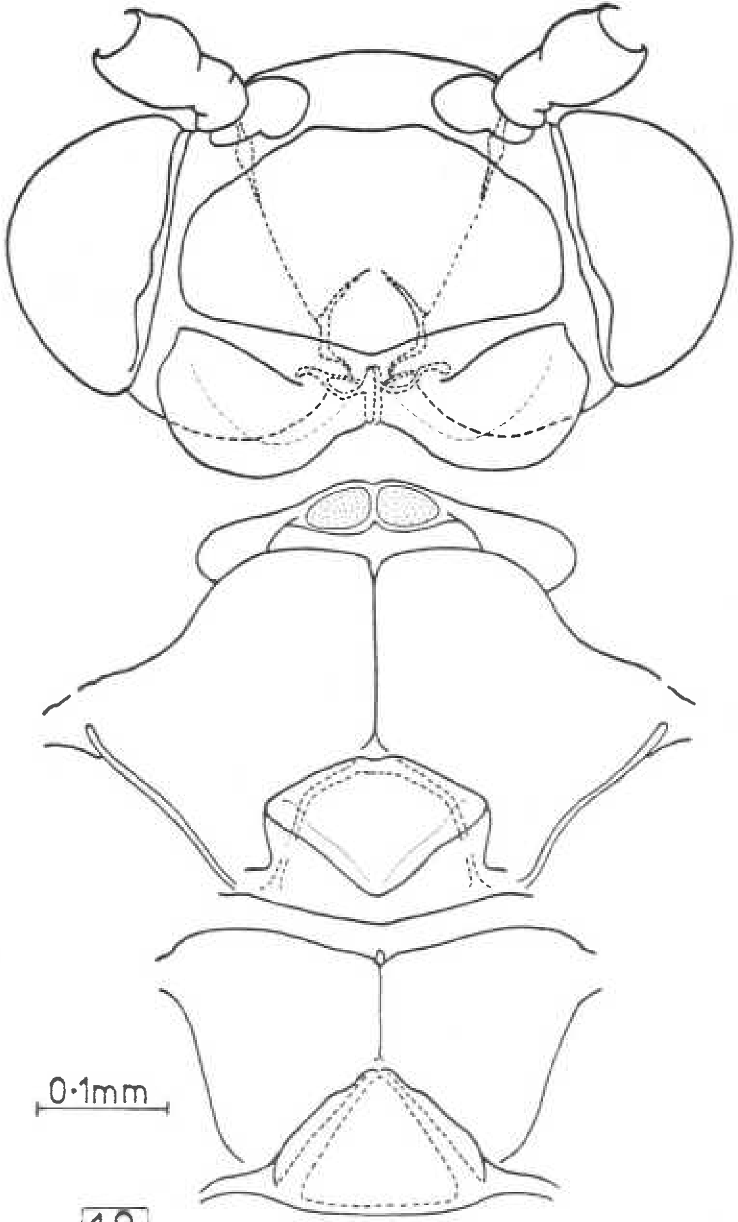
Ugandatrichia



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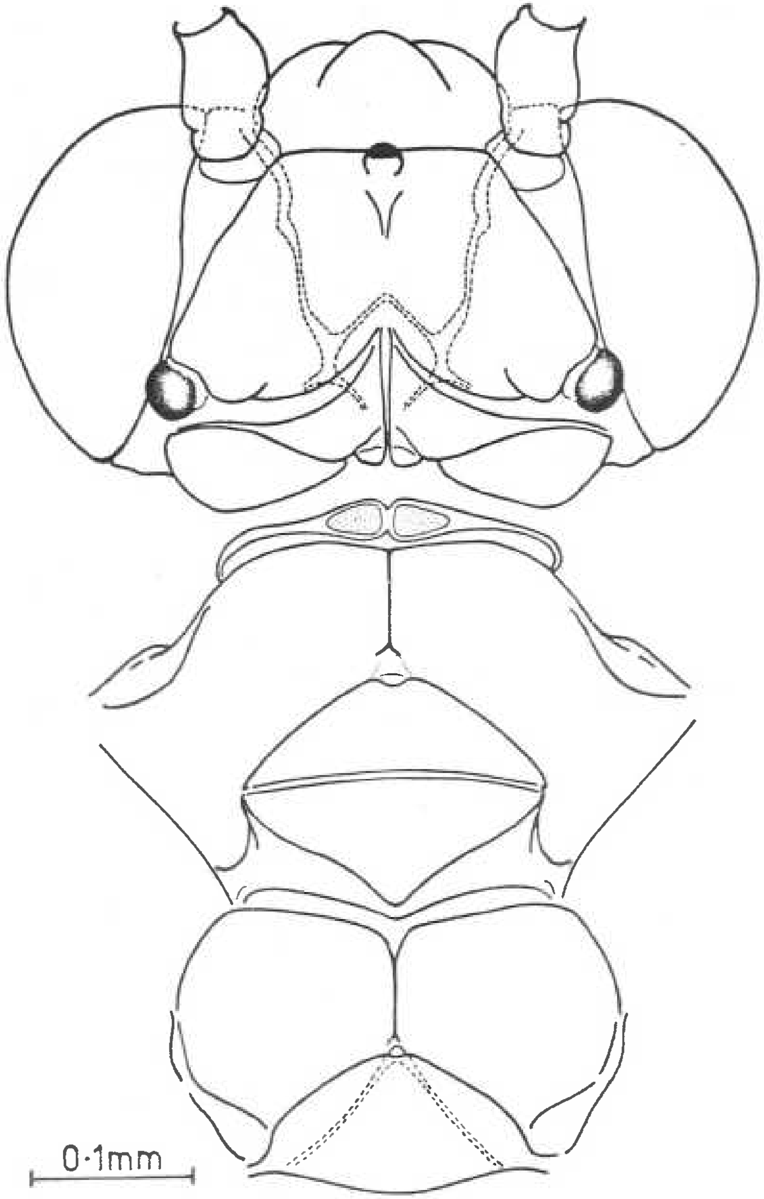
Hydroptila



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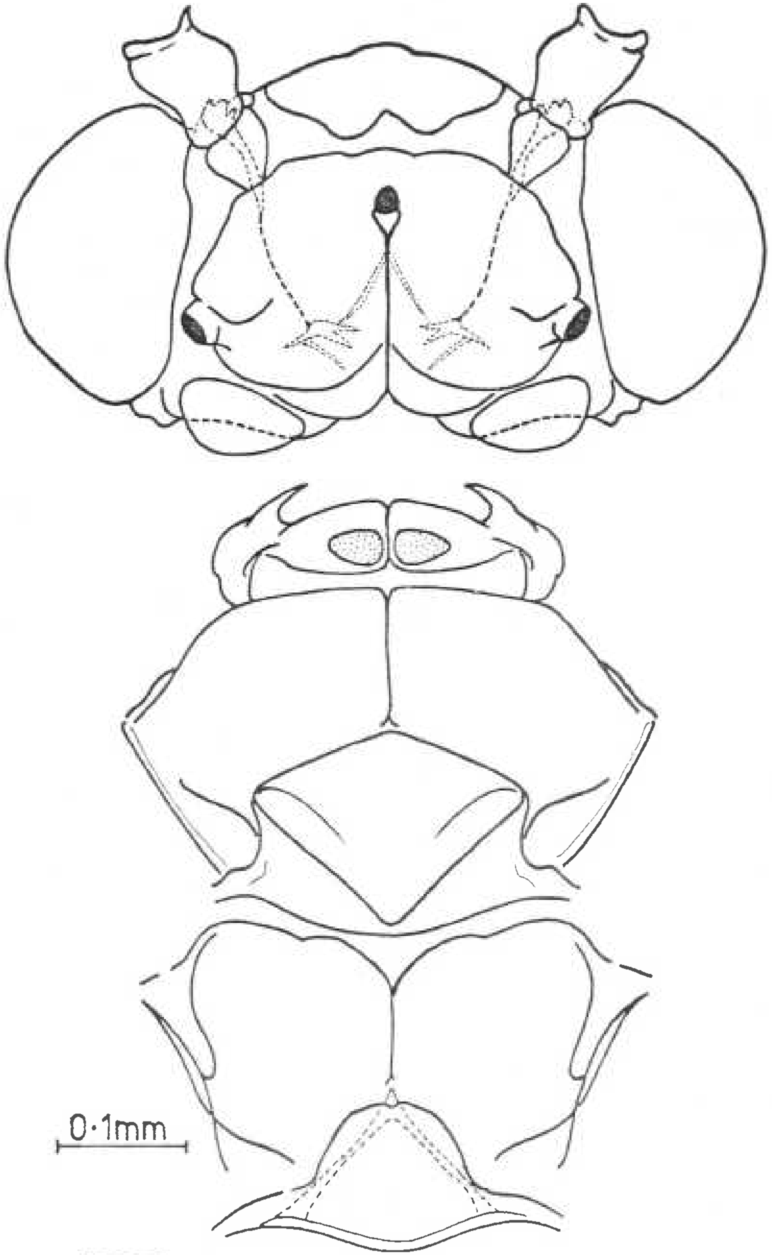
Ochrotrichia



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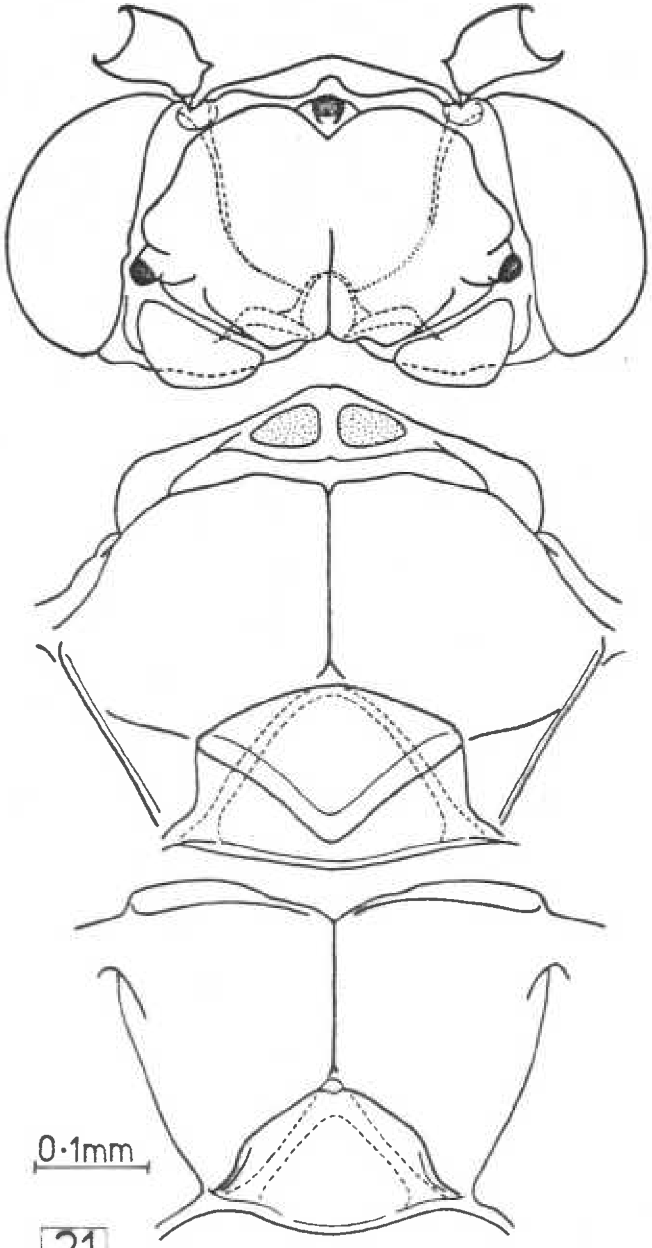
Oxyethira



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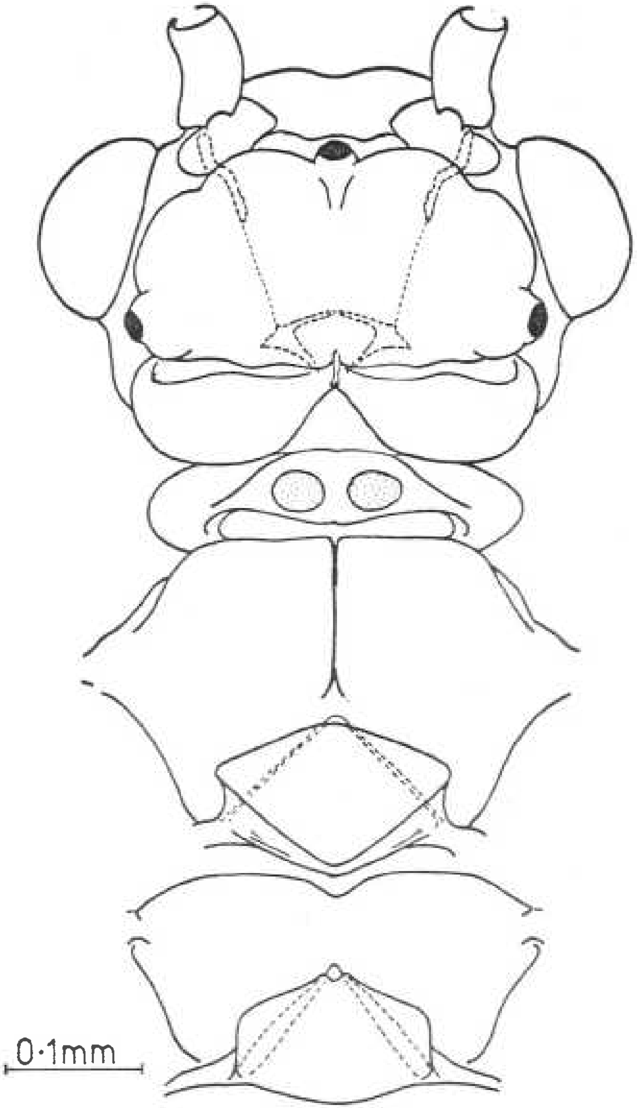
Paroxyethira



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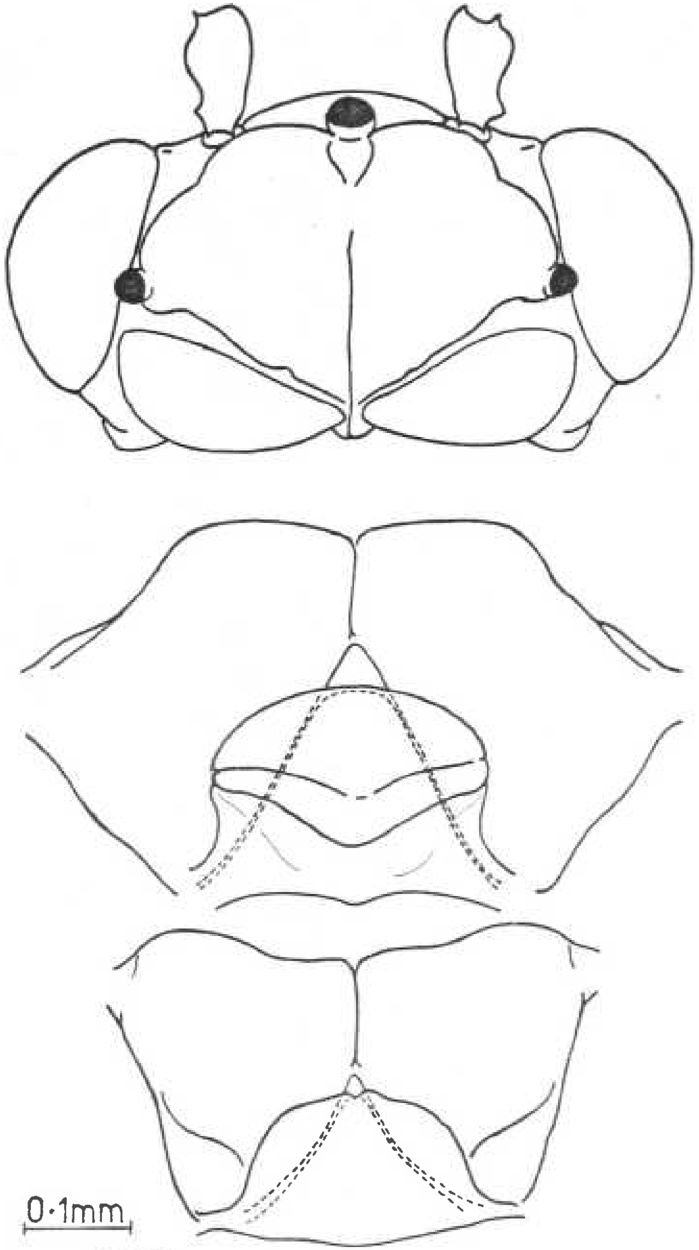
Tricholeiochiton



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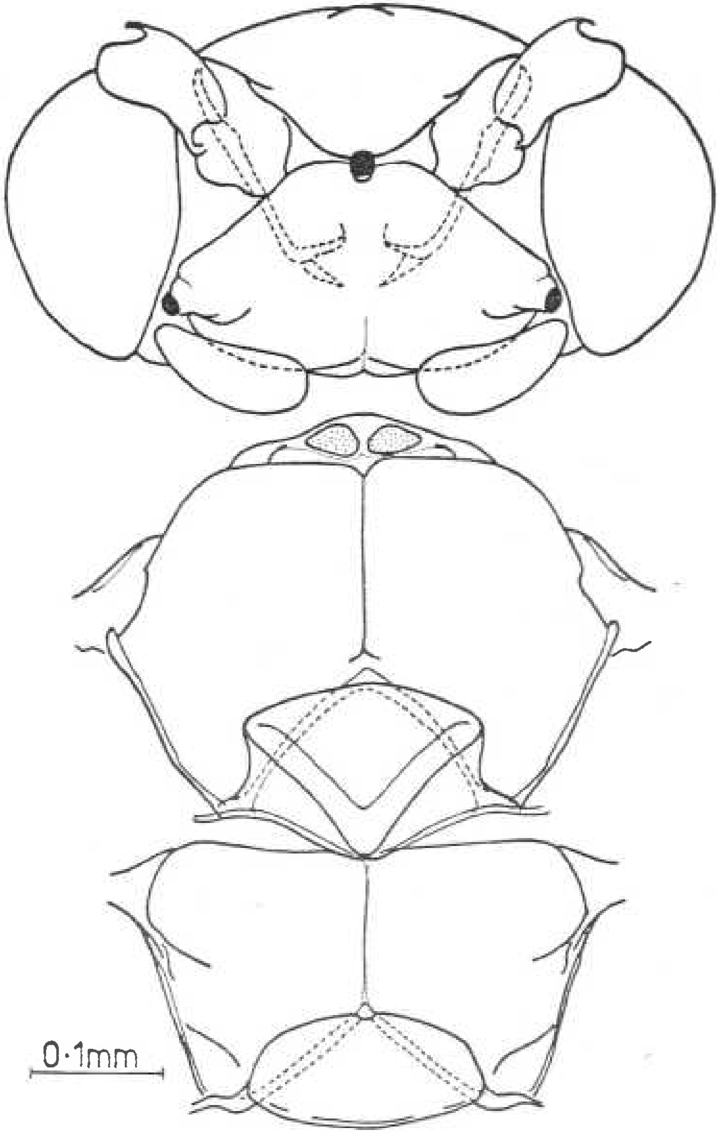
Nothotrichia



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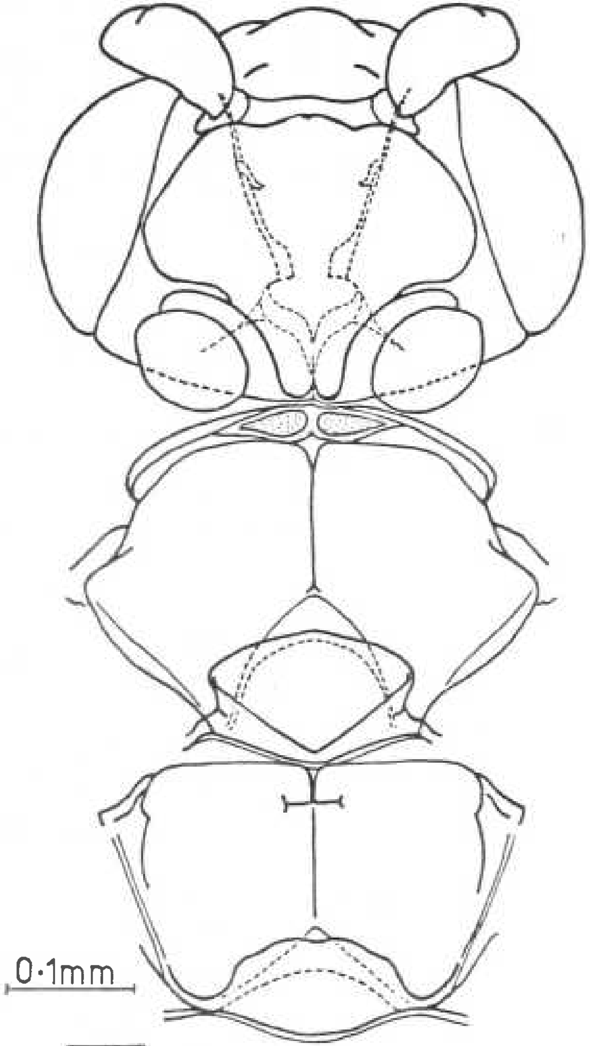
Ithytrichia



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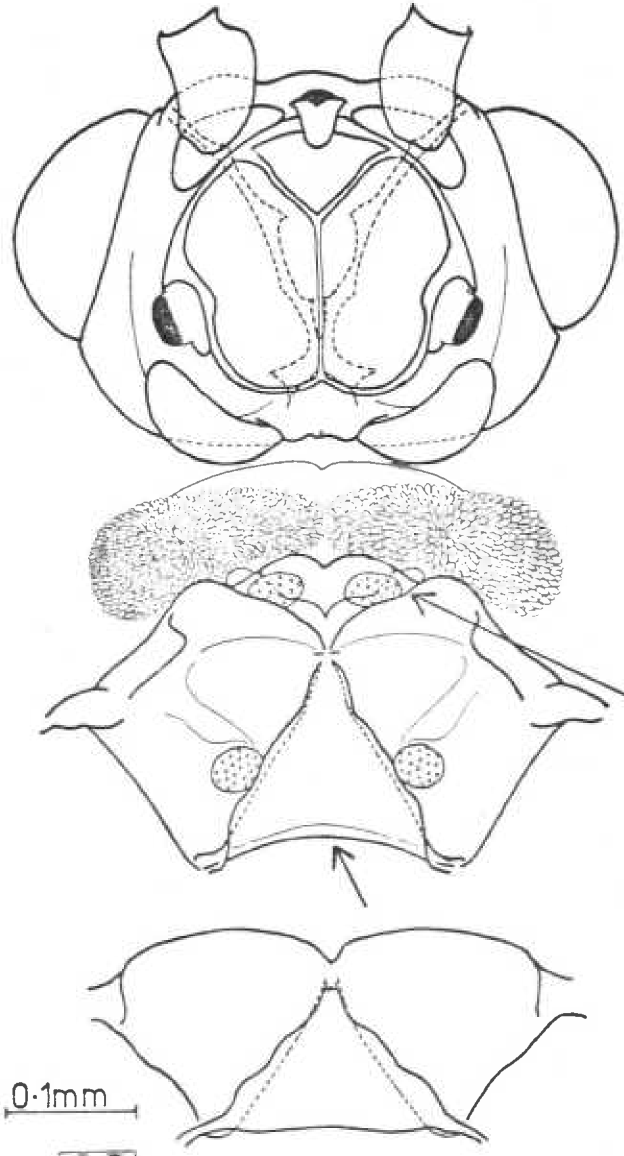
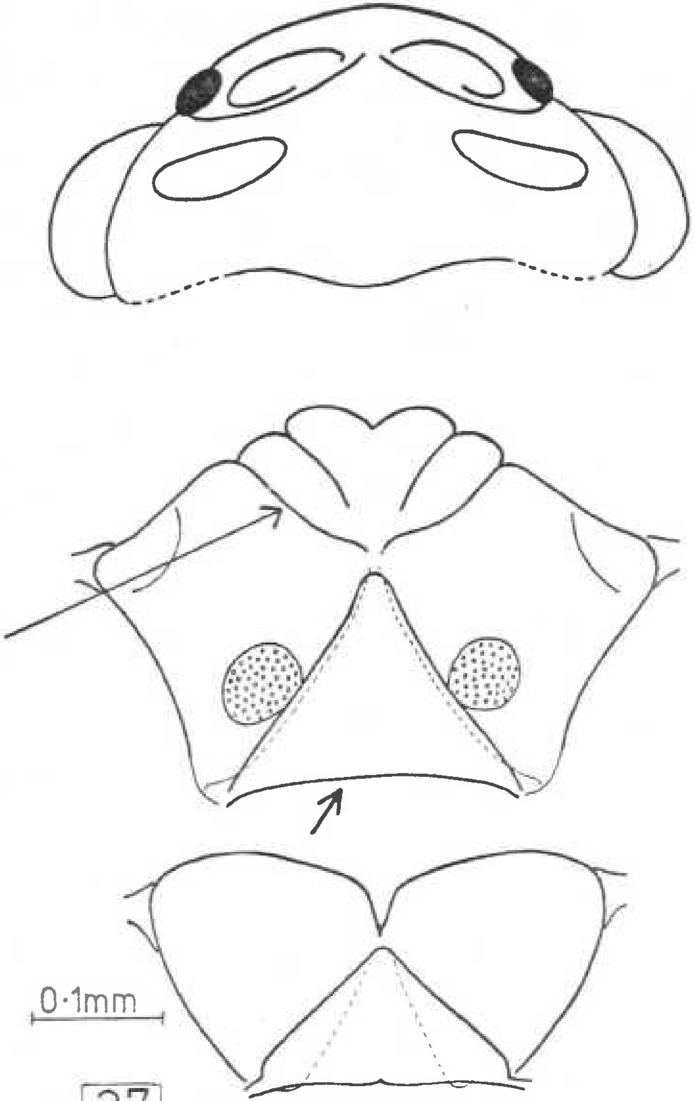
Orthotrichia



26

Nepaloptila



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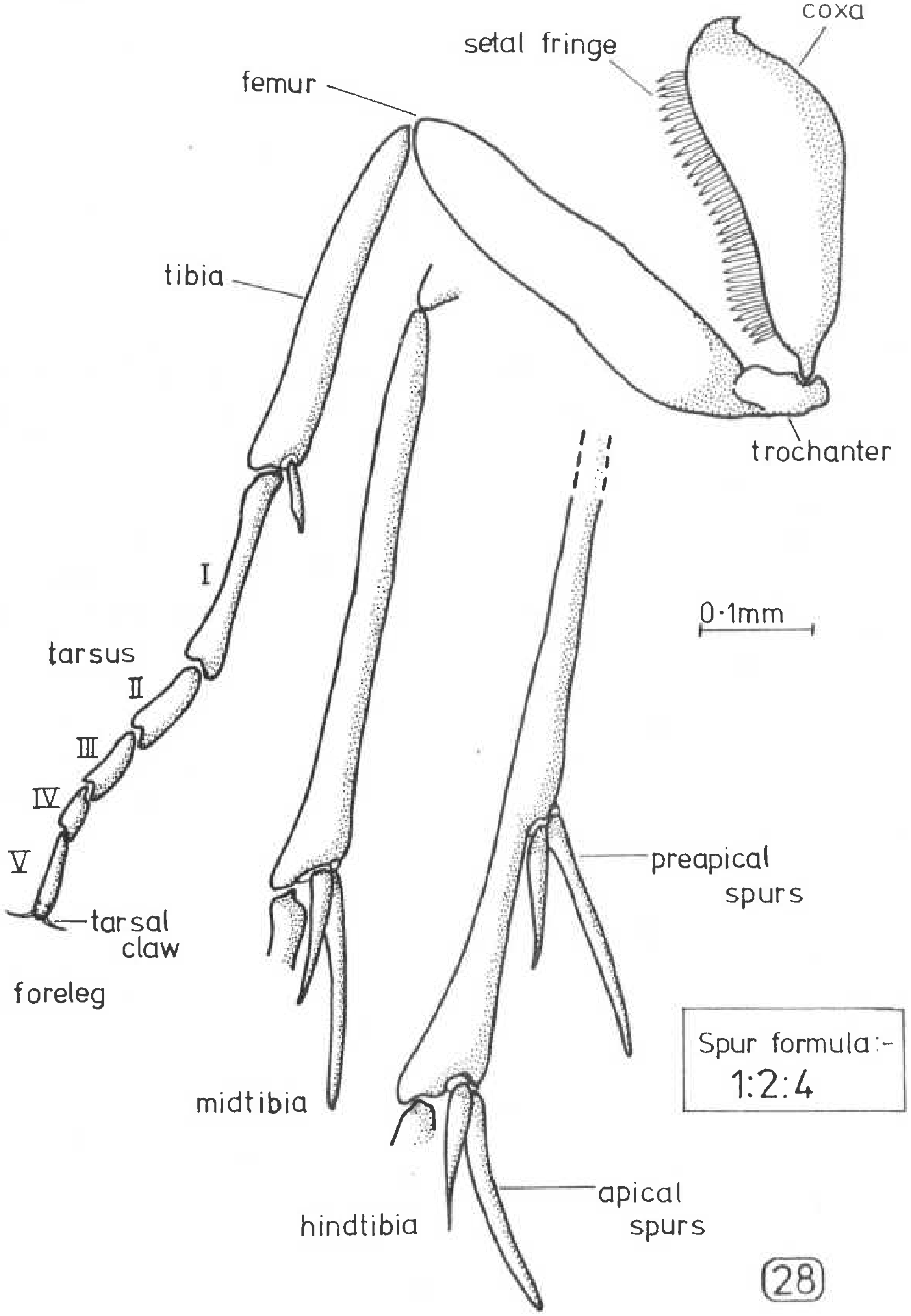
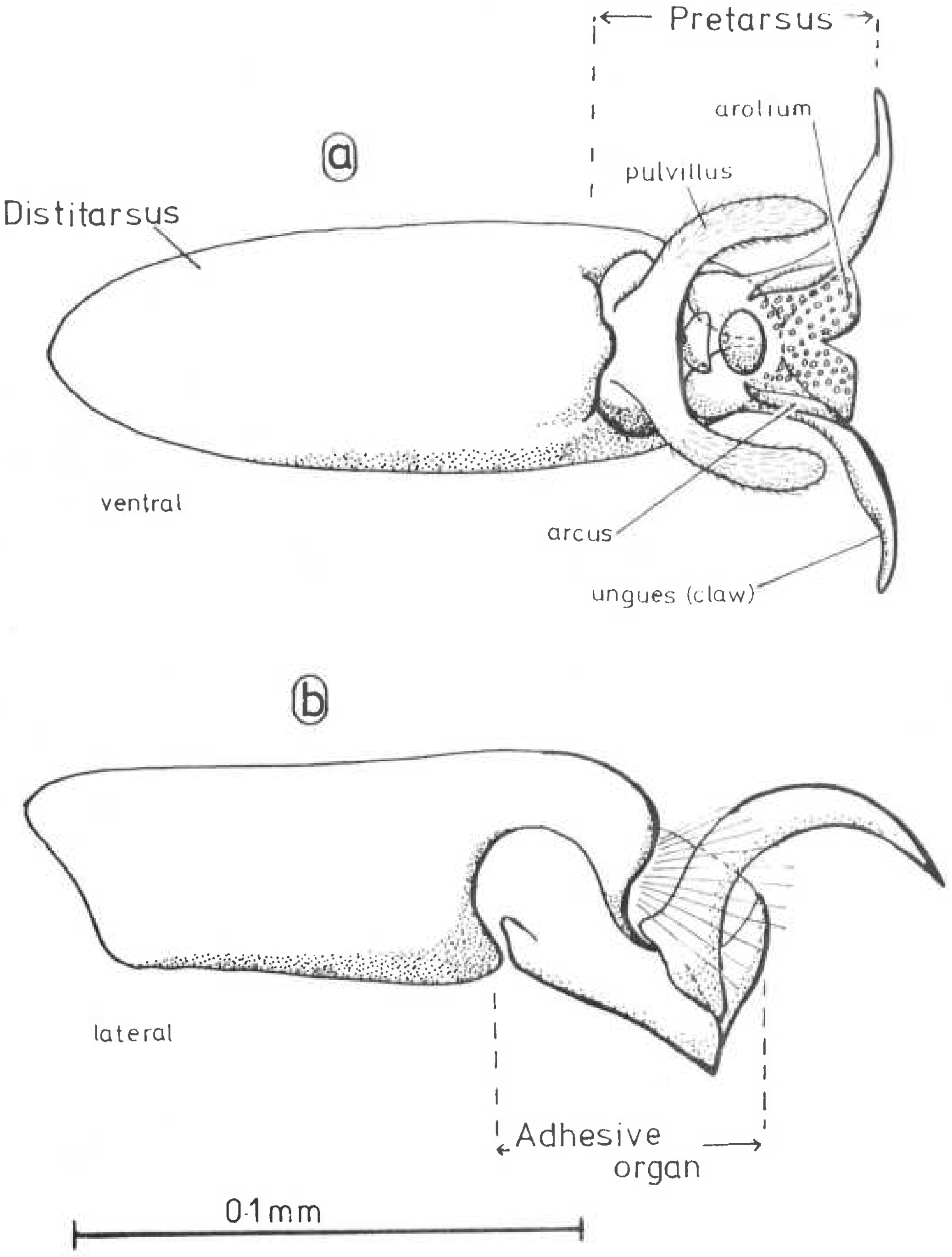
Padunia

Protoptilinae : Glossosomatidae



(28)

Adult legs - Stactobia mclachlani Kimmins



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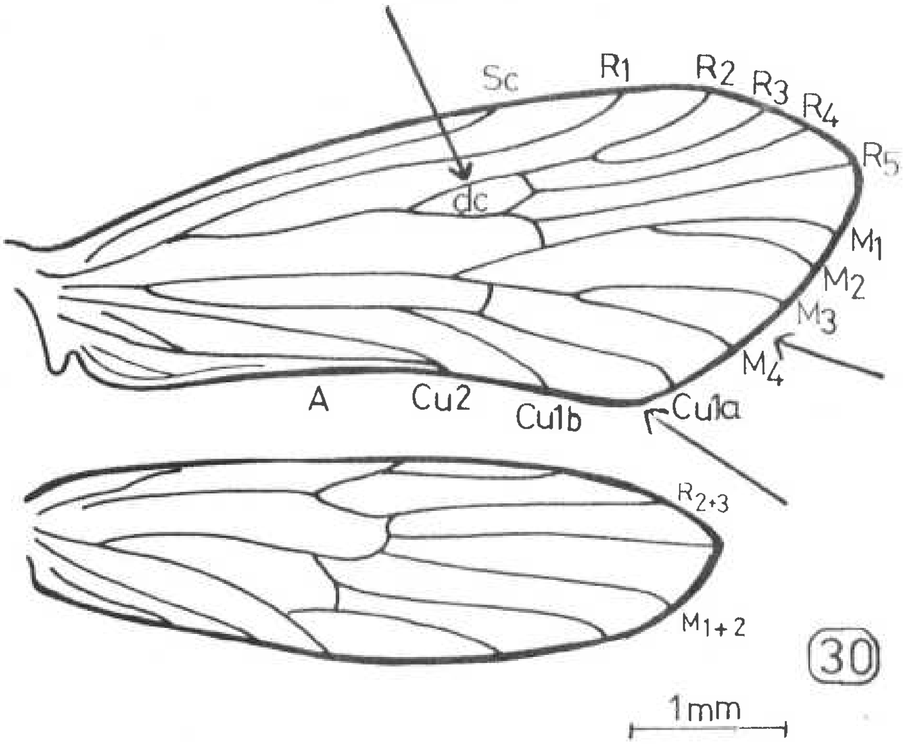
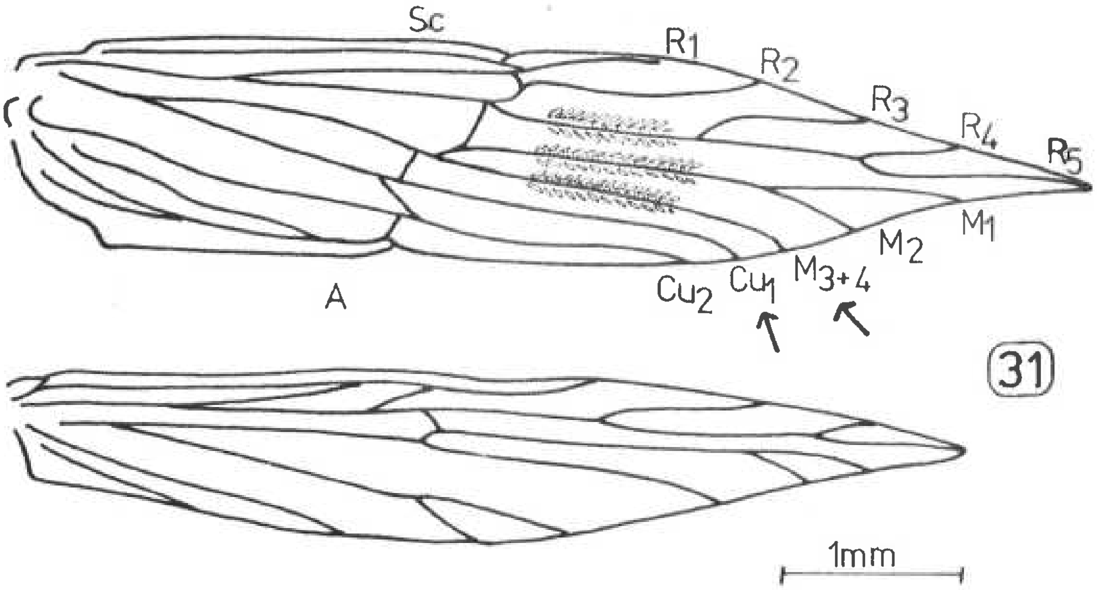
Pretarsus

Ptilocolepus — Adult



(30)

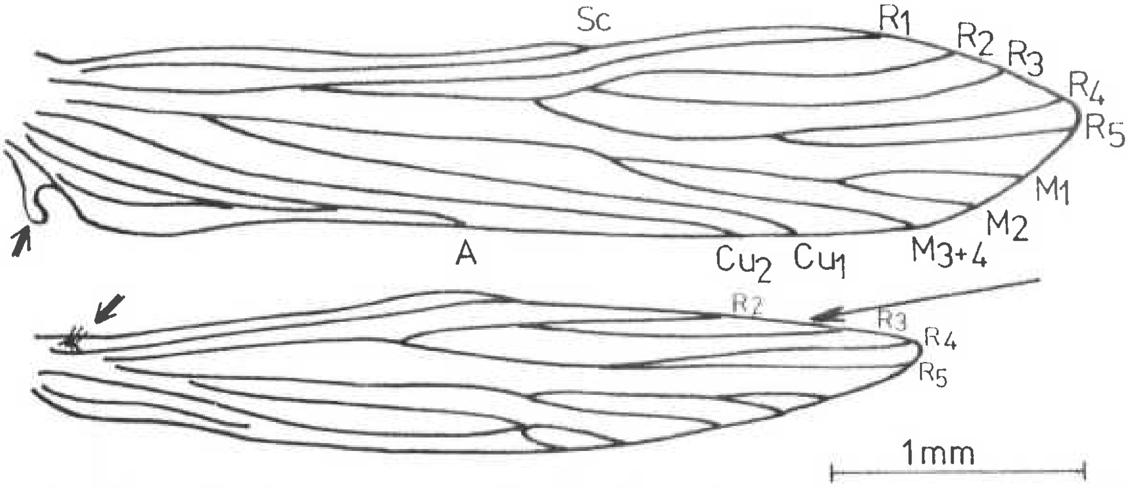
Ptilocolepus granulatus (Pictet)



(31)

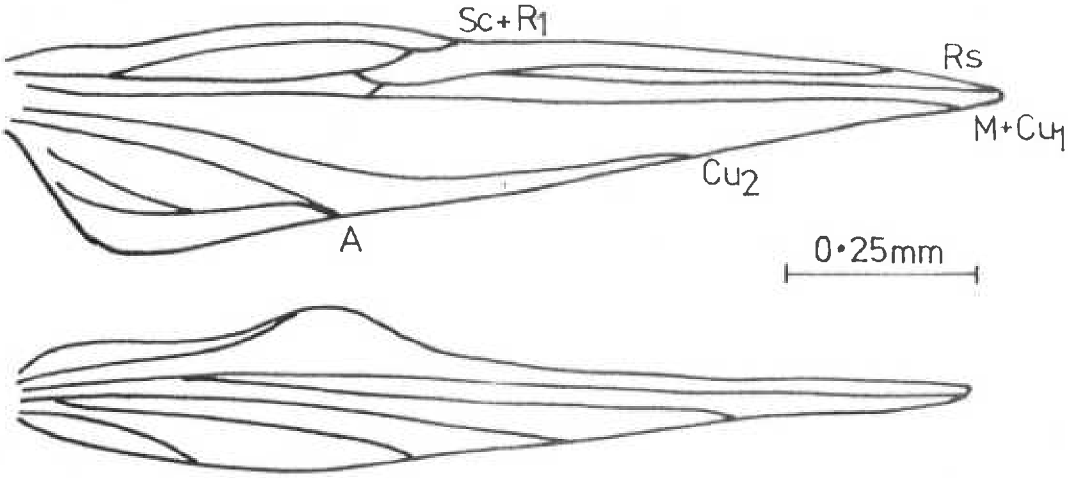
Ugandatrichia cyanotrichia (Kimmins)

Wing venation



Agraylea

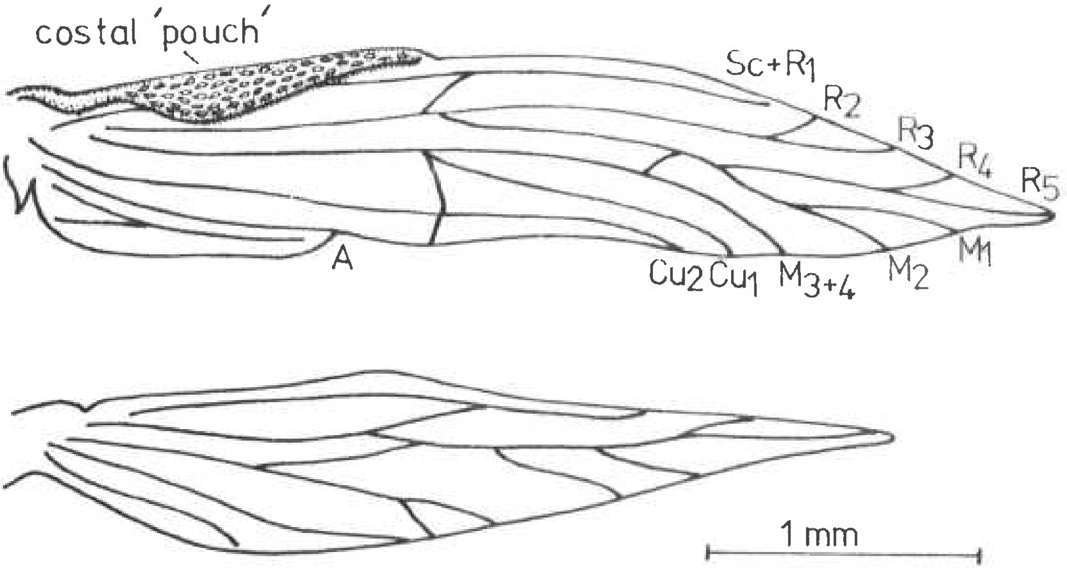
(32)



(33)

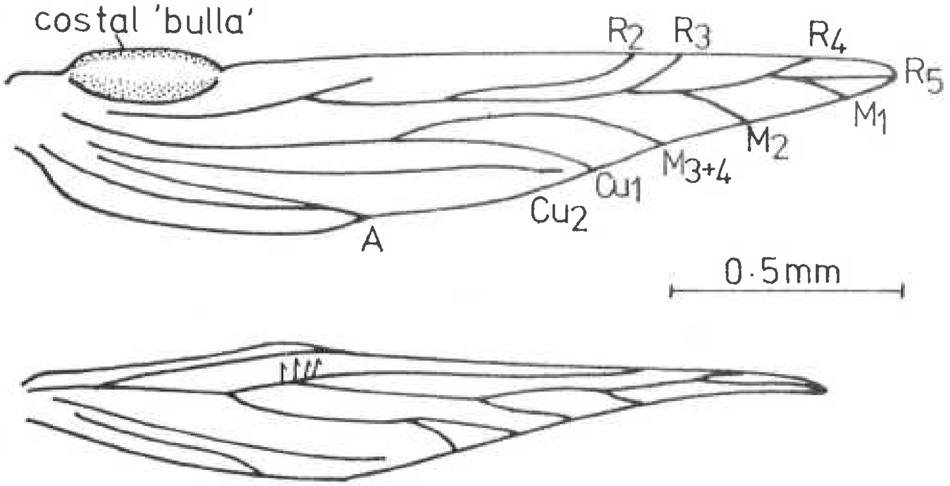
Neotrichia anahua (Mosely)

Wing venation



Abtrichia antennata Mosely ♂

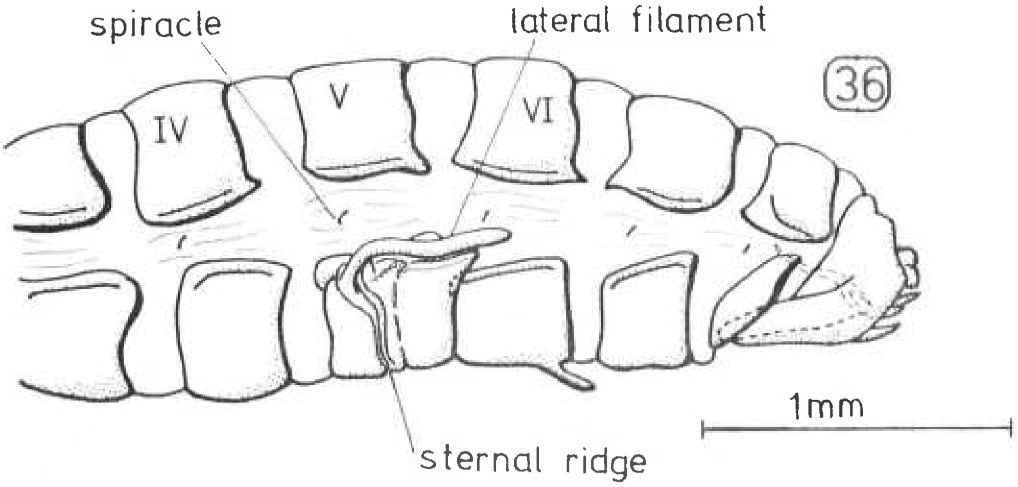
34



Costatrichia lodora Mosely ♂

35

Wing venation



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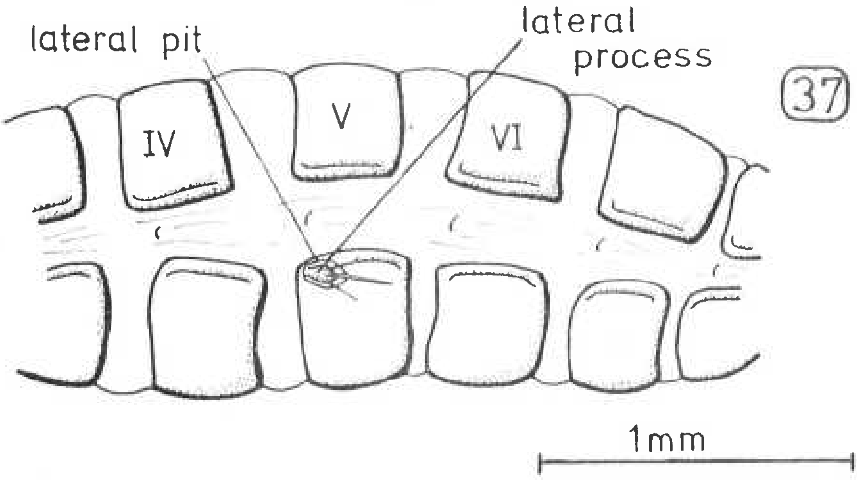
Ptilocolepus granulatus (Pictet) ♂



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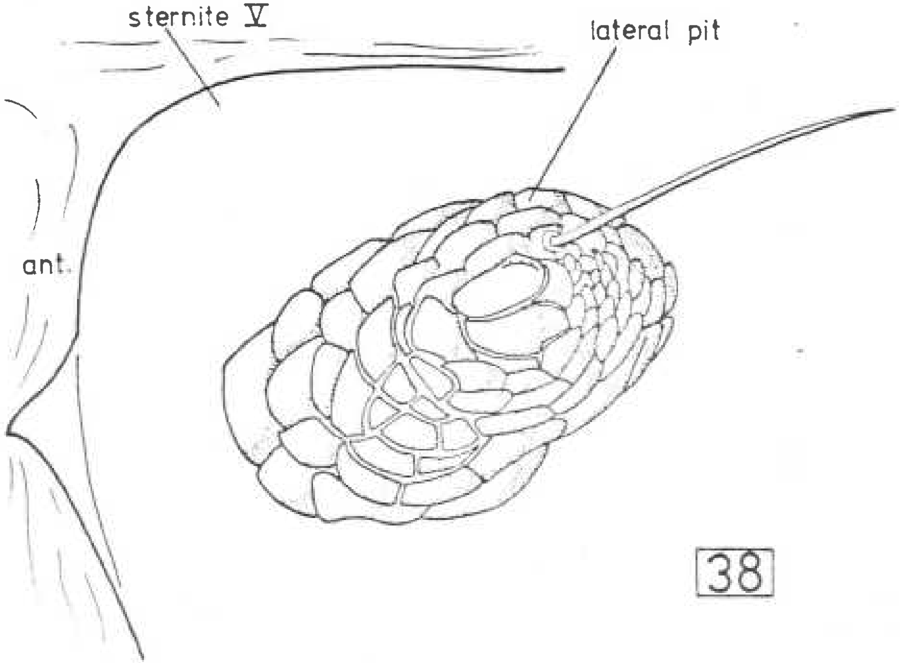
Hydroptilinae

Structures of abdominal sternite V - Adult

Hydroptilidae



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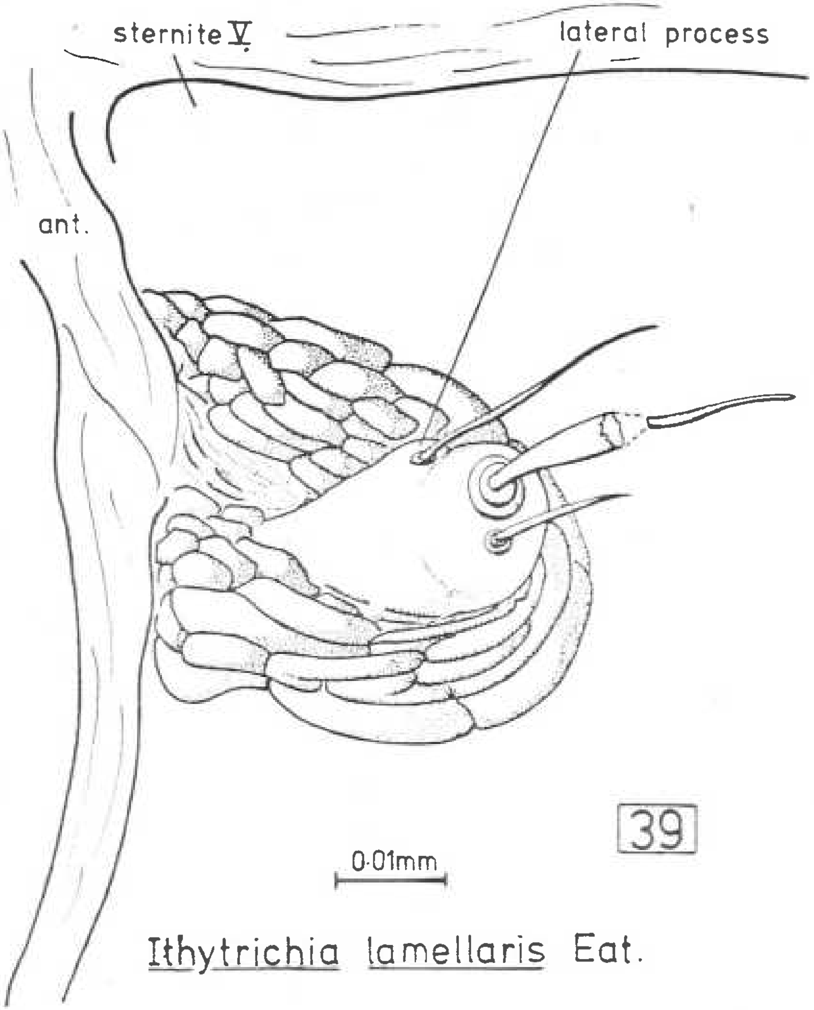
Tricholeiochiton fagesii (Guin.)



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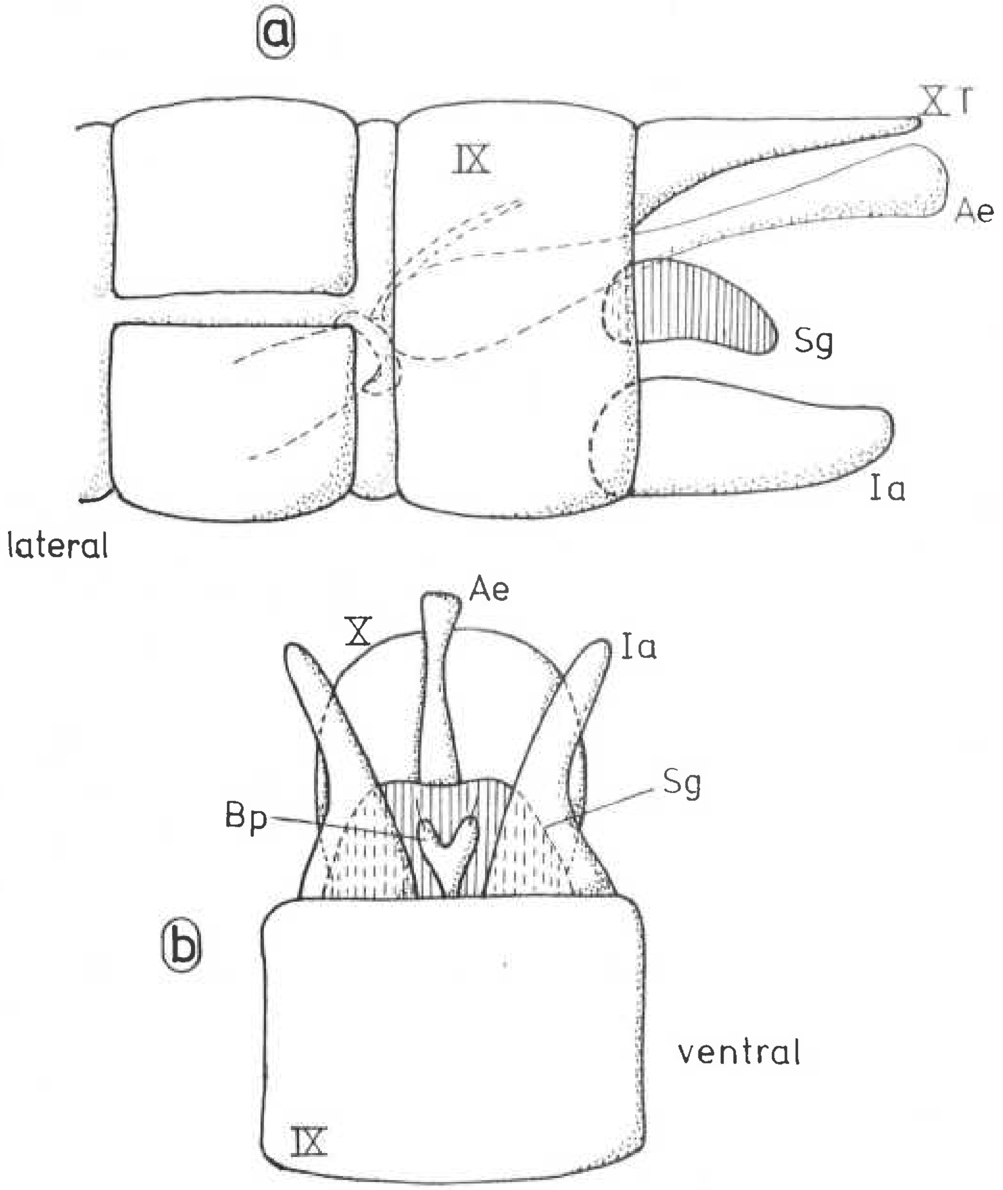
Ithytrichia lamellaris Eat.

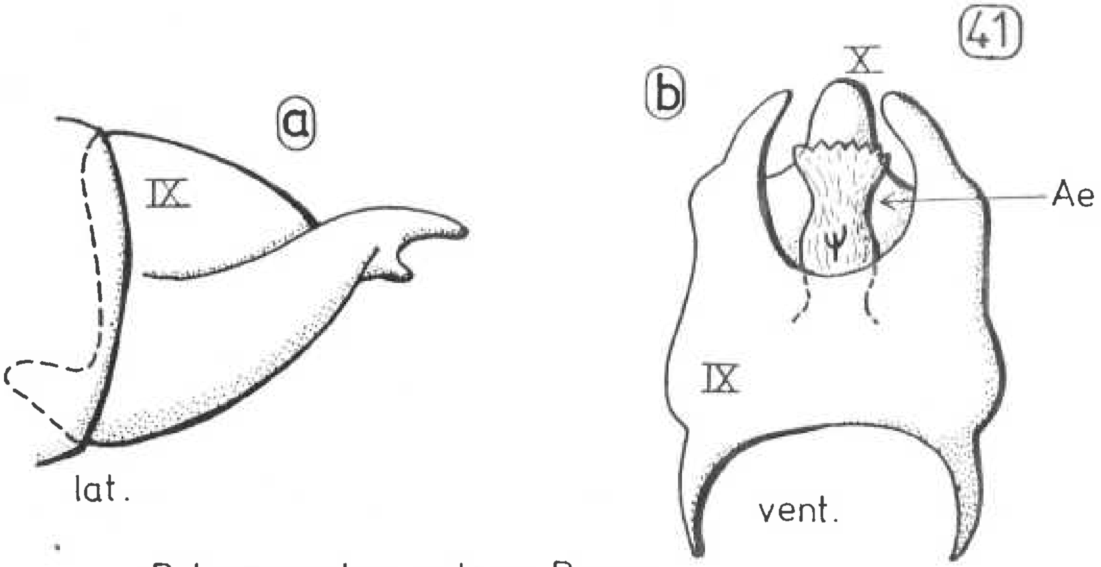
Adult Hydroptilinae - sternal gland of abdominal segment V - external appearance.



(40)

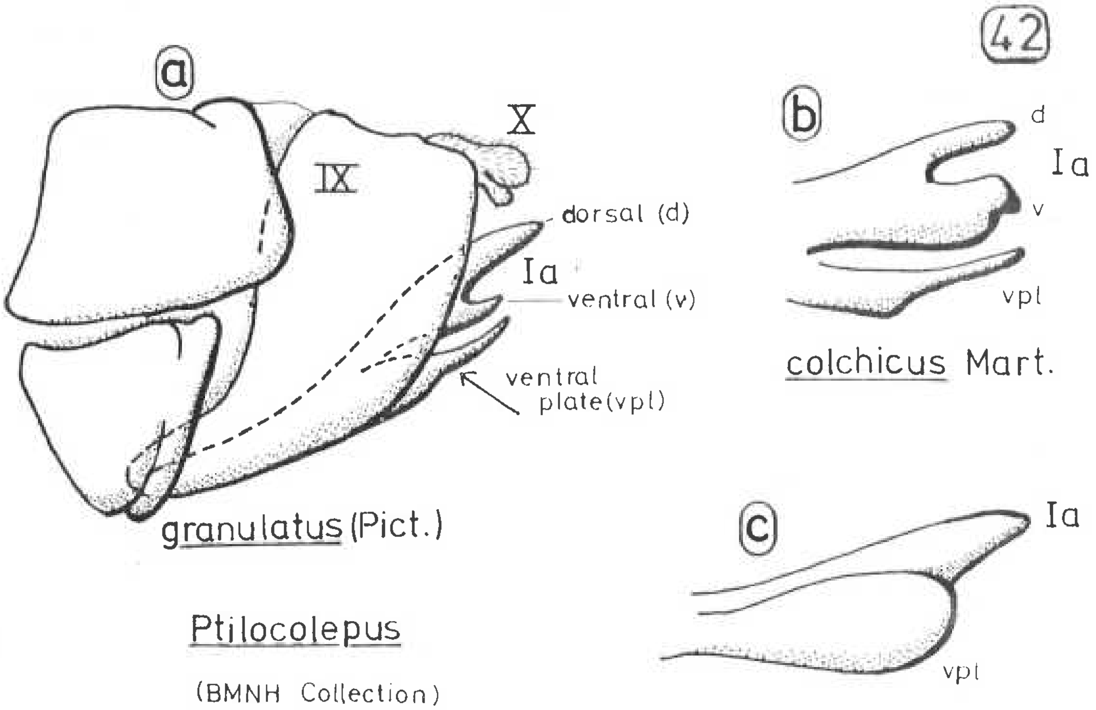
Generalized ♂ genitalia - Hydroptilidae

[Legend (figs 40-60) : Ae-aedeagus, Ia - inferior appendage ; Sg-subgenital structure, Bp-bilobed process.]



Palaeagapetus celsus Ross

(after Ross,1944)



colchicus Mart.

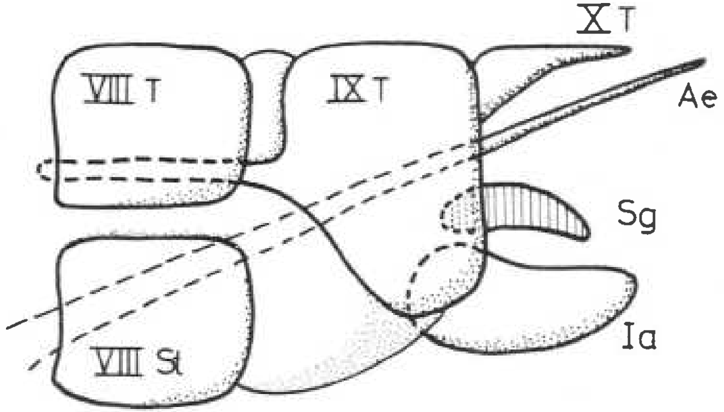
granulatus (Pict.)

Ptilocolepus

(BMNH Collection)

extensus McL.

Ptilocolepinae – ♂ genitalia



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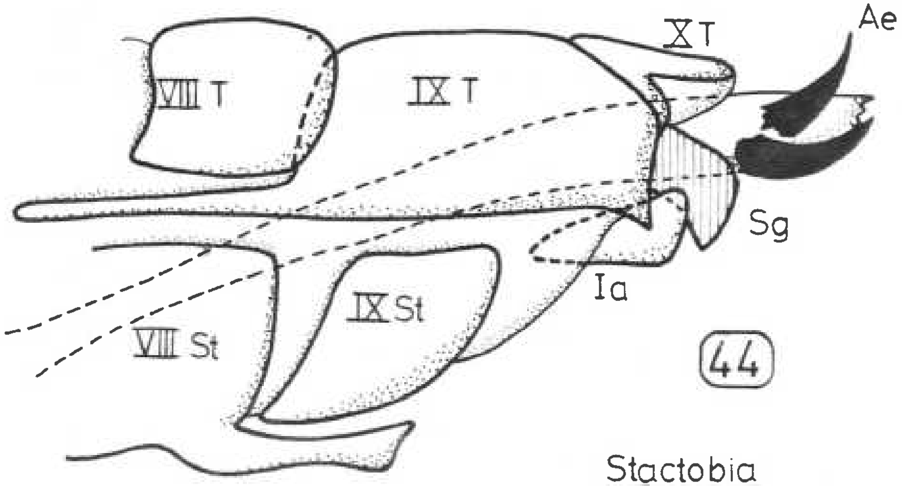
Stactobiella
Plethus
Chrysotrichia



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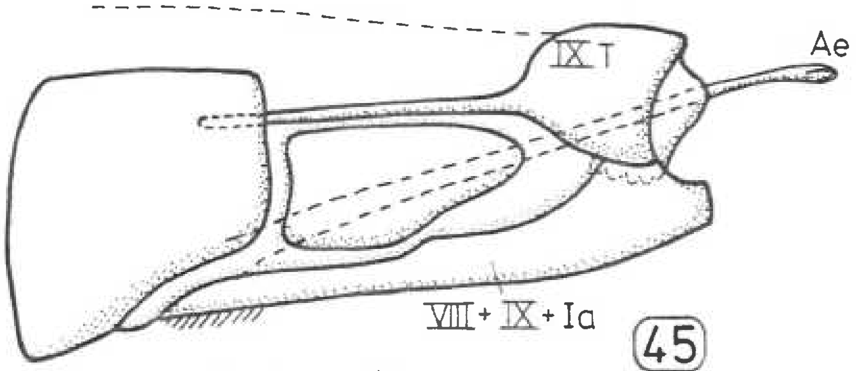
Stactobia
(after Schmid, 1959)



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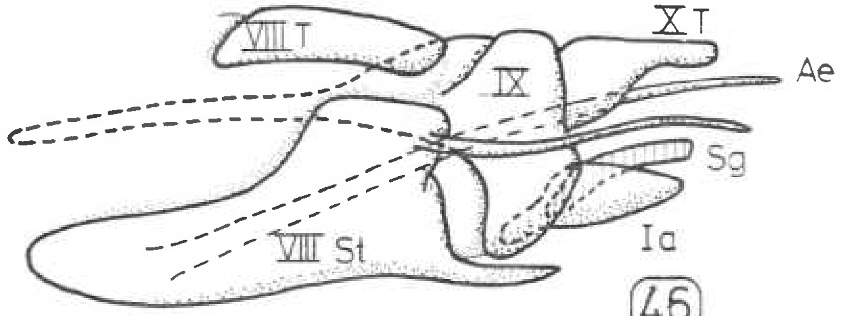
Madioxyethira



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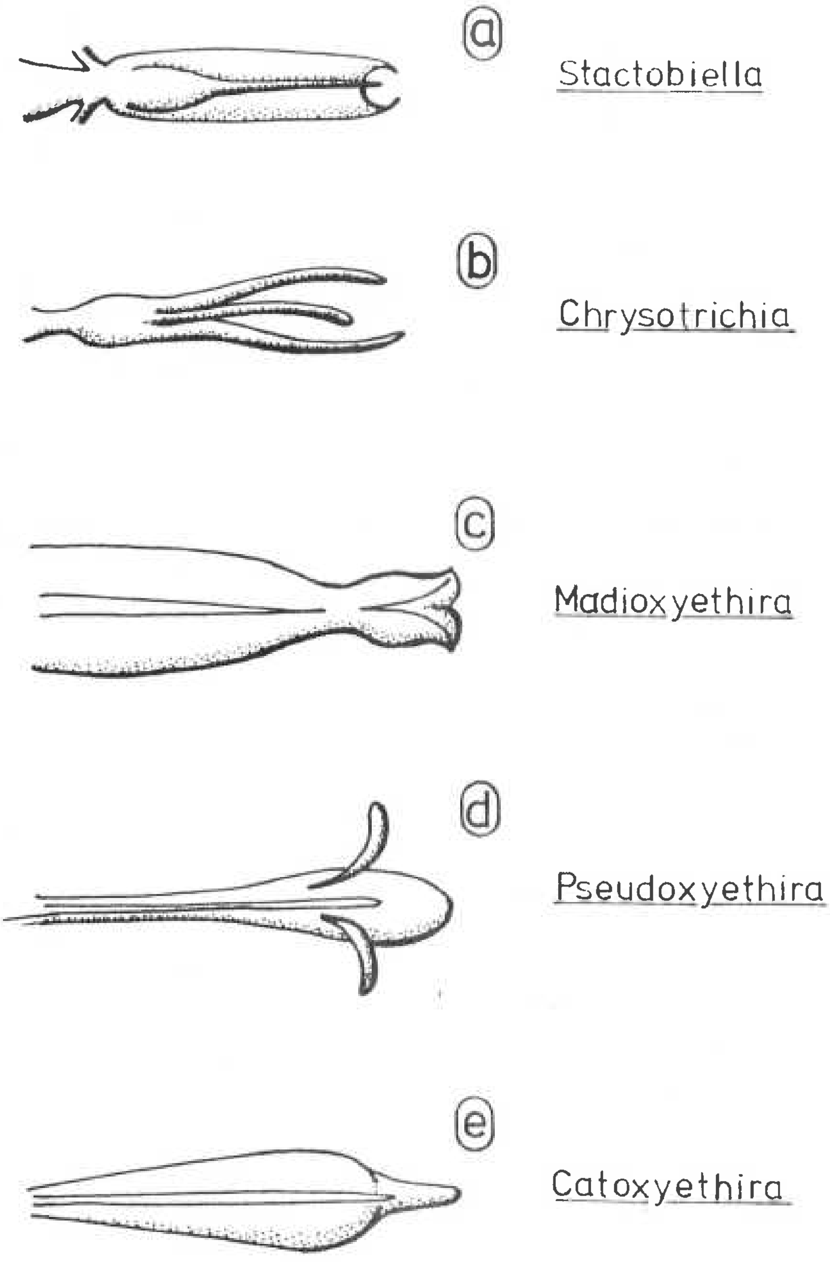
Catoxyethira

Stactobiini – ♂ genitalia - lateral



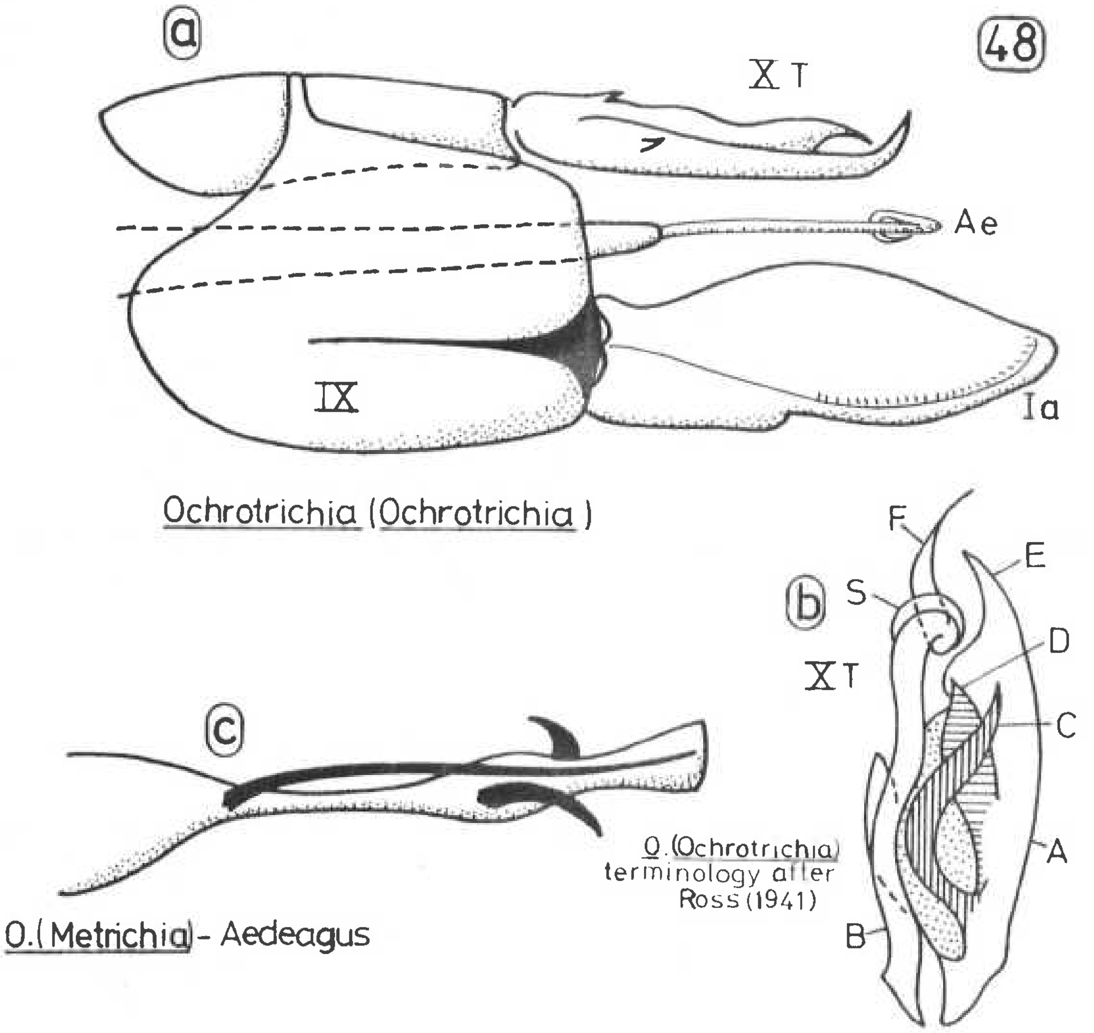
ant.

dorso-ventral views

(47)

Stactobiini — ♂ aedeagus

48



Ochrotrichia (Ochrotrichia)

O. (Ochrotrichia) terminology after Ross (1941)

O. (Metrichia) - Aedeagus

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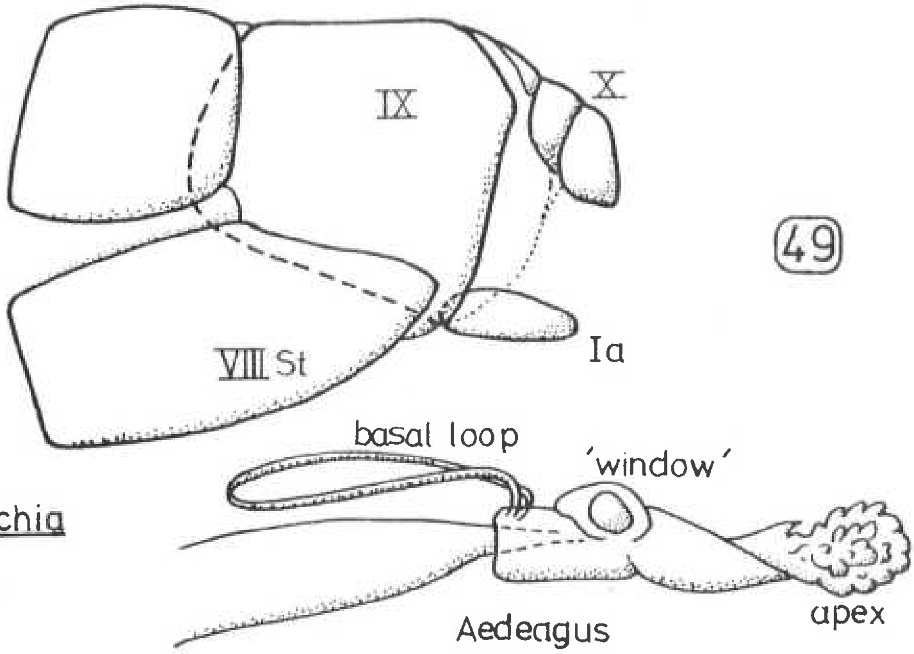
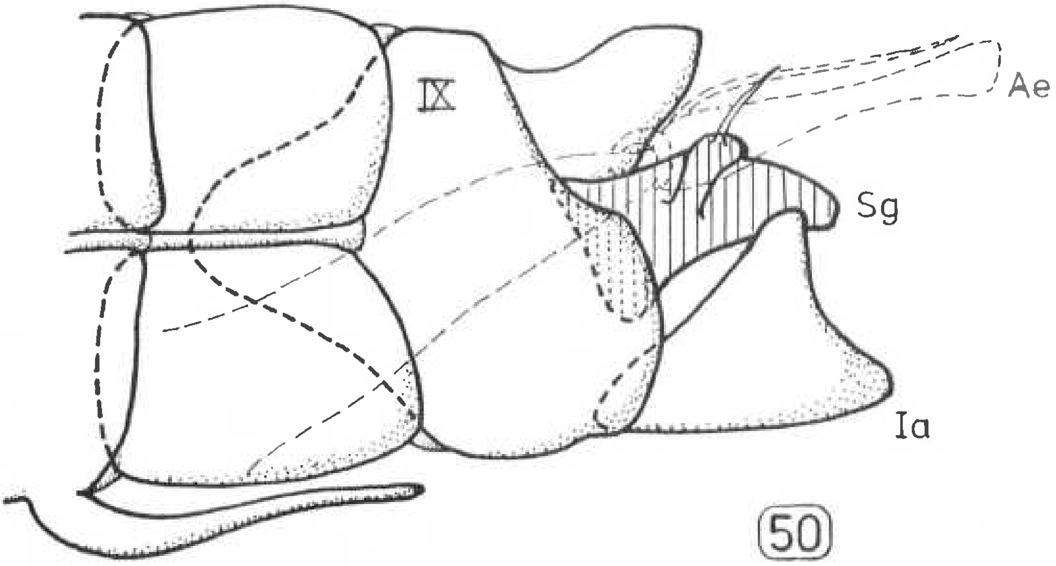


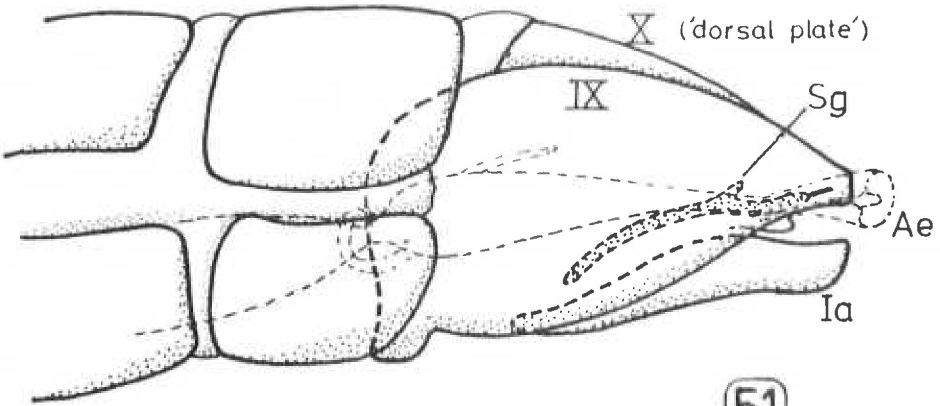
Leucotrichia

Ochrotrichiini and Leuchotrichiini
♂ genitalia - lateral



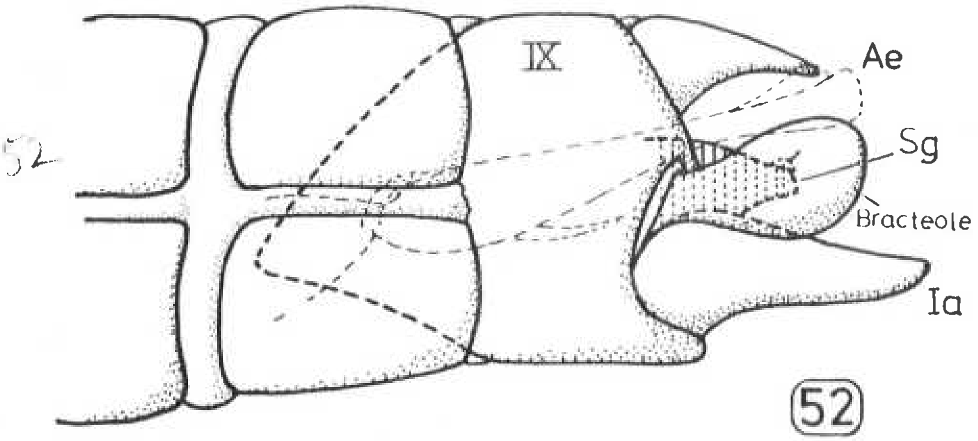
(50)

Allotrichia (*Agraylea* group)



(51)

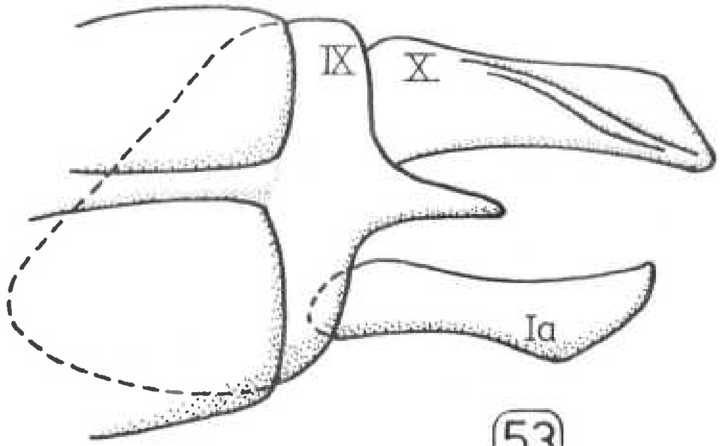
Ithytrichia



(52)

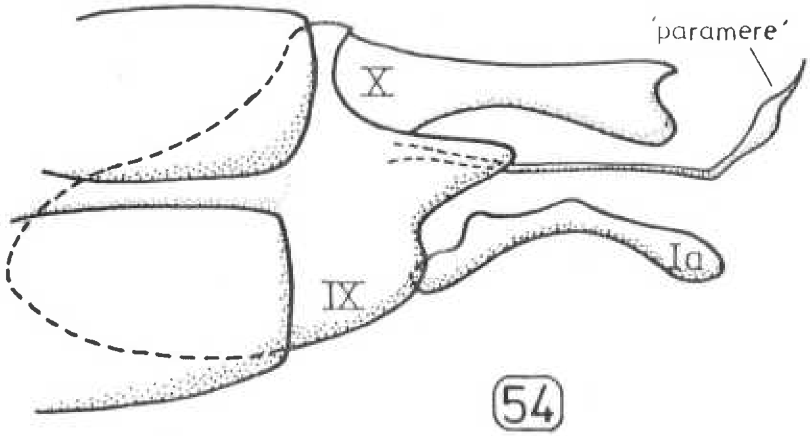
Neotrichia

♂ genitalia – lateral



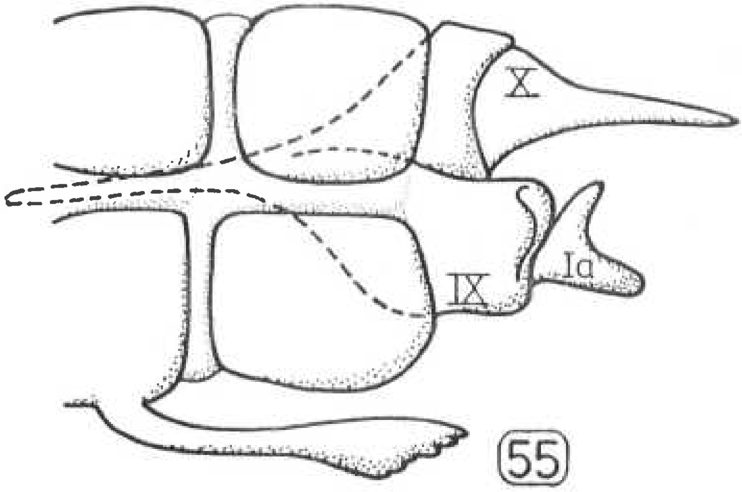
(53)

sparsa-group



(54)

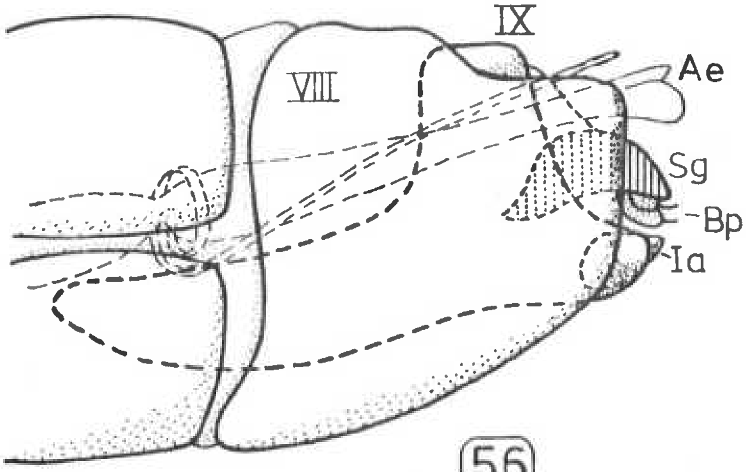
occulta-group



(55)

tineoides-group

Hydroptila – ♂ genitalia – lateral



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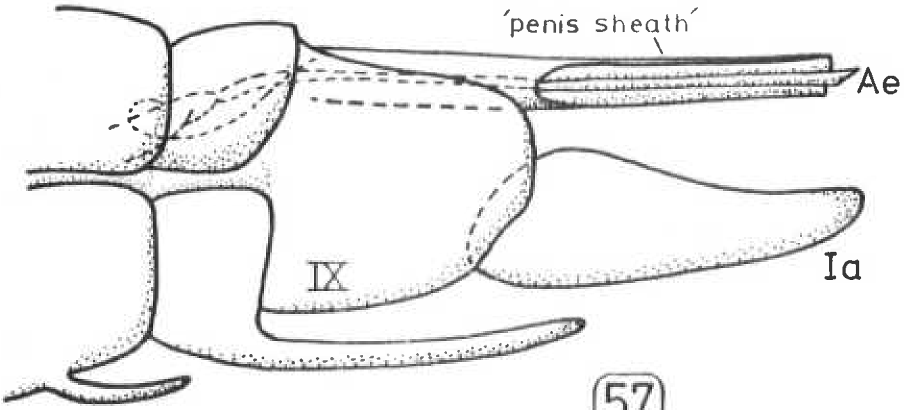
Oxyethira



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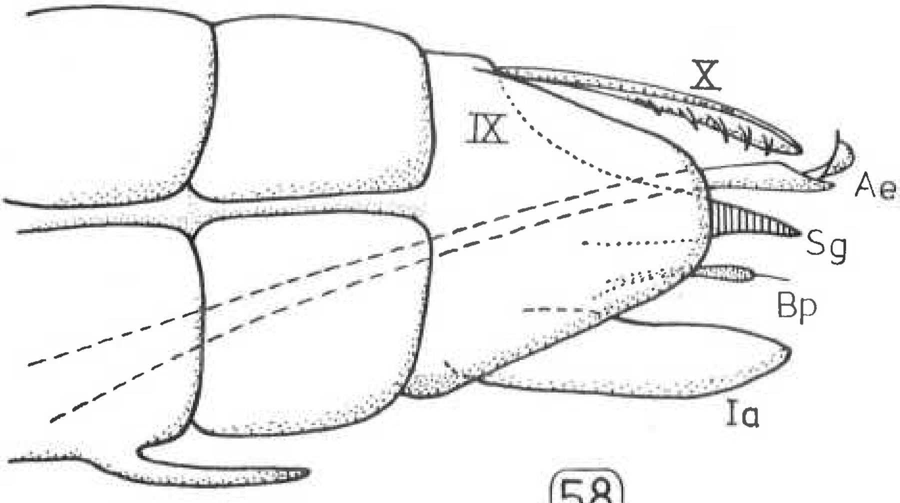
Paroxyethira



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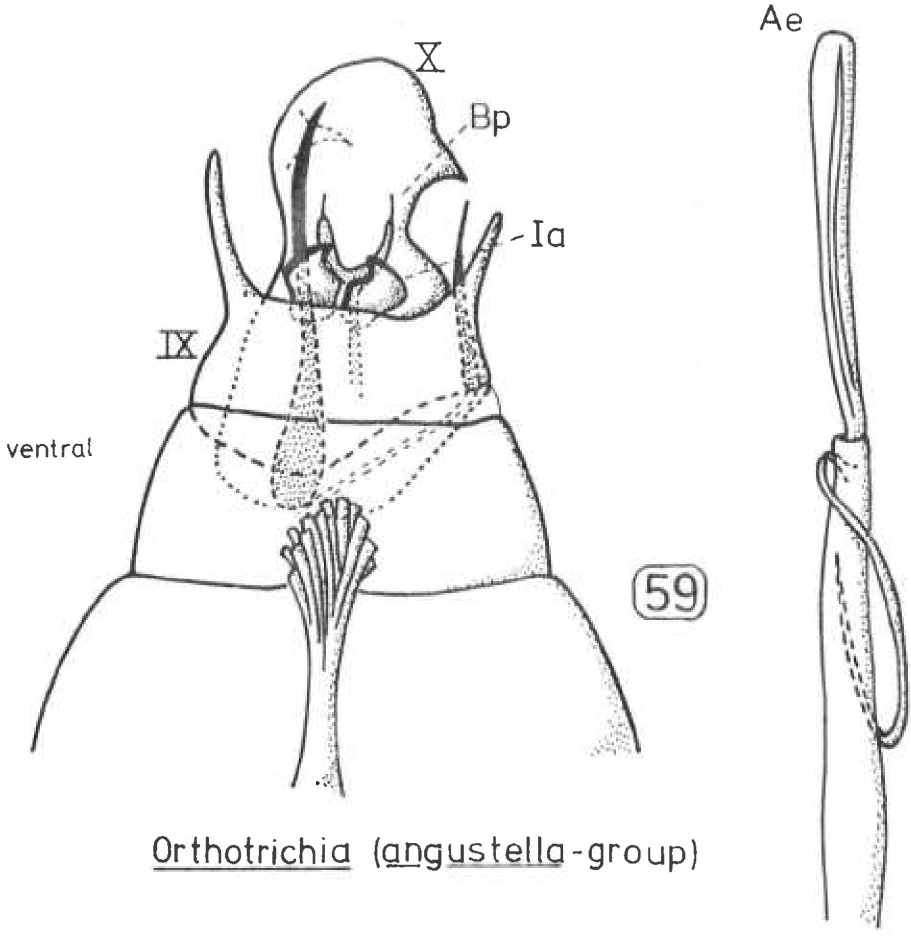
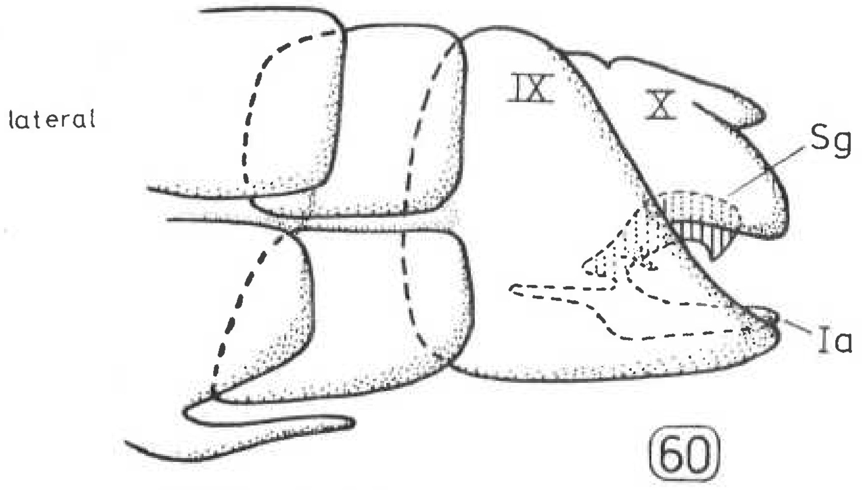
Xuthotrichia

♂ genitalia -lateral

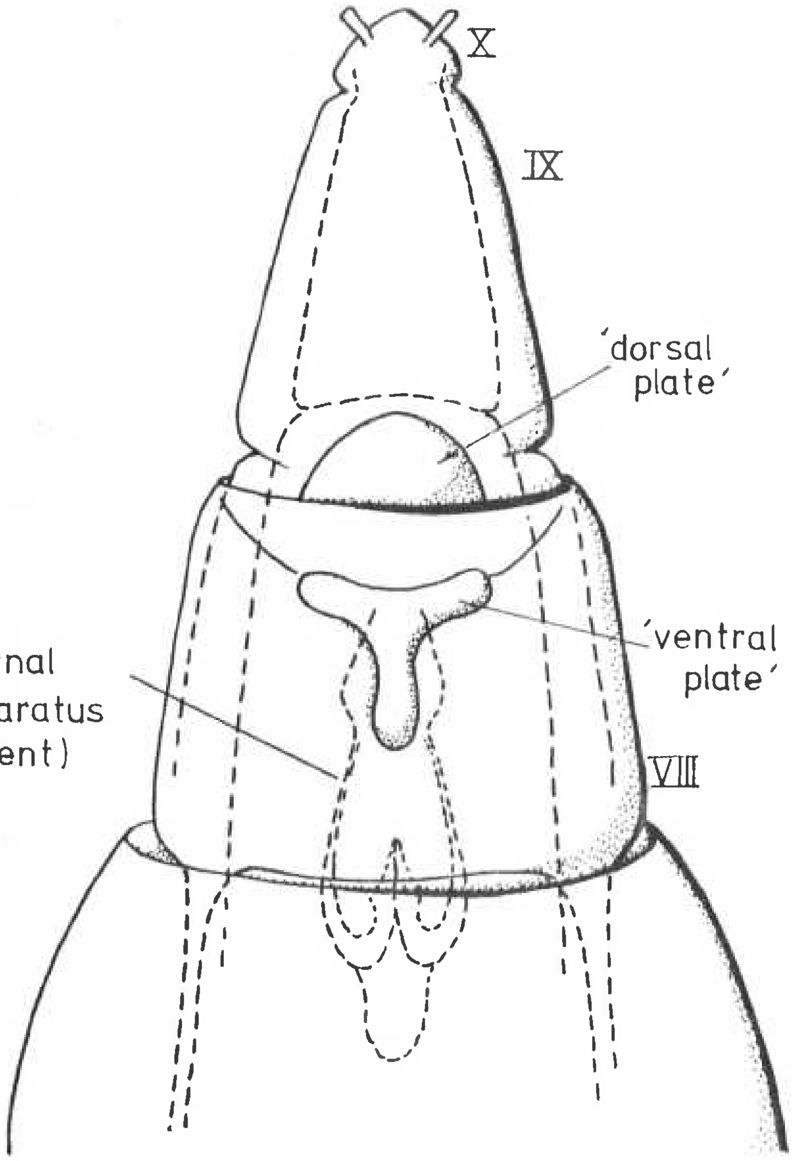


Orthotrichia (angustella-group)



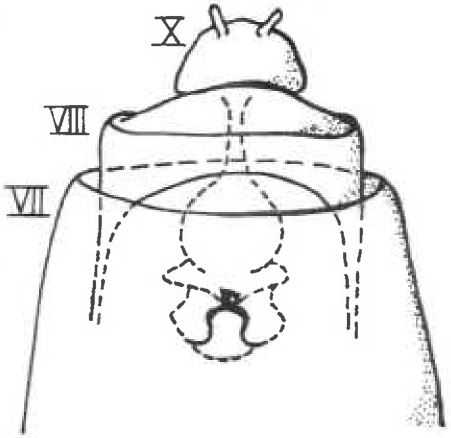
Tricholeiochiton

♂ genitalia



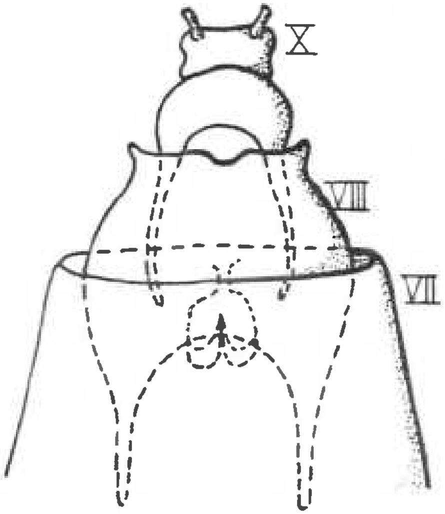
(61)

Generalized Hydroptilid ♀ genitalia
(oviscapt)



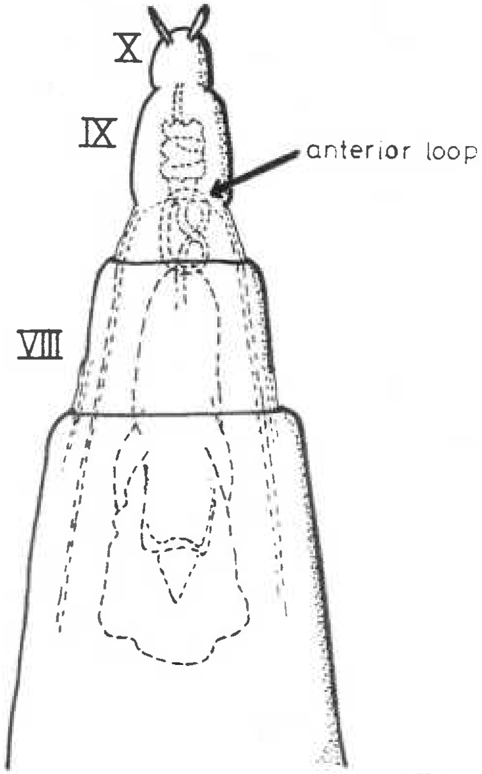
Oxyethira

(62)



Orthotrichia

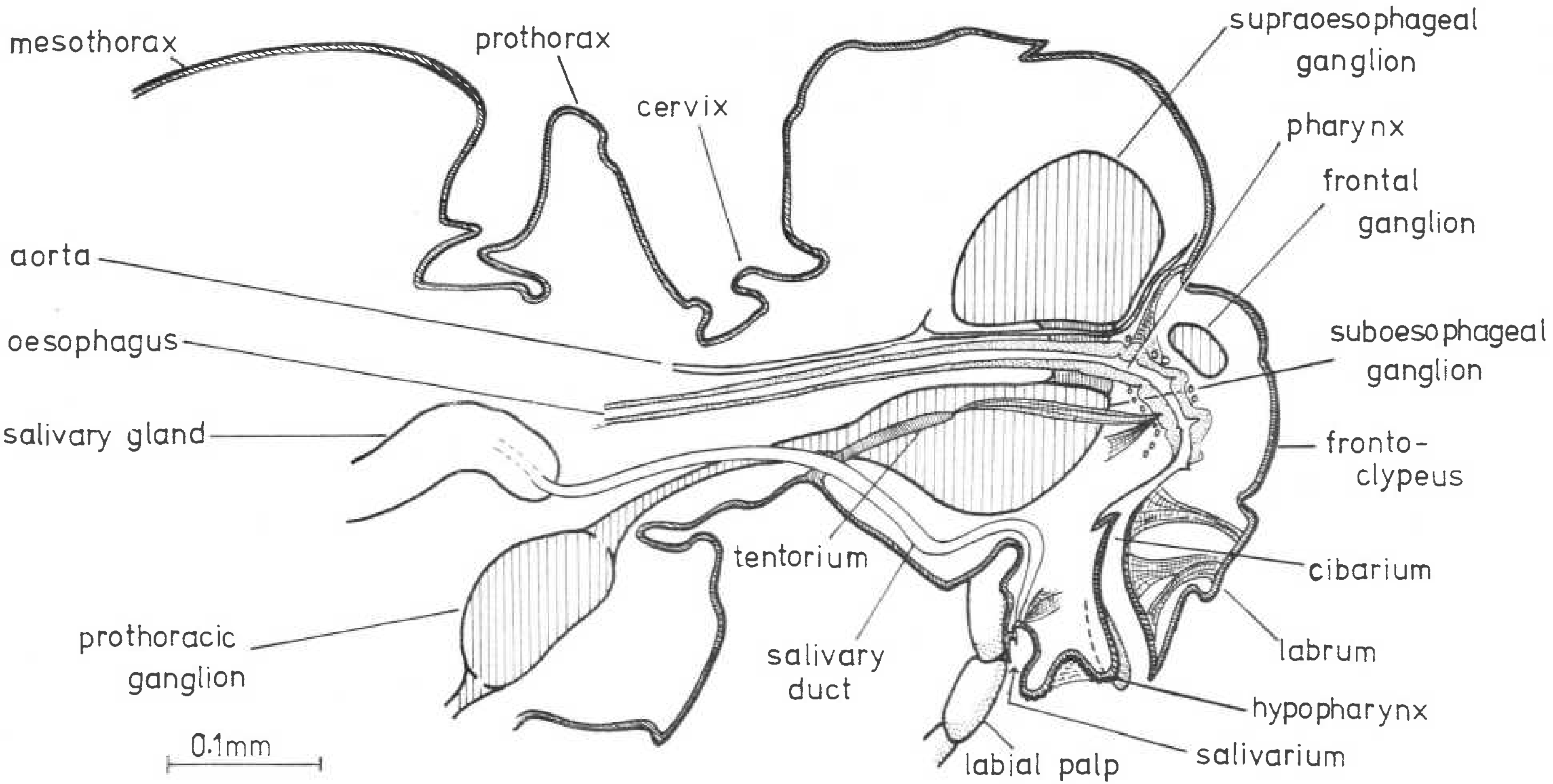
(63)



(64)

Madioxyethira

♀ genitalia – ventral



Internal anatomy - Head and prothorax - Adult Hydroptilid [LS] (65)
(Hydroptila sparsa Curtis)

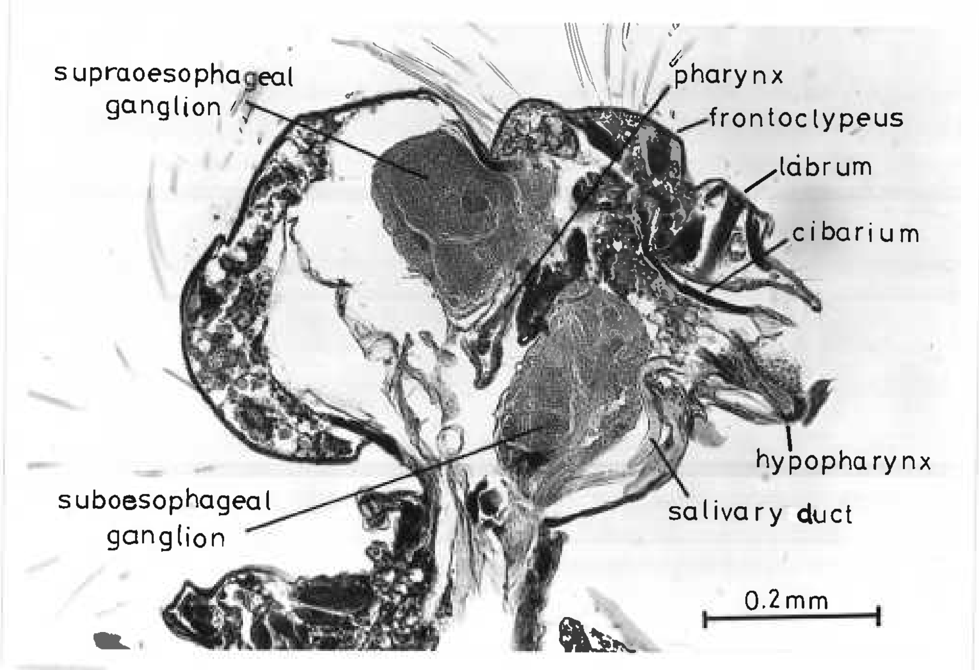
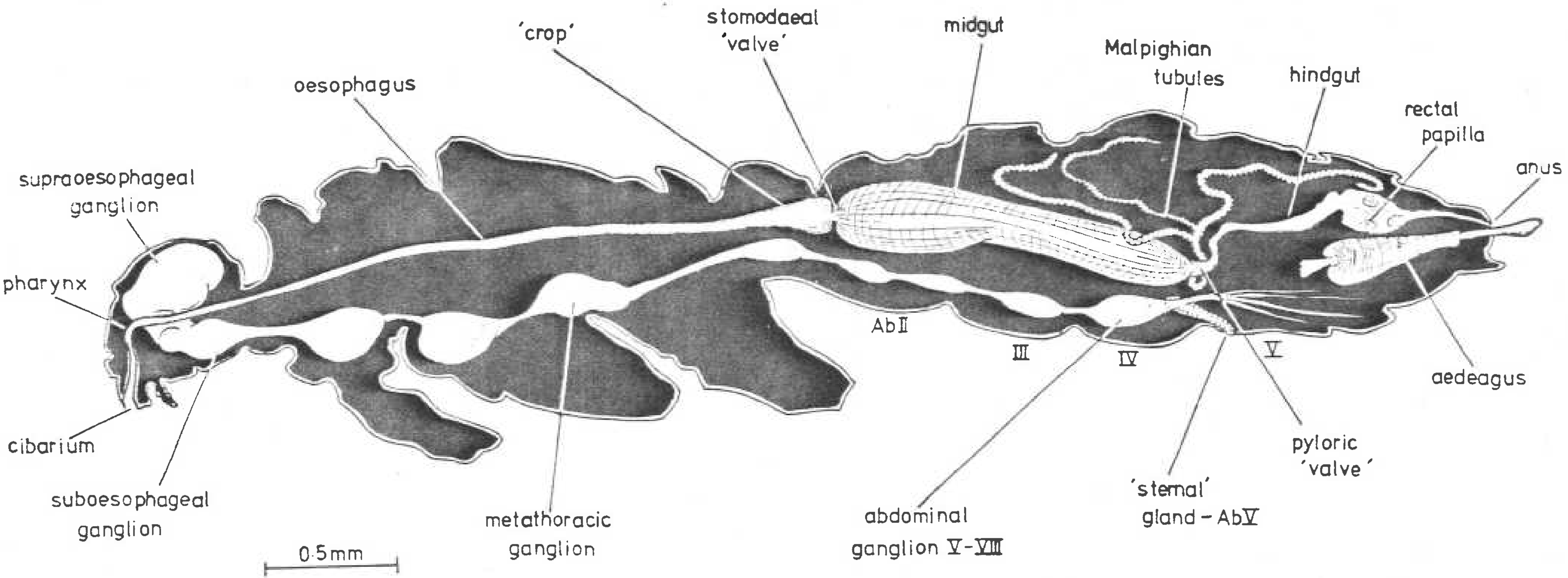


Fig. 66. Adult head L.S. *Hydroptila sparsa* Curtis.



67

Adult internal anatomy - *Agraylea* sp.

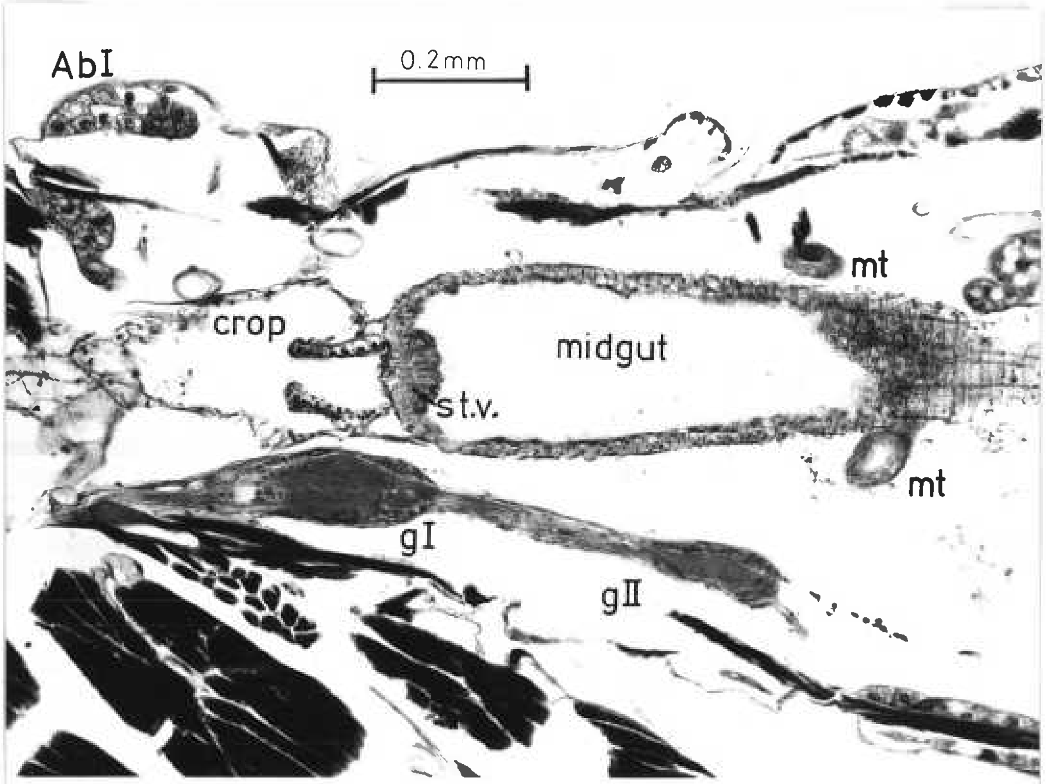


Fig. 68. Adult alimentary canal.
L.S. crop and midgut, Hydroptila sp.(Ab. abdominal segment; g. abdominal ganglion; mt. Malpighian tubule; st.v. stomodaeal valve).

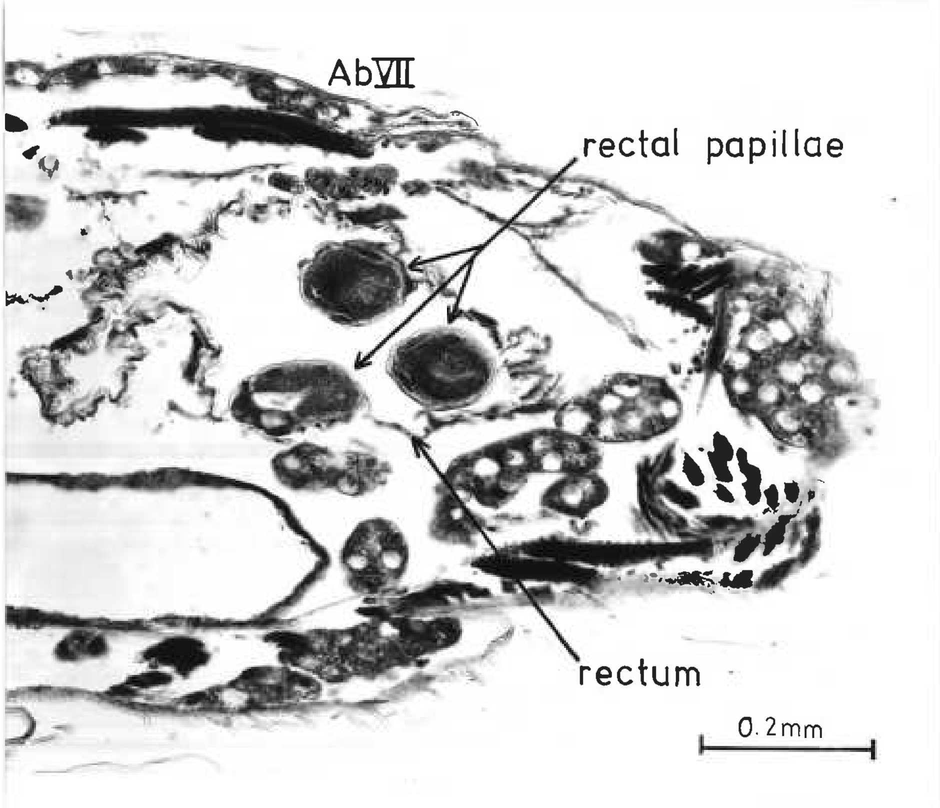


Fig. 69. Adult alimentary canal.

L.S. rectum, _Hydroptila_ sp.

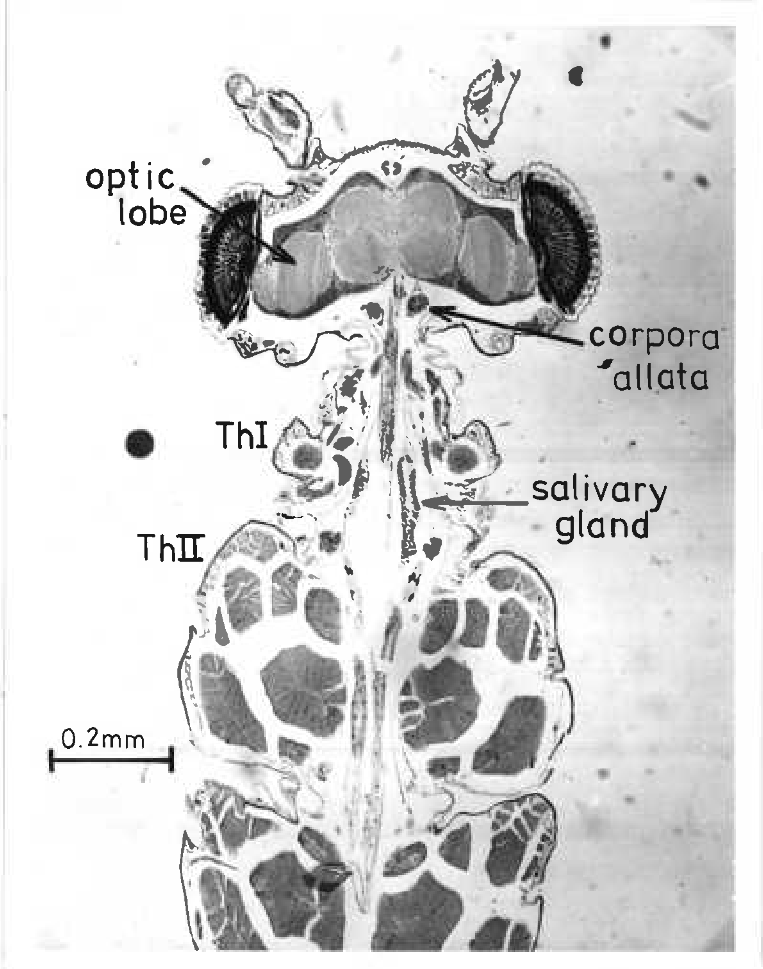


Fig. 70. Adult head and thorax H.S.

Hydroptila sp.

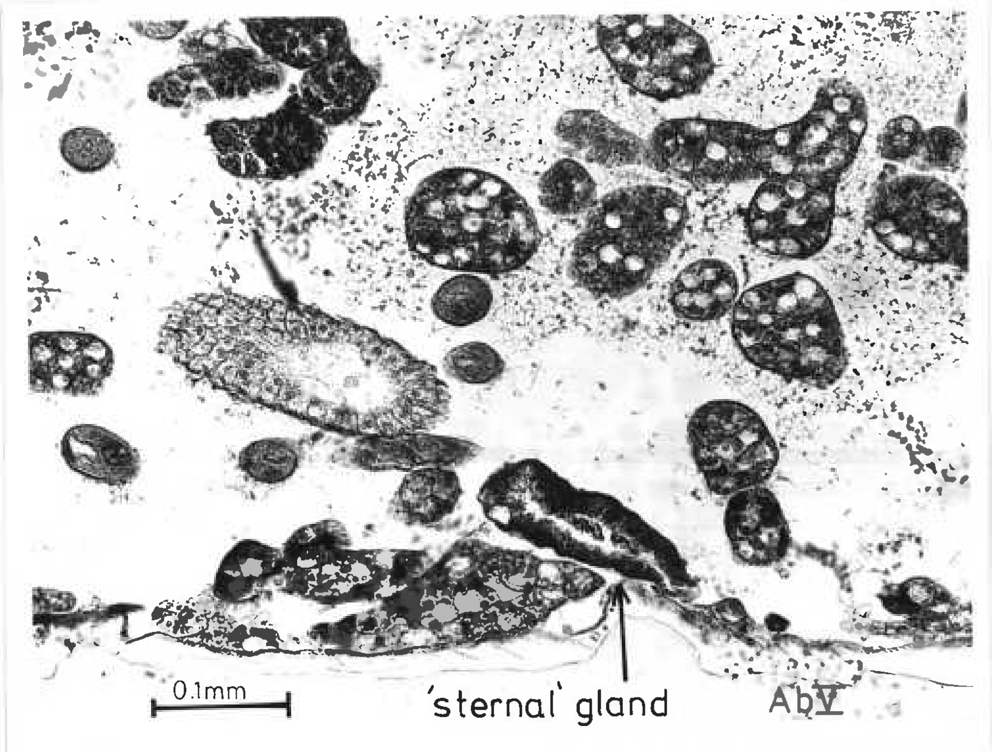
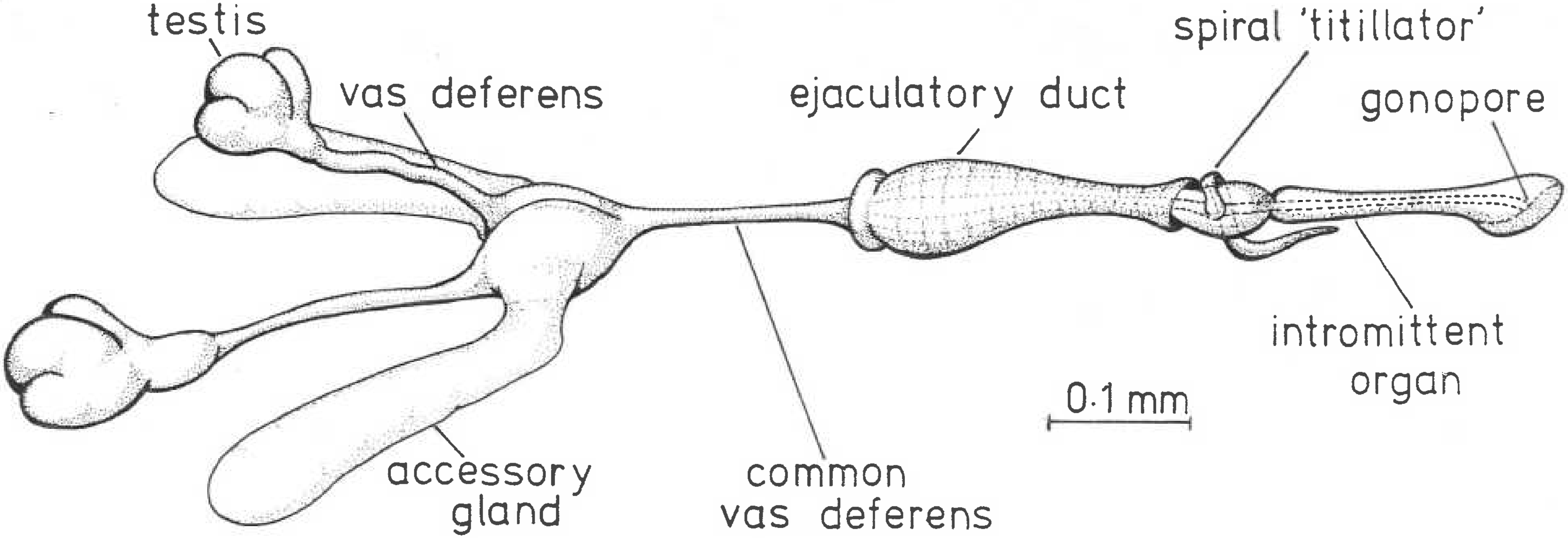


Fig. 71. Adult sternal gland.

L.S. abdominal (Ab) segments V and VI,

Hydroptila sp.



72

♂ reproductive system

Agraylea sexmaculata

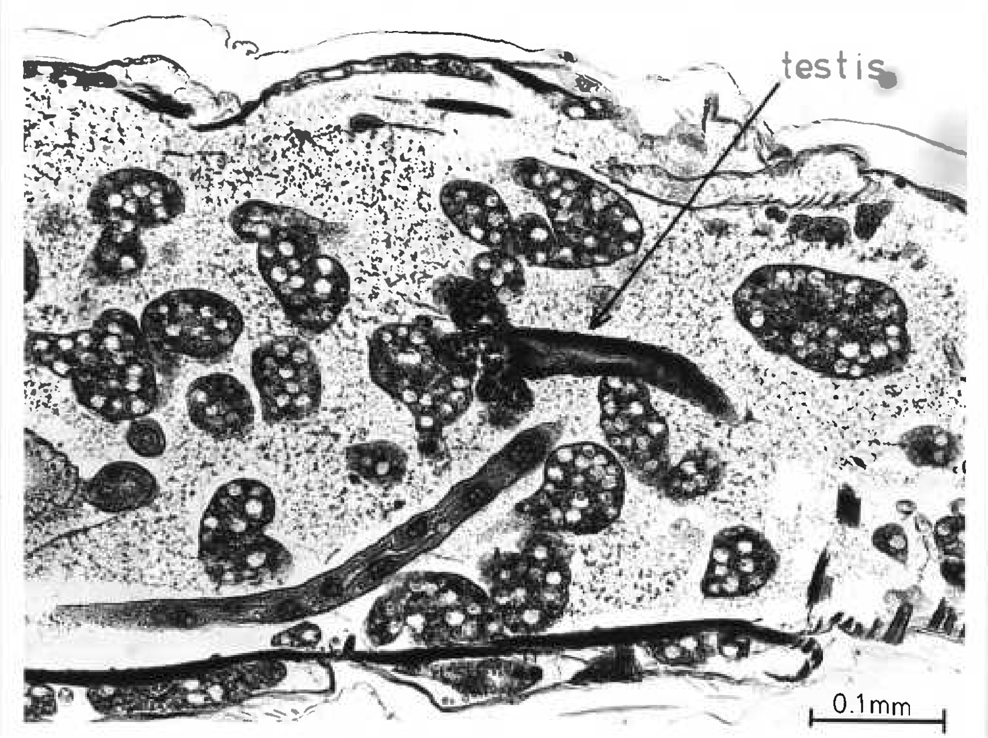
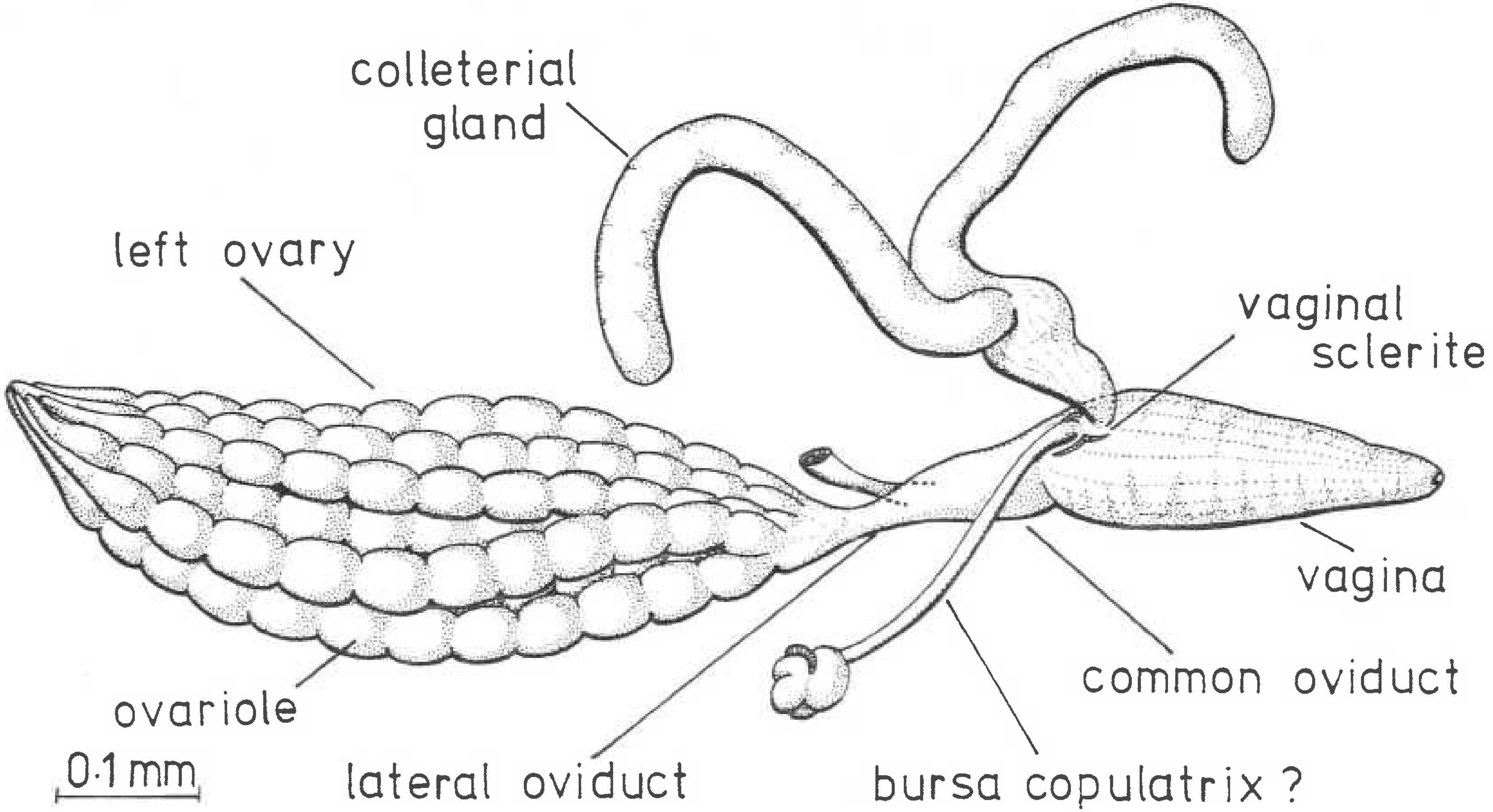


Fig. 73. L.S. trilobed testis.

Hydroptila sp.



♀ reproductive system

<u>Agraylea sexmaculata</u>

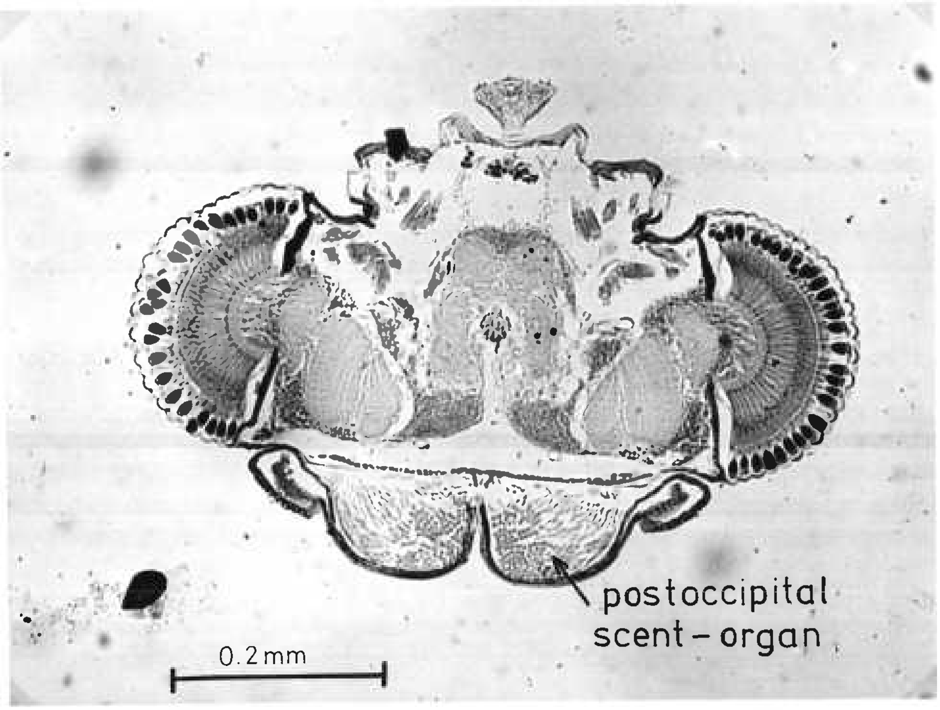
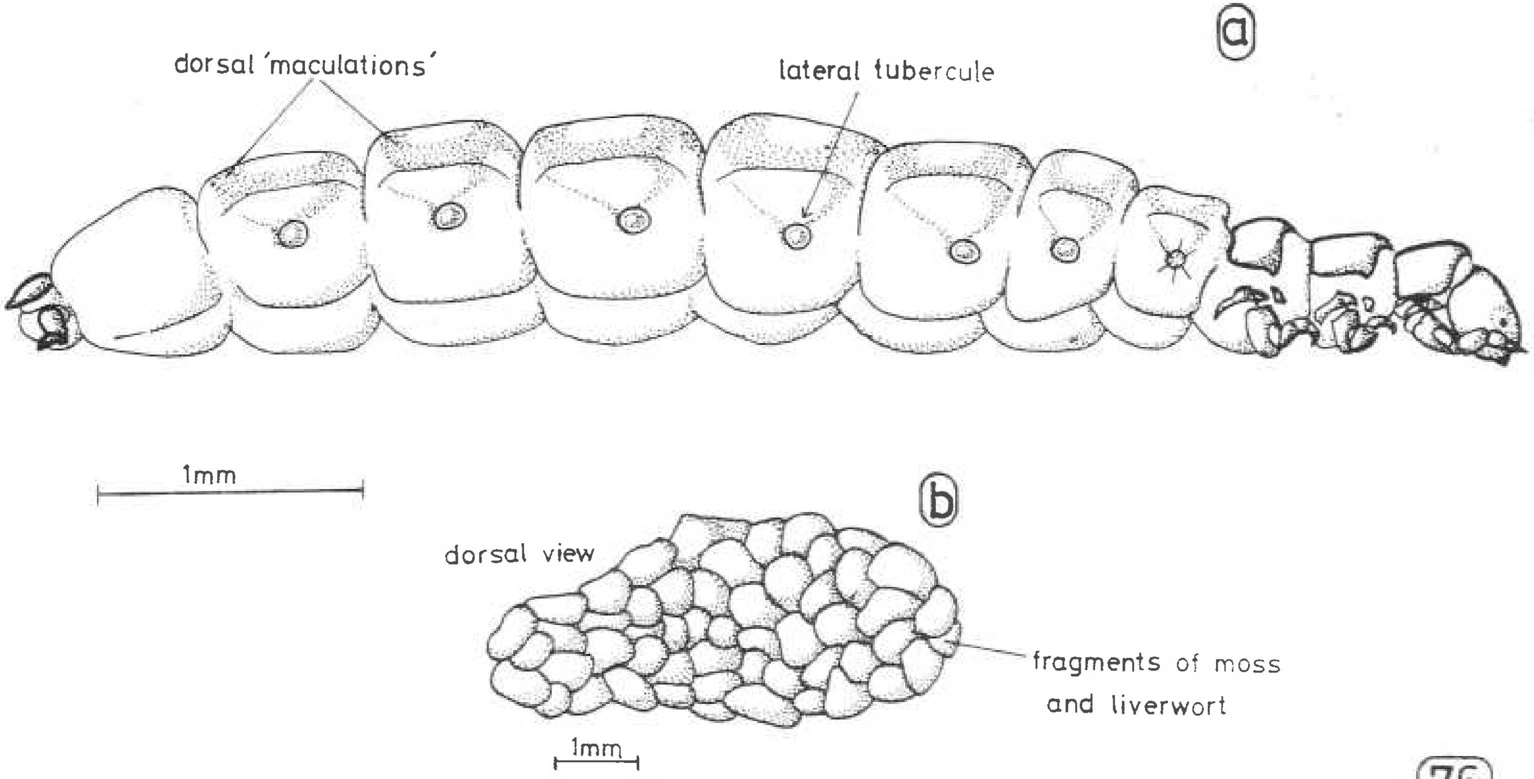


Fig. 75. H.S. head *Hydroptila* sp.

Male postoccipital 'scent' organs.

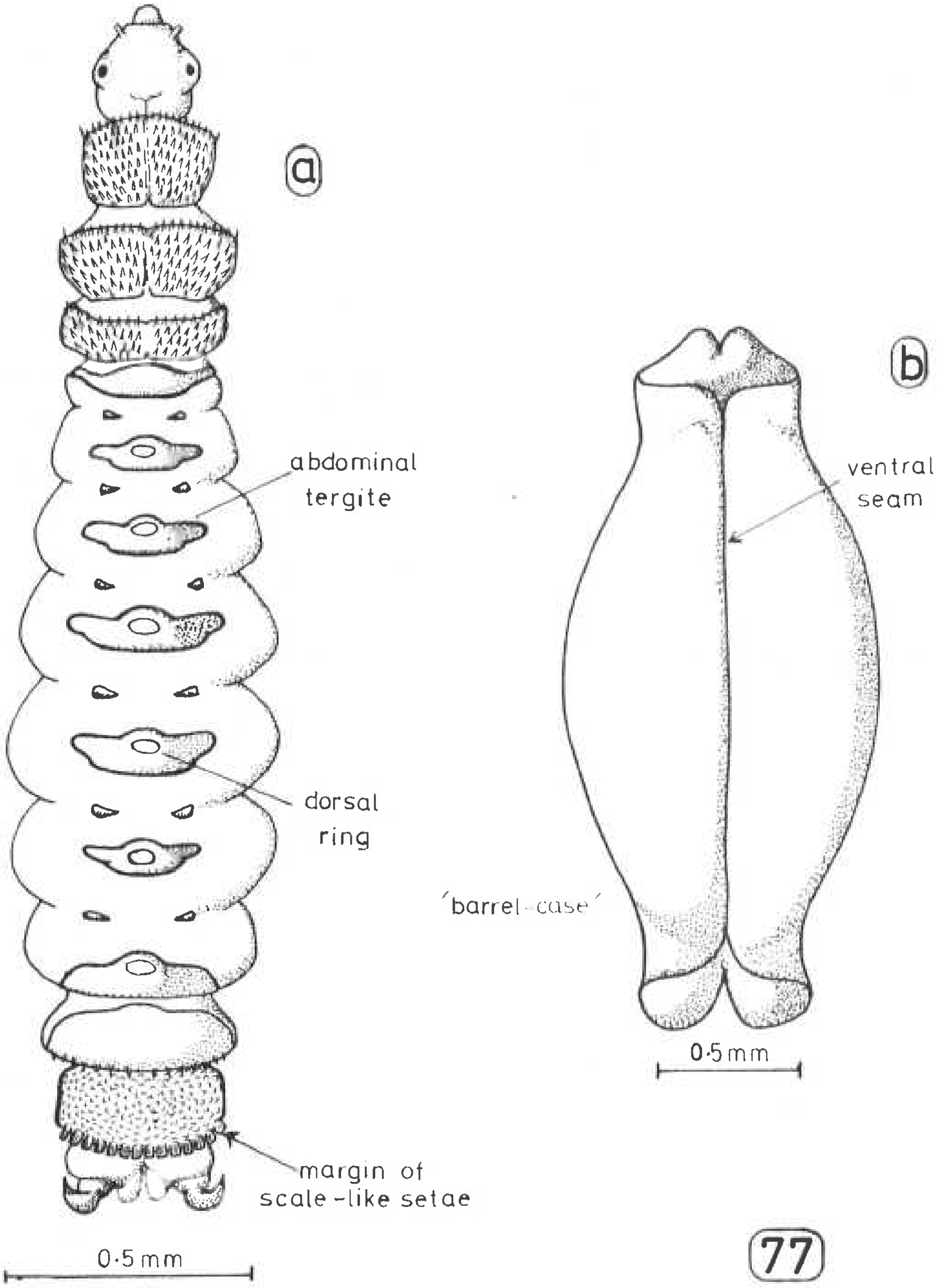


76

Palaeagapetus celsus Ross

(U.S.A.; Tennessee; Gt.Smoky Mts; N.P. Indian Gap, 7.vi.1961; O.S.Flint.)

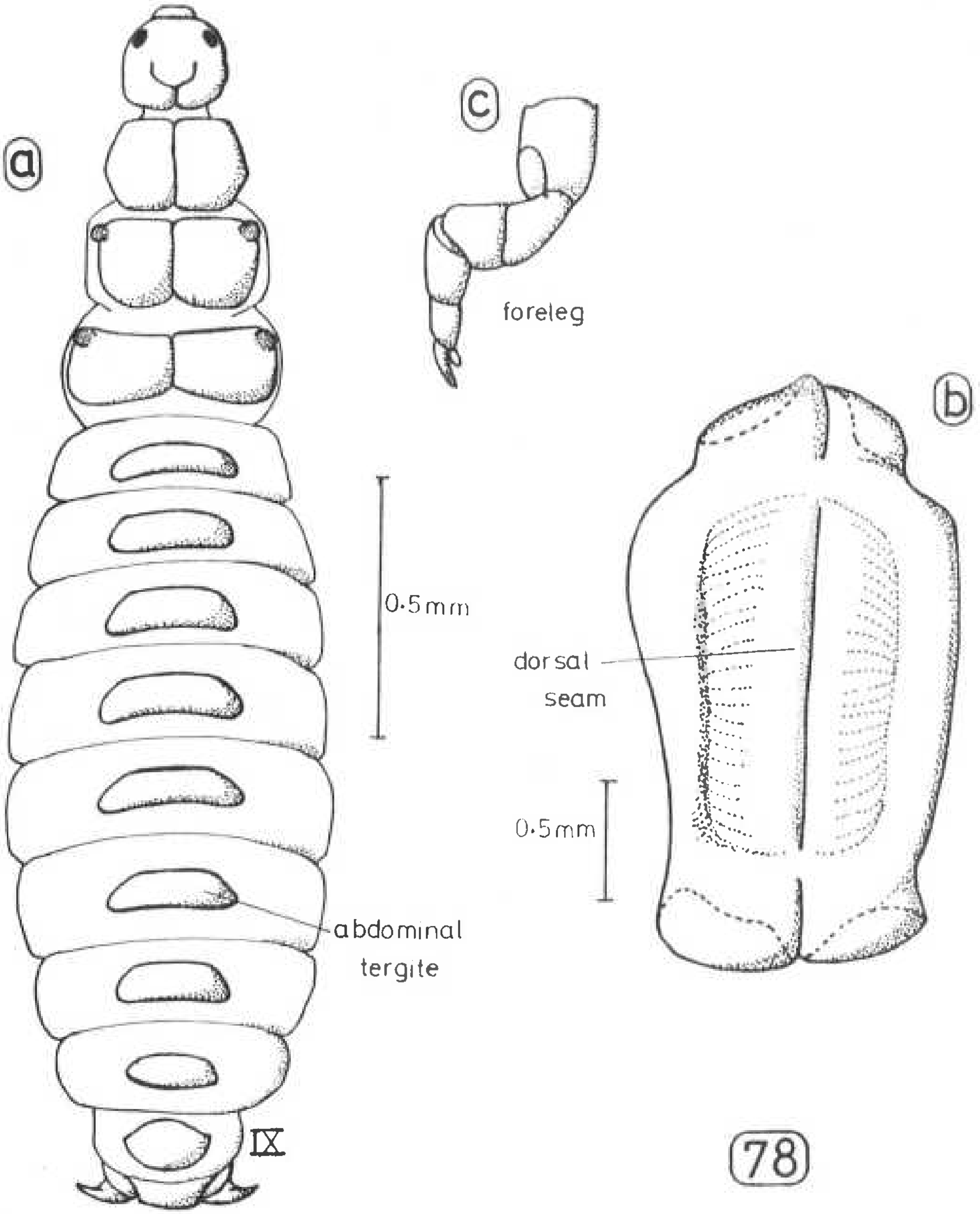
(USNM Collection)



77

Stactobia

(adapted from Vaillant, 1951b)

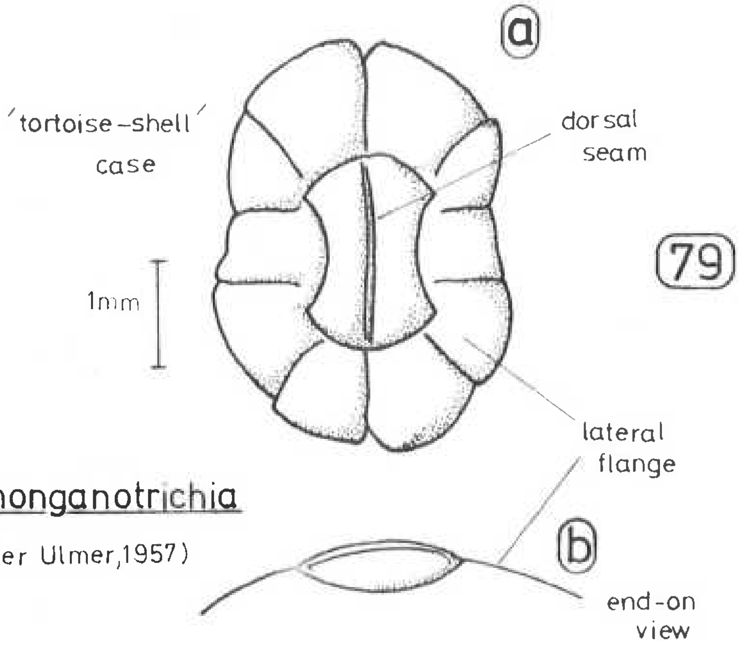


(78)

Plethus cruciatus Ulmer

(after Ulmer, 1957)

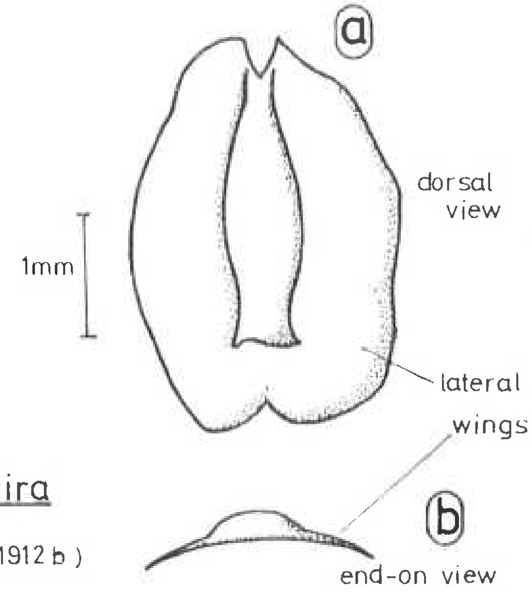
79



Lamonganotrichia

(after Ulmer, 1957)

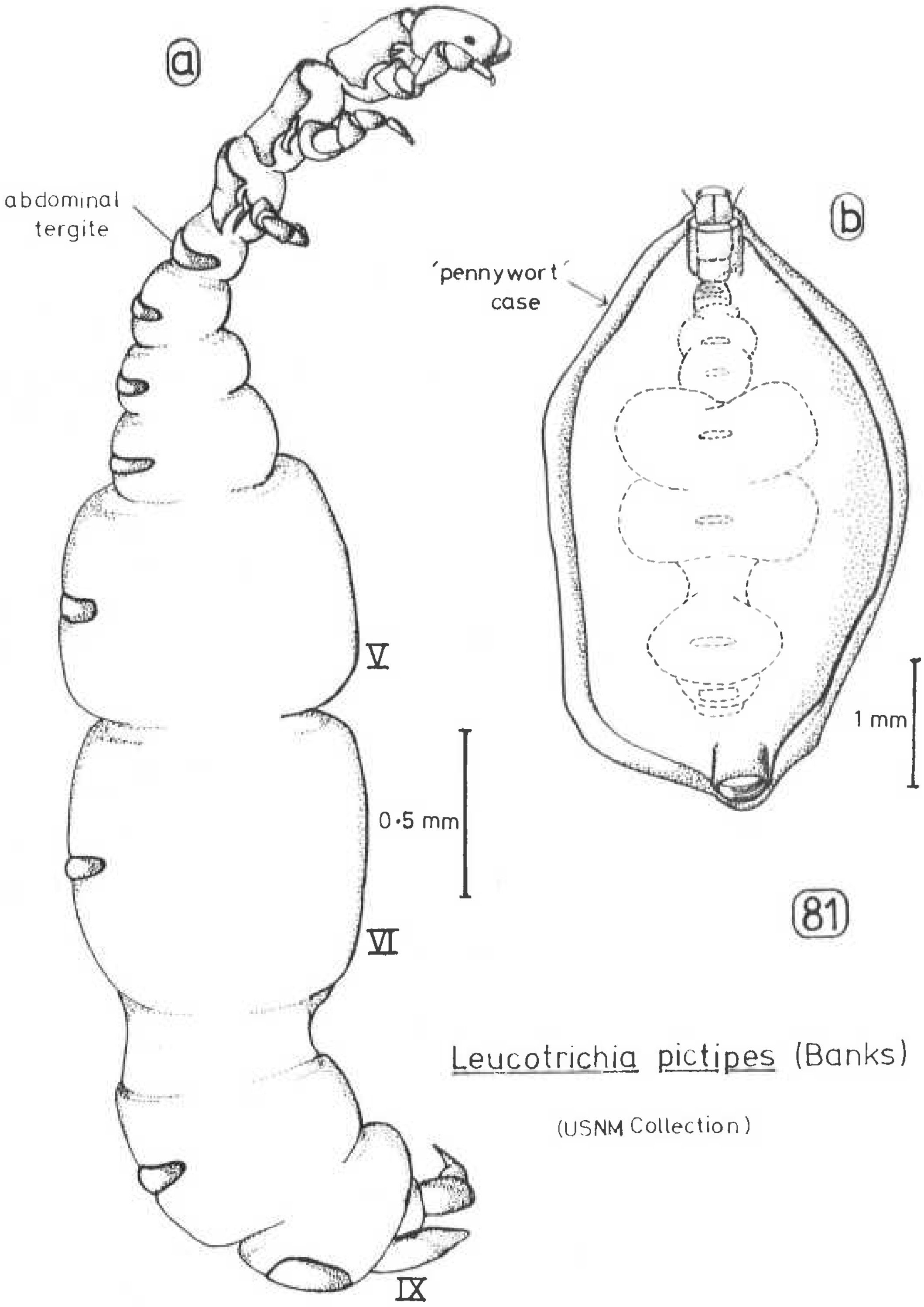
80



Catoxyethira

(after Ulmer, 1912 b)

Stactobiini - larval cases



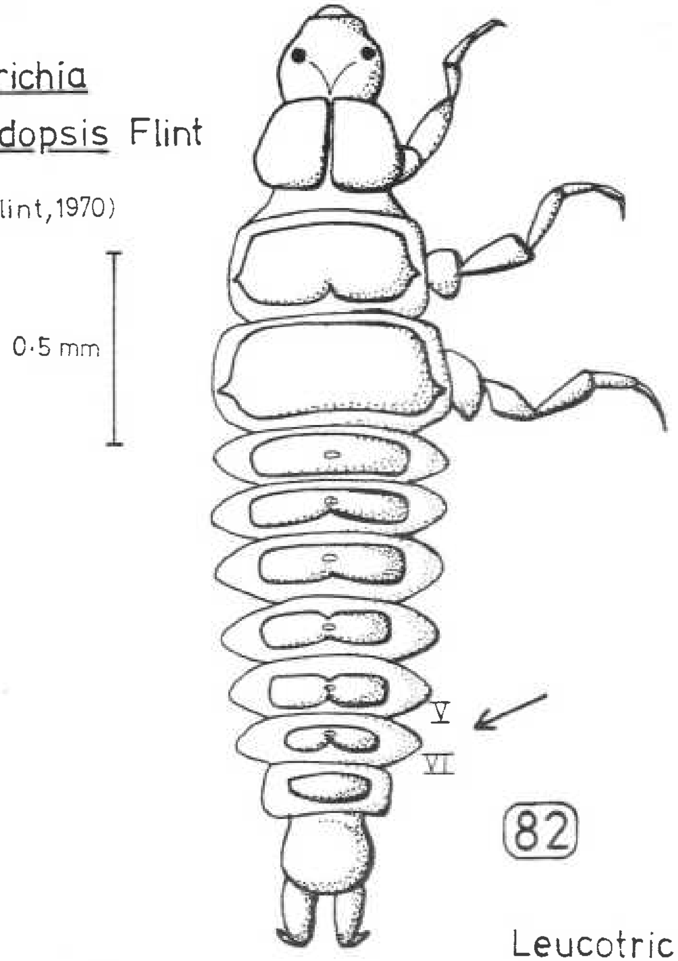
(81)

Leucotrichia pictipes (Banks)

(USNM Collection)

Alisotrichia
hirudopsis Flint

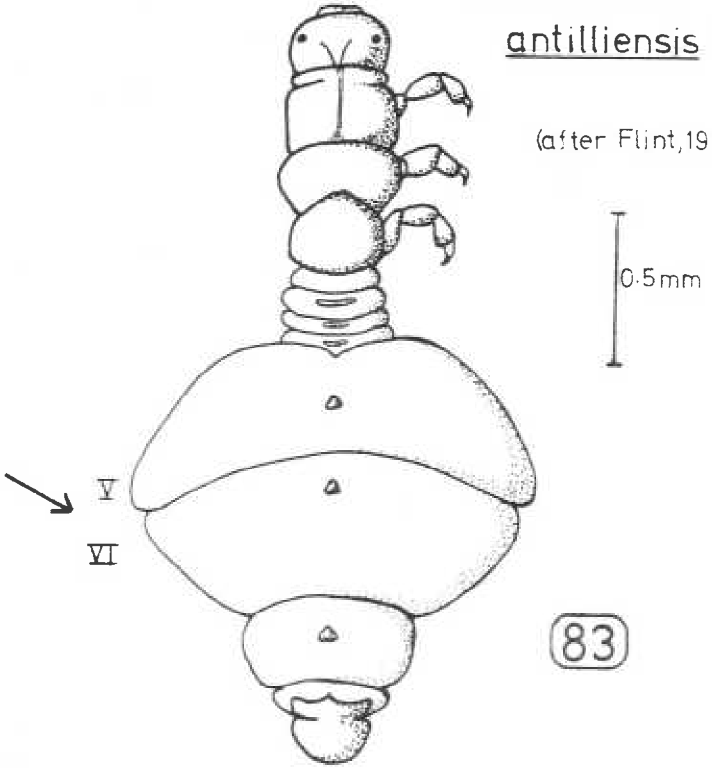
(after Flint, 1970)



82

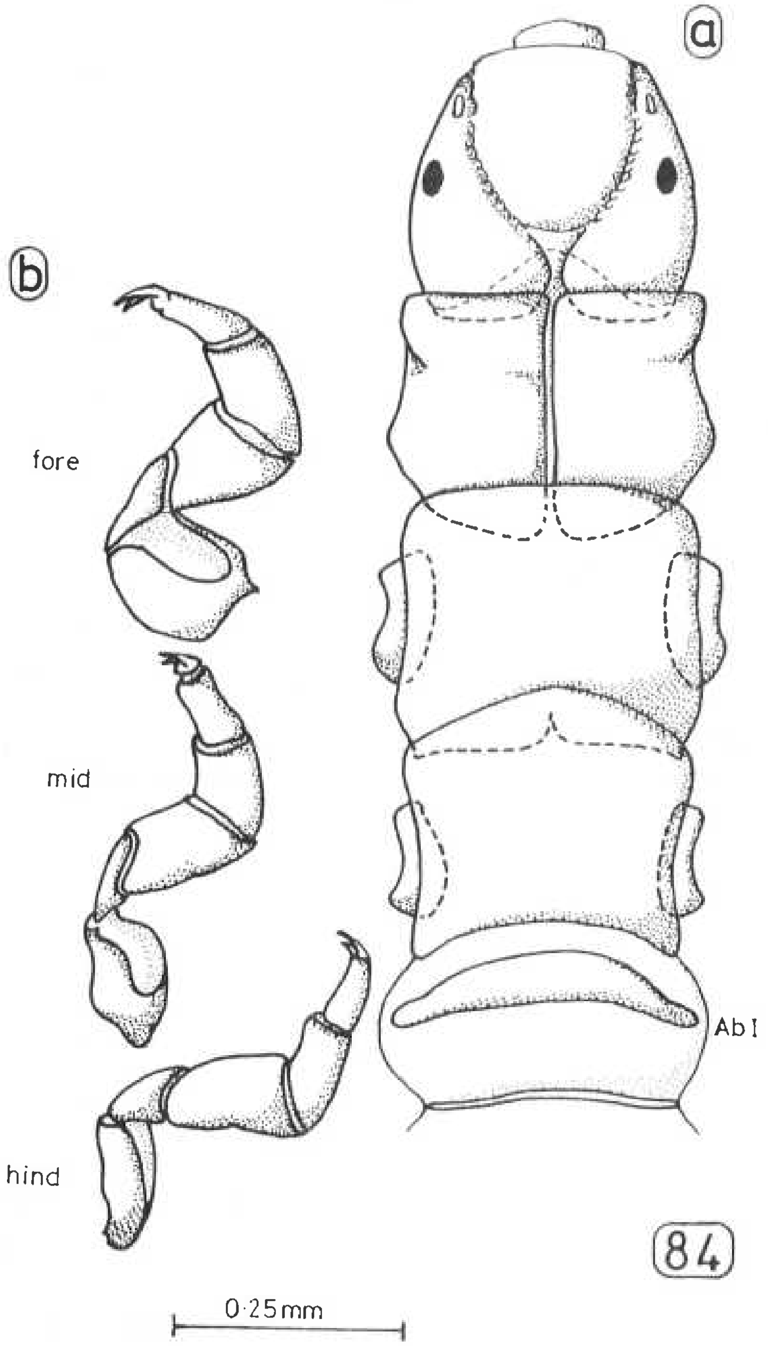
Zumatrichia
antilliensis Flint

(after Flint, 1970)



83

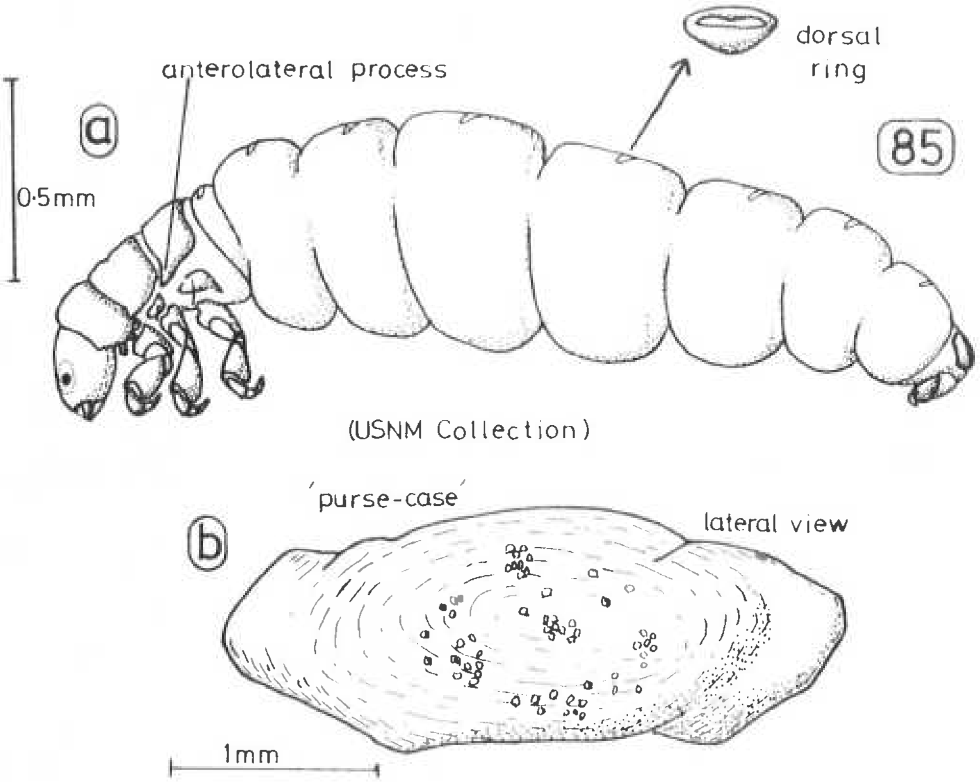
Leucotrichiini – larvae



84

Peltopsyche sieboldii Müller

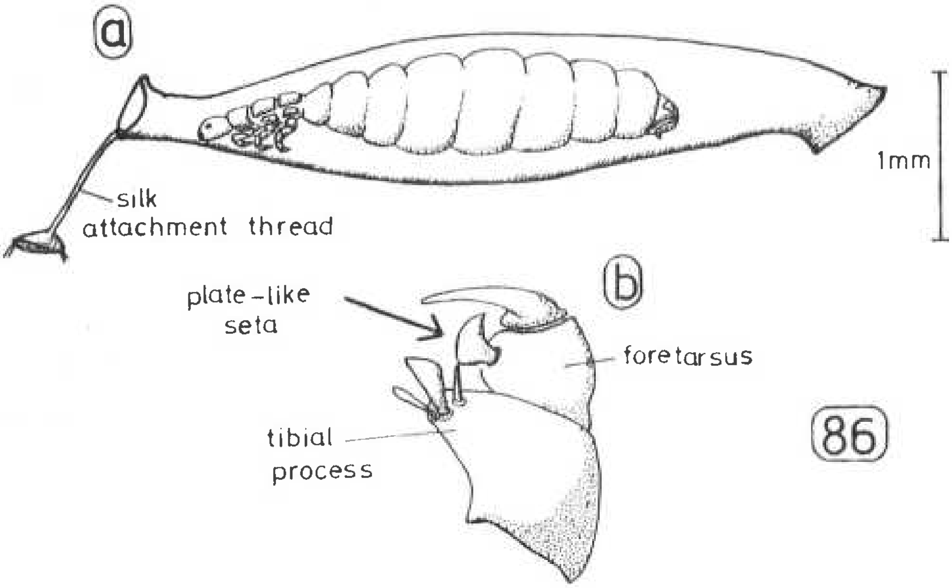
(BMNH Collection)



85

(USNM Collection)

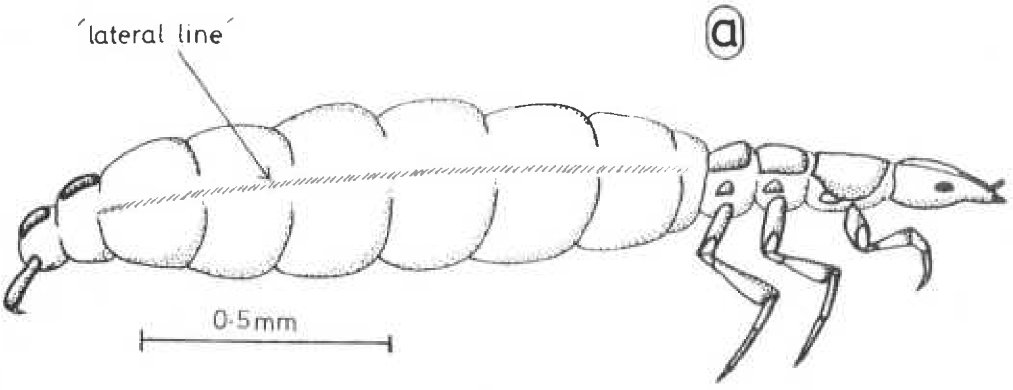
Ochrotrichia (*O.*) *juana* Flint

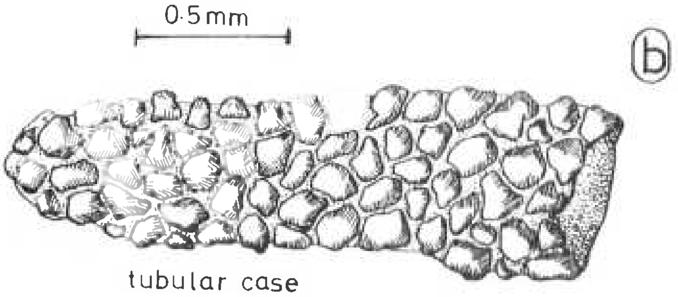


86

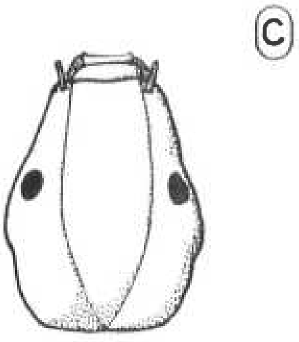
Rhyacopsyche mexicana (Flint)

(USNM Collection)





tubular case

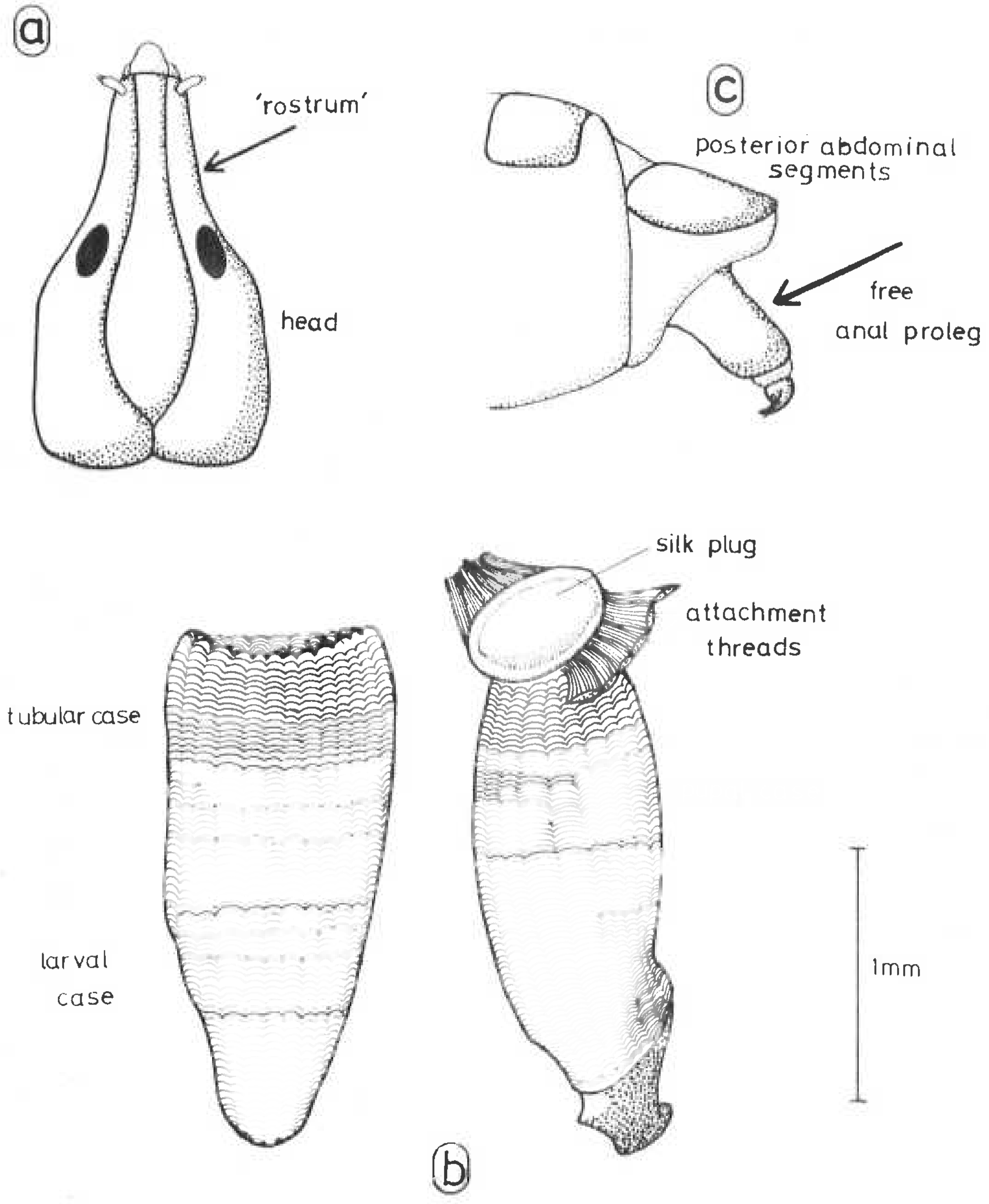


head

87

Neotrichia sp.

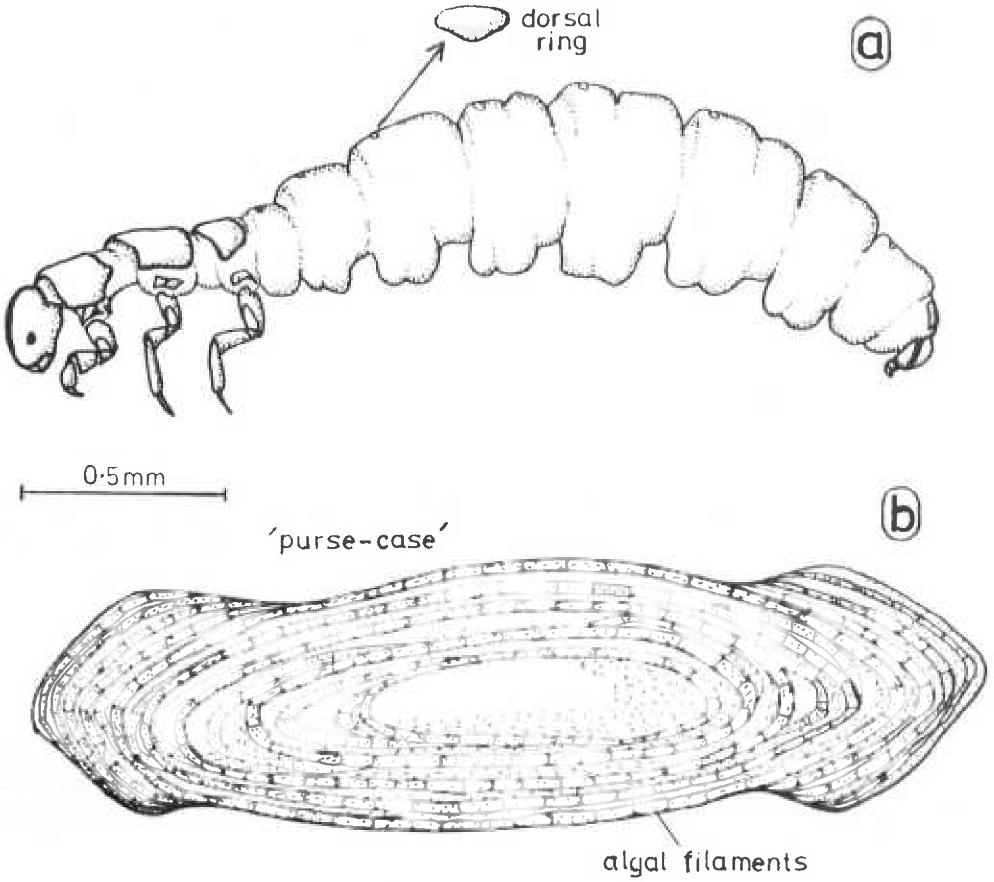
(USNM Collection)



88

Mayatrichia ayama Mosely

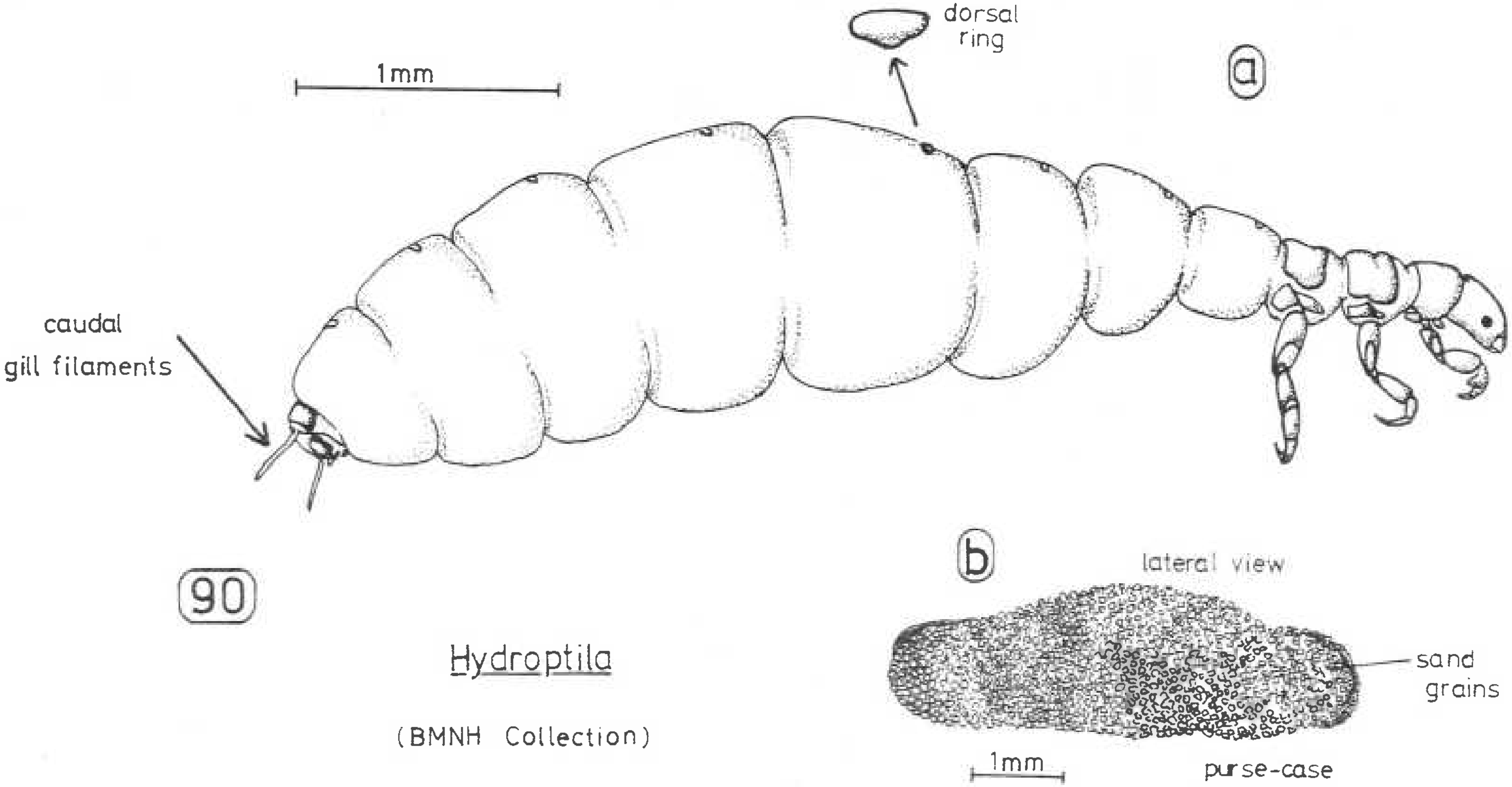
(USNM Collection)



89

Agraylea multipunctata Curtis

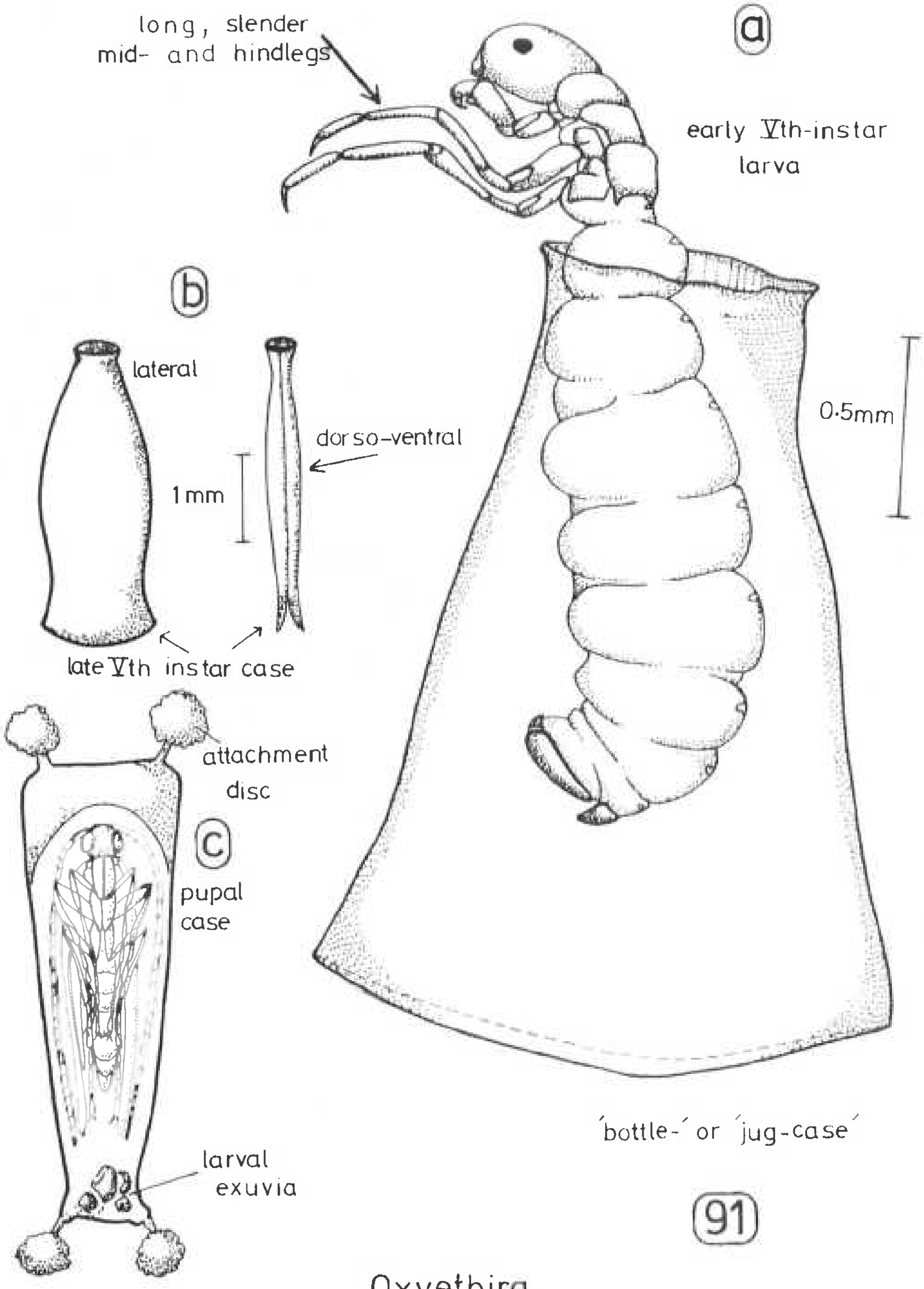
(BMNH Collection)



90

Hydroptila

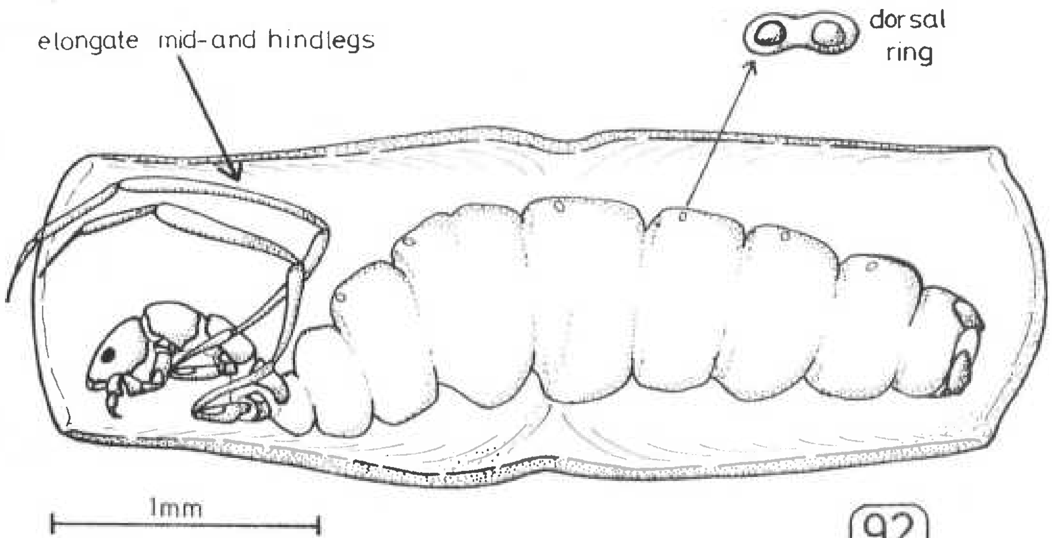
(BMNH Collection)



91

Oxyethira

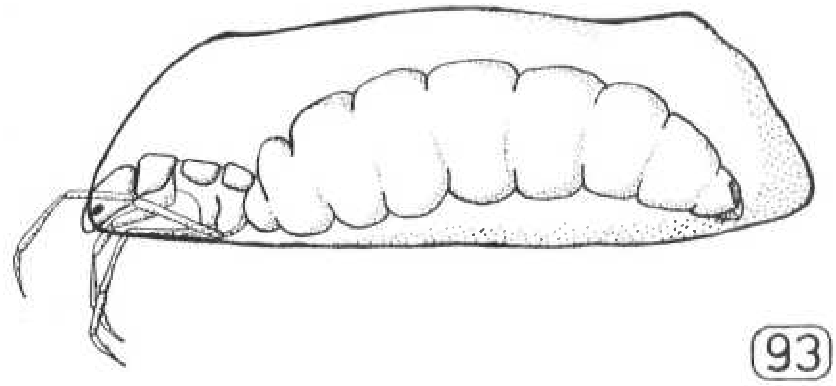
(BMNH Collection)



92

Tricholeiochiton fagesii (Guinard)

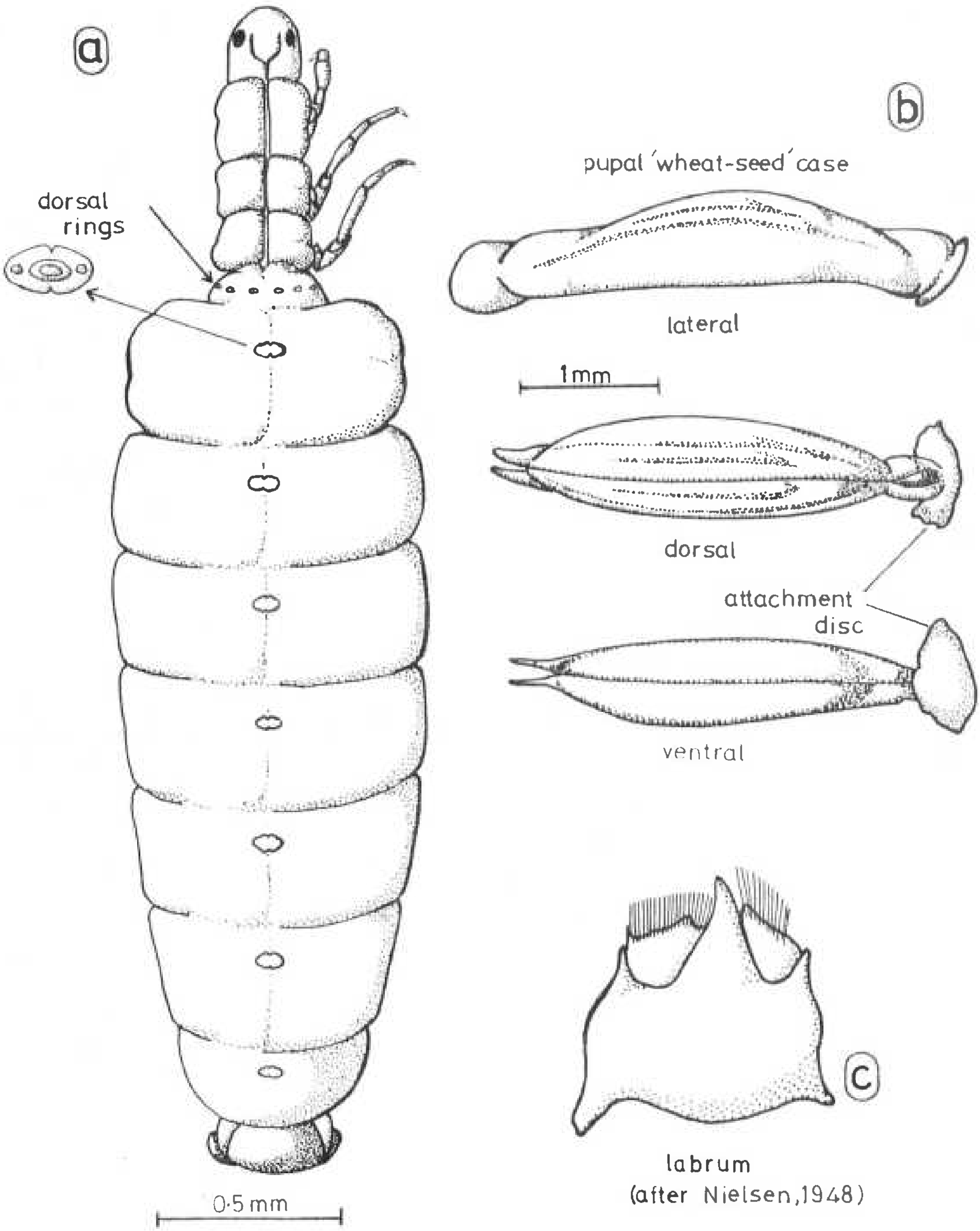
(Netherlands material,
BMNH Collection)



93

Paroxyethira

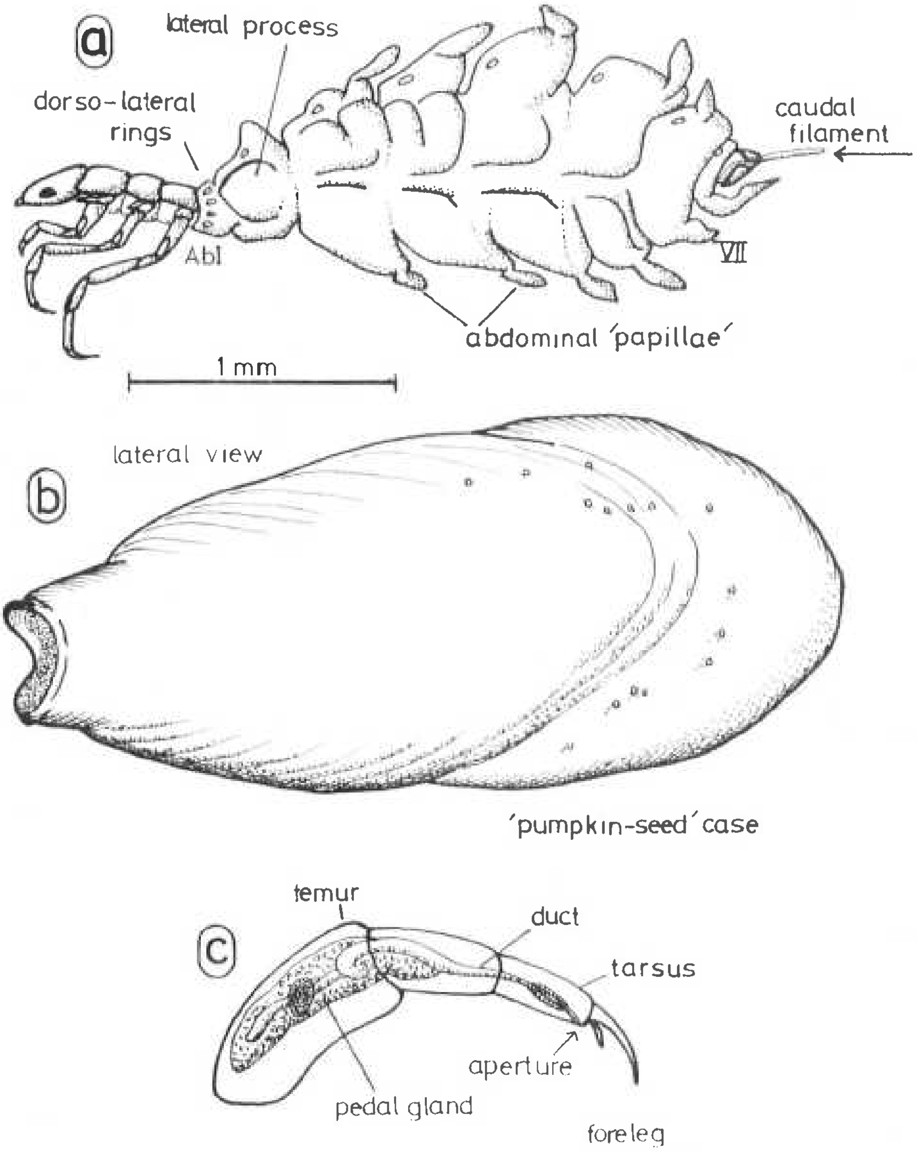
(after Leader, 1972)



94

Orthotrichia

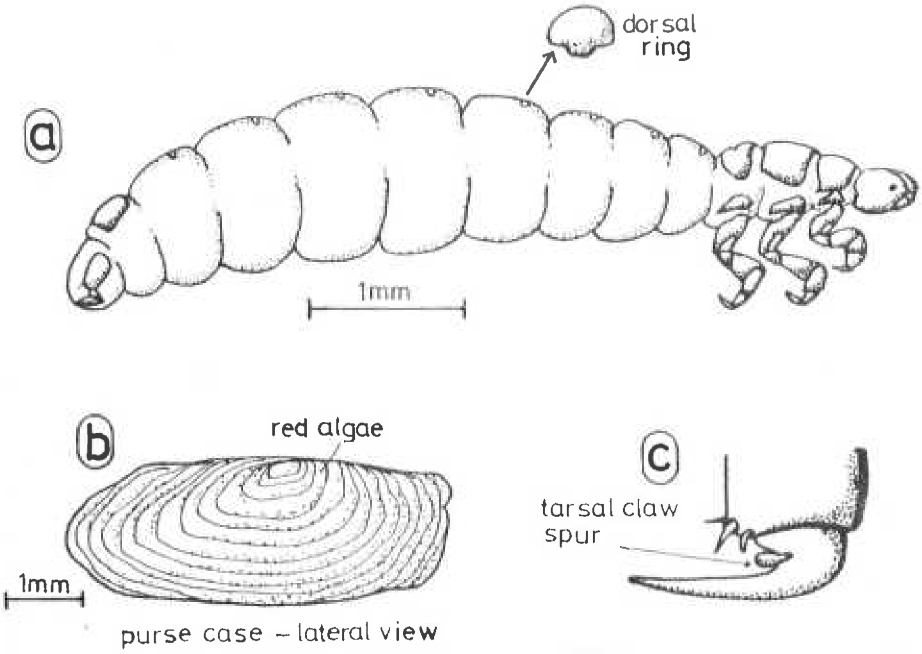
(BMNH Collection)



95

Ithytrichia lamellaris Eaton

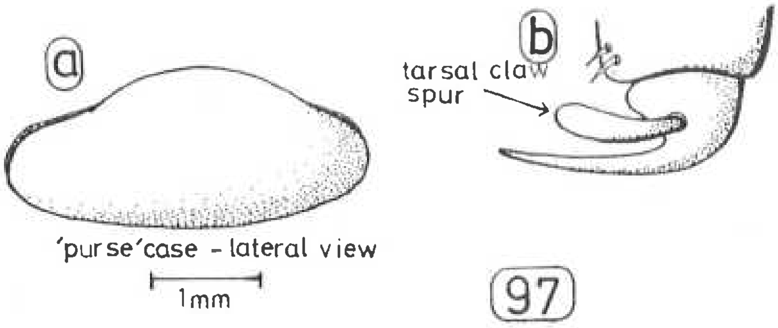
(BMNH Collection)



96

Dibusa

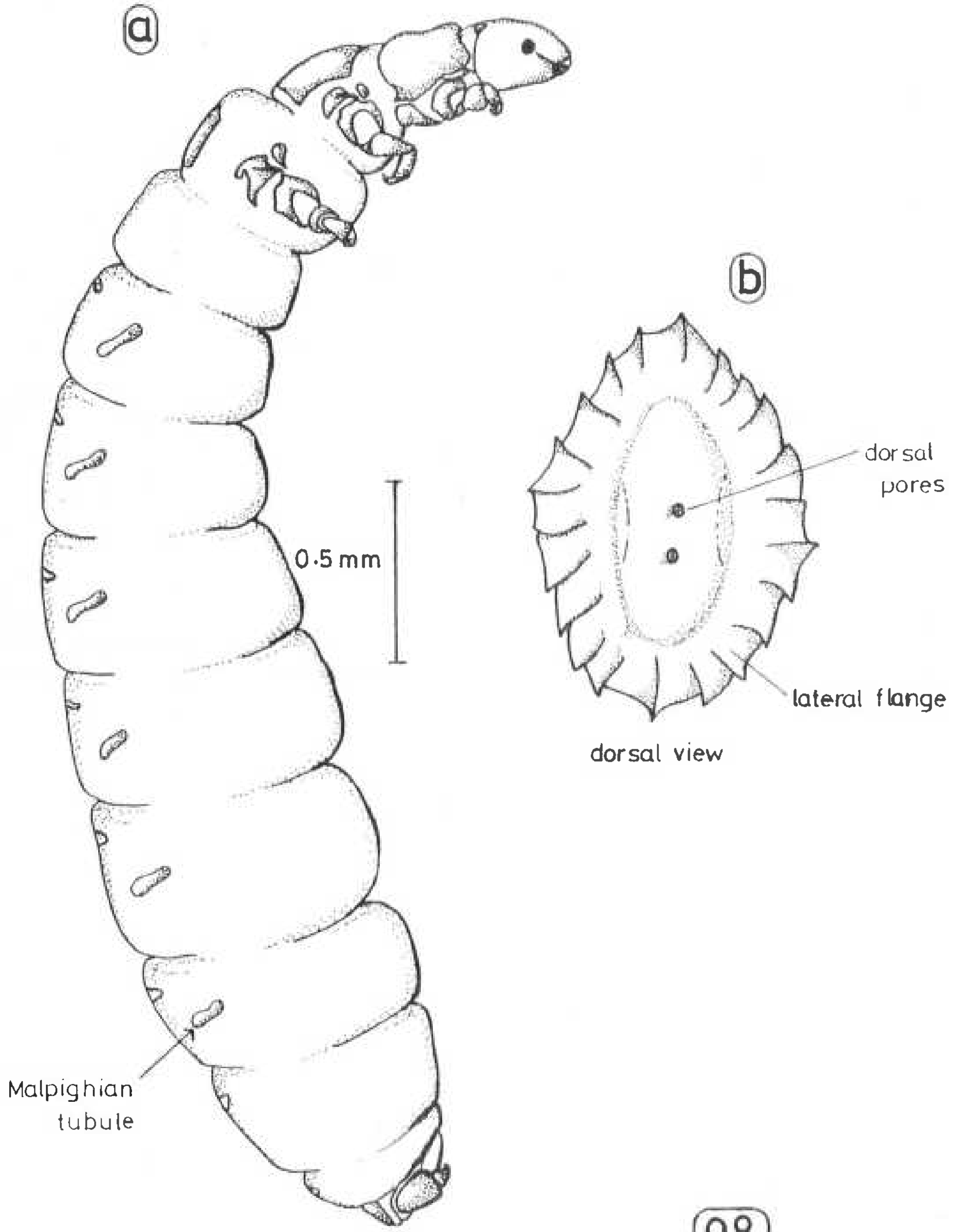
(USNM Collection)



97

Stactobiella

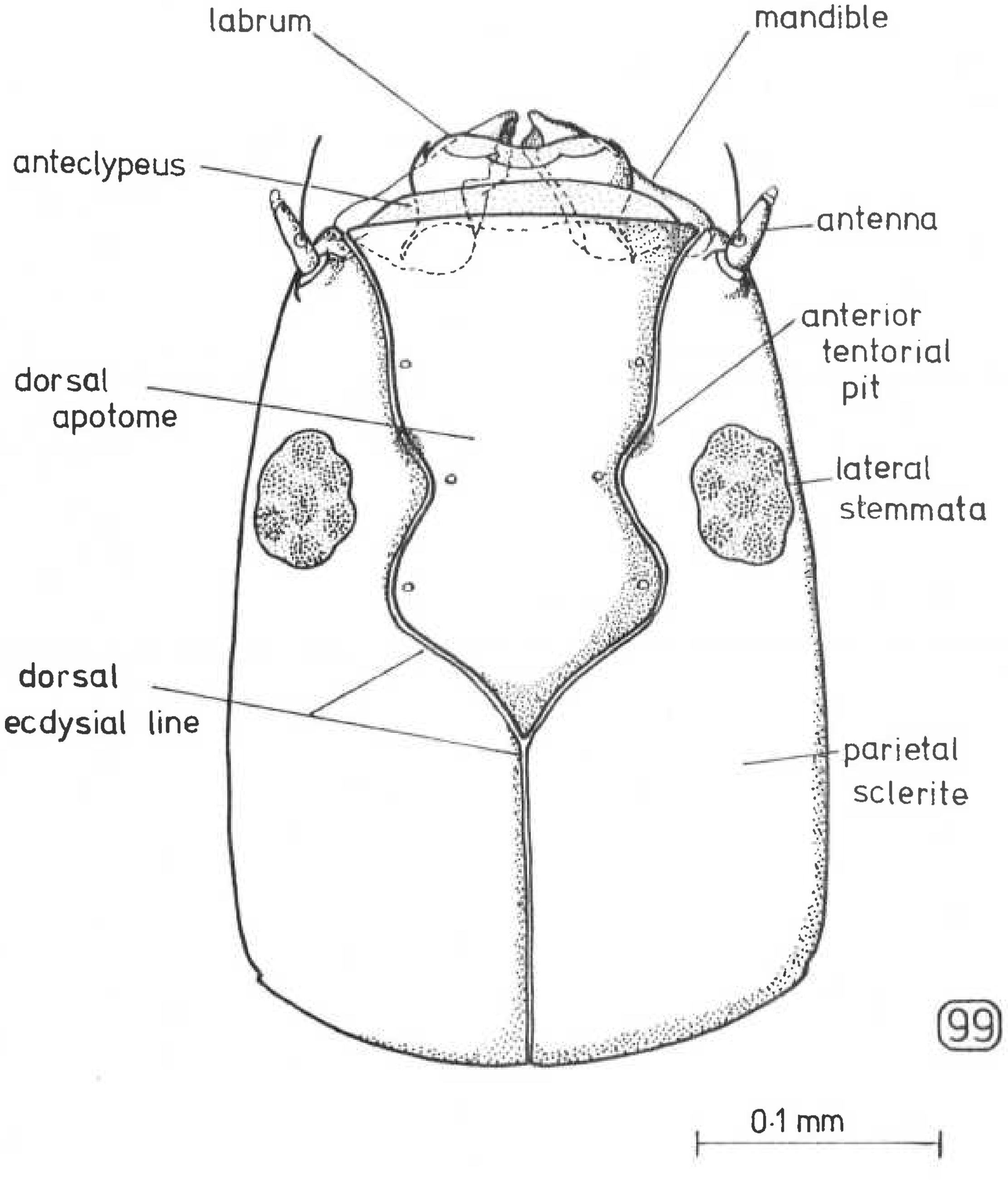
(USNM Collection)



98

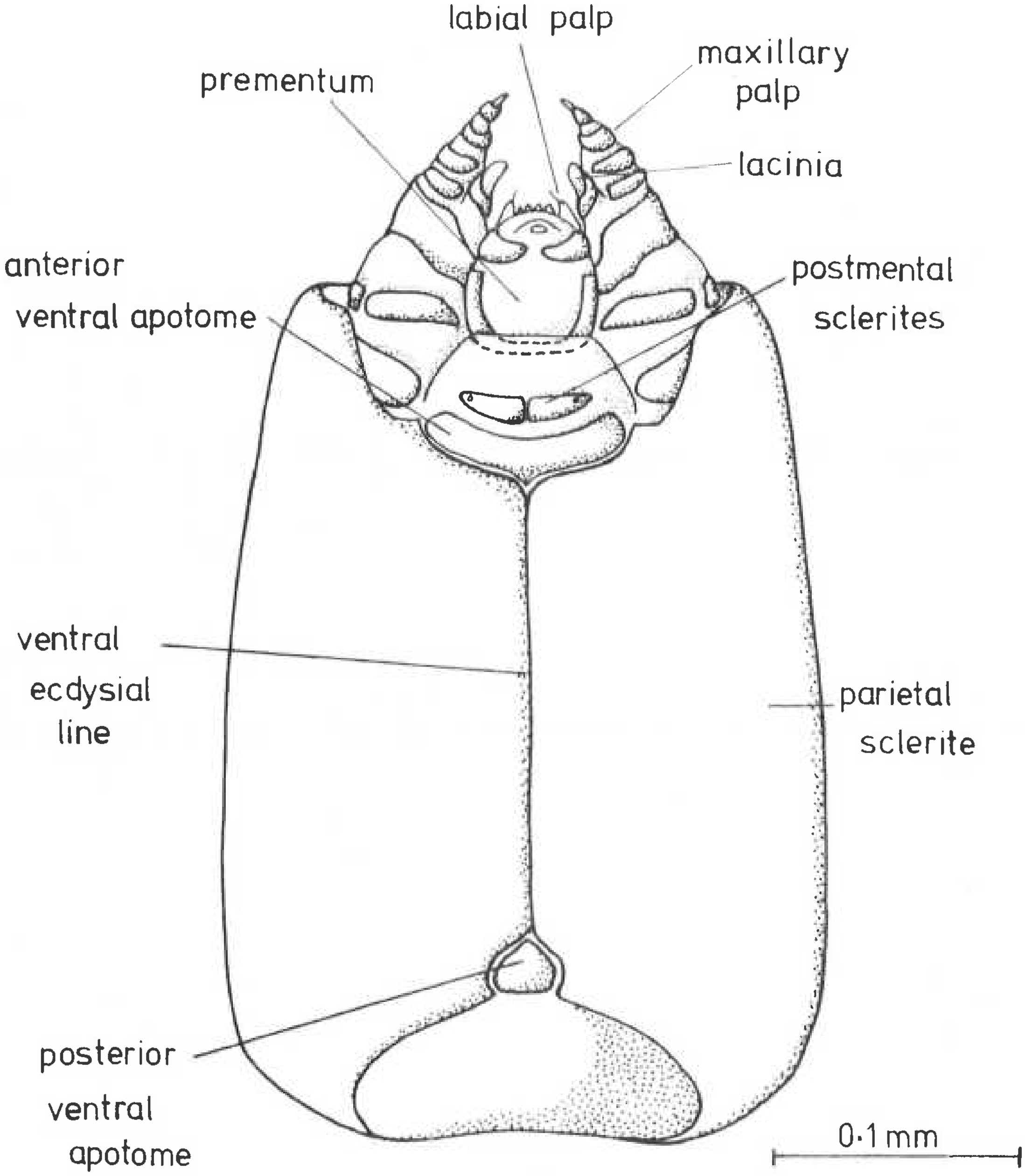
Caledonotrichia

(Ross Collection)



Generalized Head of a Hydroptilid Larva

Dorsal View

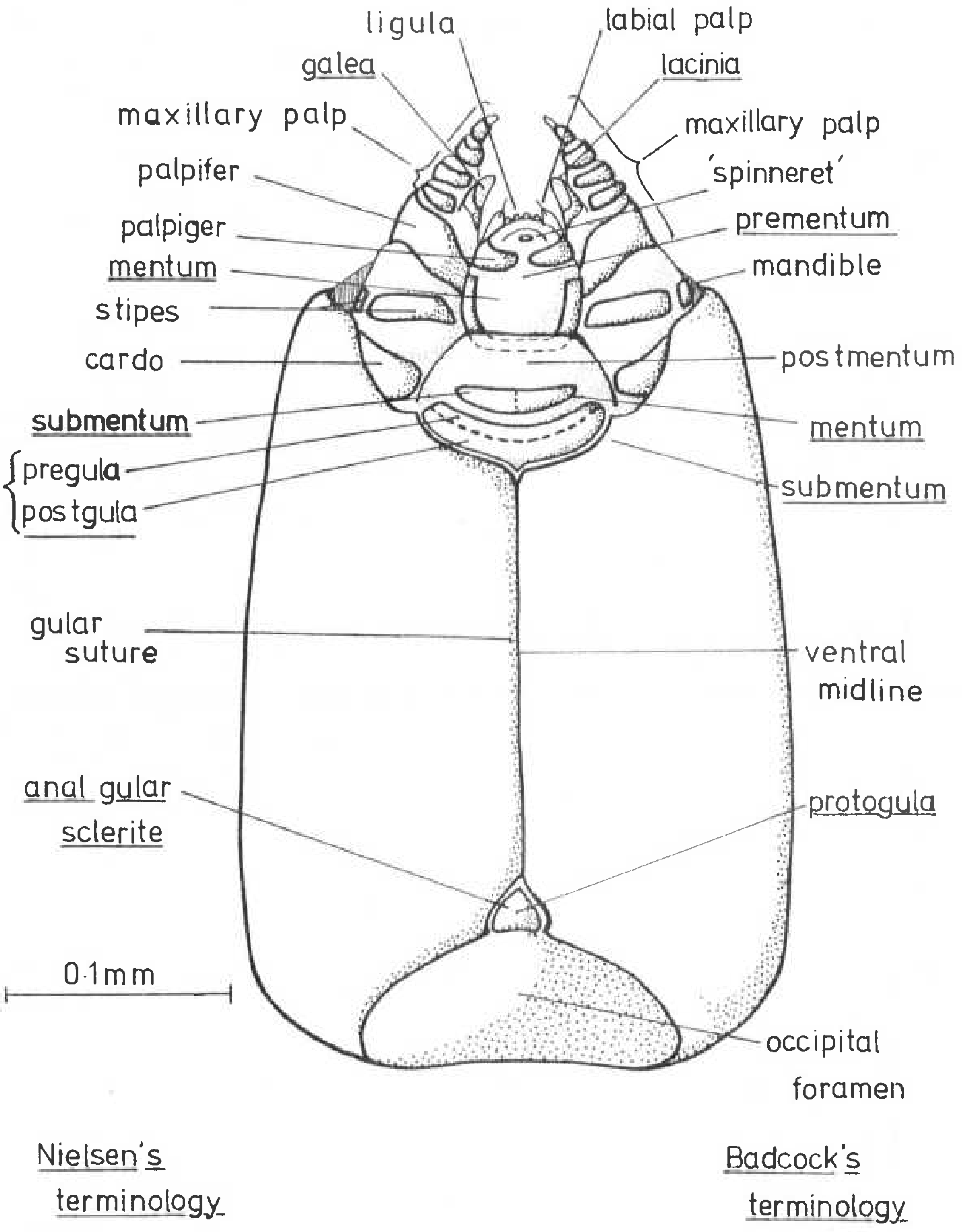


100

Generalized Head of a Hydroptilid Larva

Ventral View

Terminology based on Hinton (1963)

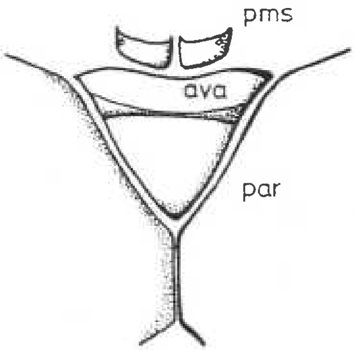


Generalized Head of a Hydroptilid Larva

Ventral View

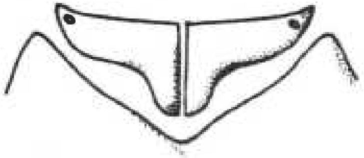
Comparison of the Terminologies of Nielsen (1948) and Badcock (1961)

102



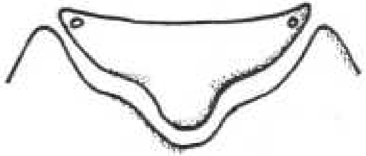
Palaeagapetus

103



Agraylea sexmaculata

104

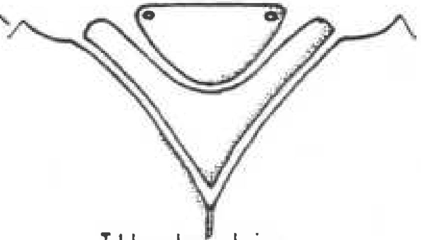


Agraylea multipunctata

105

Tricholeiochiton

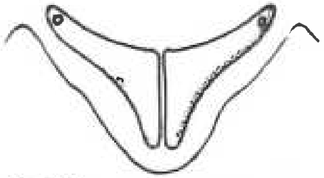
106



Ithytrichia

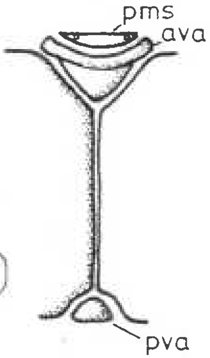
107

Stactobia



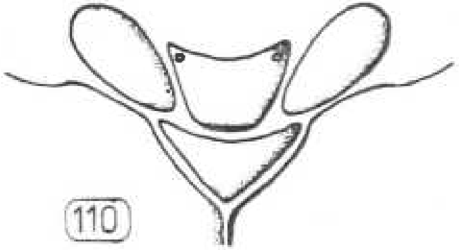
108

Hydroptila



109

Oxyethira

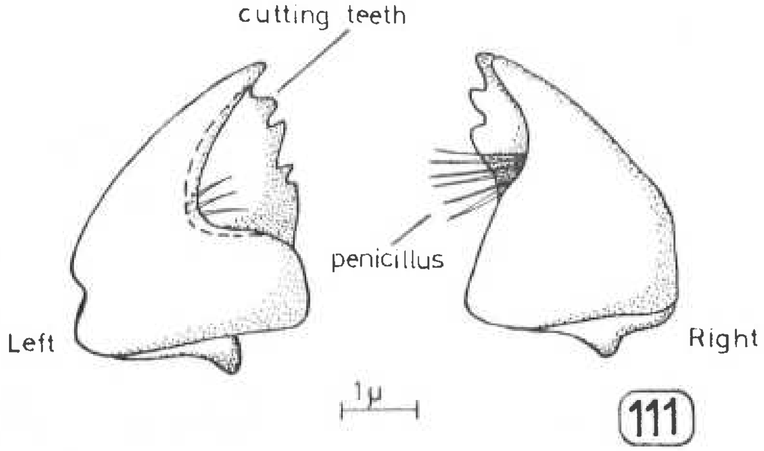


110

Orthotrichia

Ventral Apotomes and Postmental Sclerites

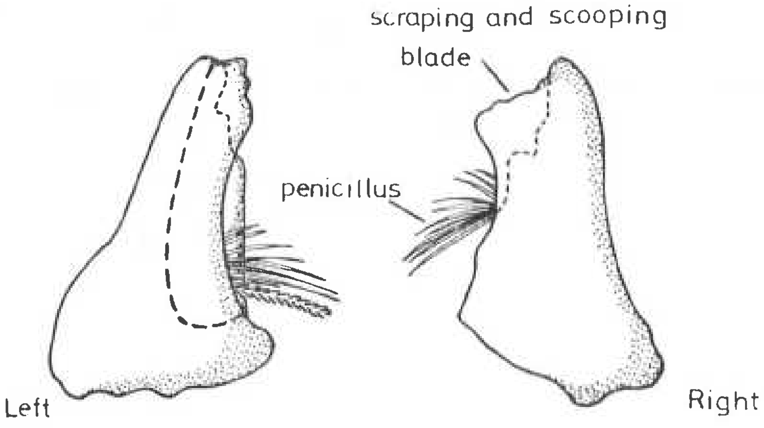
ava, pva. anterior and posterior ventral apotomes; par. parietal sclerites, pms. postmental sclerites



111

Palaeagapetus celsus Ross

After Flint (1962)

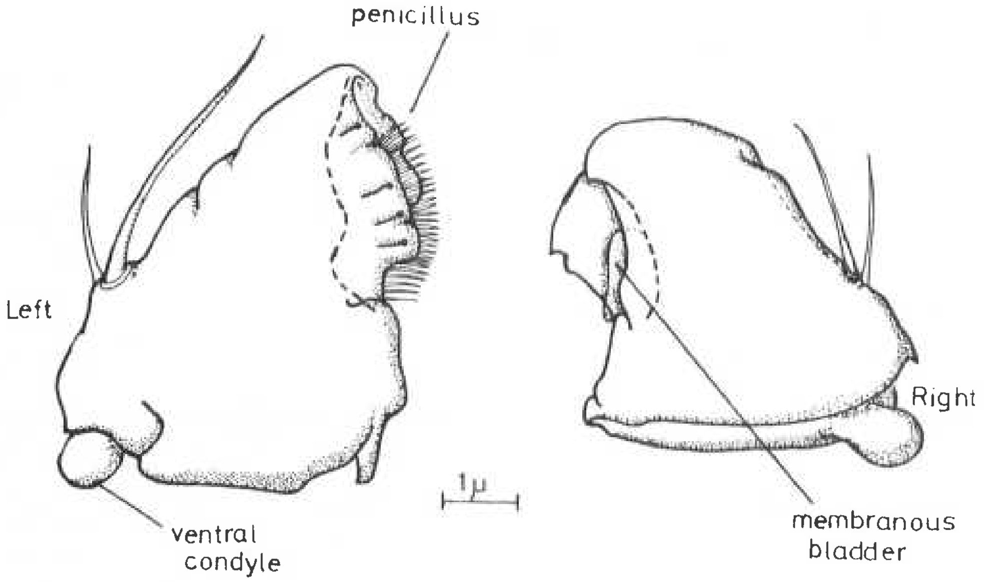


112

Stactobia caspersi Ulmer

After Botosaneanu (1956)

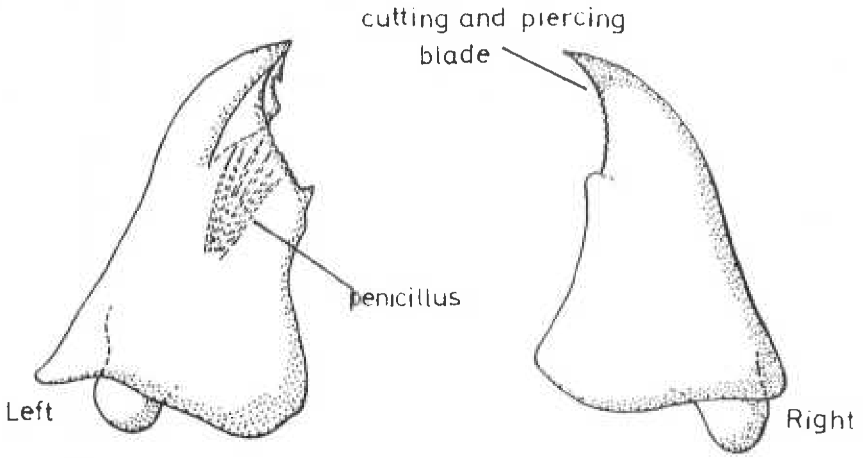
Larval Mandibles – dorsal view



Hydroptila occulta (Eaton)

(BMNH Collection)

(113)

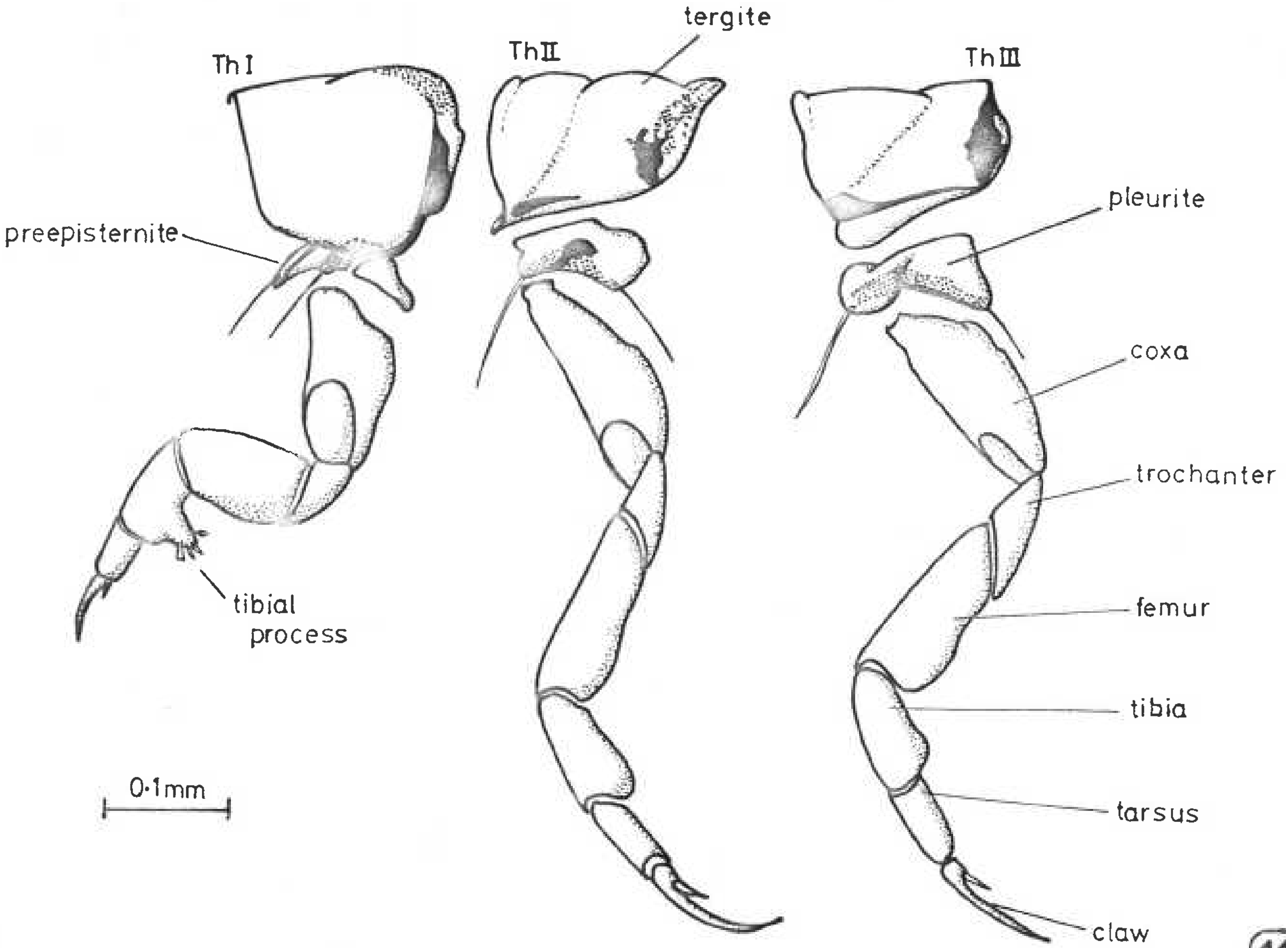


Orthotrichia costalis (Curtis)

After Nielsen (1948)

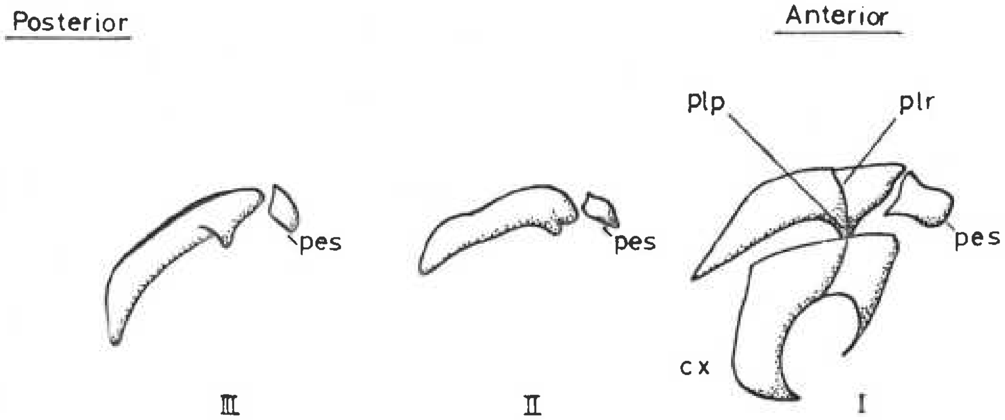
(114)

Larval Mandibles - dorsal view



115

Thorax and Legs, *Hydroptila* sp., lateral view



Palaeagapetus

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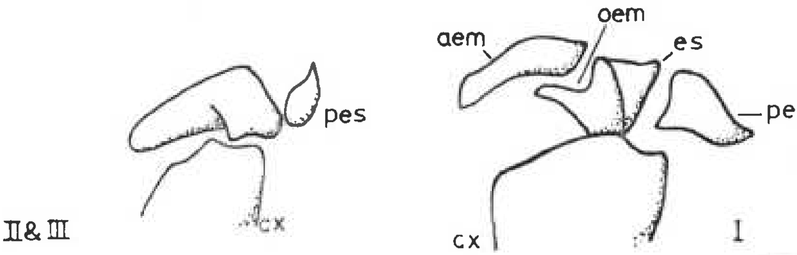
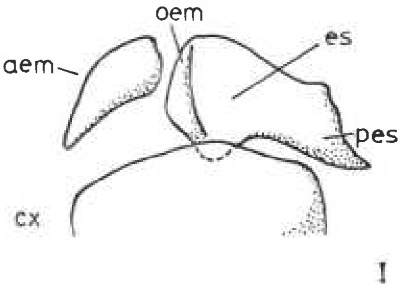


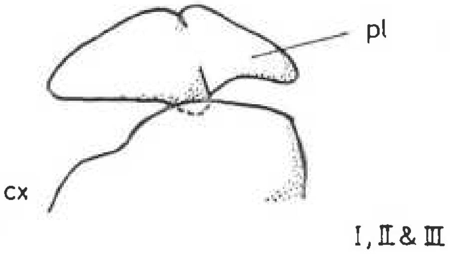
Agraylea

117



Oxyethira

118



Dibusa

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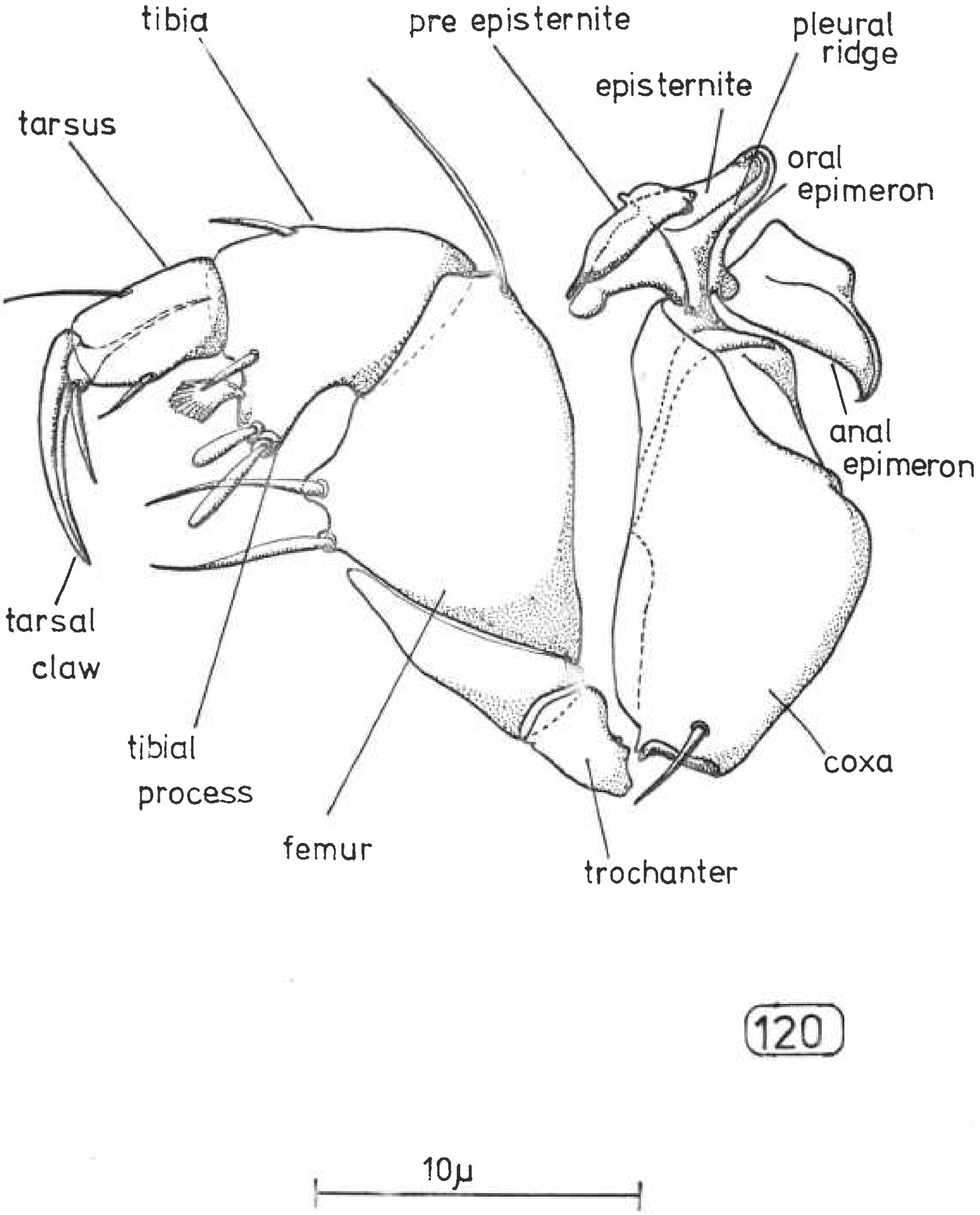
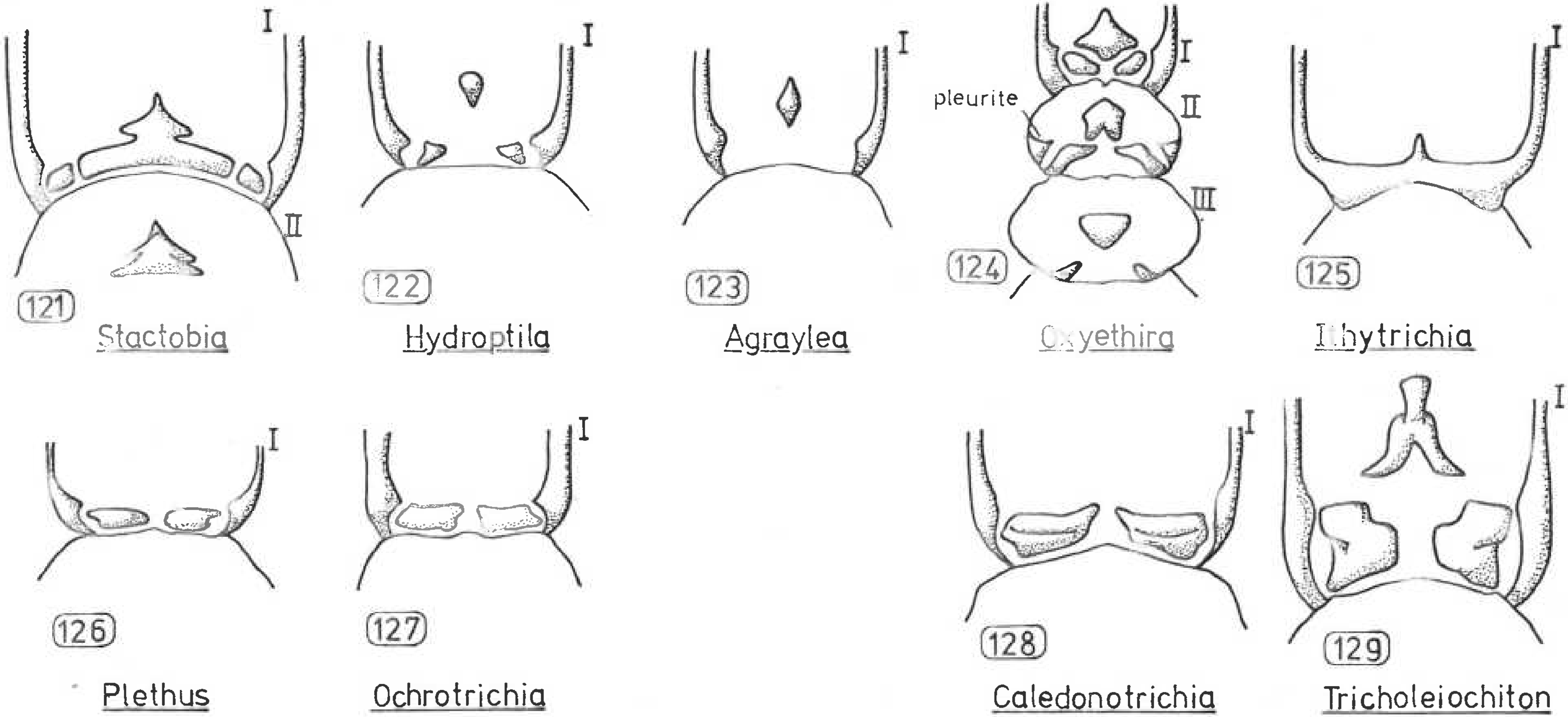
Thoracic Pleurites, Hydroptilid larvae, lateral views

aem, anal epimeron; cx, coxa; es, episternite; oem, oral epimeron; pl, pleurite; plp, pleural process; plr, pleural ridge; pes, preepisternite.

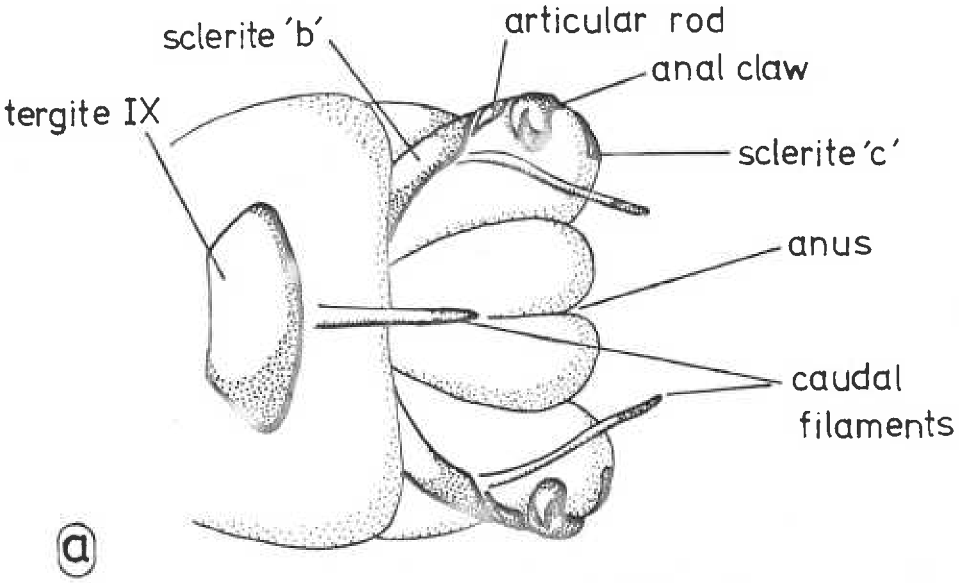


120

Foreleg and Pleurites, Hydroptila sp. larva

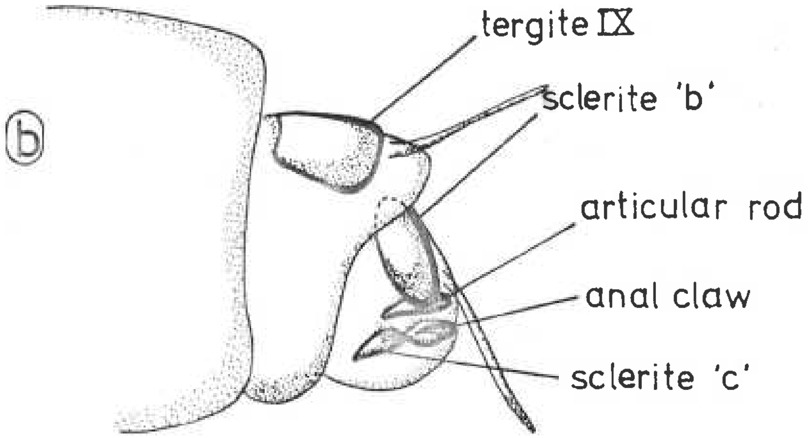


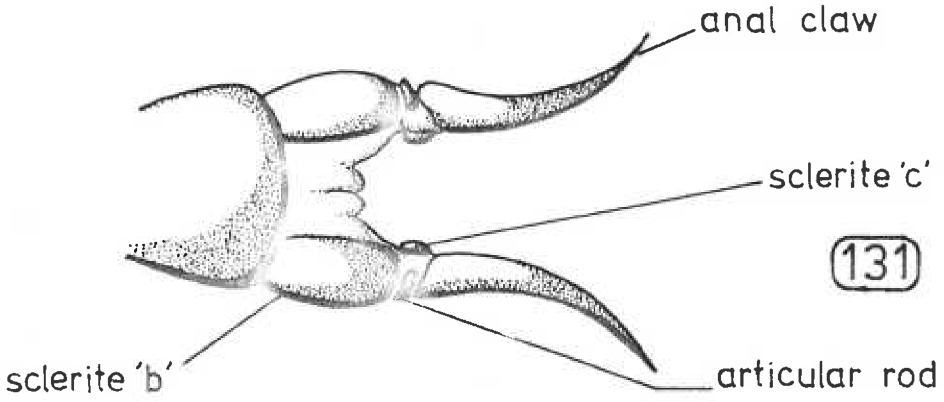
Thoracic sternites, Hydroptilid larvae, ventral views



Vth-instar, a. dorsal b. lateral

130

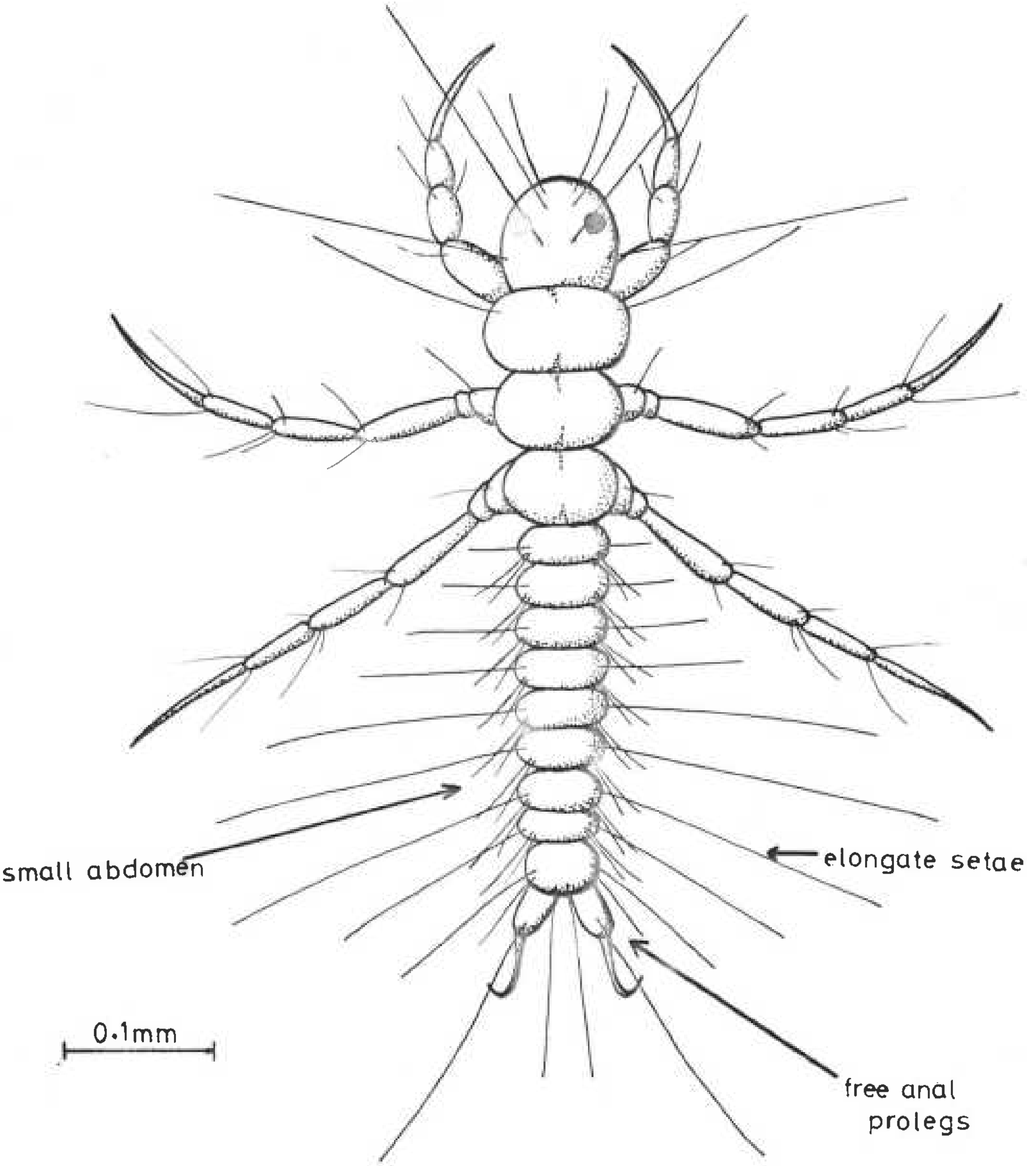




131

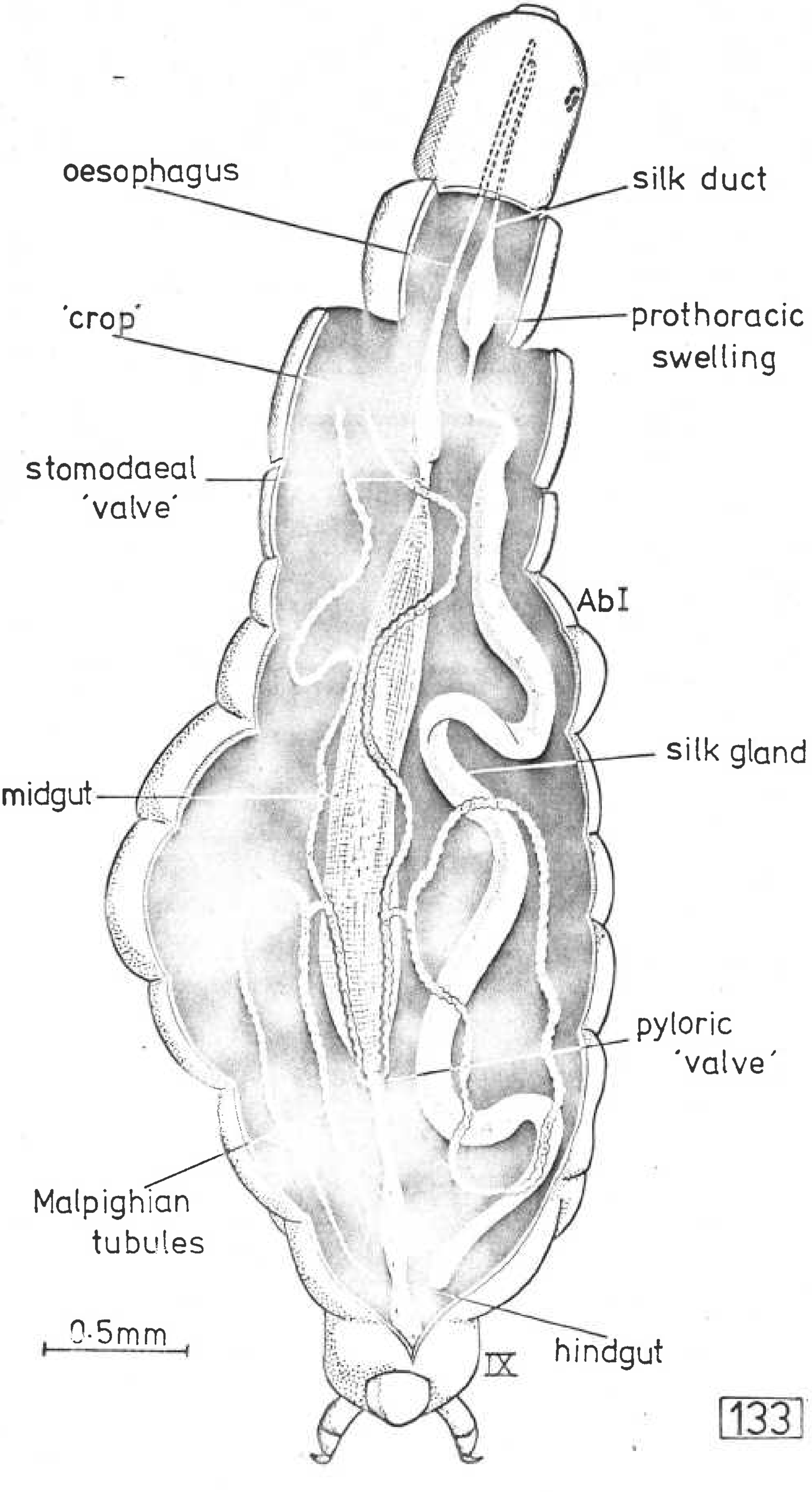
Early instar, dorsal view

Anal prolegs, generalized Early and Vth-instar Hydroptilid larvae [after Nielsen (1948)]

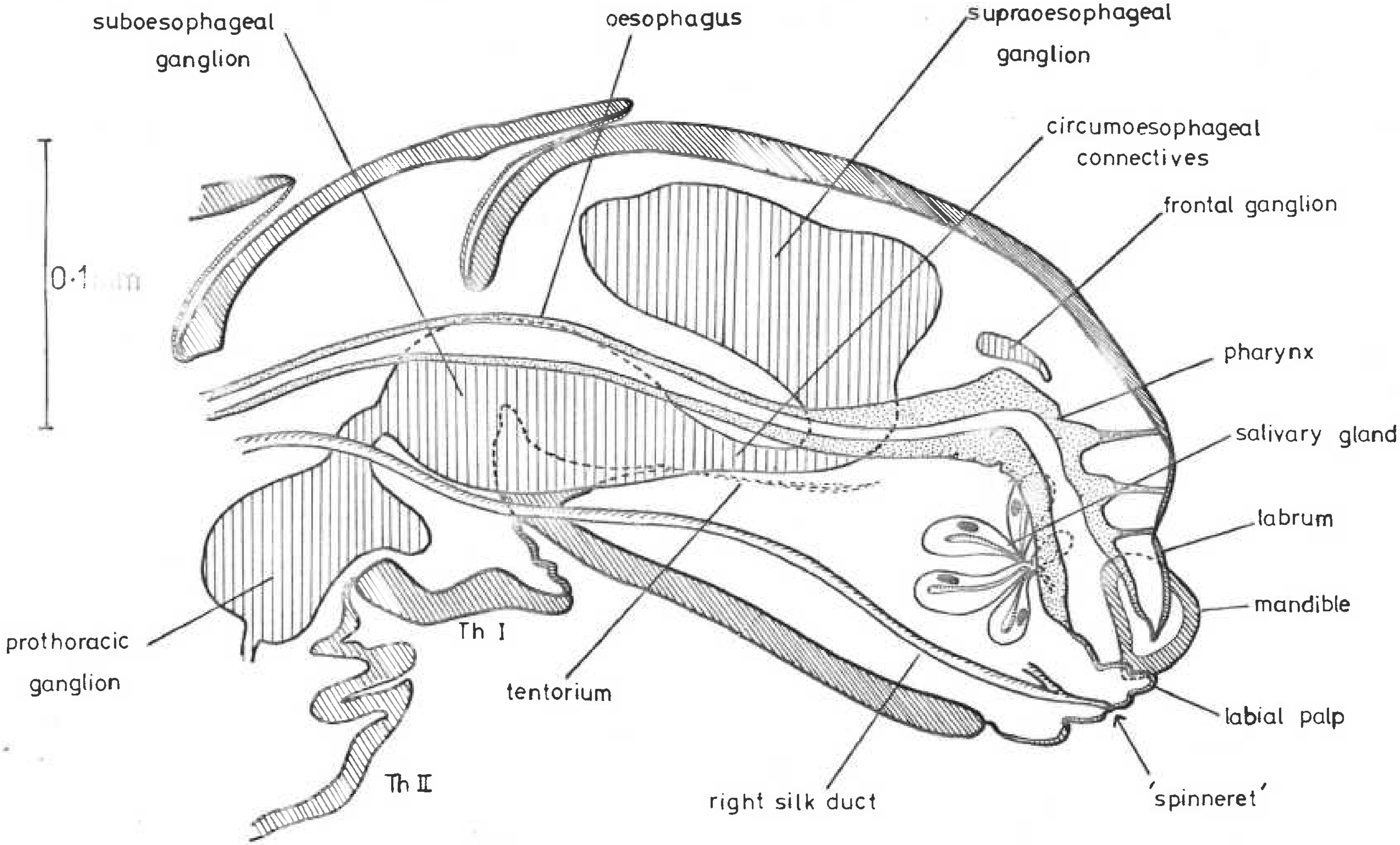


Generalized Early Instar Hydroptilid Larva, dorsal

Adapted from Nielsen (1948)



Larval internal anatomy - Agraylea sp.



134

Internal anatomy-Head and prothorax-Larval Hydroptilid
Hydroptila sp.

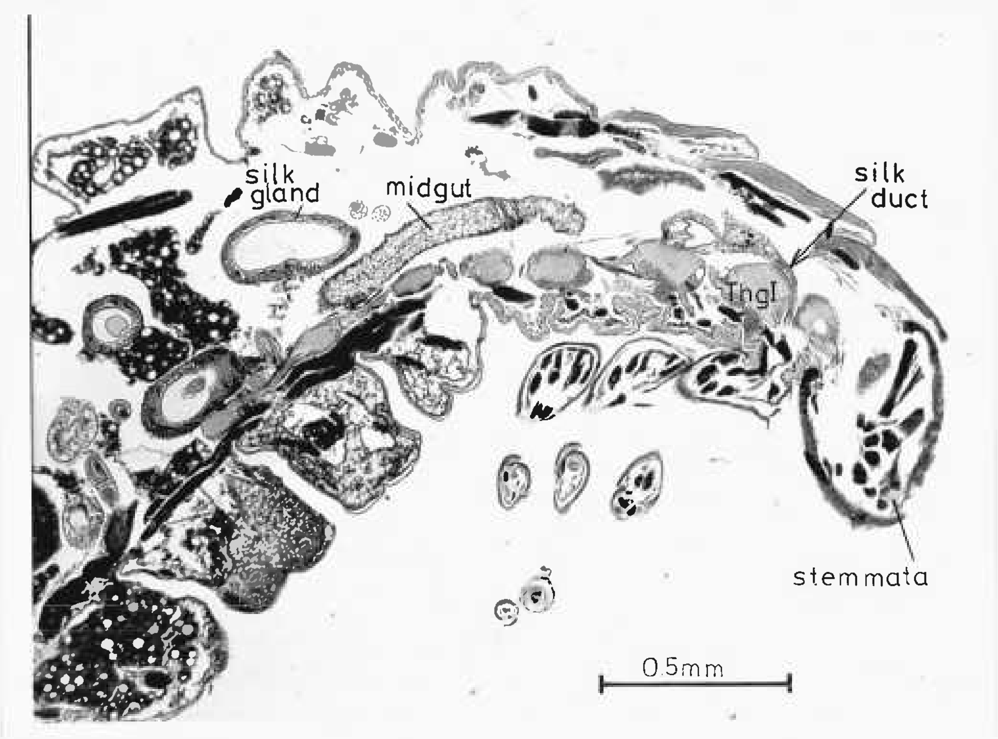


Fig. 135. Larval internal anatomy.

L.S. head and anterior segments, *Hydroptila* sp.

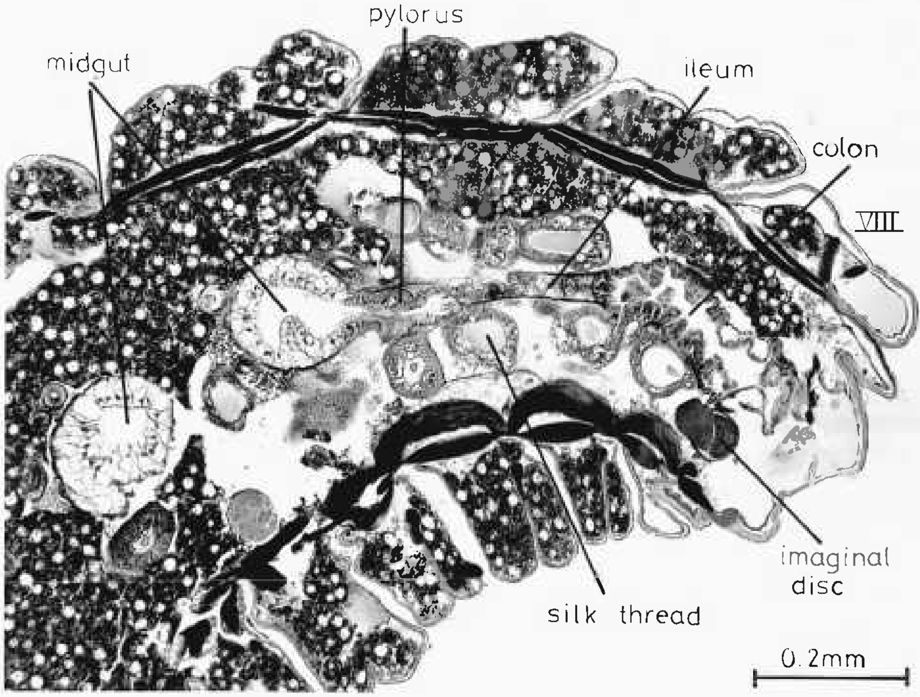
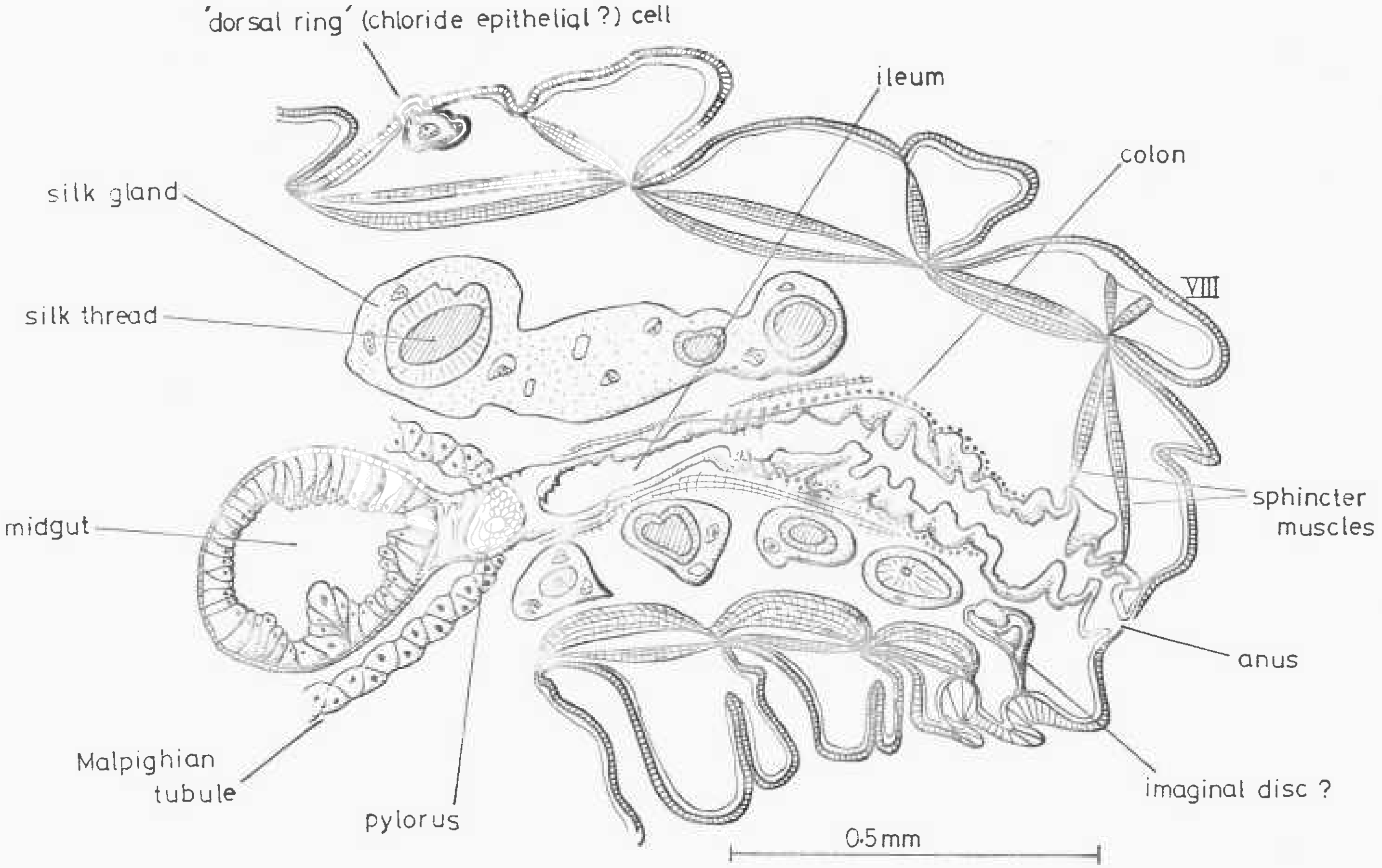


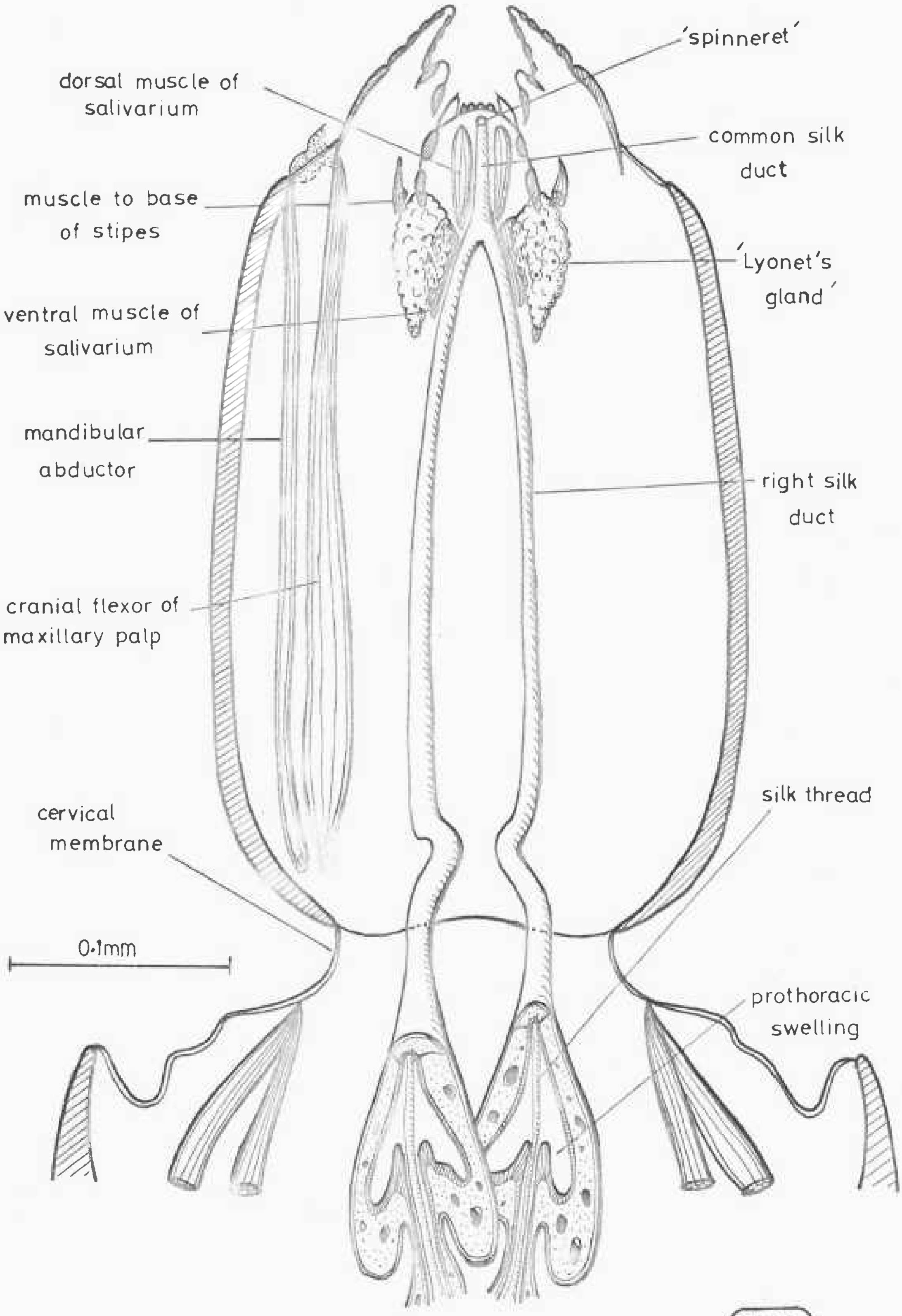
Fig. 136. Larval internal anatomy.
L.S. posterior abdominal segments, mid- and hind-gut, *Hydroptila* sp.



137

Larval internal anatomy - Hind gut

(L.S. posterior abdominal segments)



138

Larval labial silk ducts

(H.S. head)

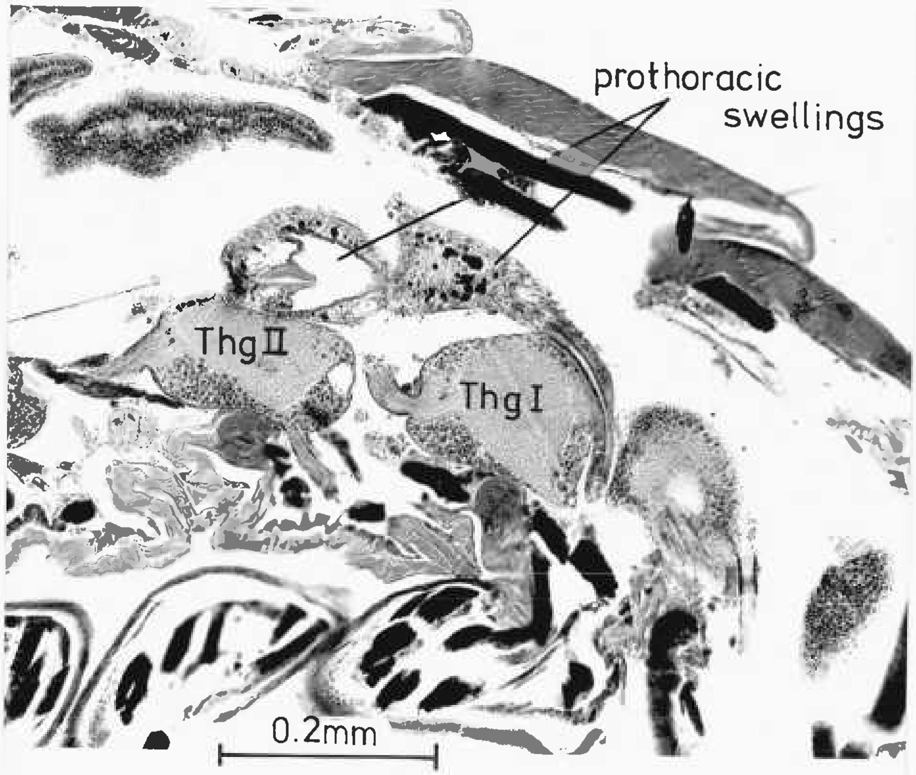


Fig. 139. Prothoracic swellings of labial silk glands. L.S. prothorax, Hydroptila sp. larva. (Thg, thoracic ganglion).

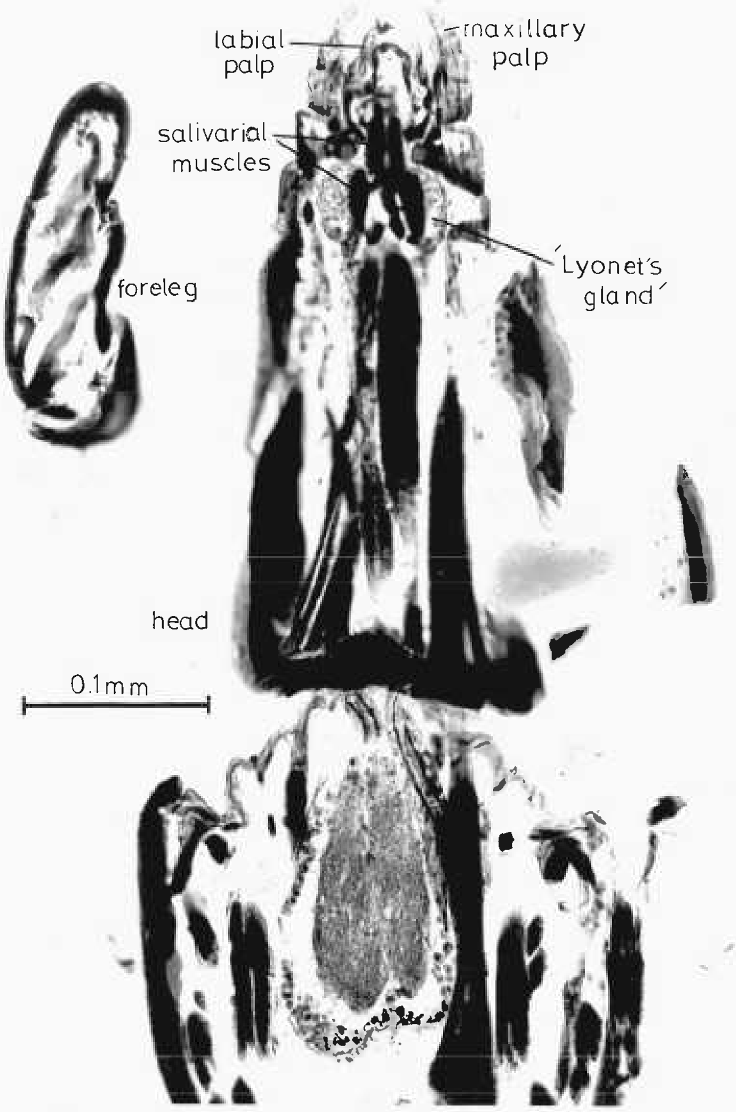


Fig. 140. 'Lyonet's glands'.

H.S. head, *Hydroptila* sp. larva.

Fig. 141. Labial silk press.

H.S. head, *Hydroptila* sp. larva.

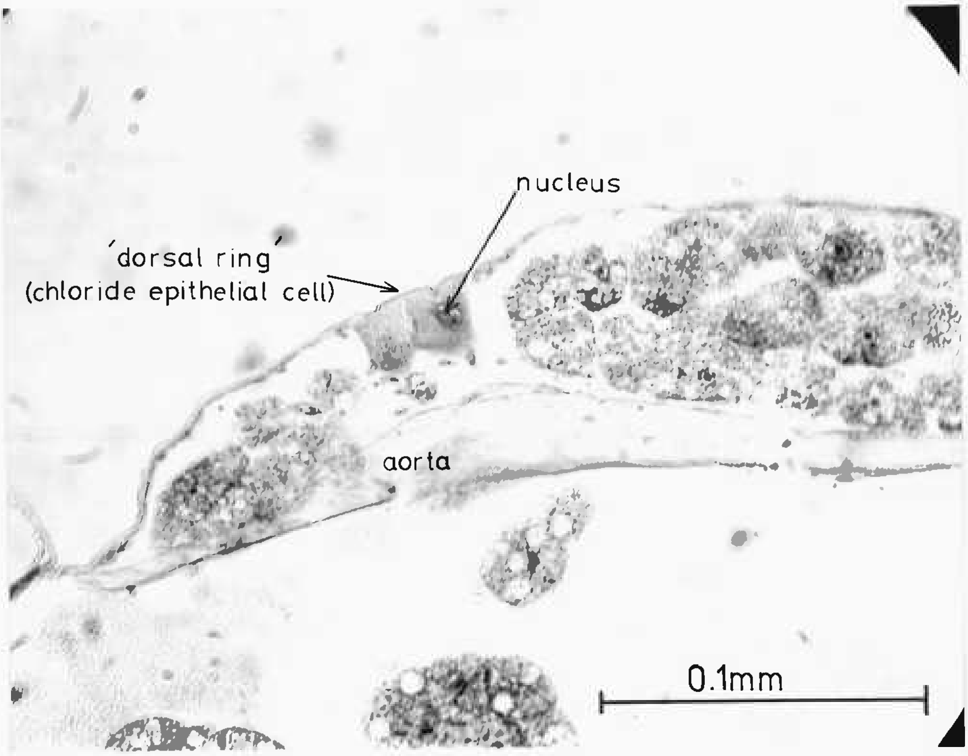
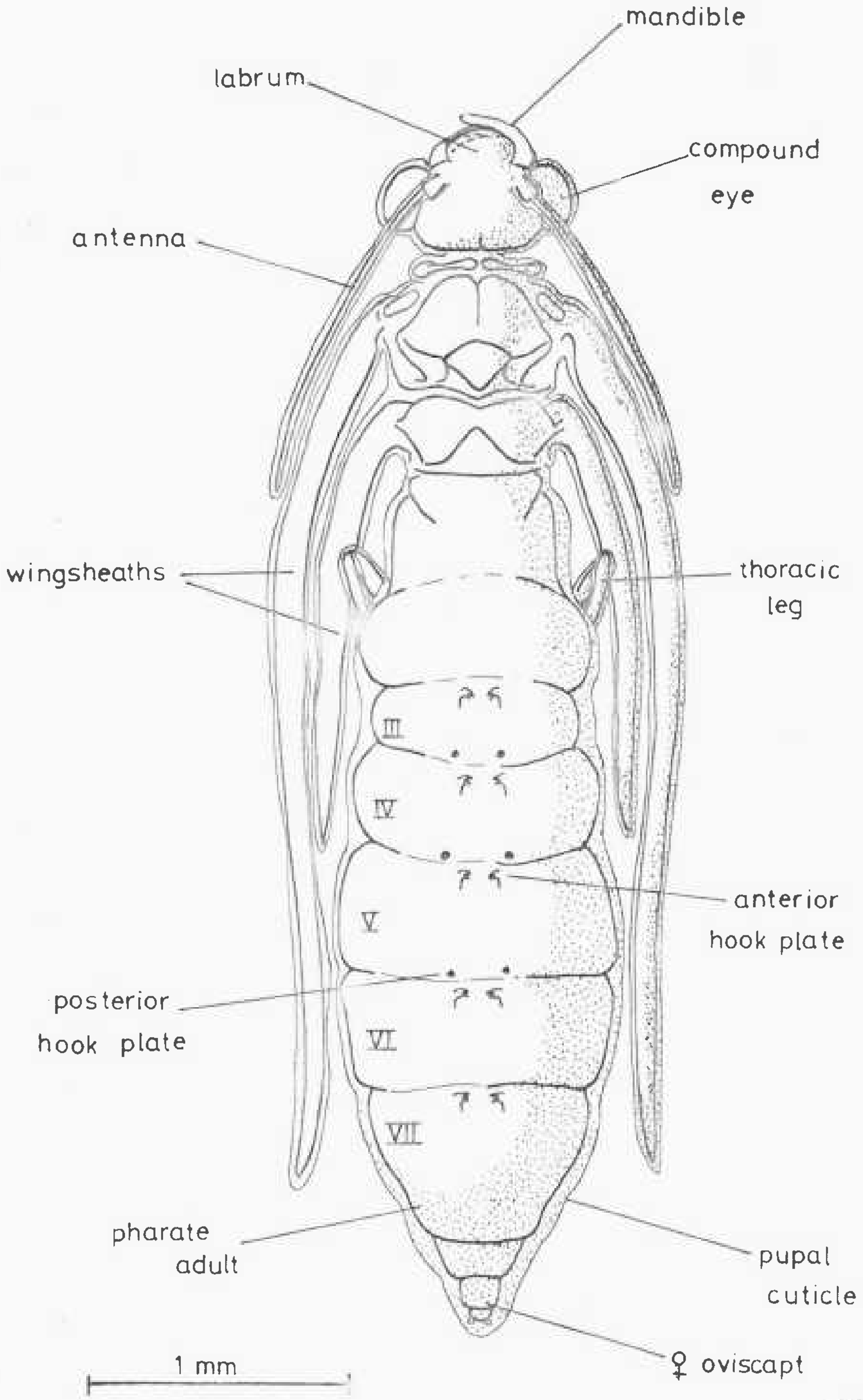


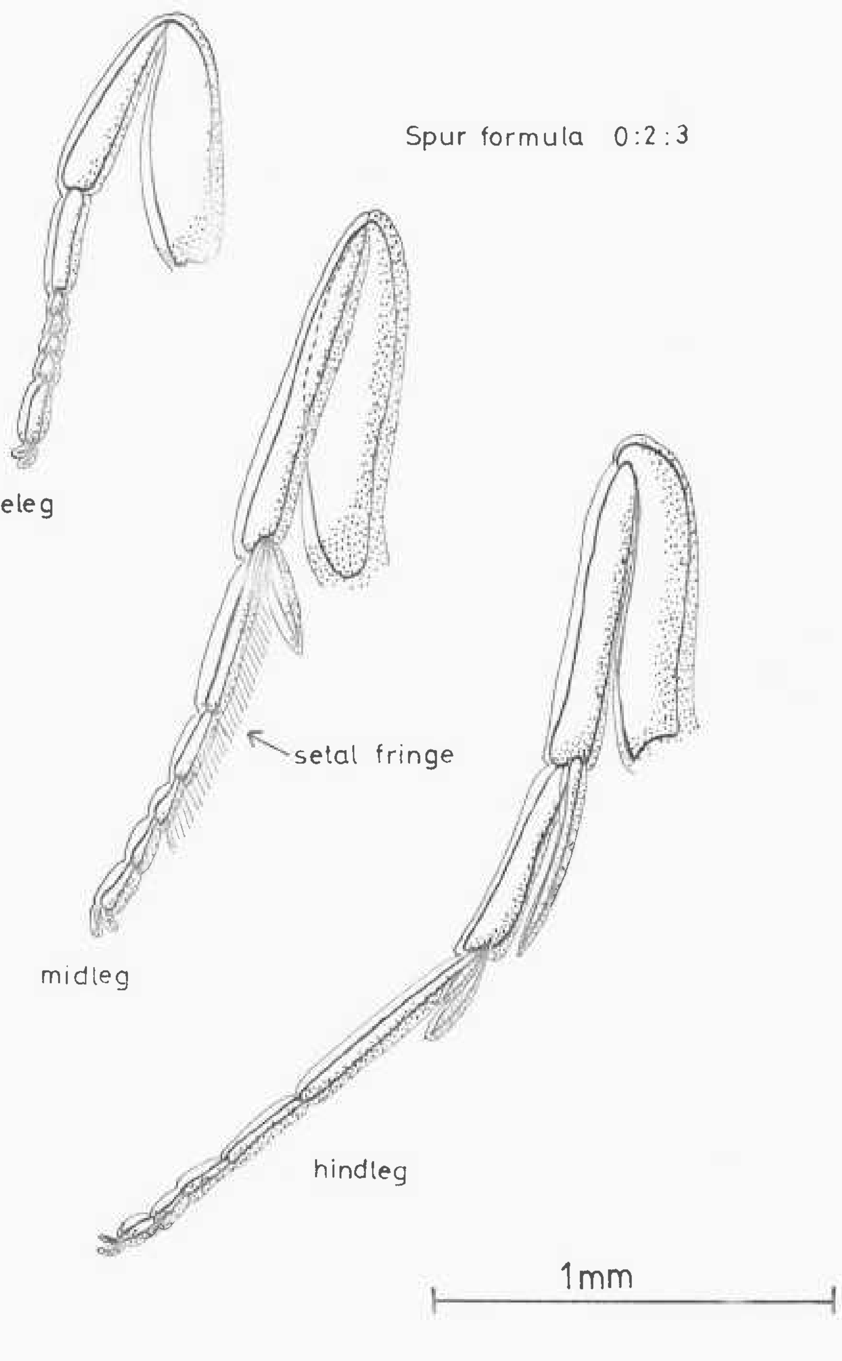
Fig. 142. 'Dorsal ring' (chloride epithelial cell), L.S. anterior dorsal wall, abdominal segment. *Hydroptila* sp. larva.



143

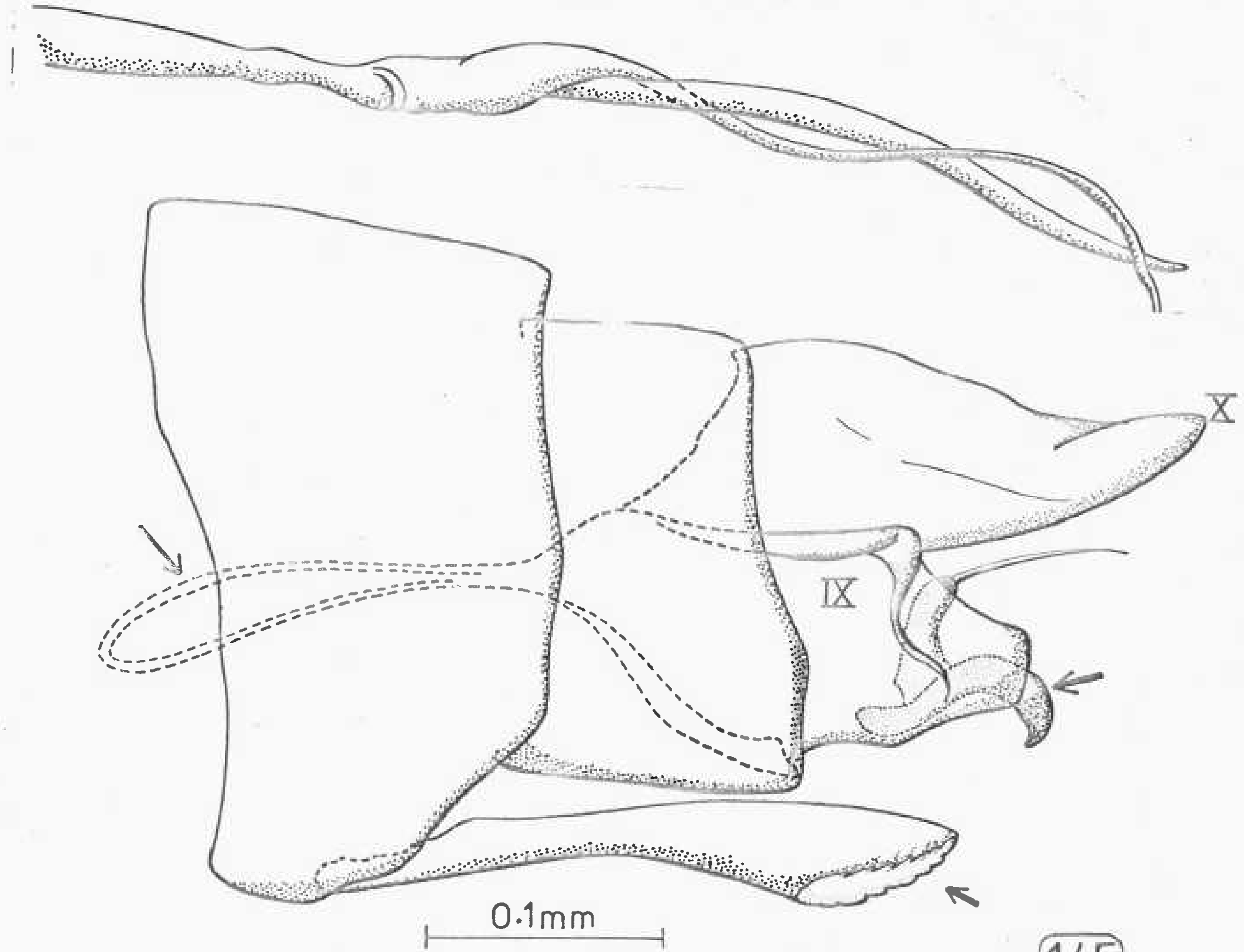
Pharate adult ('pupa'), Hydroptila vectis Curtis, ♀

dorsal view



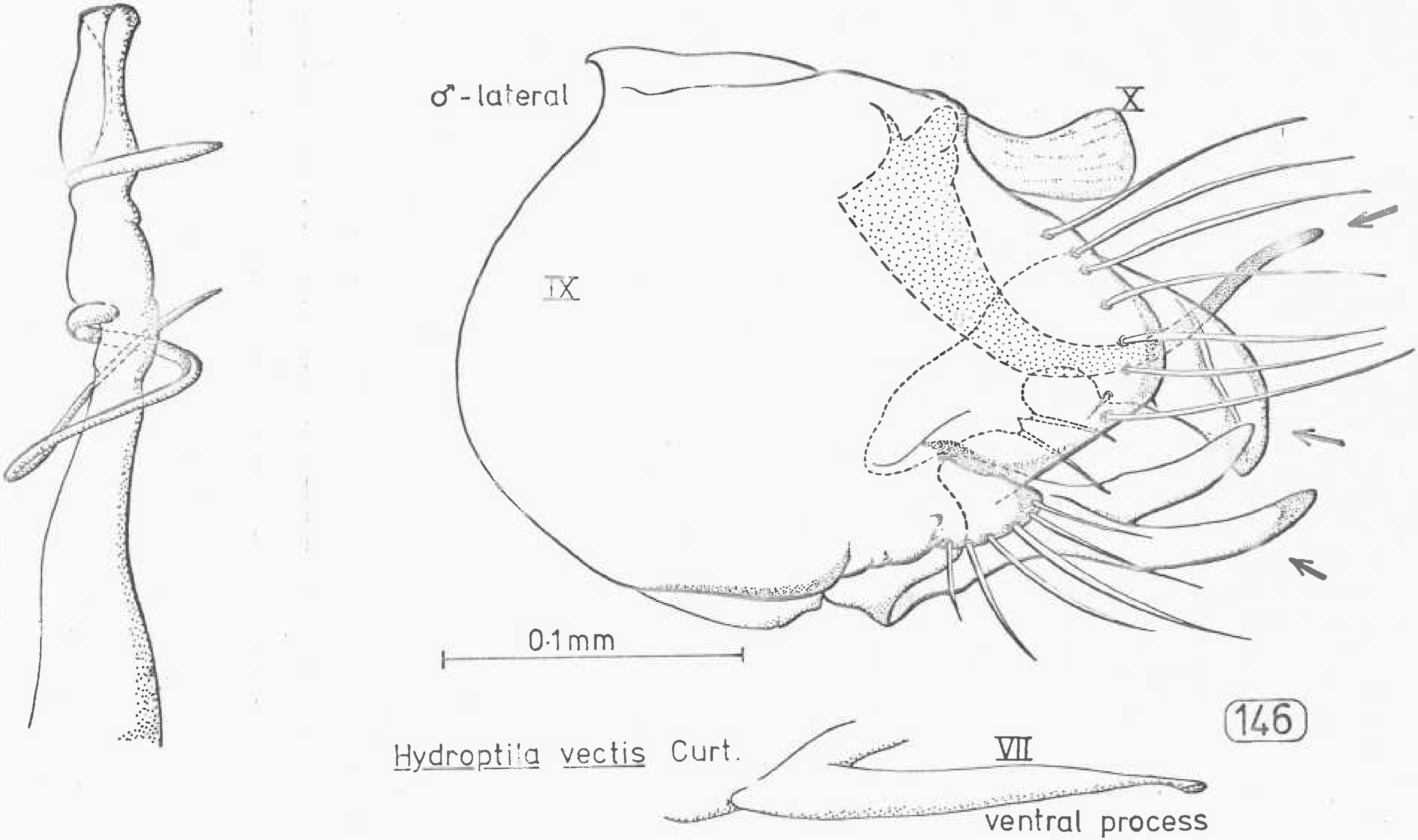
144

Thoracic Legs, Pharate Adult, *Hydroptila* sp.



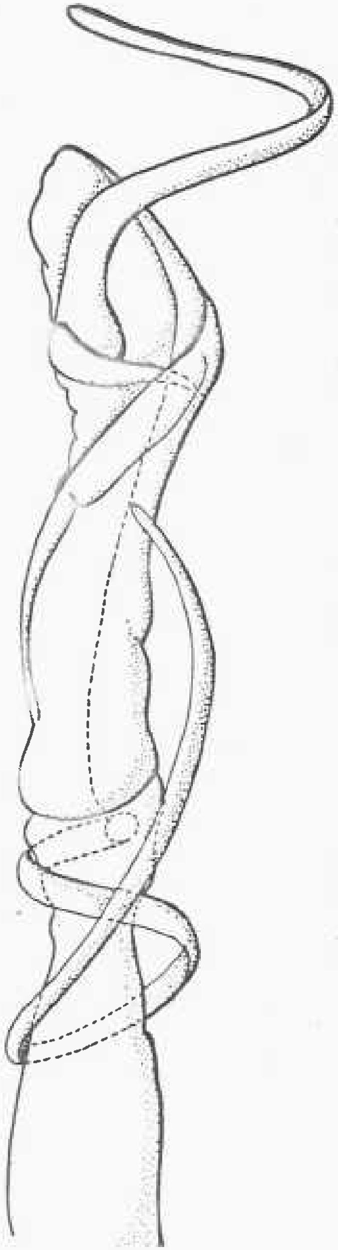
145

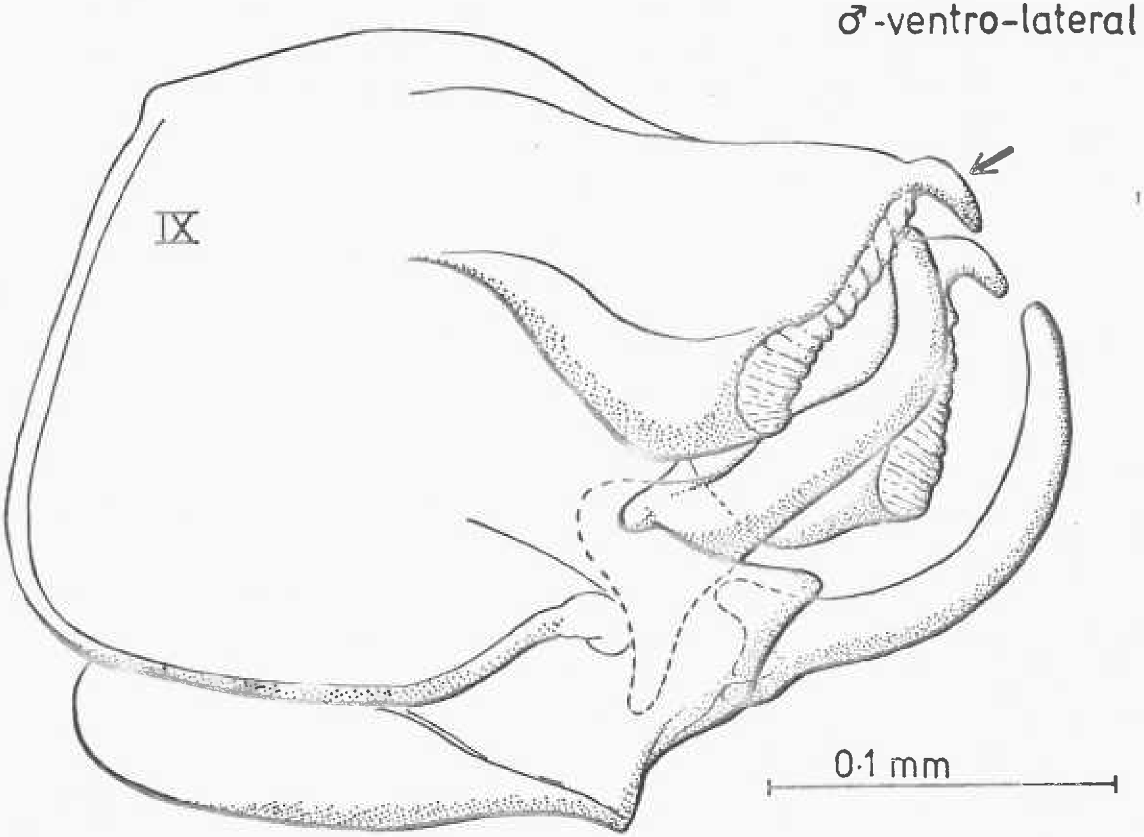
Hydroptila tineoides Dalm.



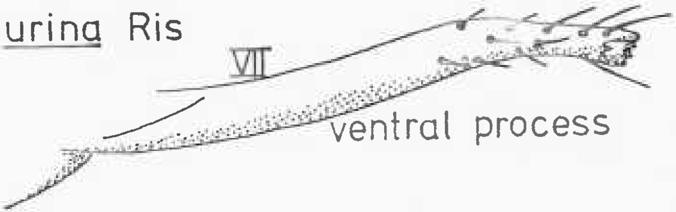
146

Hydroptila vectis Curt.





Hydroptila tigurina Ris



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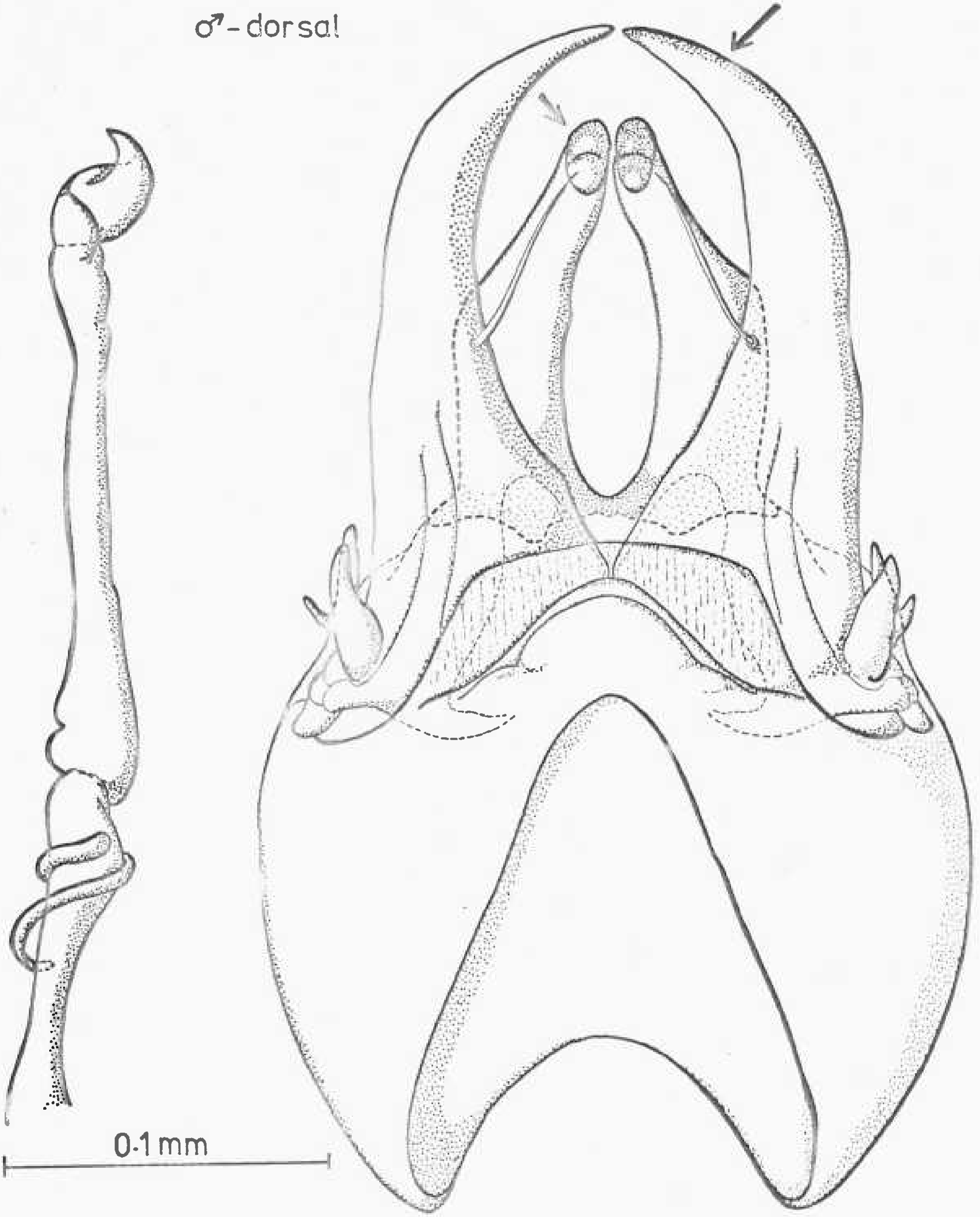
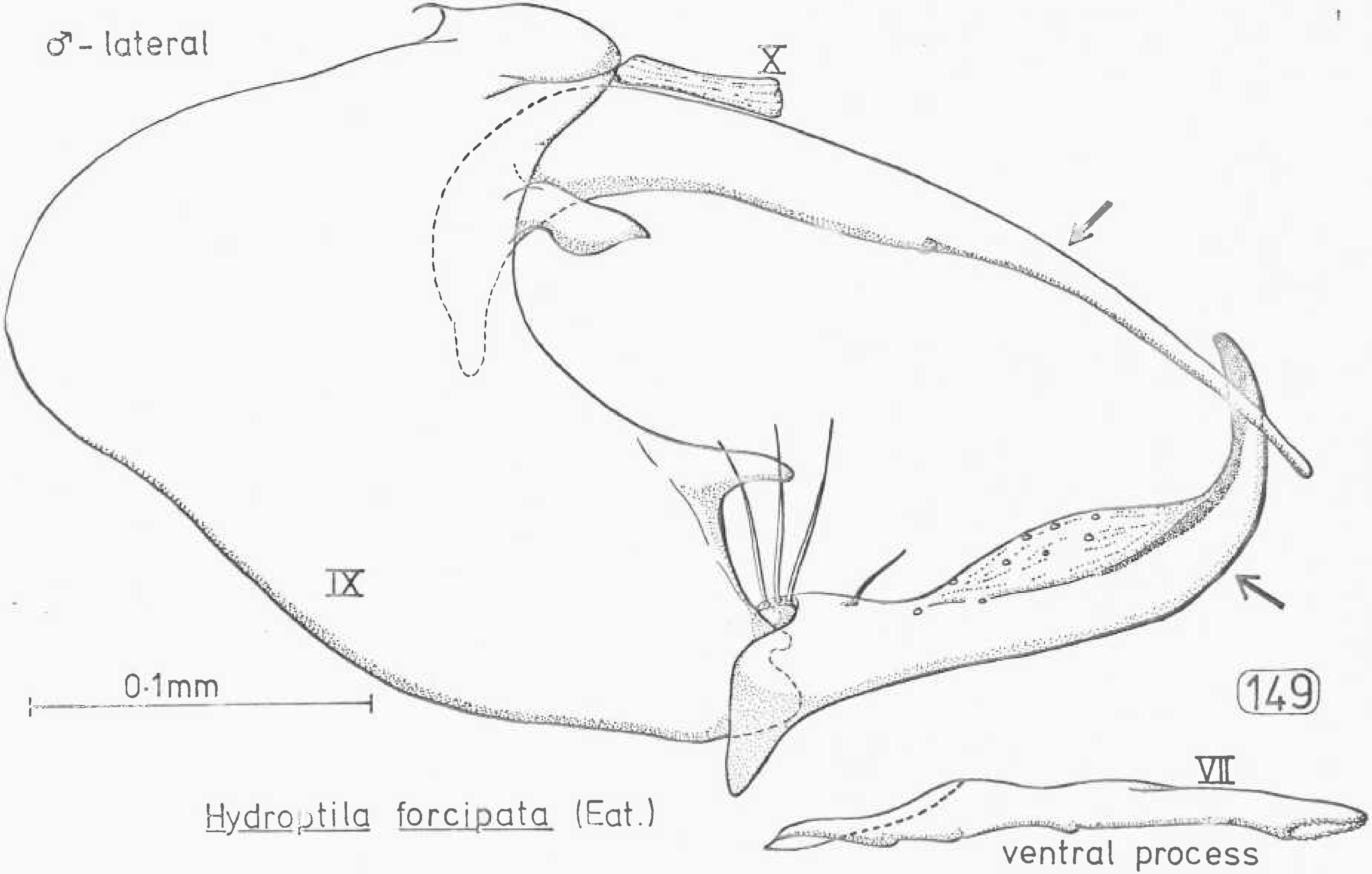


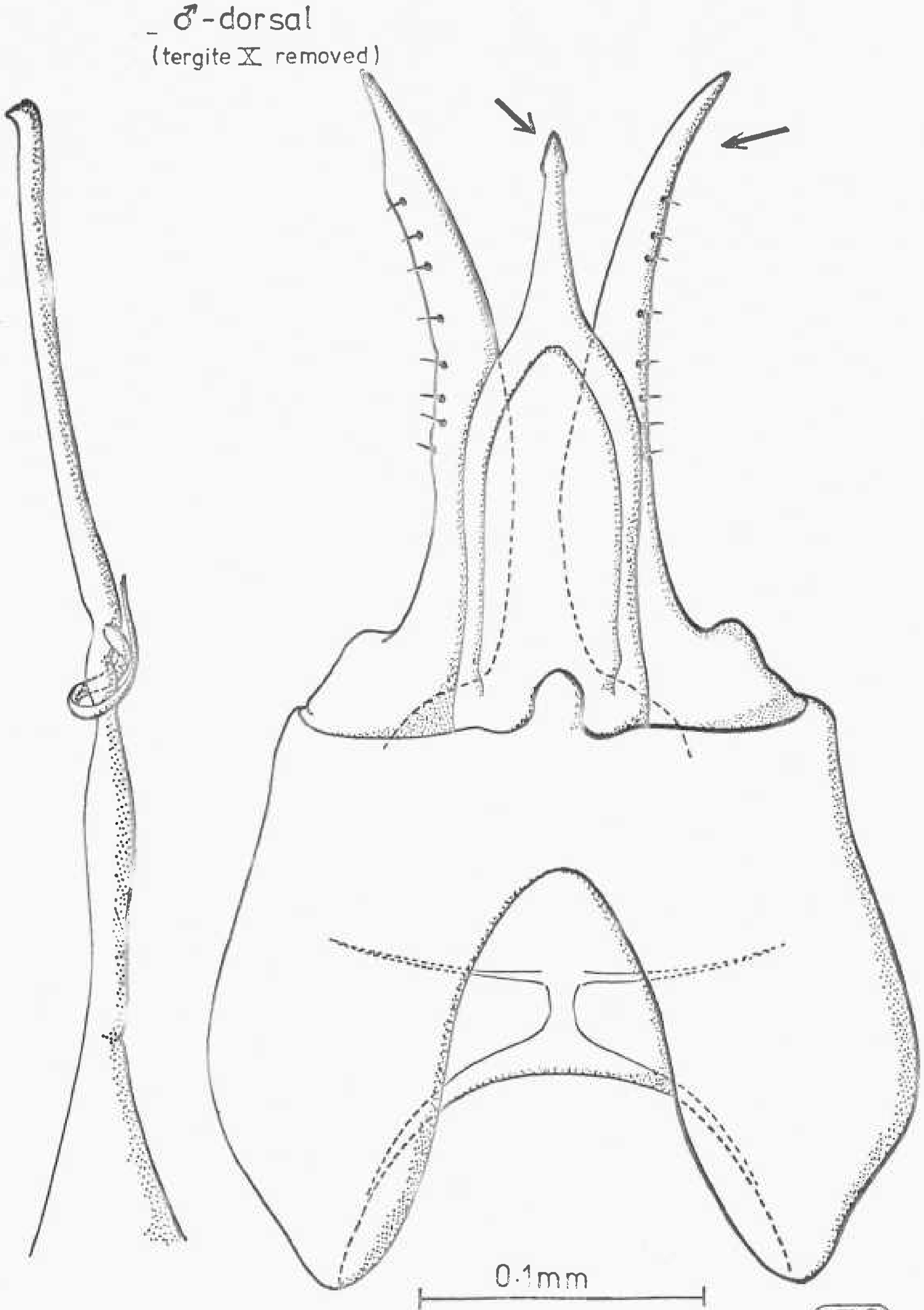
148

Hydroptila forcipata (Eat.)



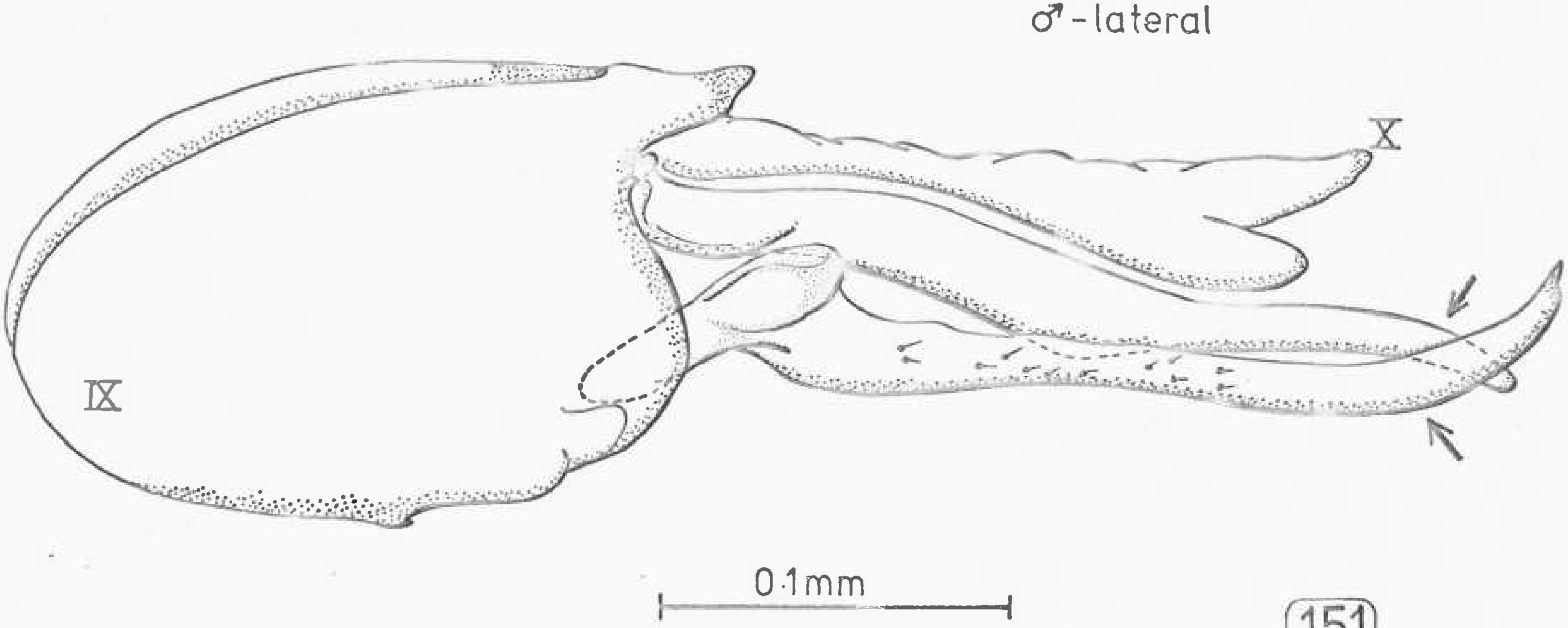
149

Hydroptila forcipata (Eat.)



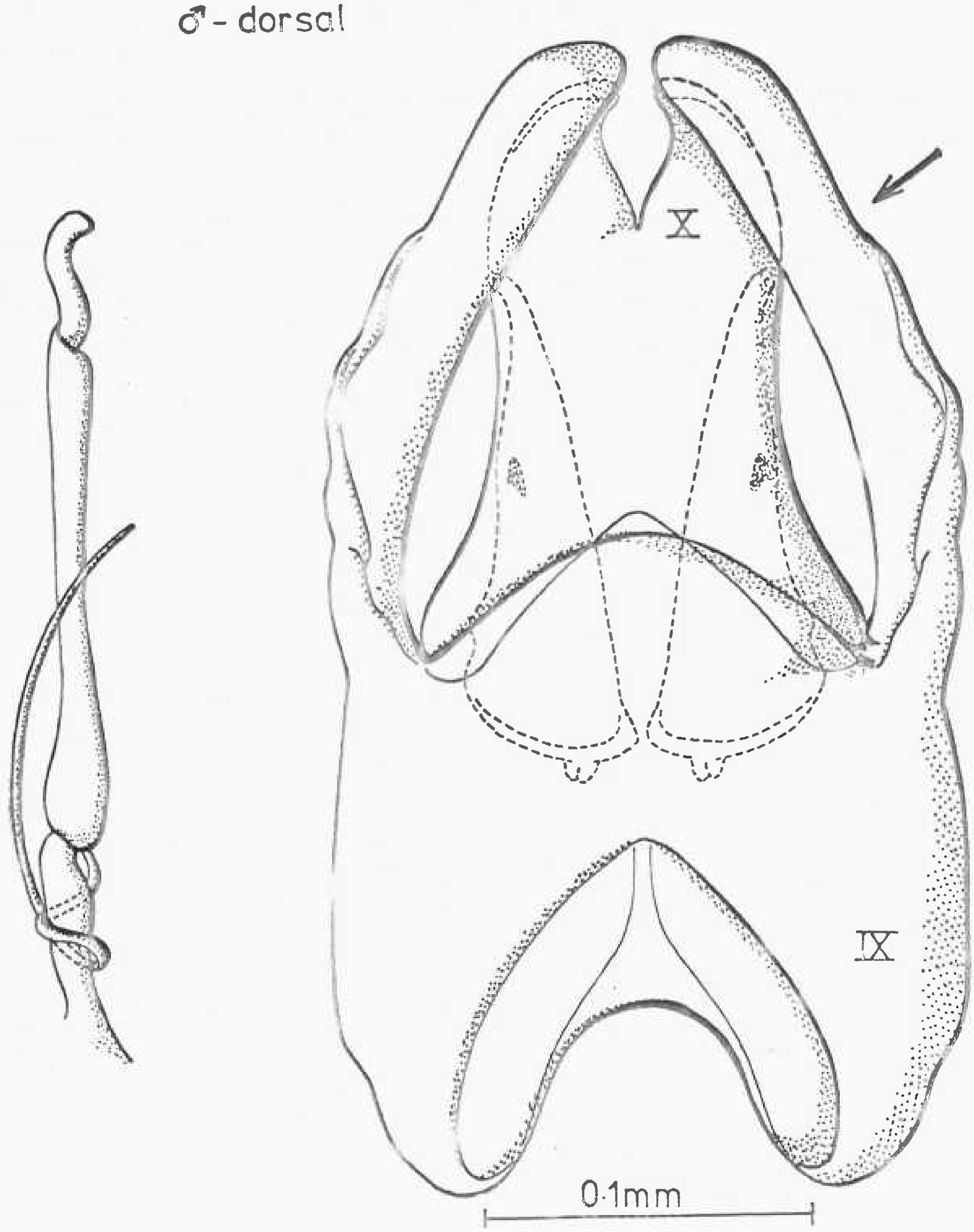
150

Hydroptila pulchricornis Pict.



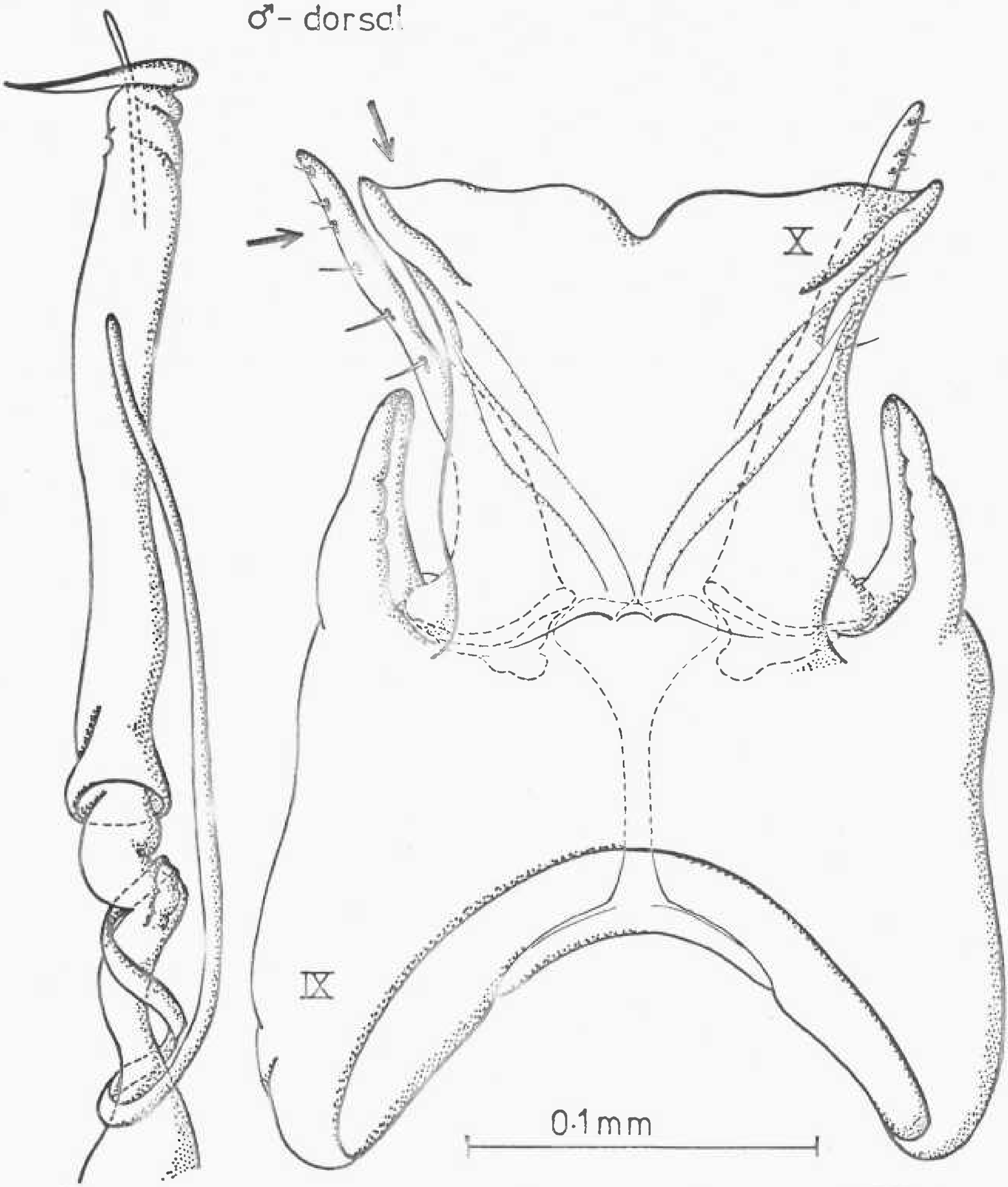
151

Hydroptila pulchricornis Pict.



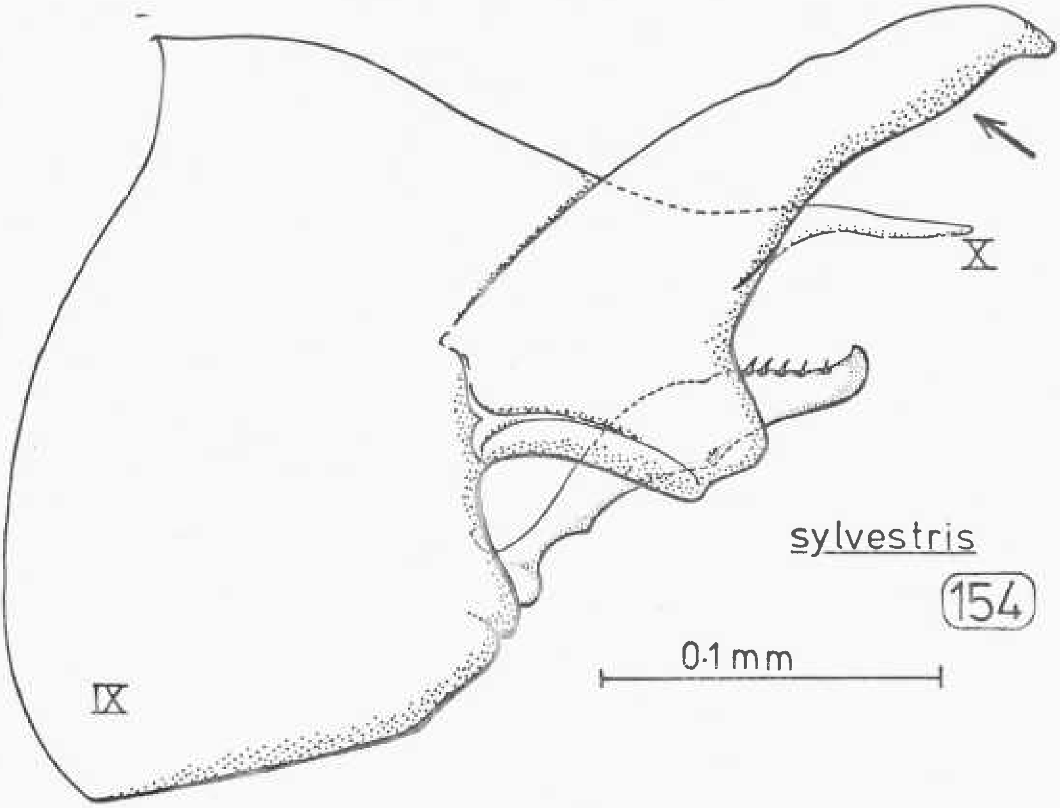
(152)

Hydroptila sylvestris Mort.



153

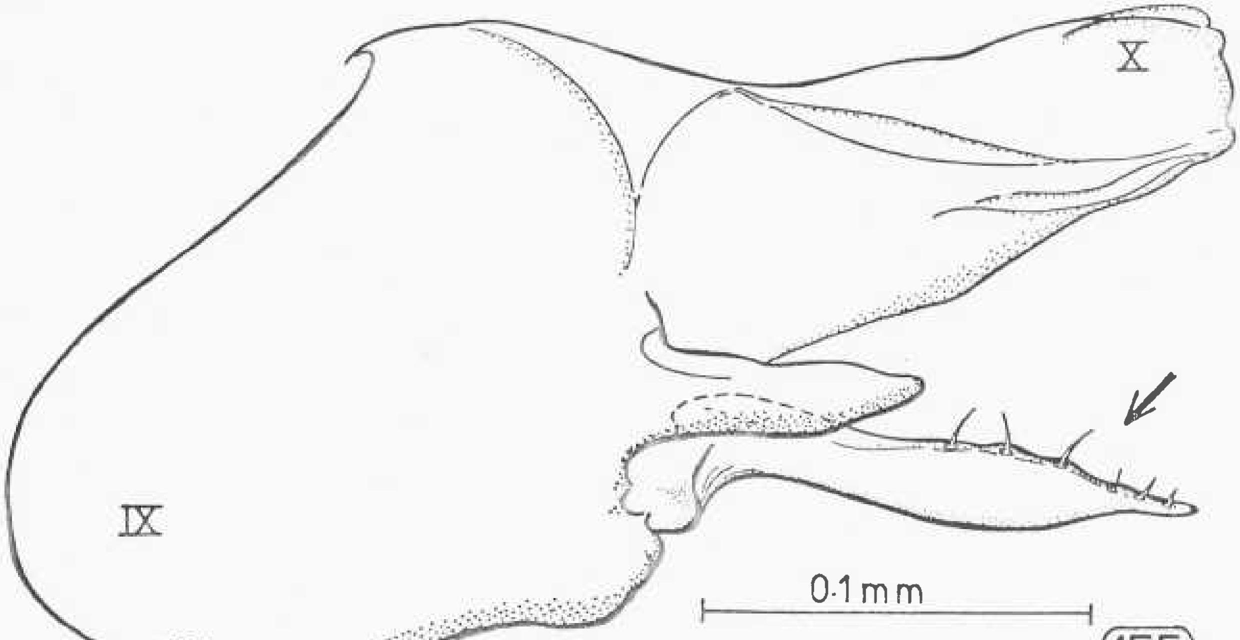
Hydroptila sparsa Curt.



sylvestris

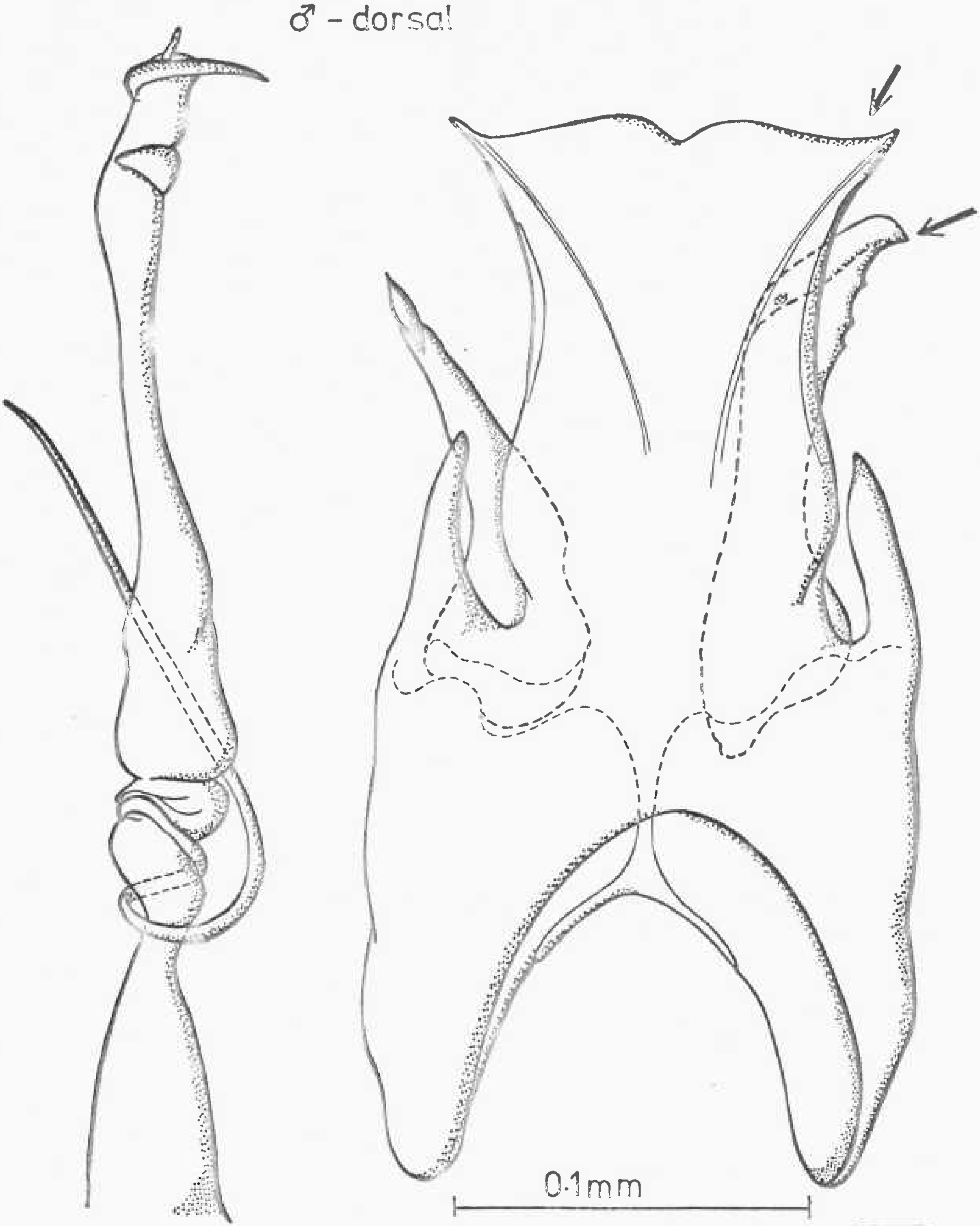
154

Hydroptila ♂♂ - lateral



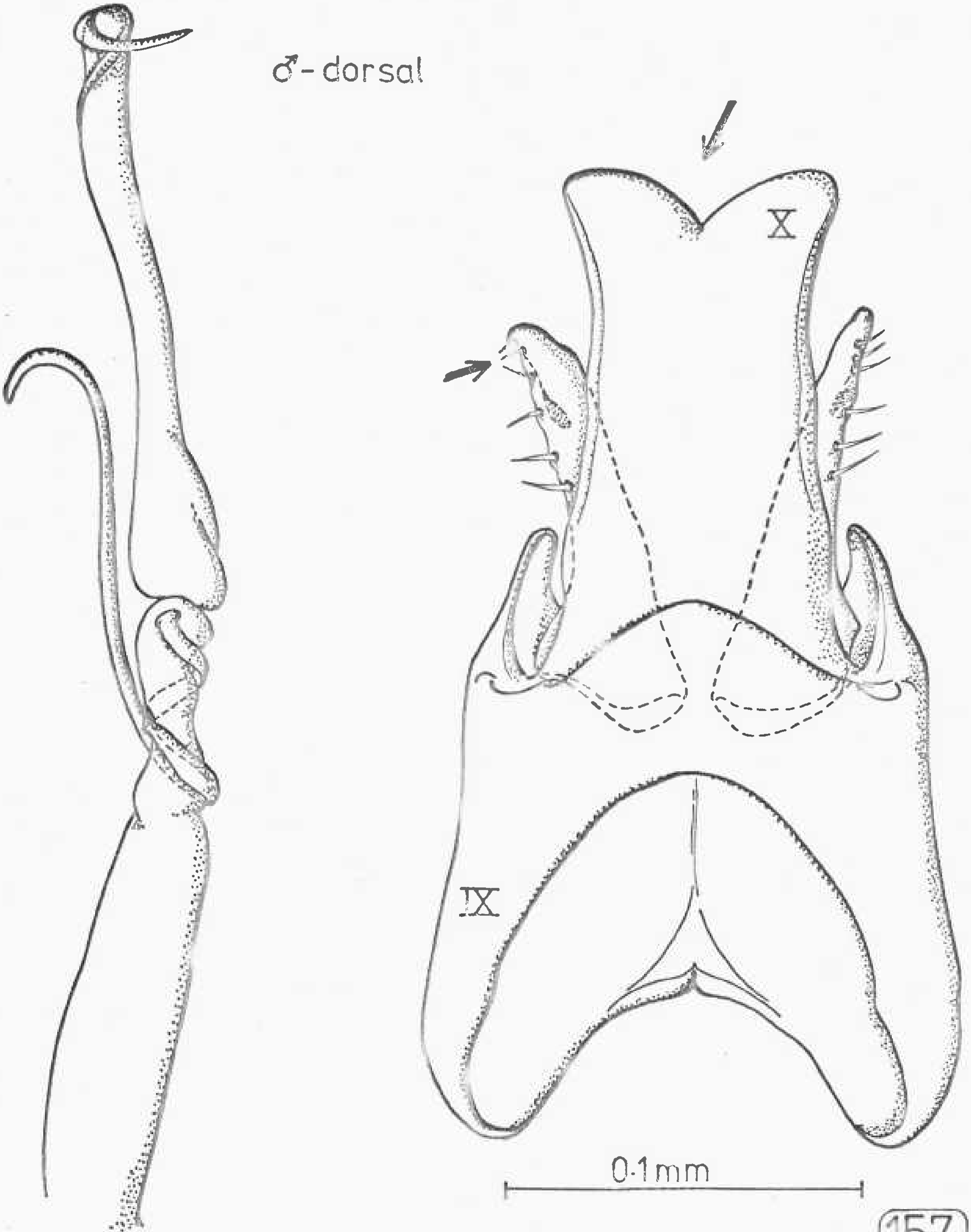
155

sparsa



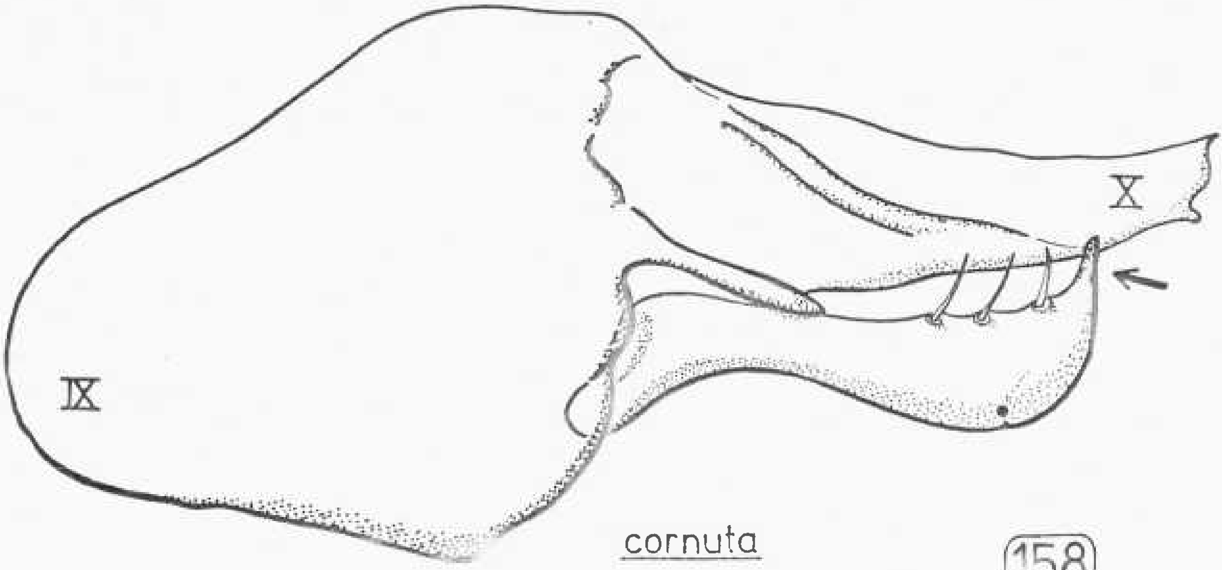
156

Hydroptila cornuta Mos.



157

Hydroptila simulans Mos.

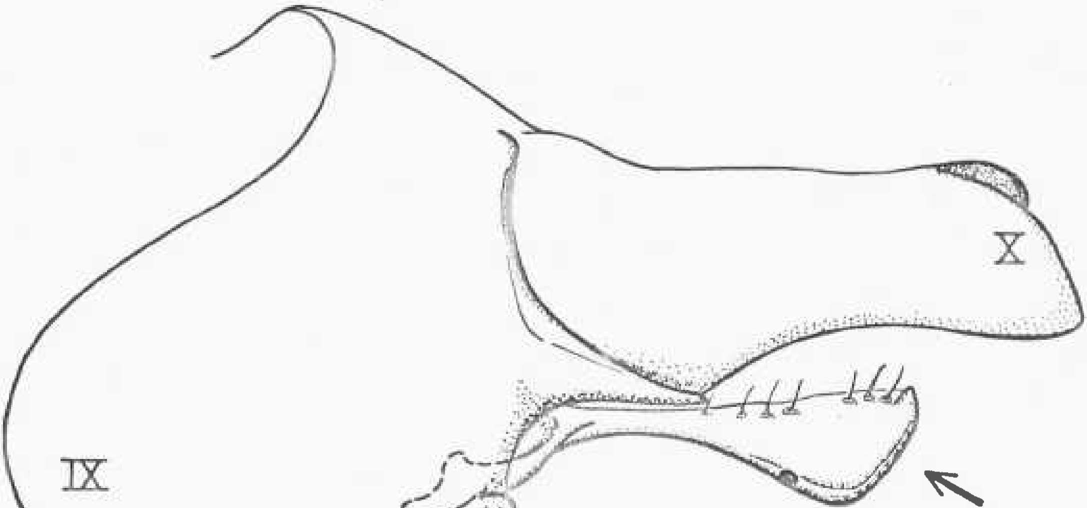


cornuta

158

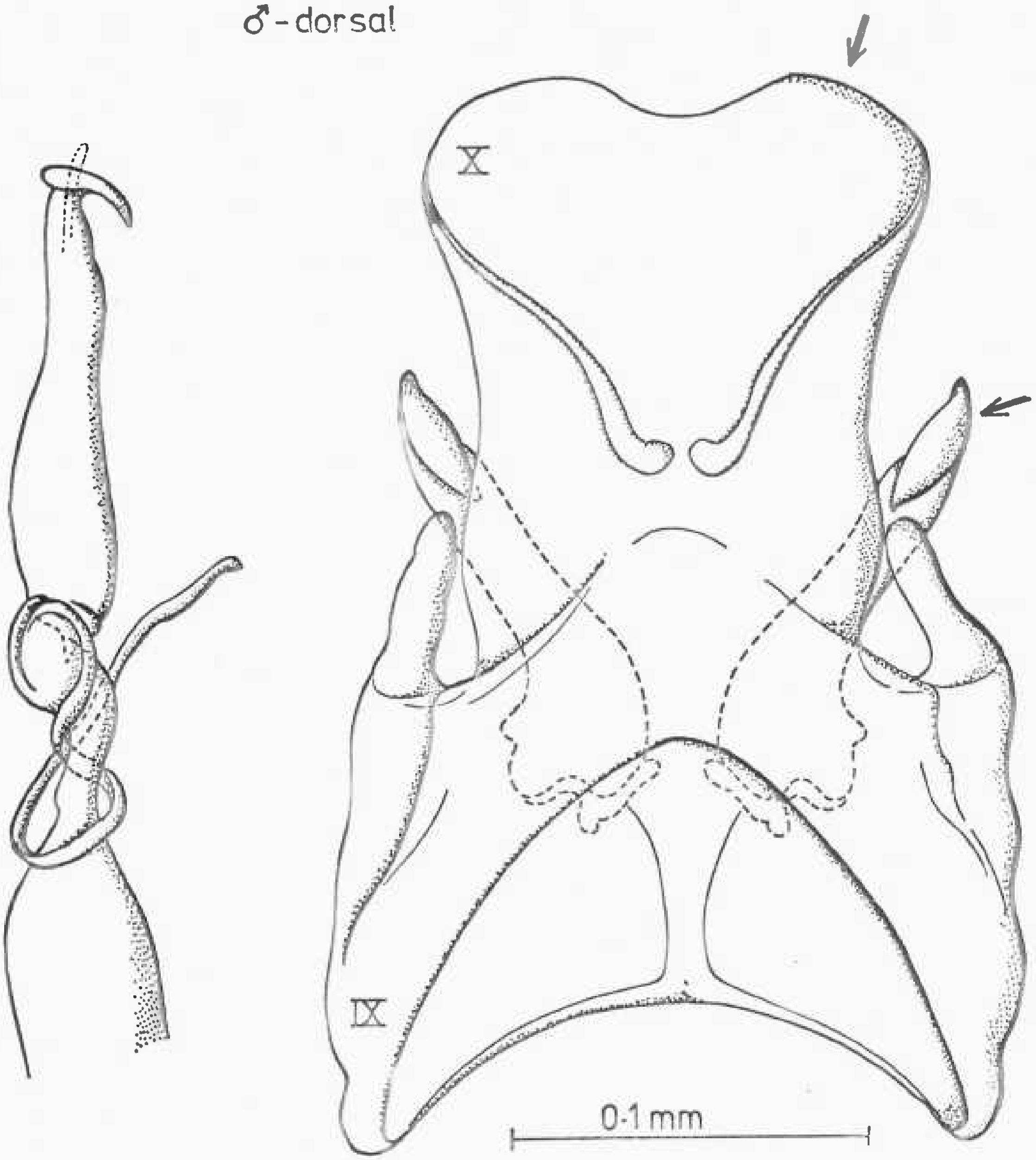
Hydroptila ♂♂ - lateral

0·1mm



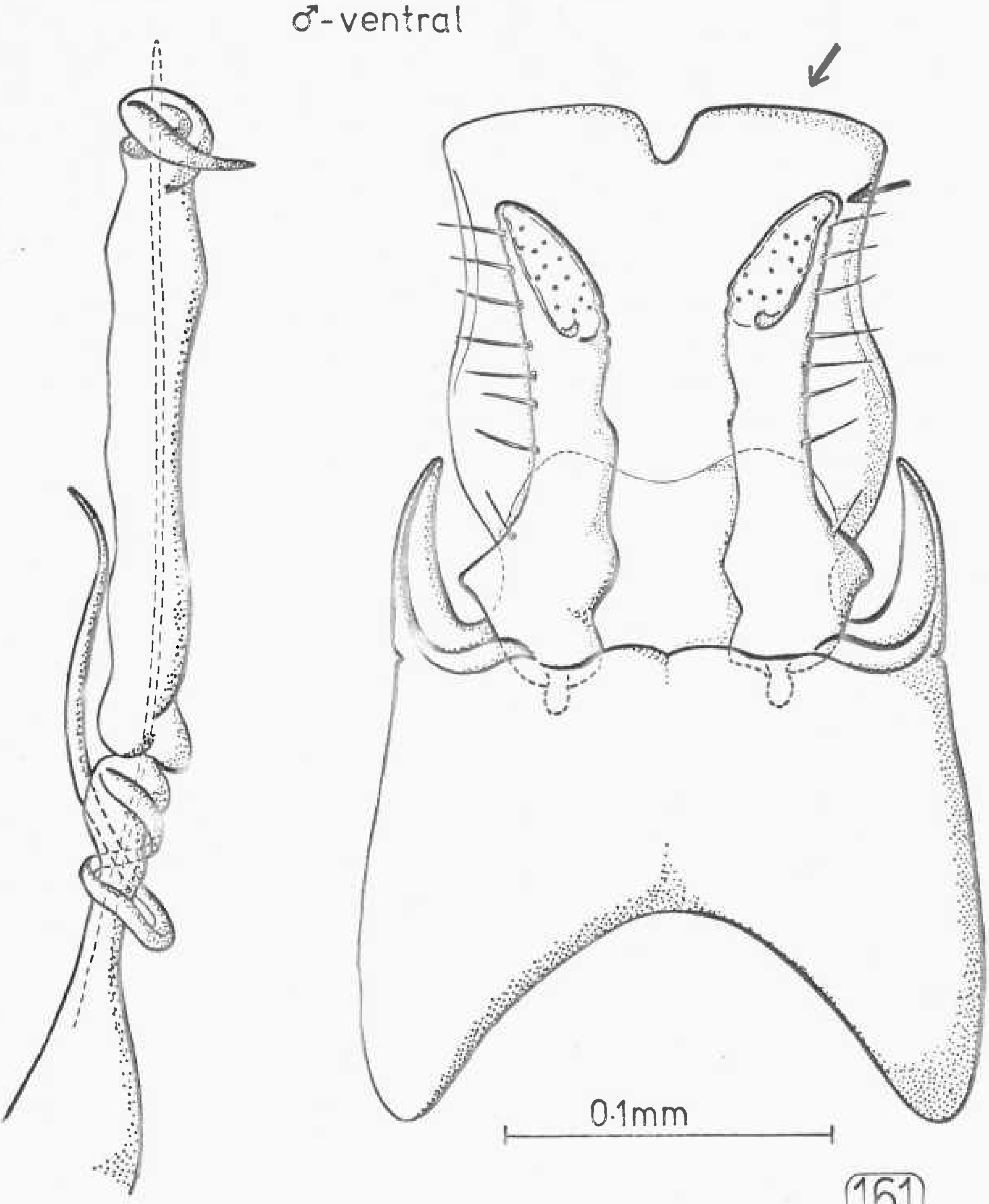
simulans

159



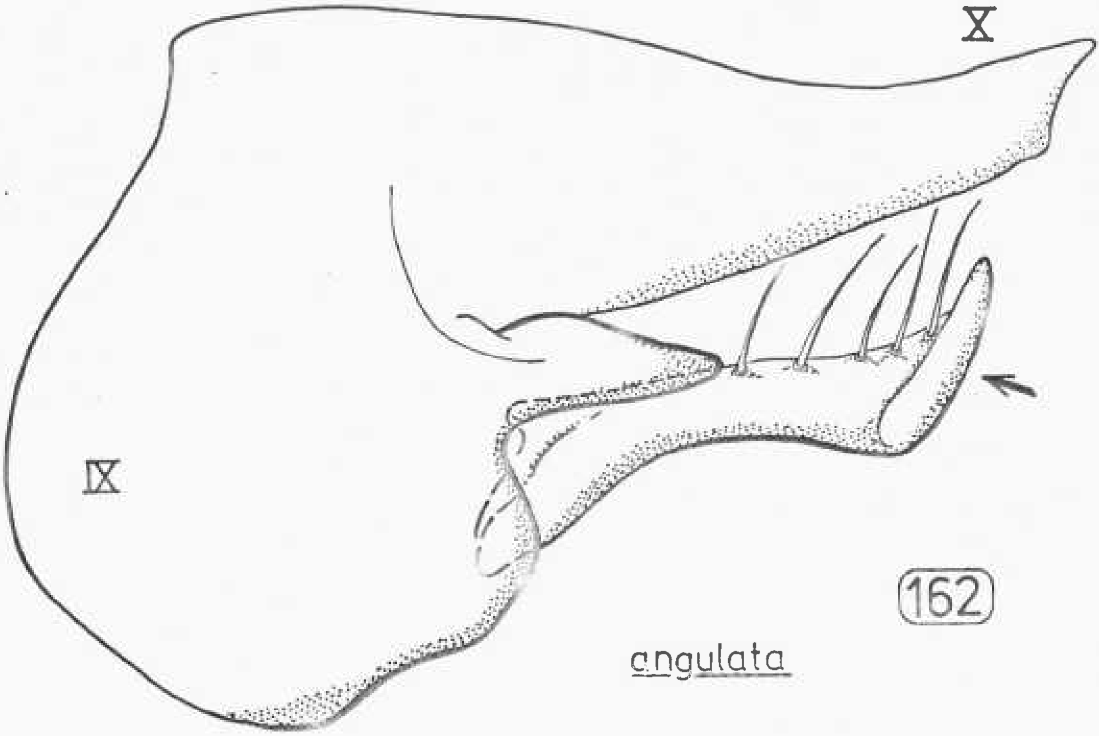
160

Hydroptila angulata Mos.



161

Hydroptila lotensis Mos.

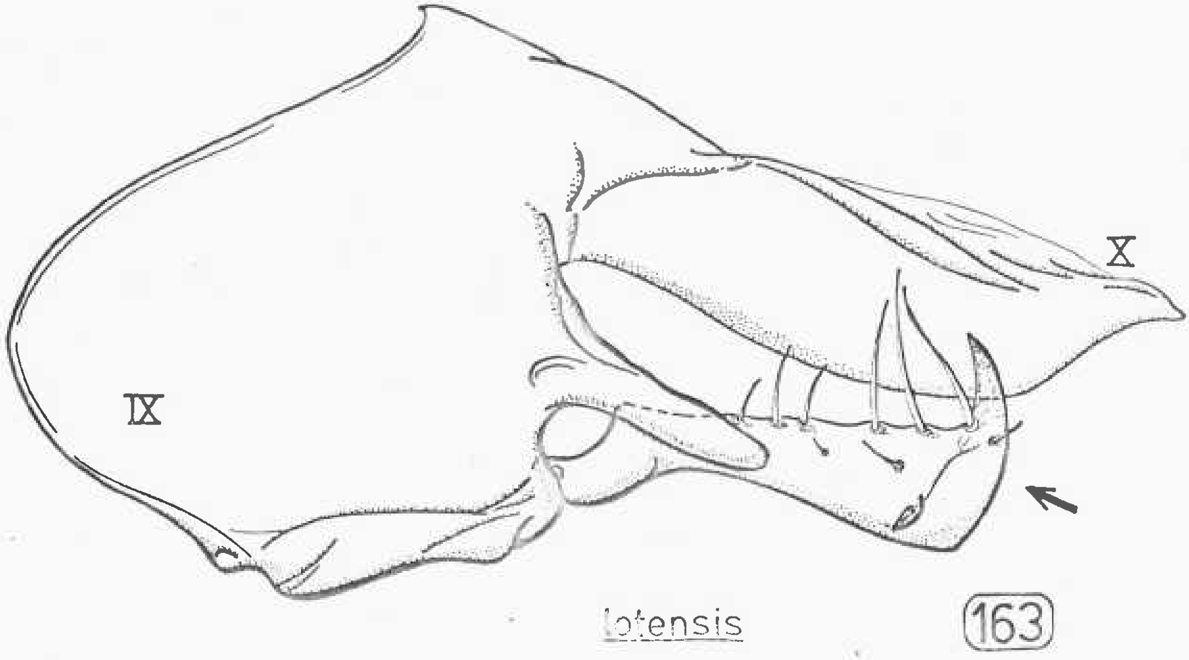


162

angulata

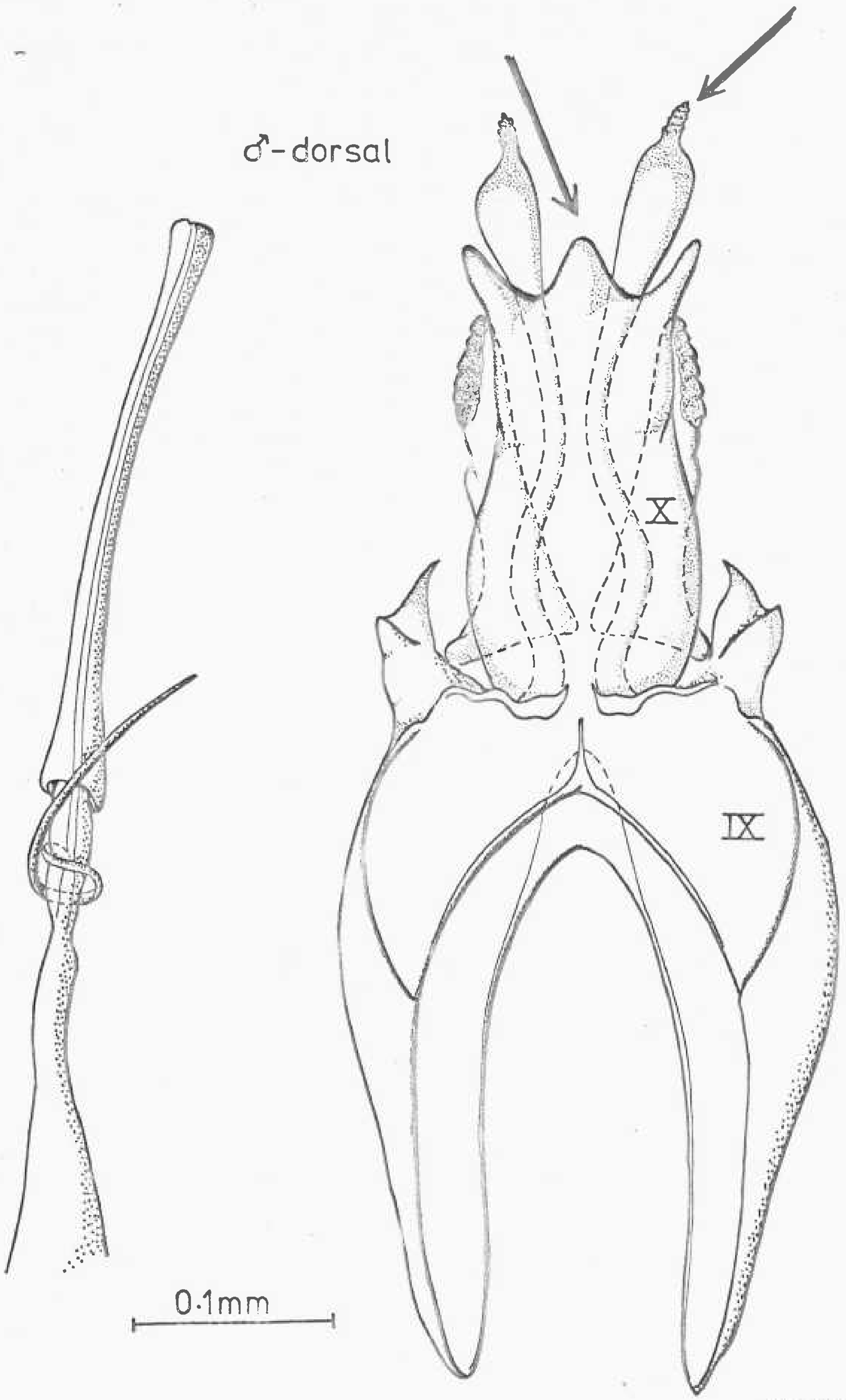
Hydroptila ♂♂ -lateral

0·1mm



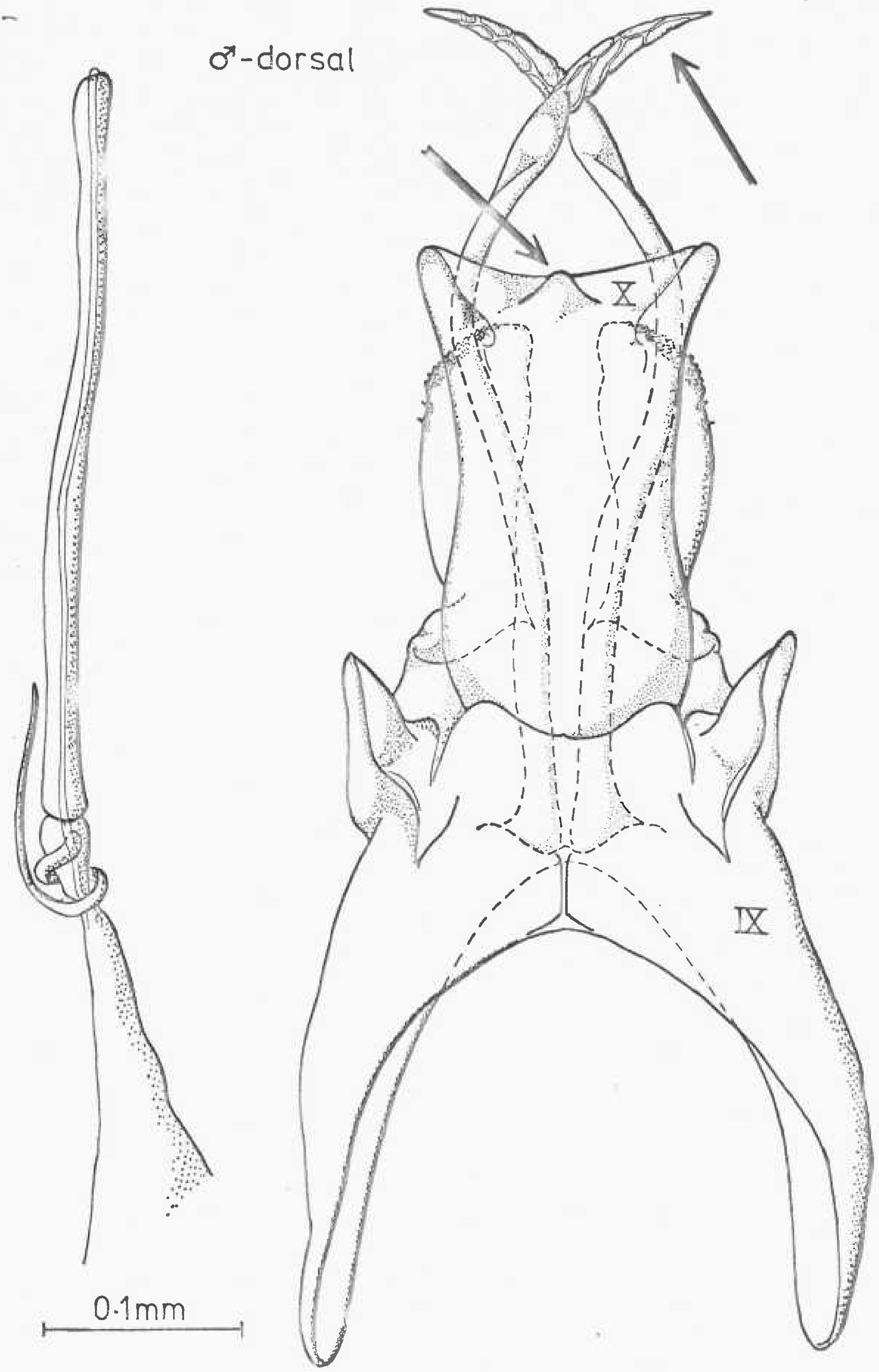
lotensis

163



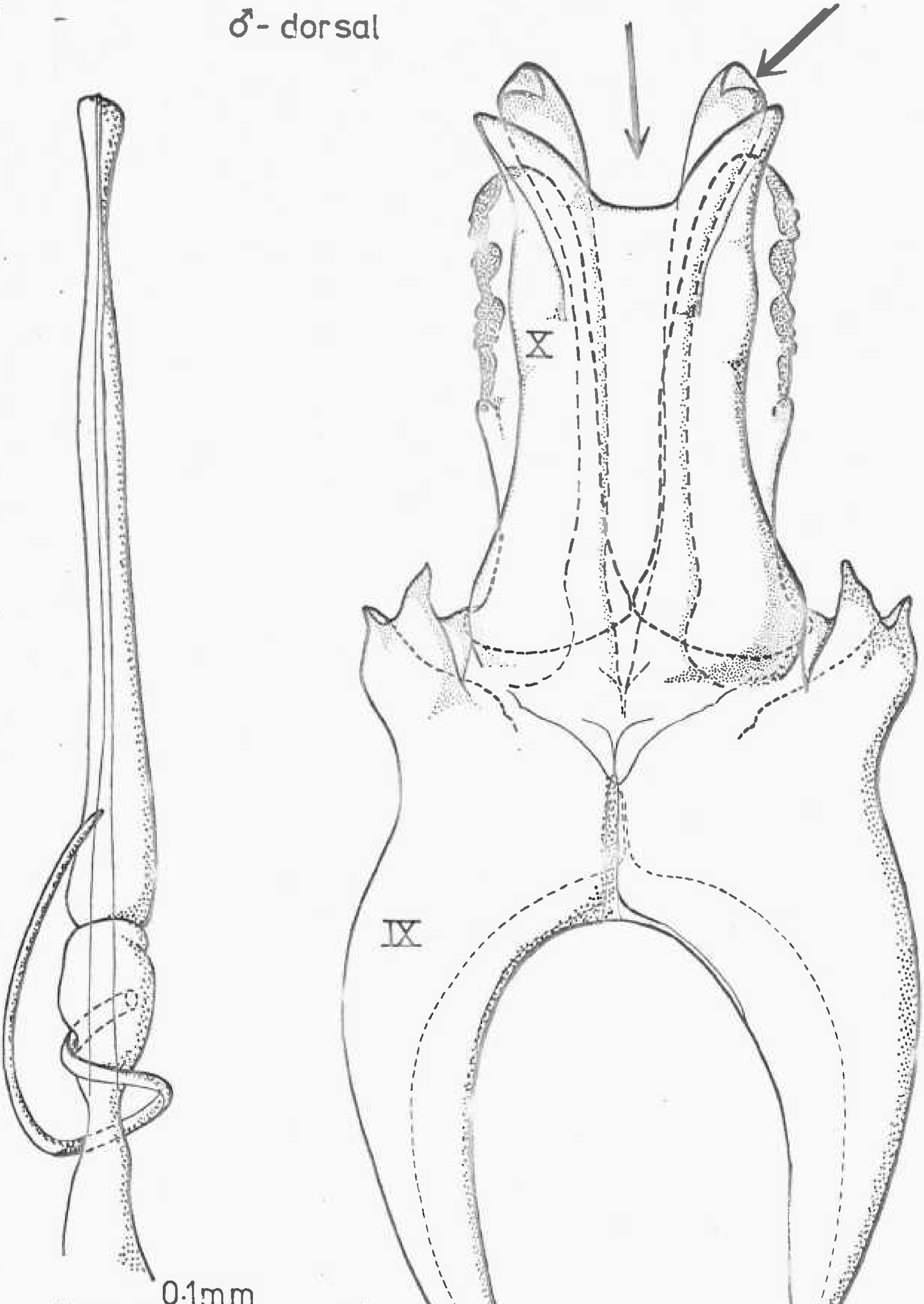
164

Hydroptila martini sp.n.



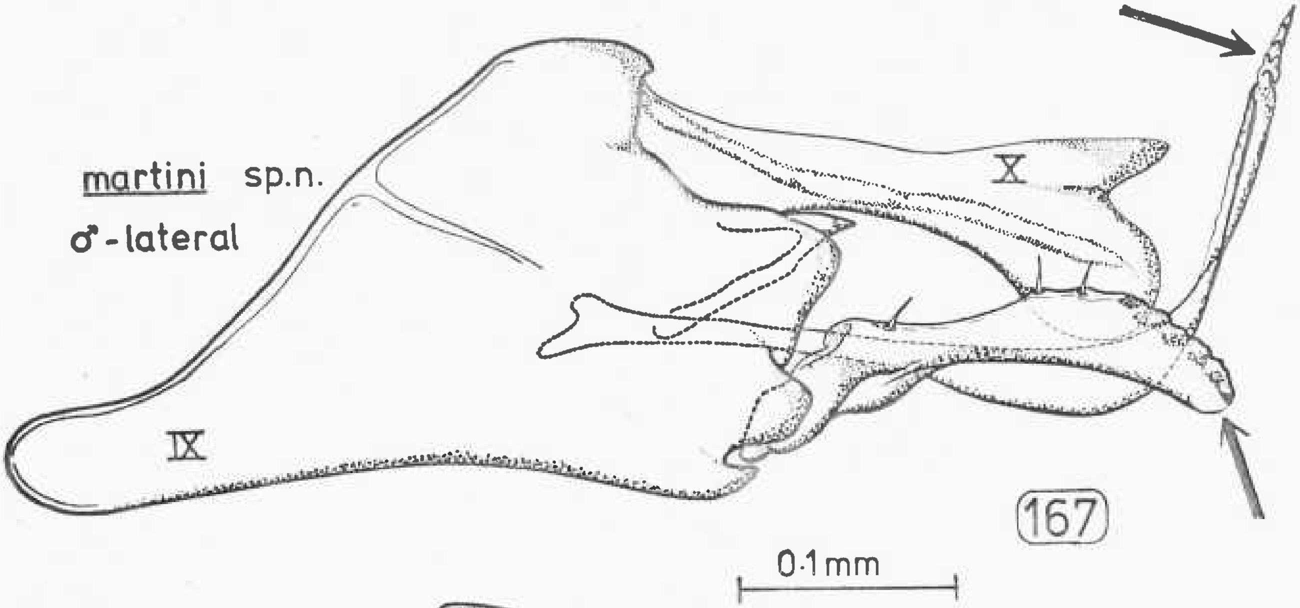
Hydroptila occulta (Eat.)

165

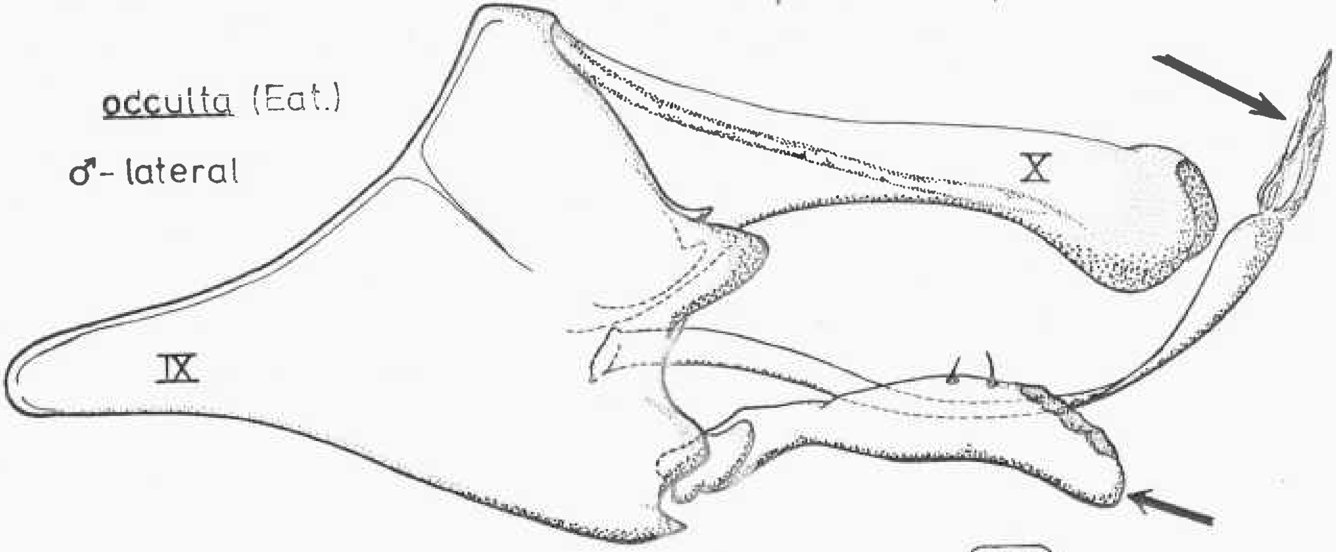


166

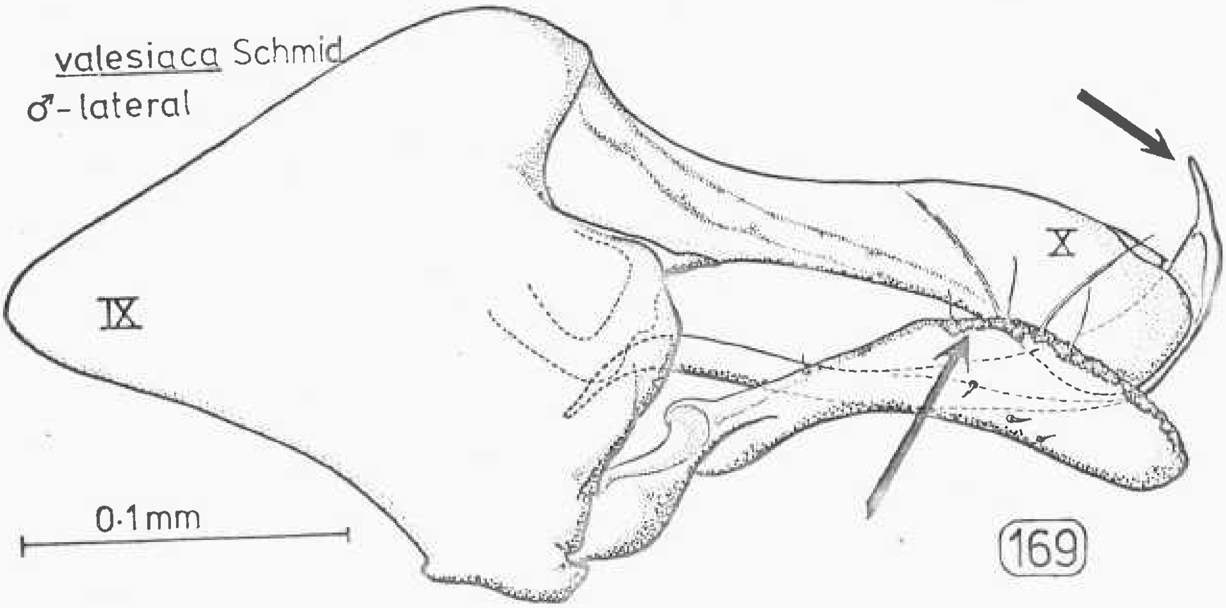
Hydroptila valesiaca Schmid


martini sp.n.
♂-lateral
X
IX
0·1mm

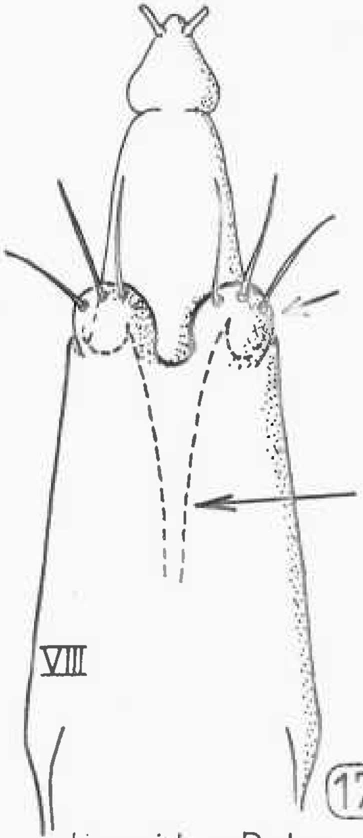
167


occulta (Eat.)
♂- lateral
X
IX

168

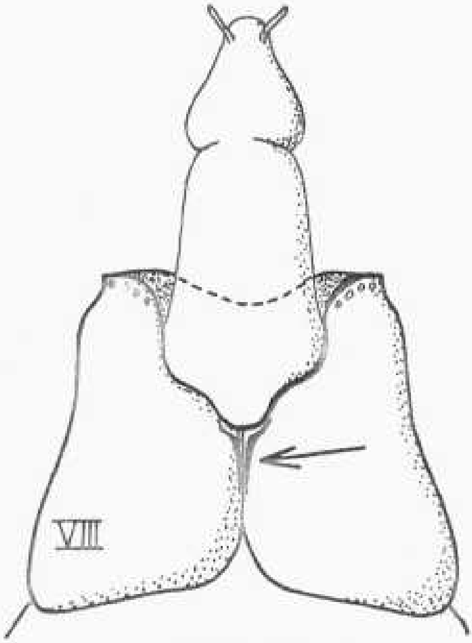

valesiaca Schmid
♂- lateral
X
IX
0·1mm

169



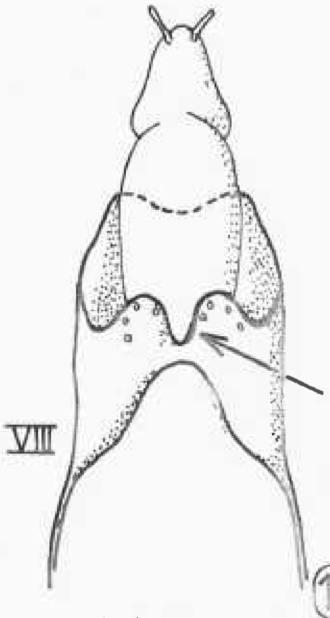
(170)

tineoides Dalm.



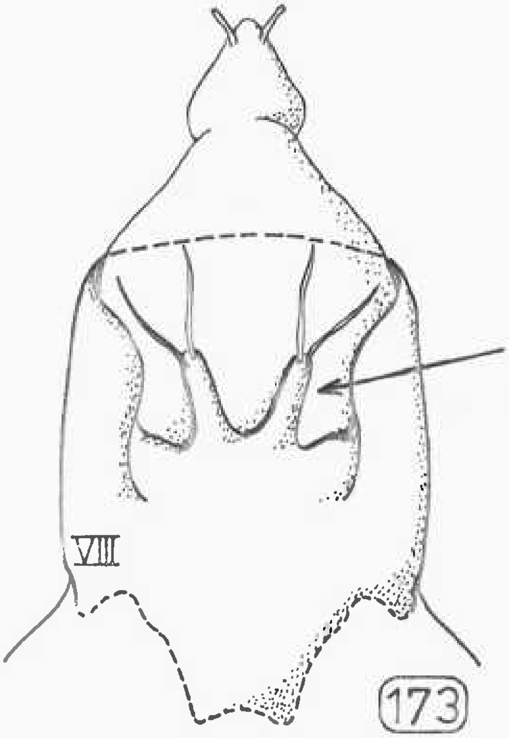
vectis Curt.

(171)



(172)

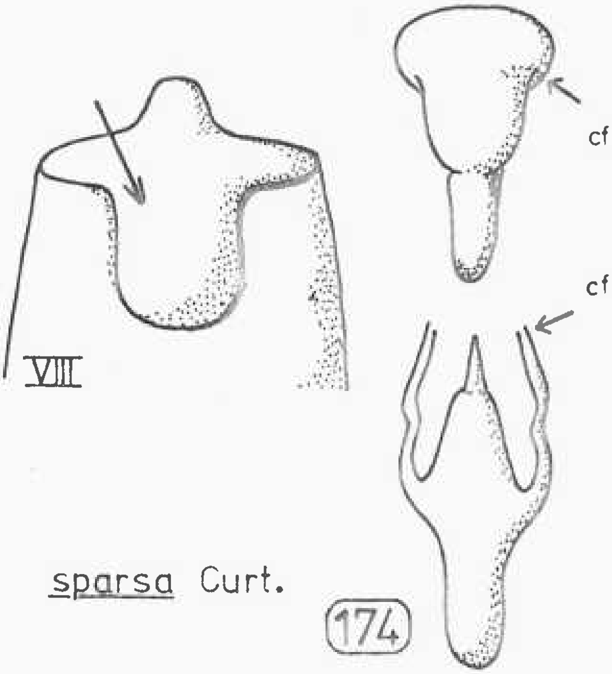
pulchricornis Pict.



(173)

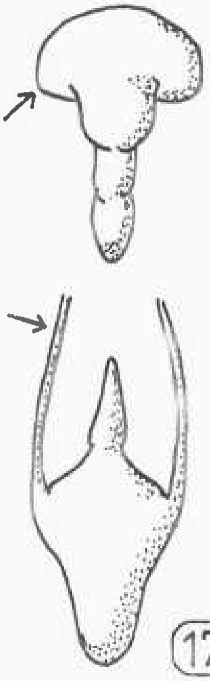
forcipata (Eat.)

Hydroptila ♀♀ – ventral



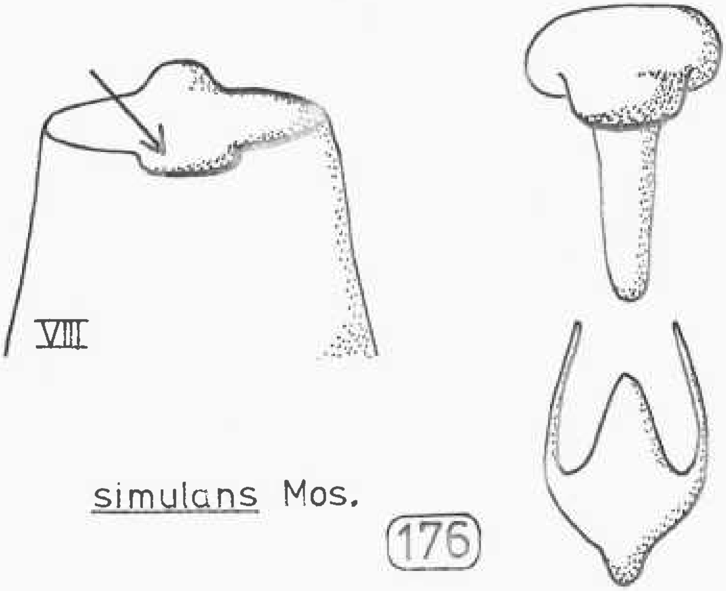
sparsa Curt.

174



175

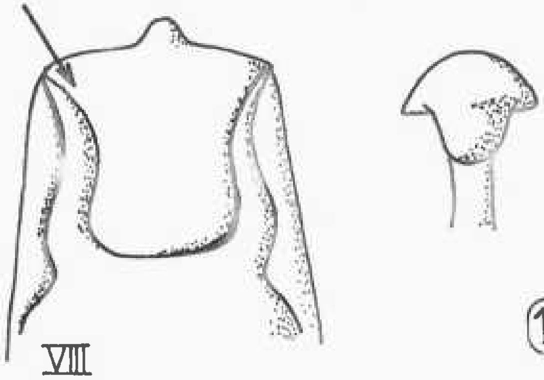
lotensis Mos.



simulans Mos.

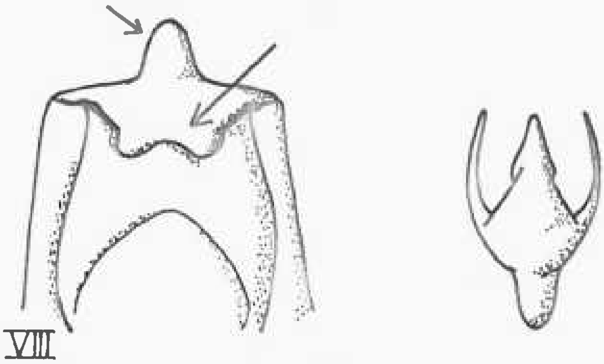
176

Hydroptila ♀♀ - dorsal



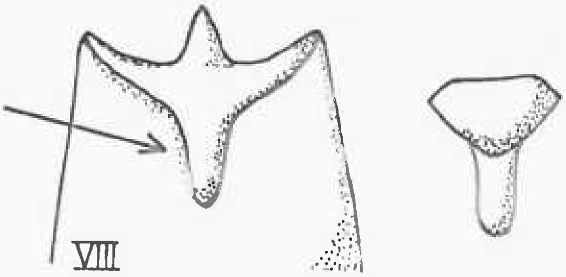
177

angulata Mos.



cornuta Mos.

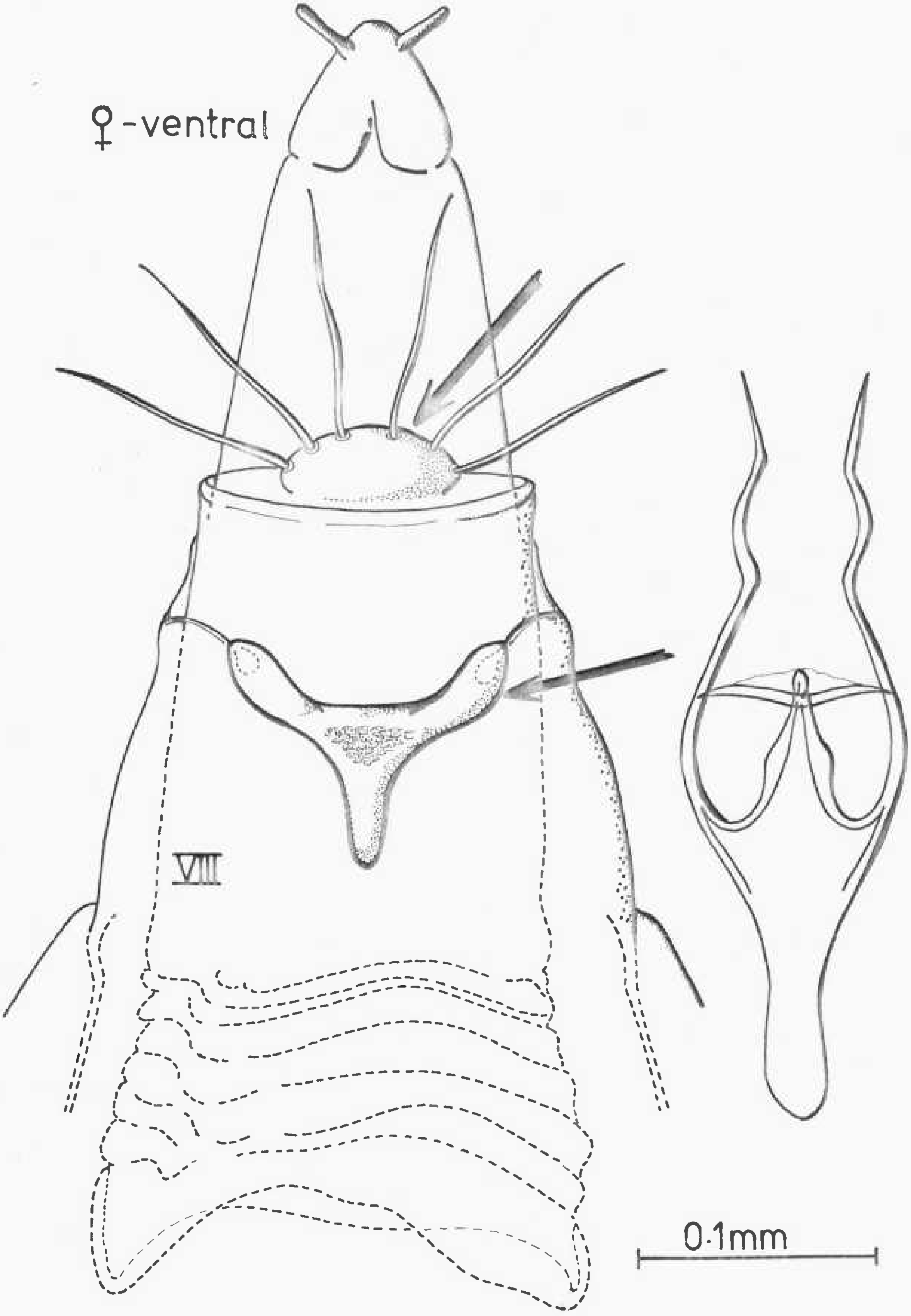
178



179

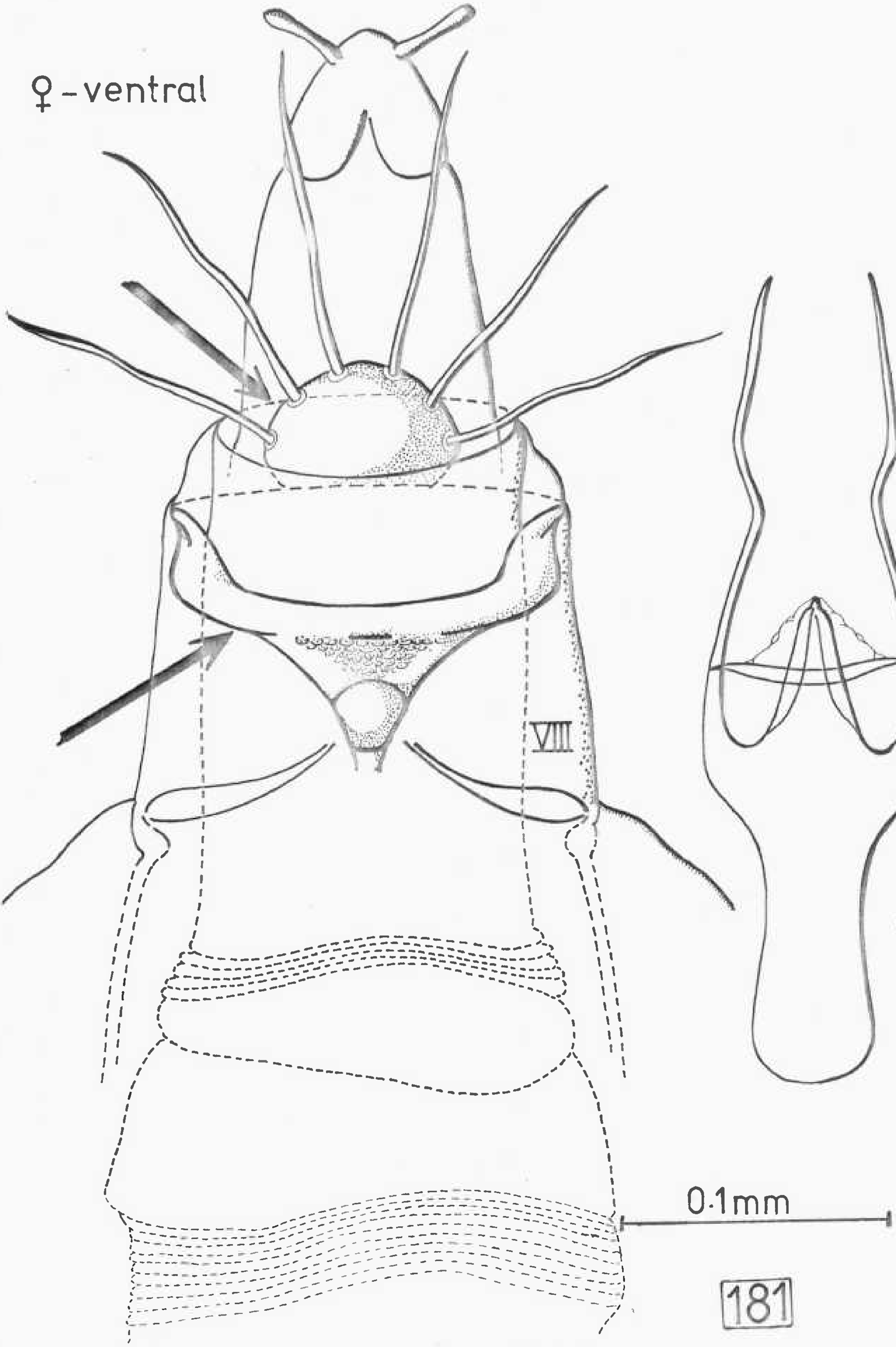
sylvestris Mort.

Hydroptila ♀♀ - dorsal



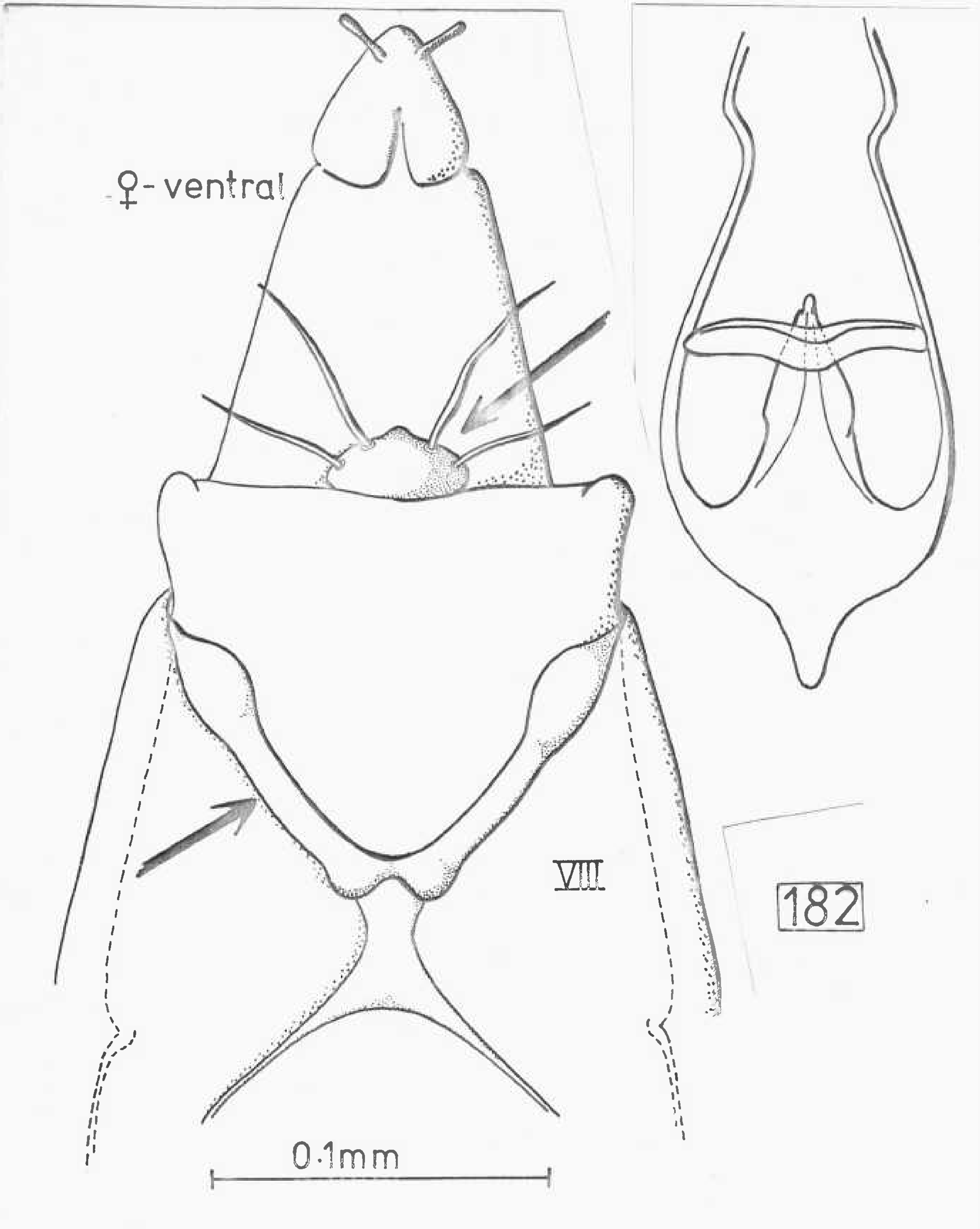
180

Hydroptila martini sp.n.



181

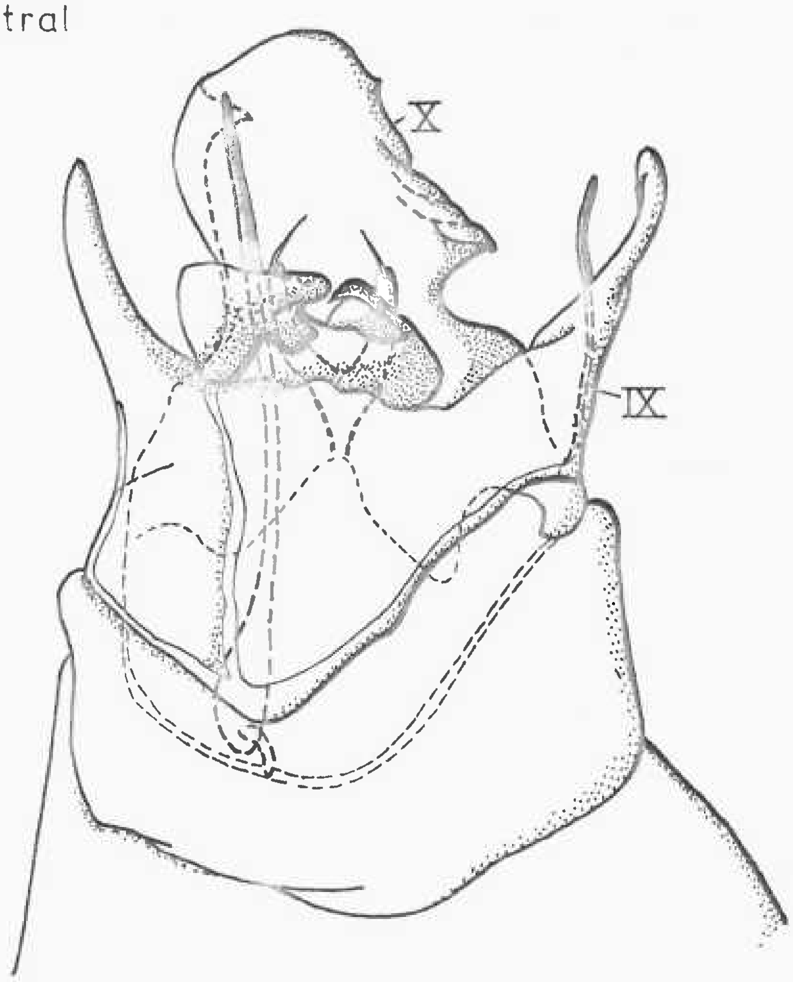
Hydroptila occulta (Eat.)

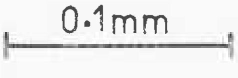


182

Hydroptila valesiaca Schmid

♂ - ventral

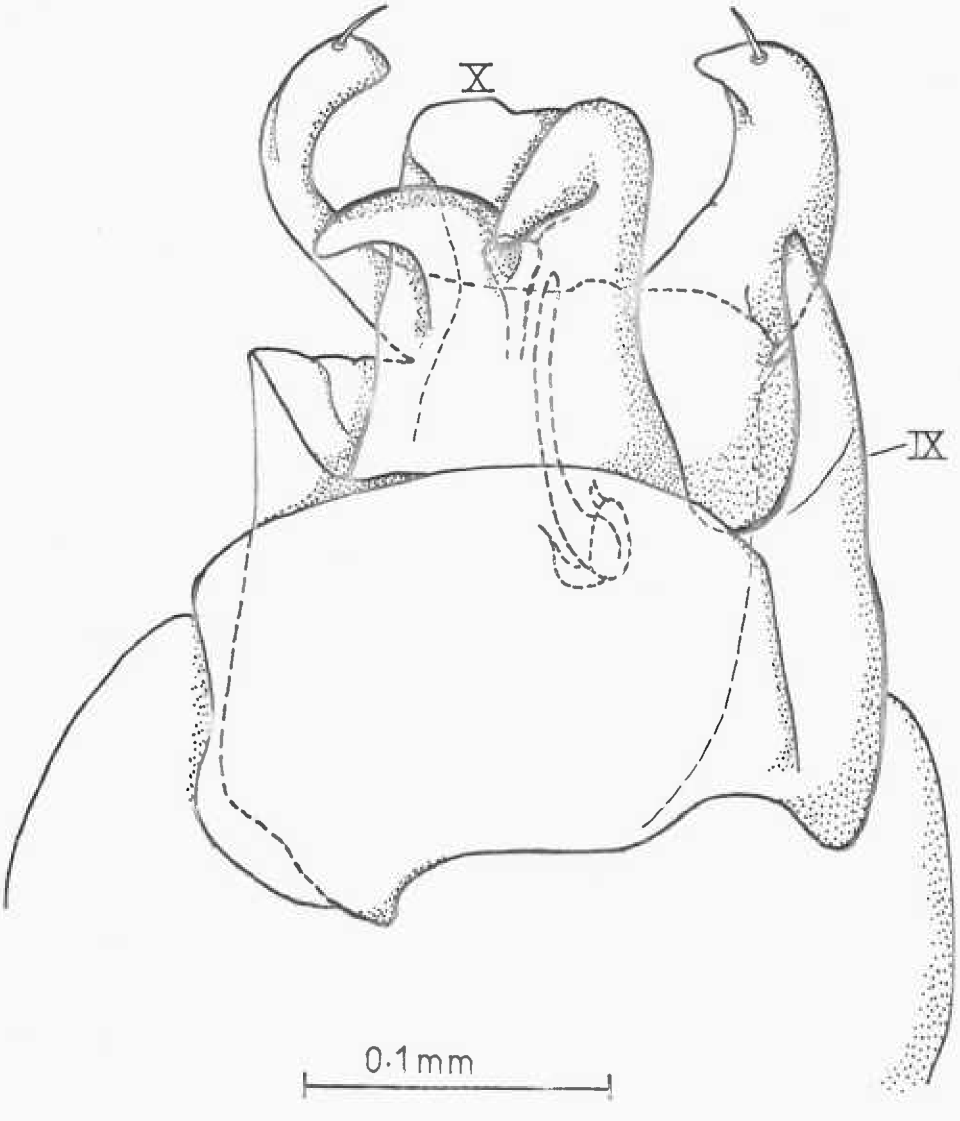




(183)

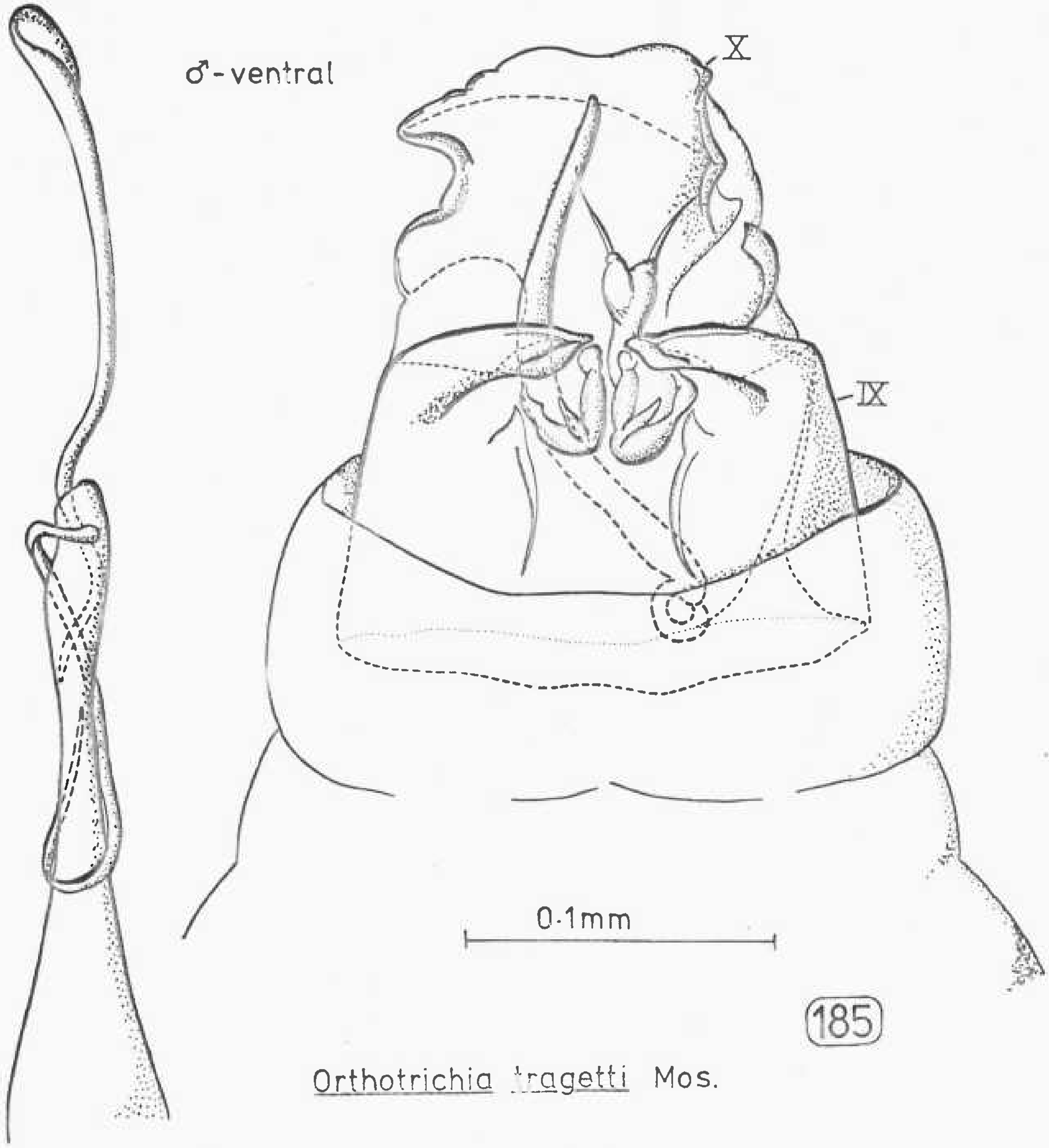
Orthotrichia angustella (McL.)

♂ - dorsal



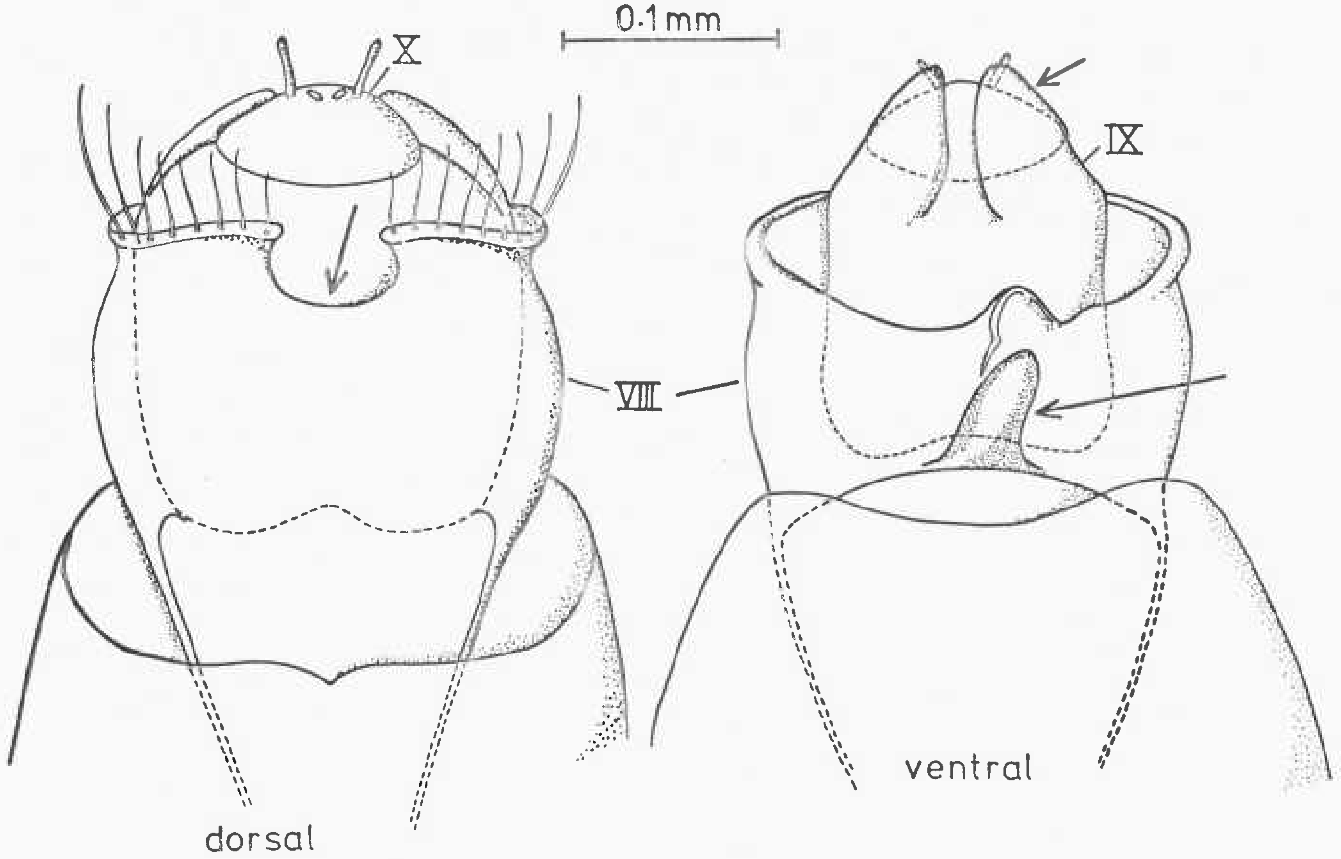
184

Orthotrichia costalis (Curt.)



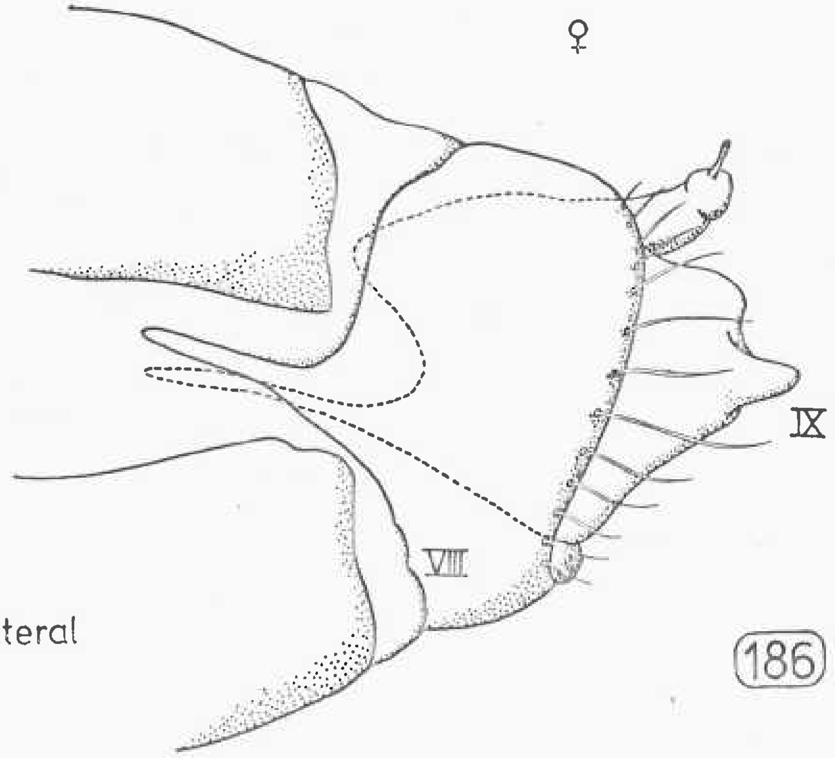
185

Orthotrichia tragetti Mos.

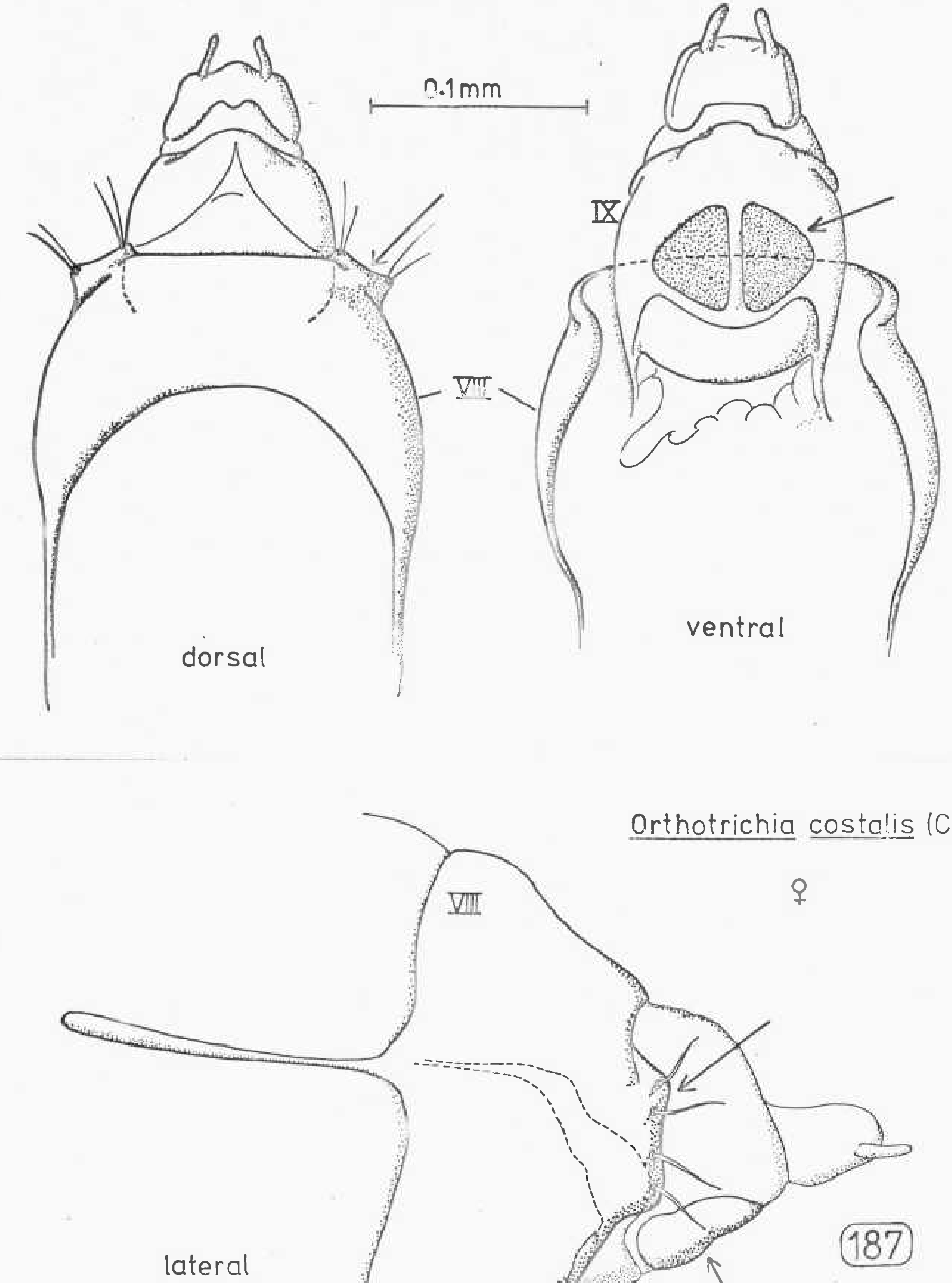


Orthotrichia angustella (McL.)

♀



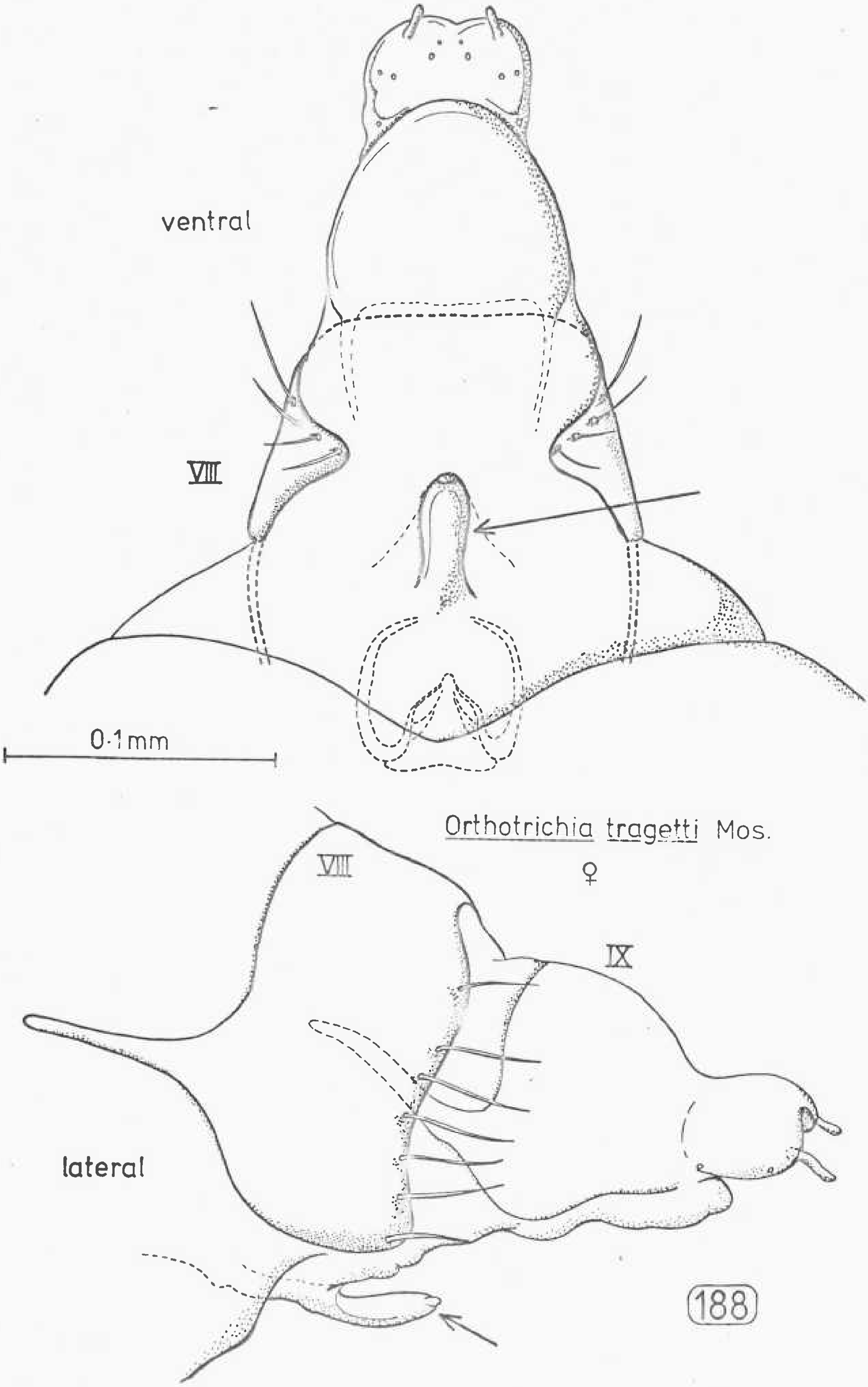
186



Orthotrichia costalis (Curt.)

♀

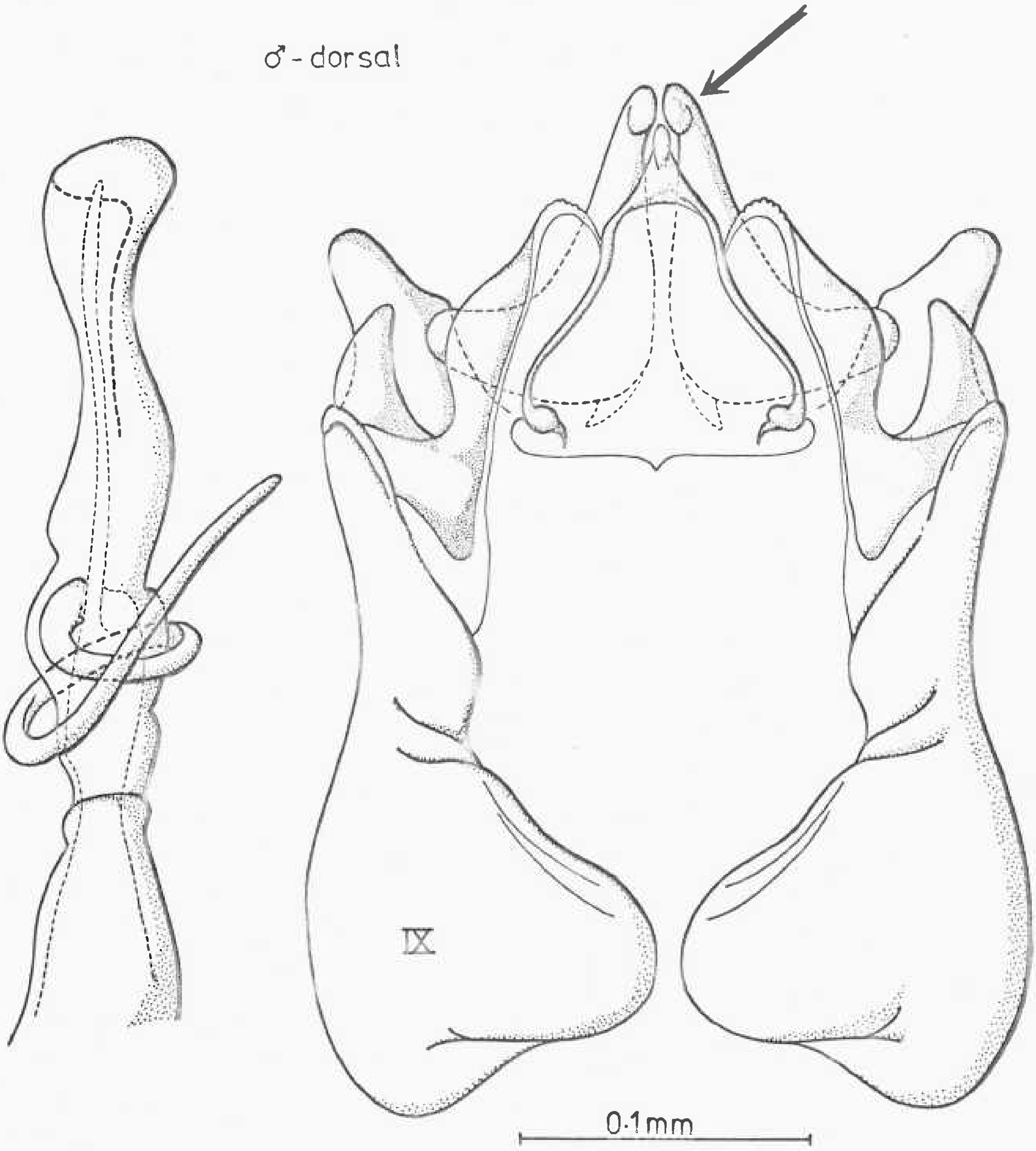
187



Orthotrichia tragetti Mos.

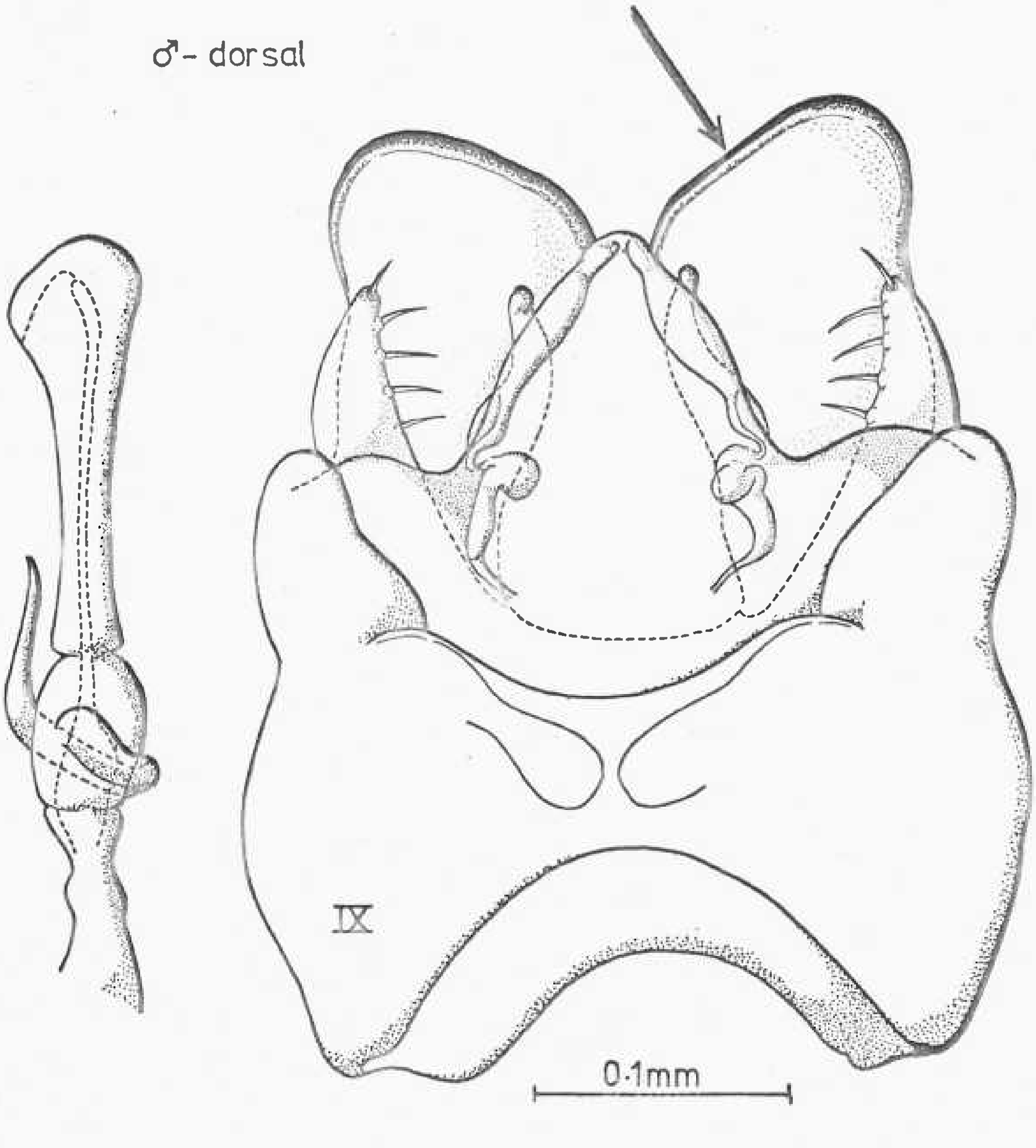
♀

188



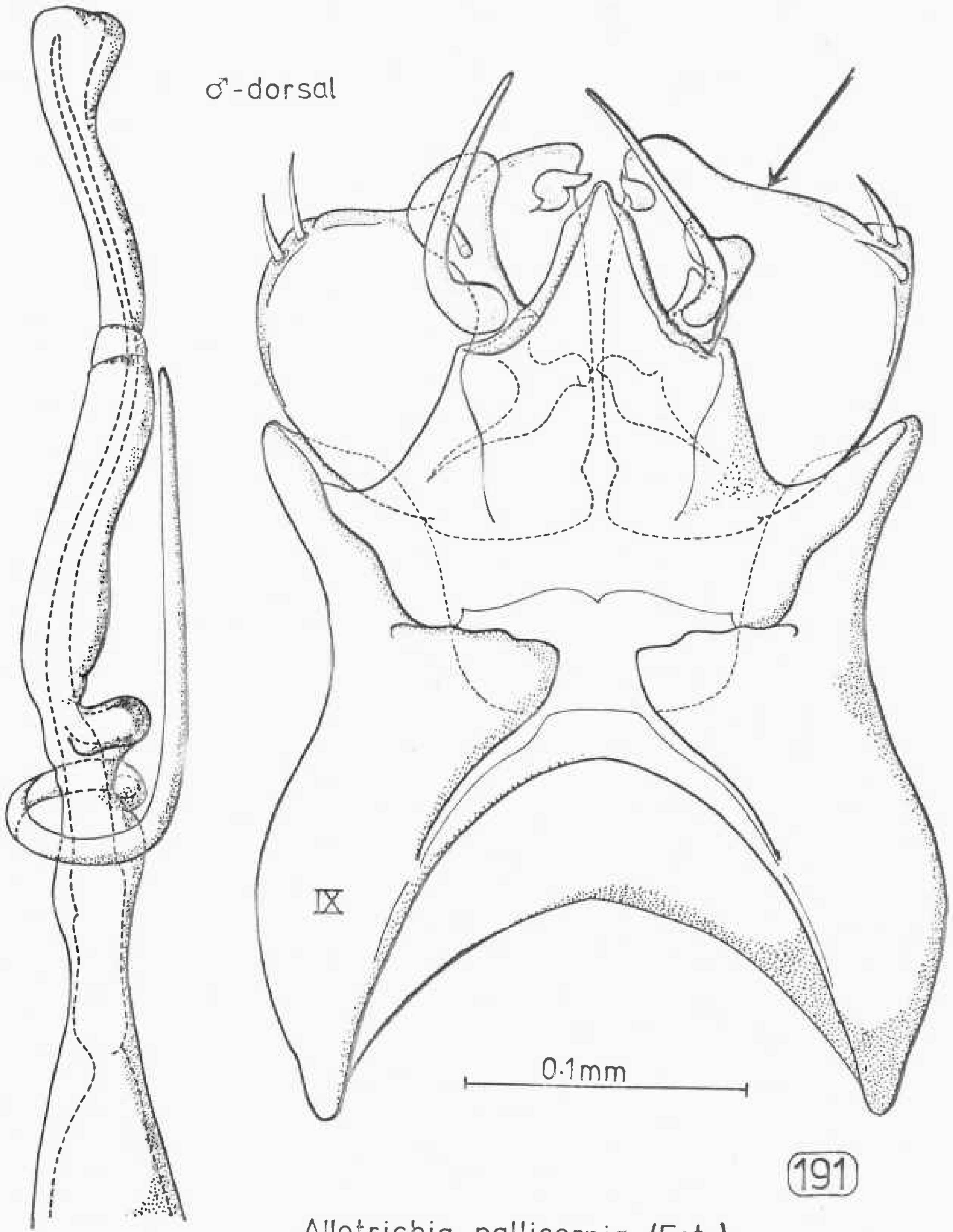
189

Agraylea multipunctata Curt.



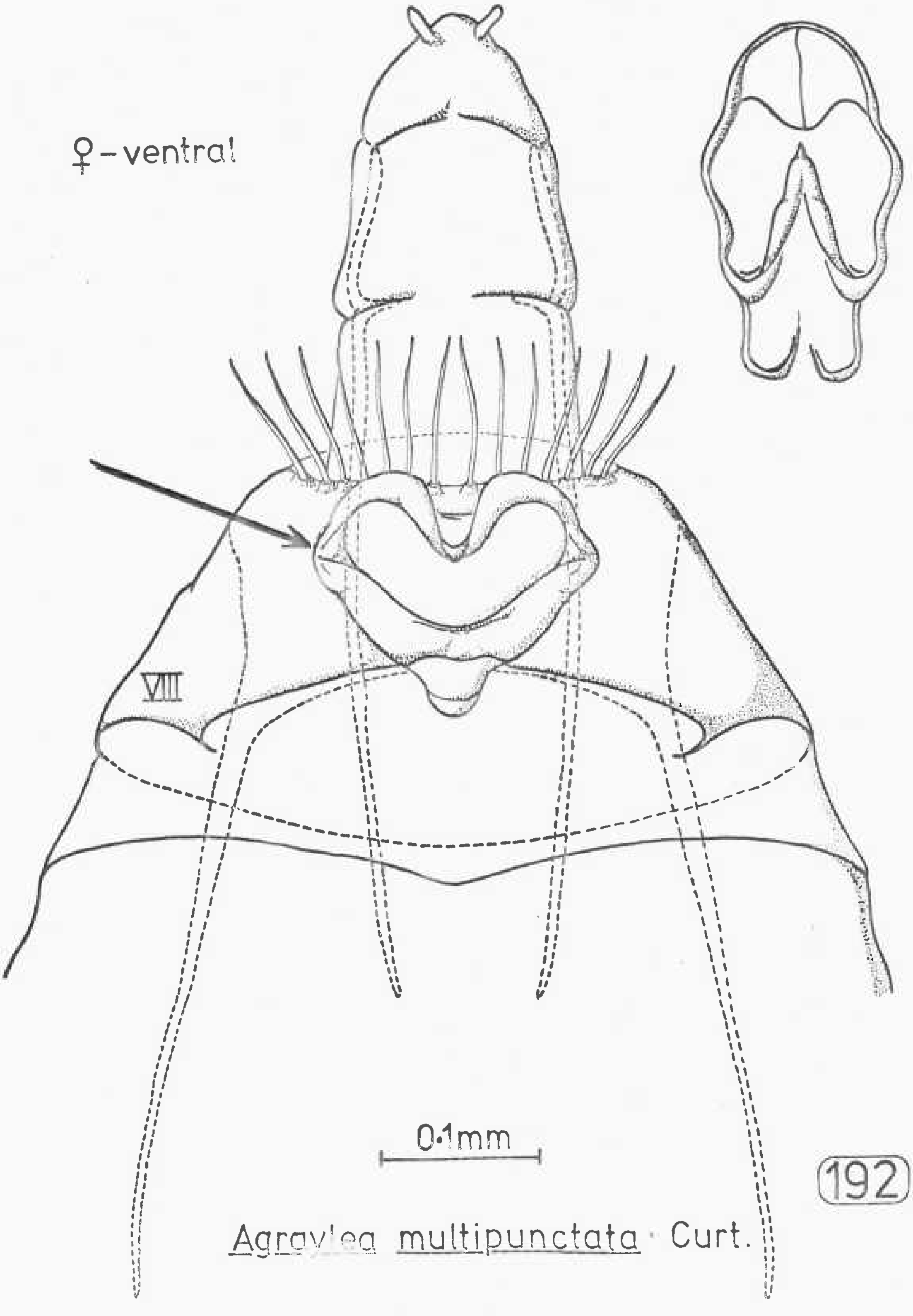
190

Agraylea sexmaculata Curt.



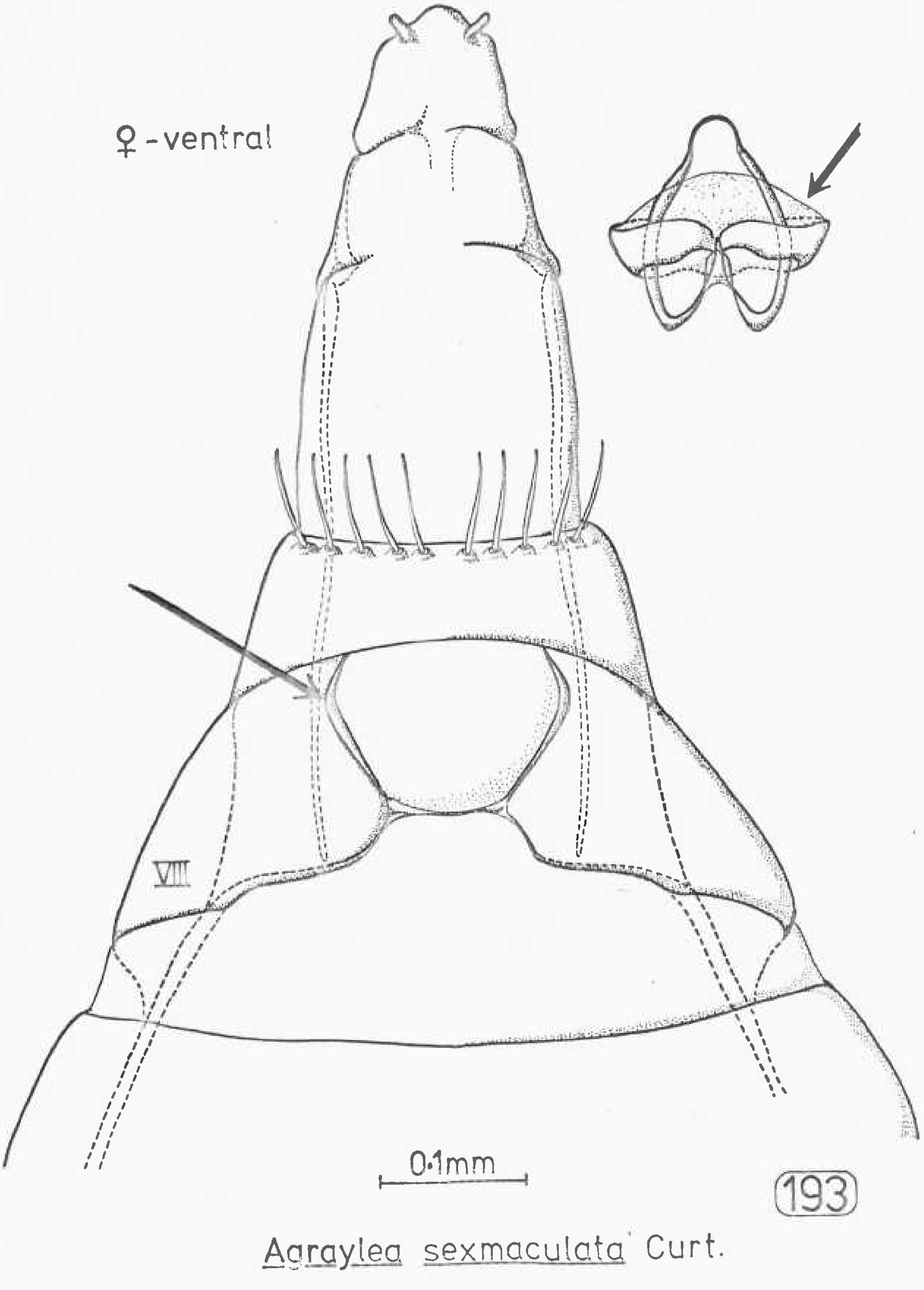
191

Allotrichia pallicornis (Eat.)



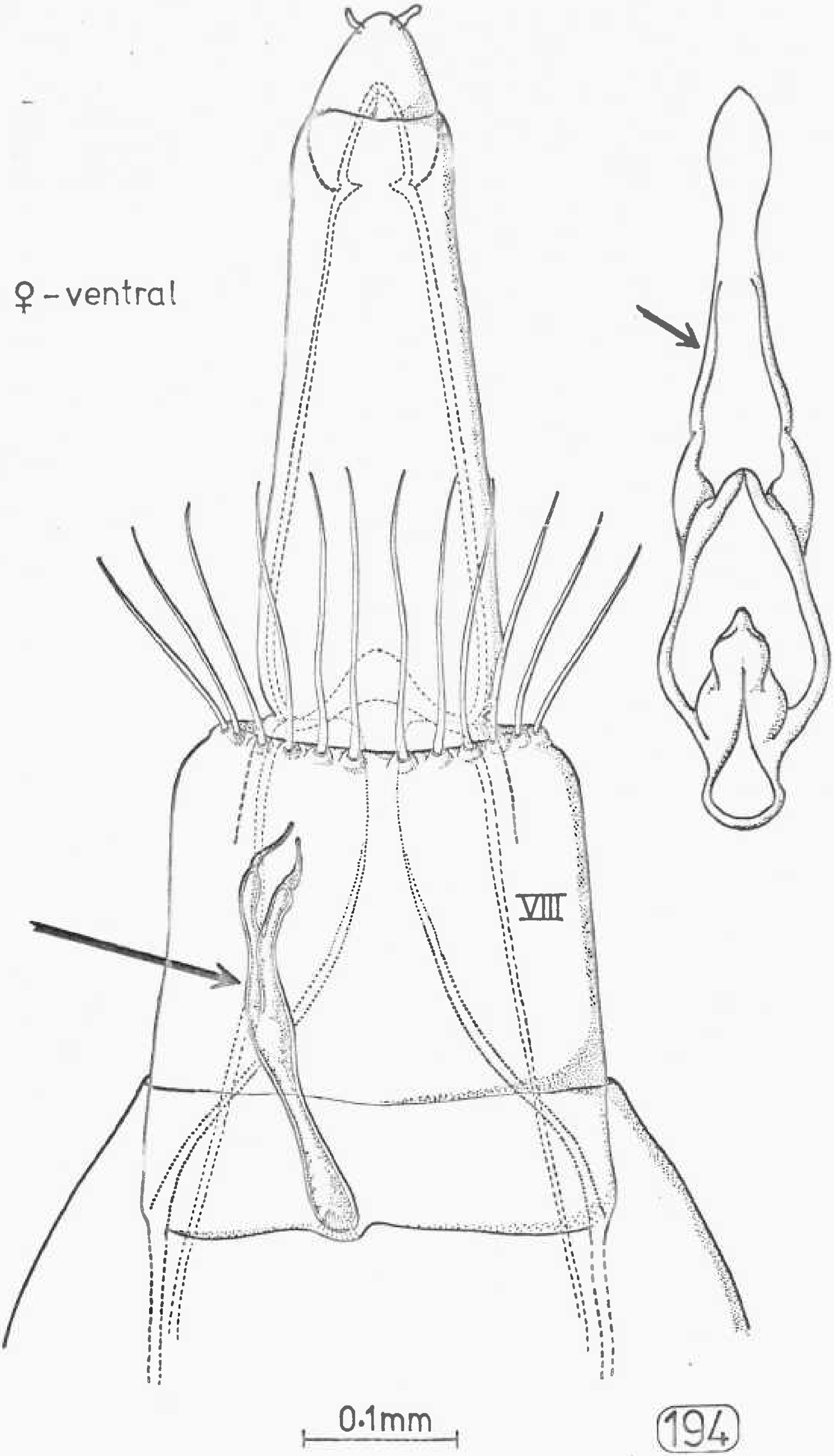
192

Agraylea multipunctata Curt.



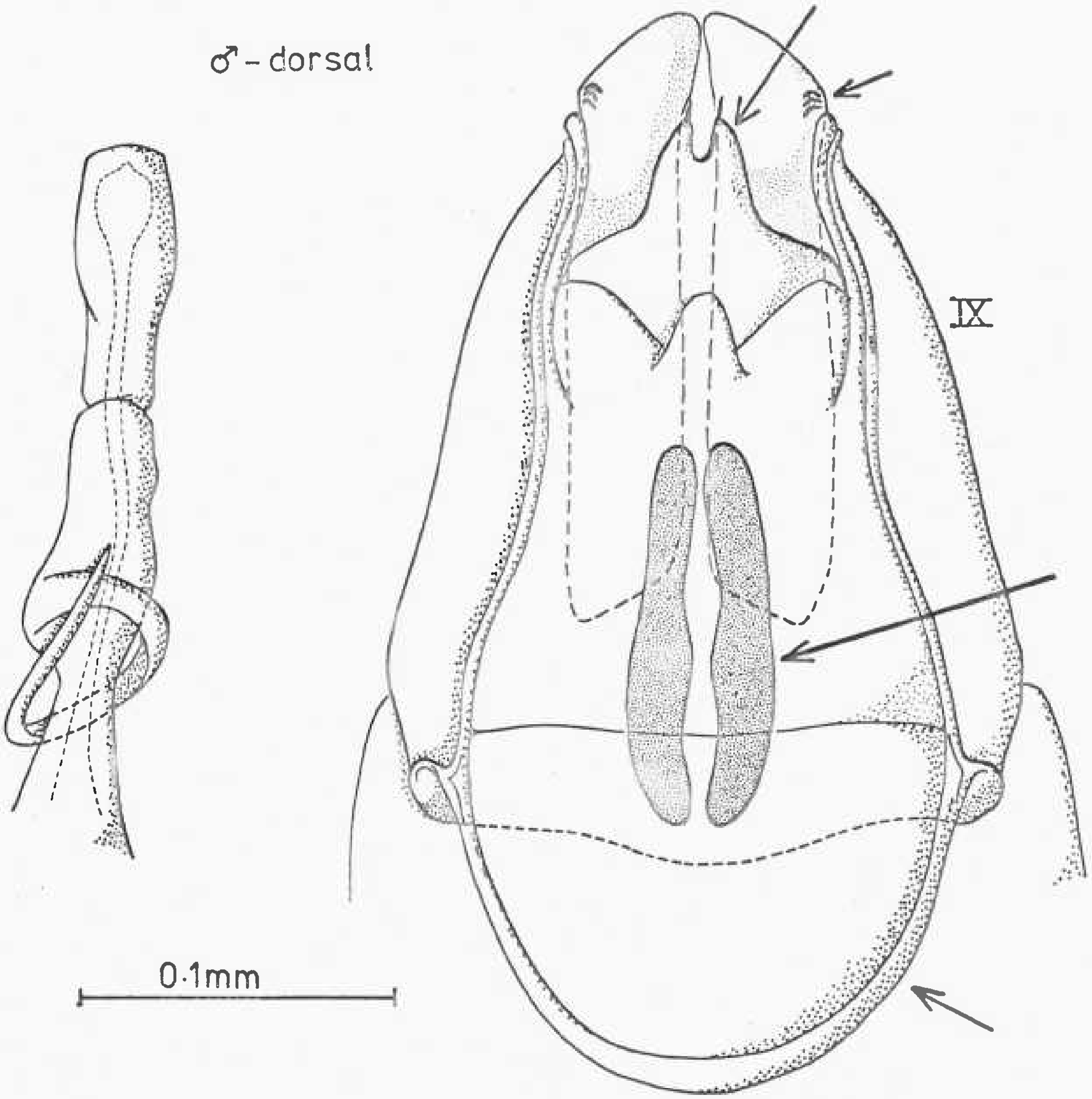
193

Agraylea sexmaculata Curt.



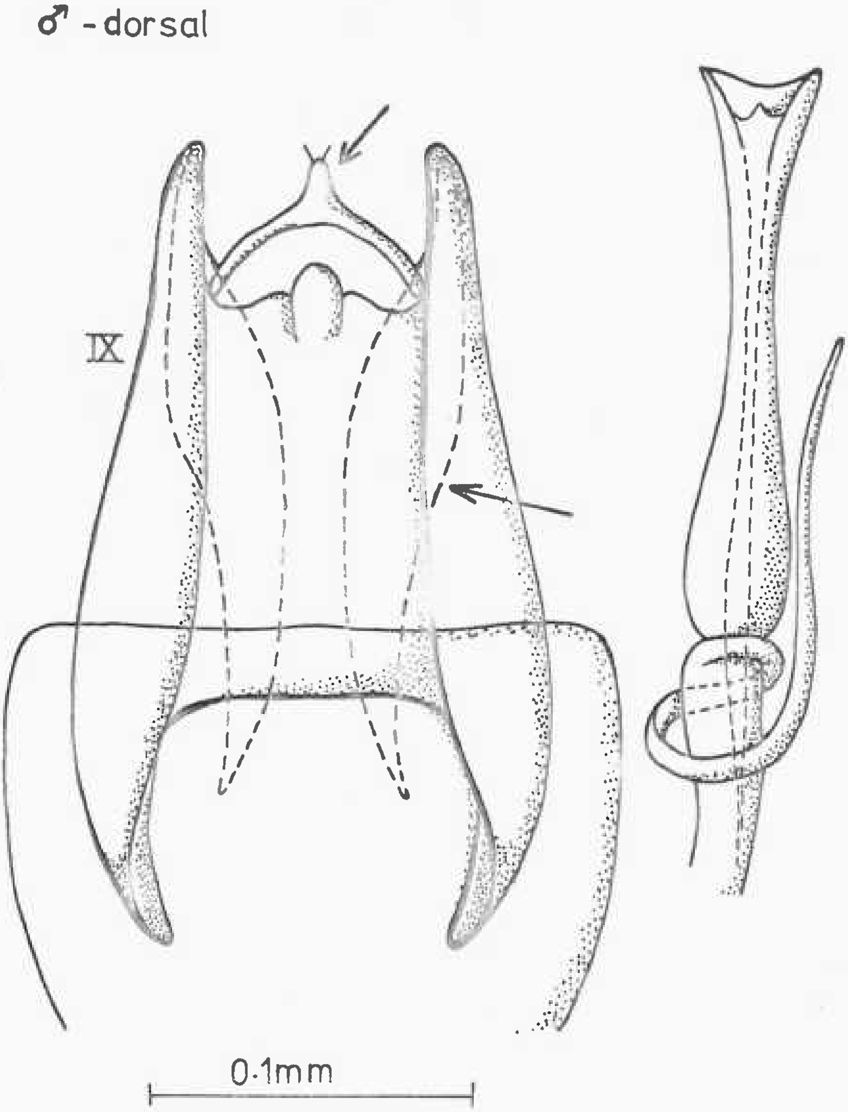
194

Allotrichia pallicornis (Eat.)



195

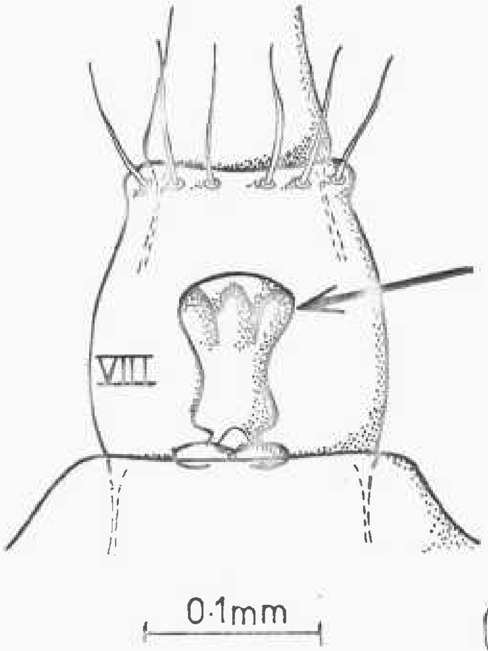
Ithytrichia lamellaris Eat.



196

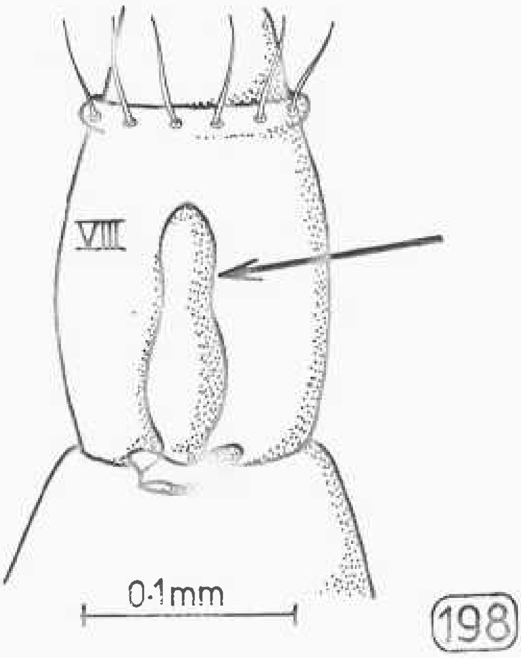
Ithytrichia clavata Mort.

after Tjeder (1930)

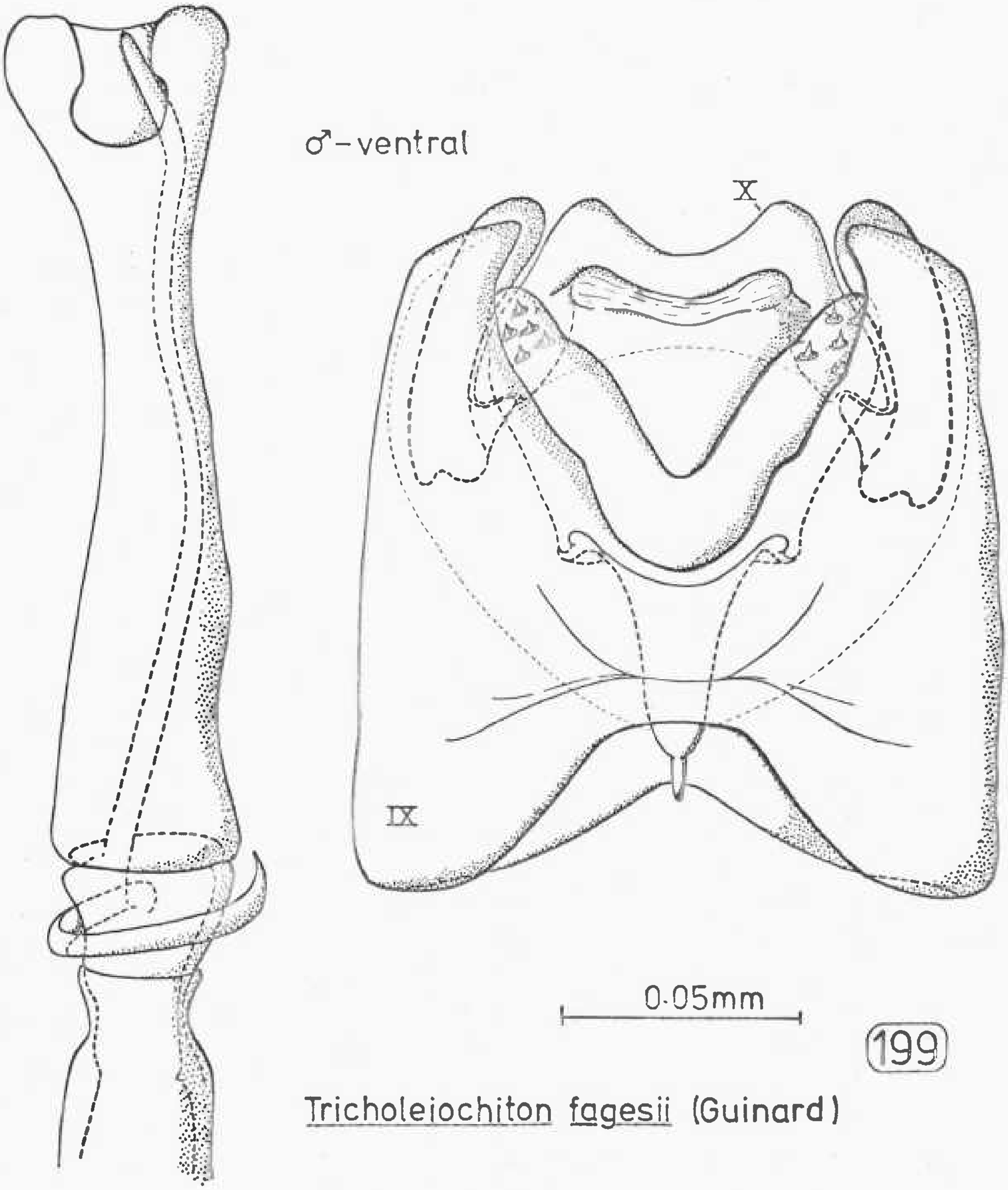


<u>Ithytrichia</u> <u>lamellaris</u> Eat.

♀♀ – ventral

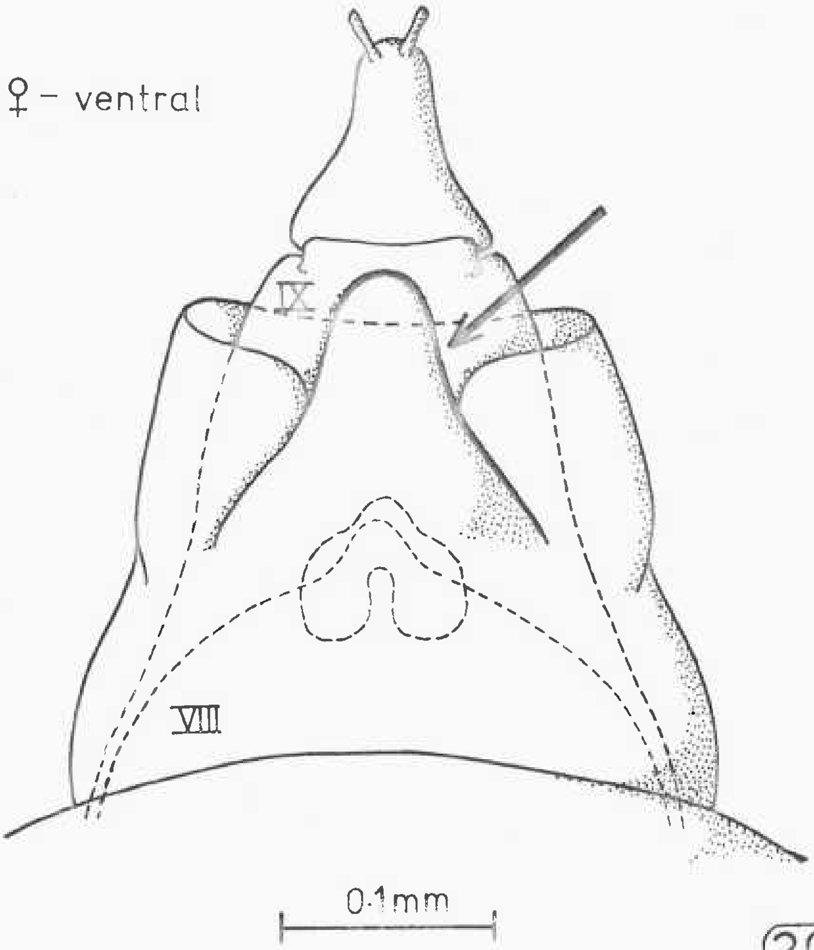


<u>Ithytrichia</u> <u>clavata</u> Mort.



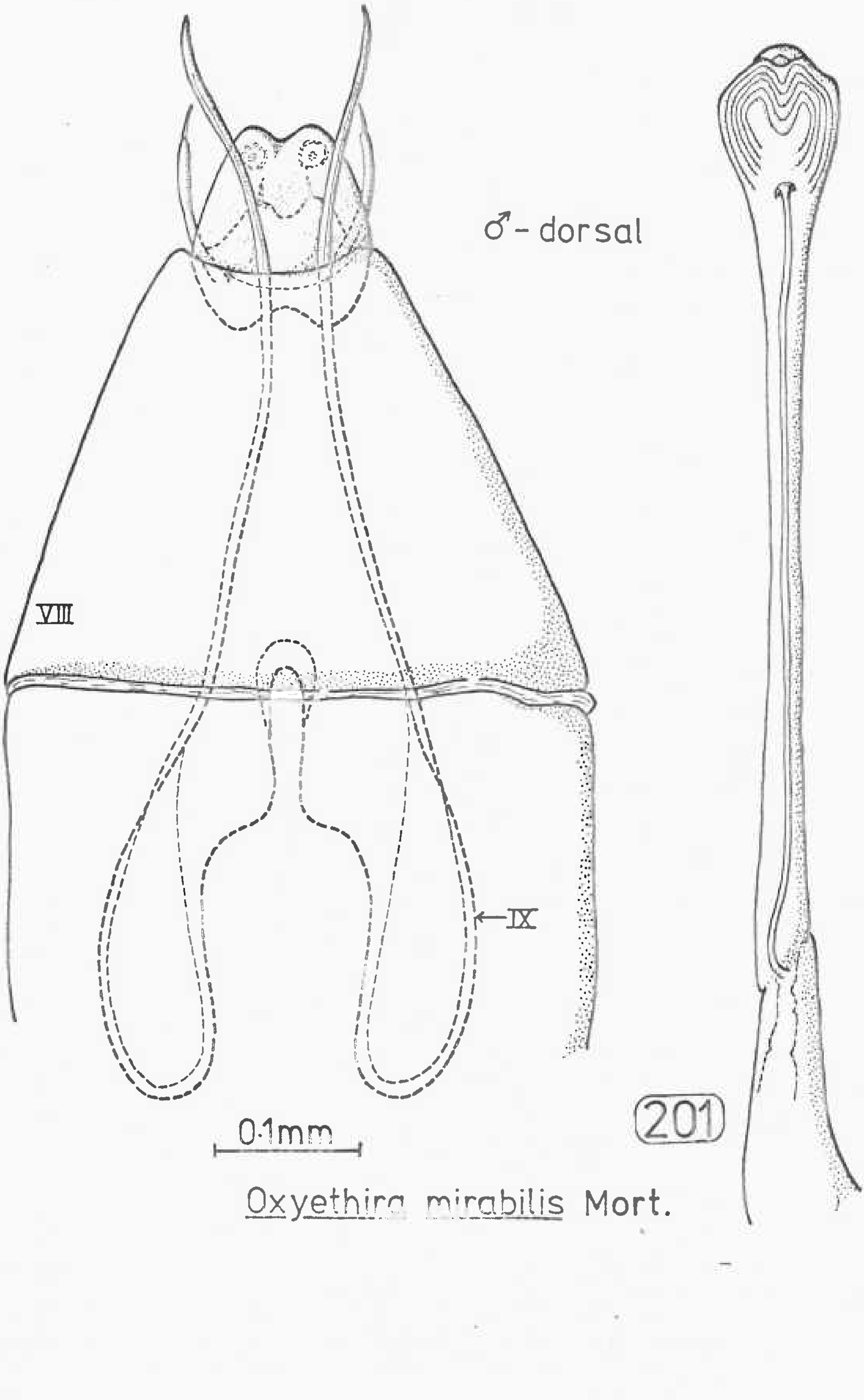
199

Tricholeiochiton fagesii (Guinard)



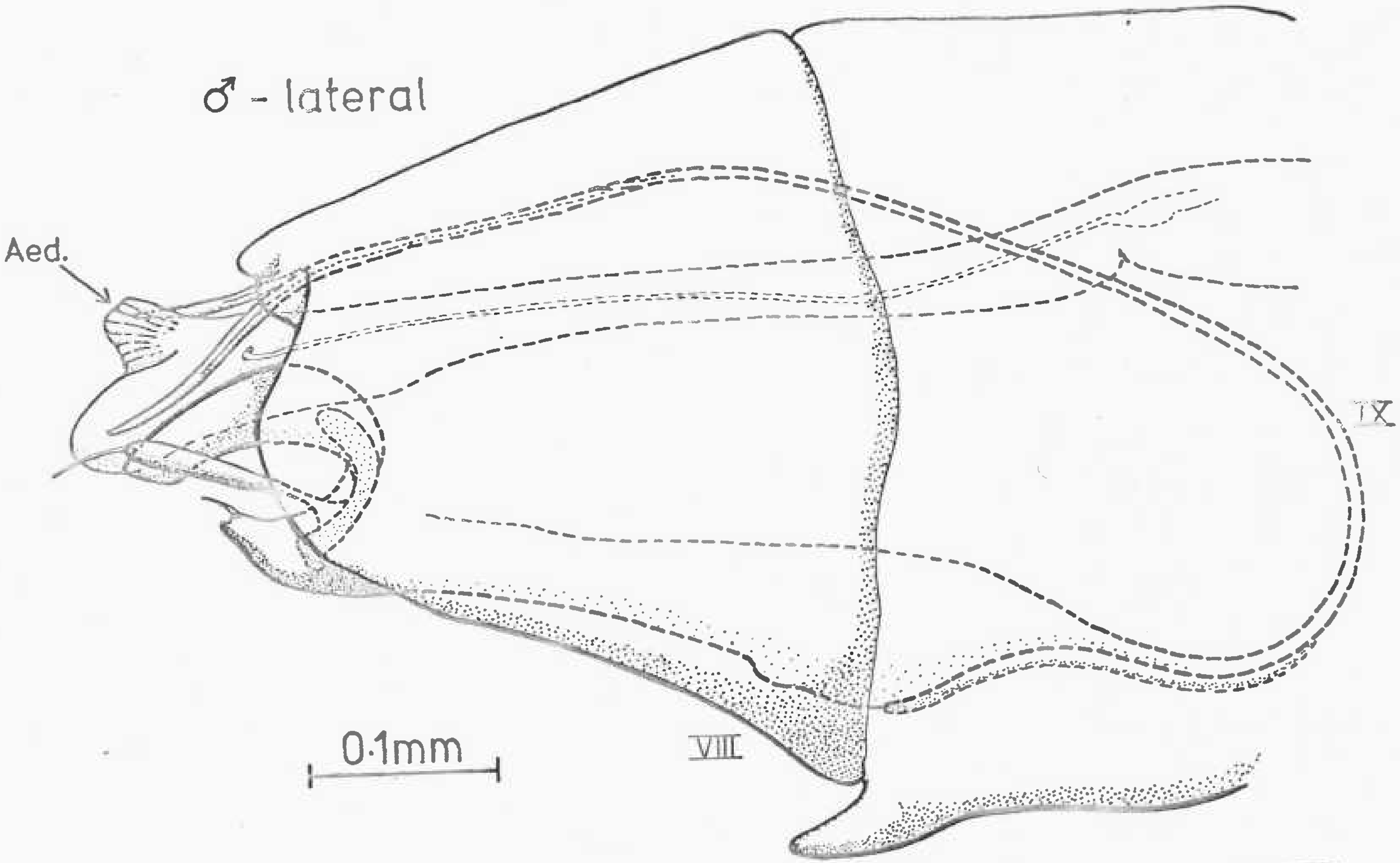
(200)

Tricholeiochiton fagesii (Guinard)



201

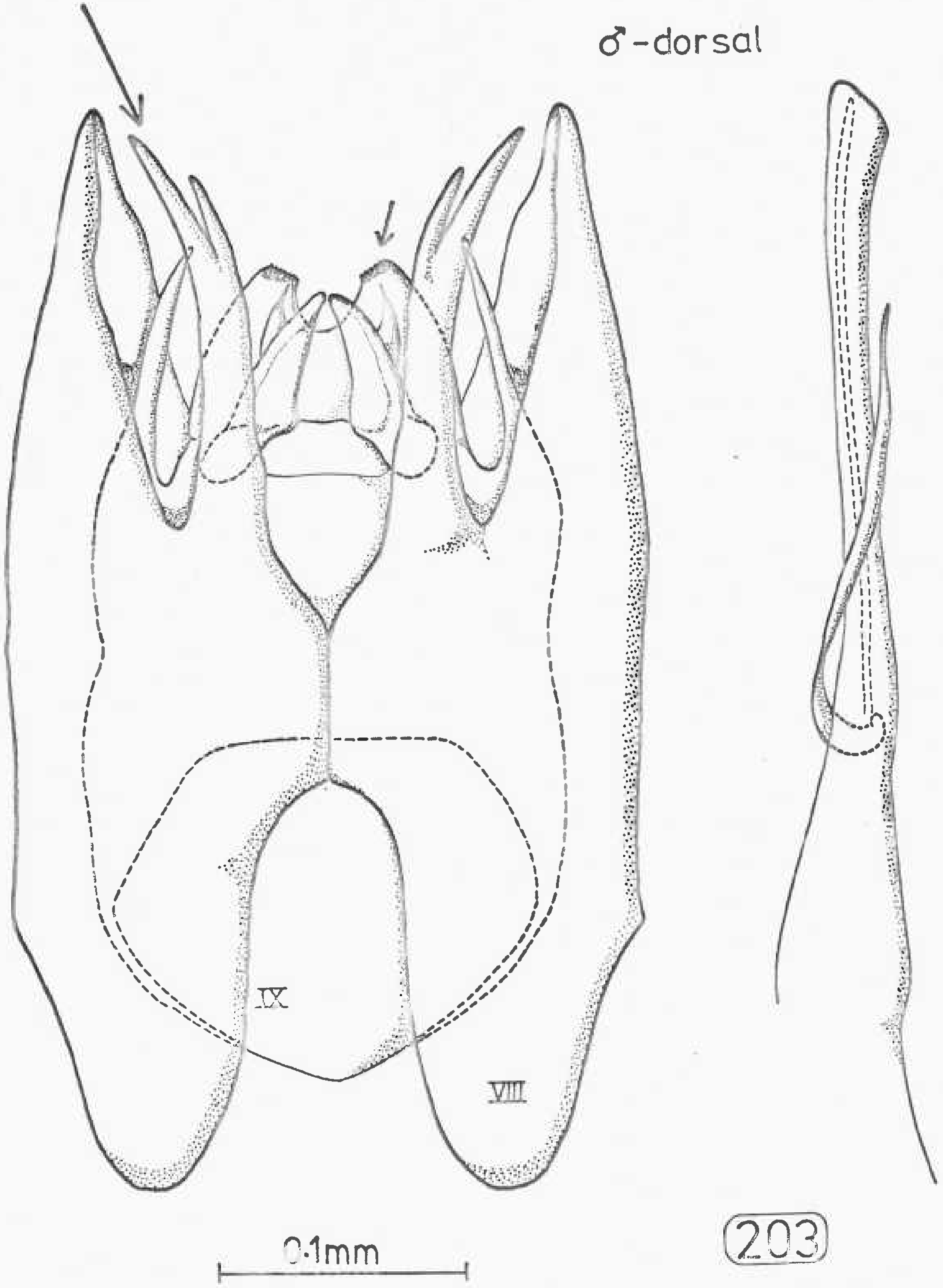
Oxyethira mirabilis Mort.



202

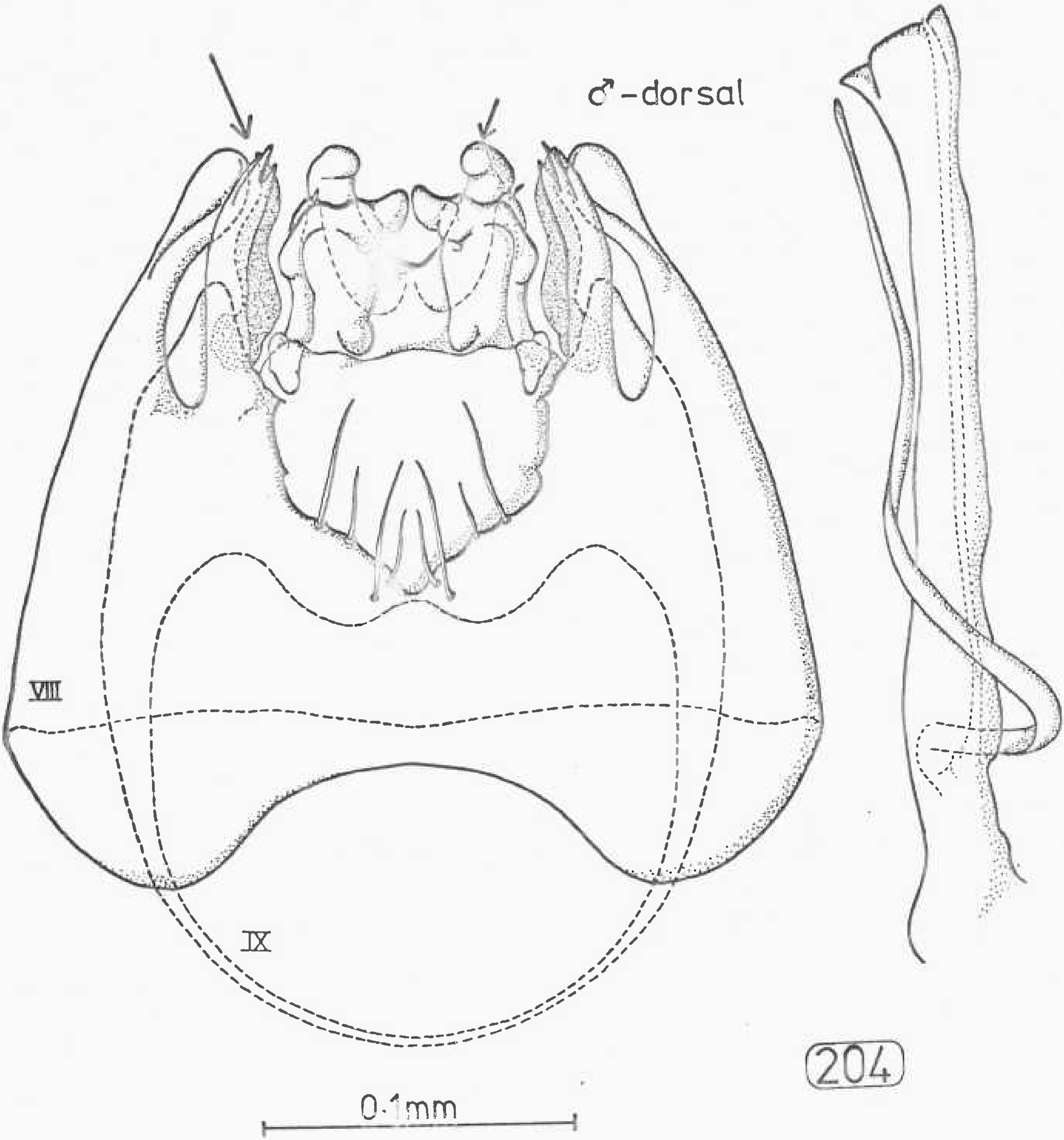
Oxyethira mirabilis Mort.

♂-dorsal



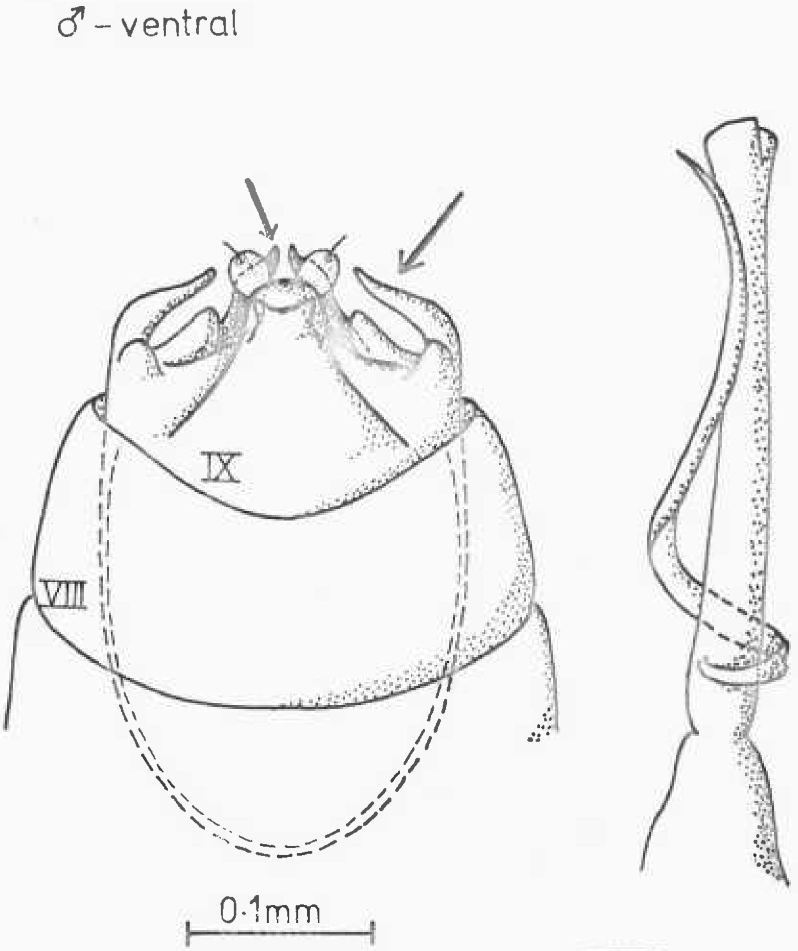
203

Oxyethira distinctella McL.



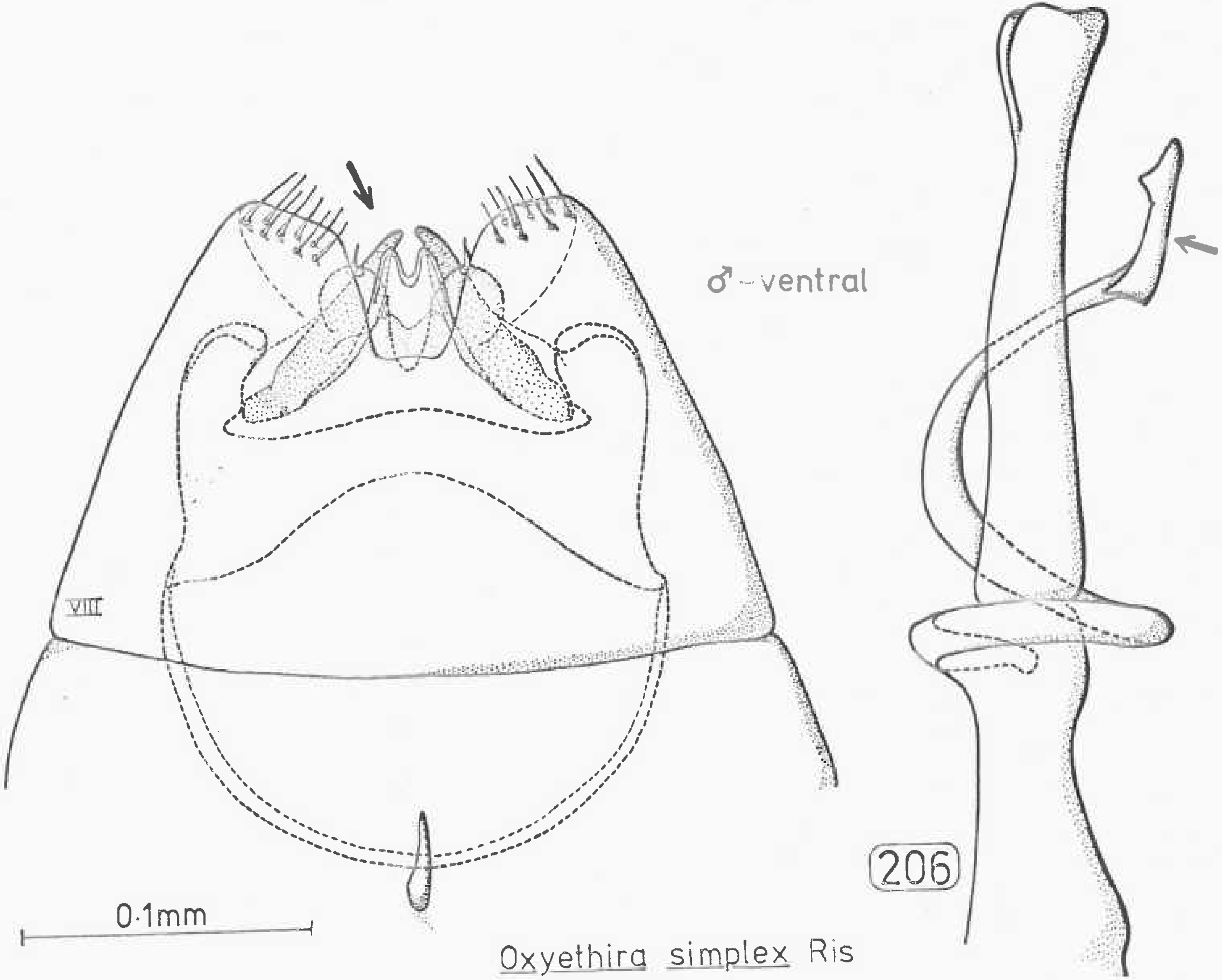
204

Oxyethira sagittifera Ris



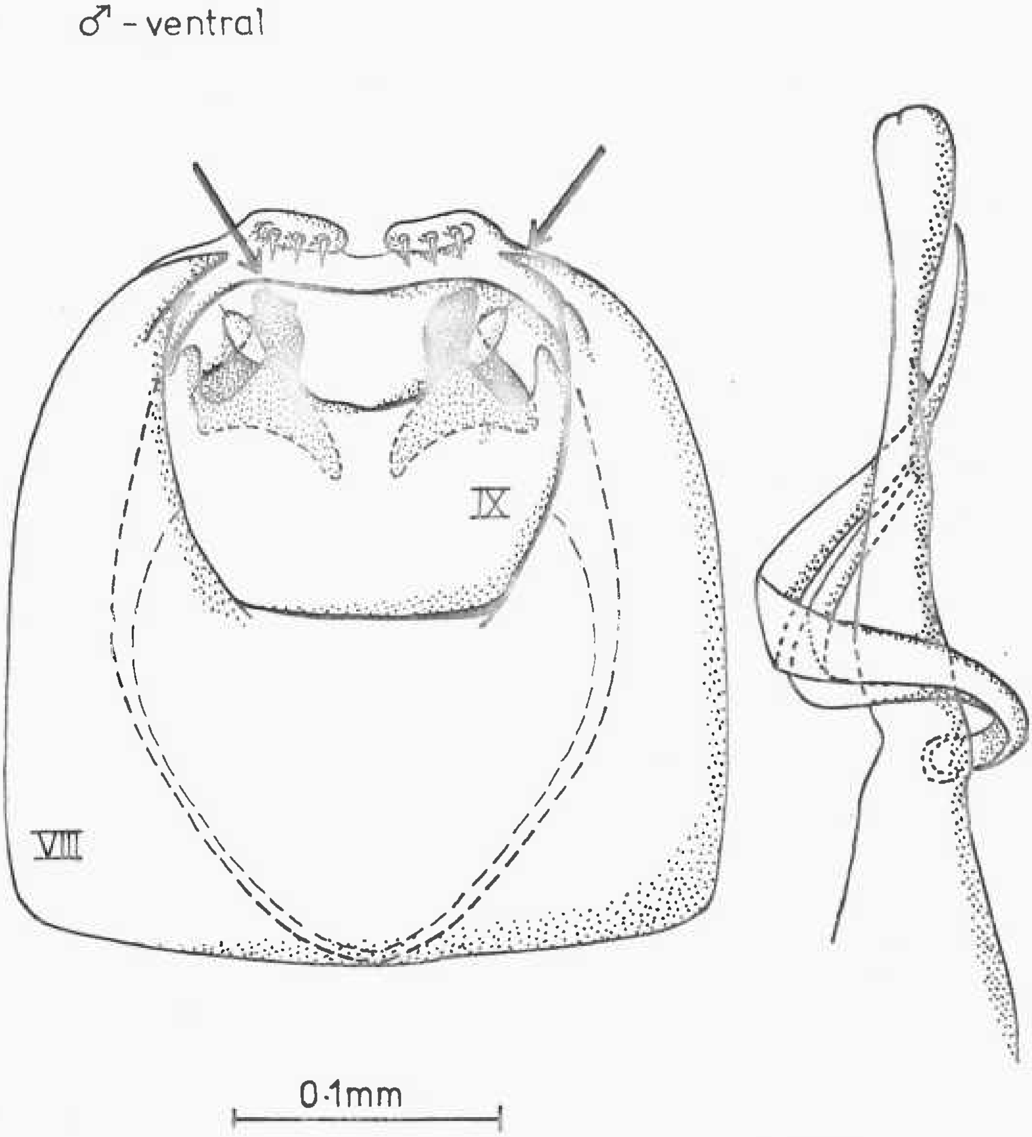
205

Oxyethira tristella Klap.



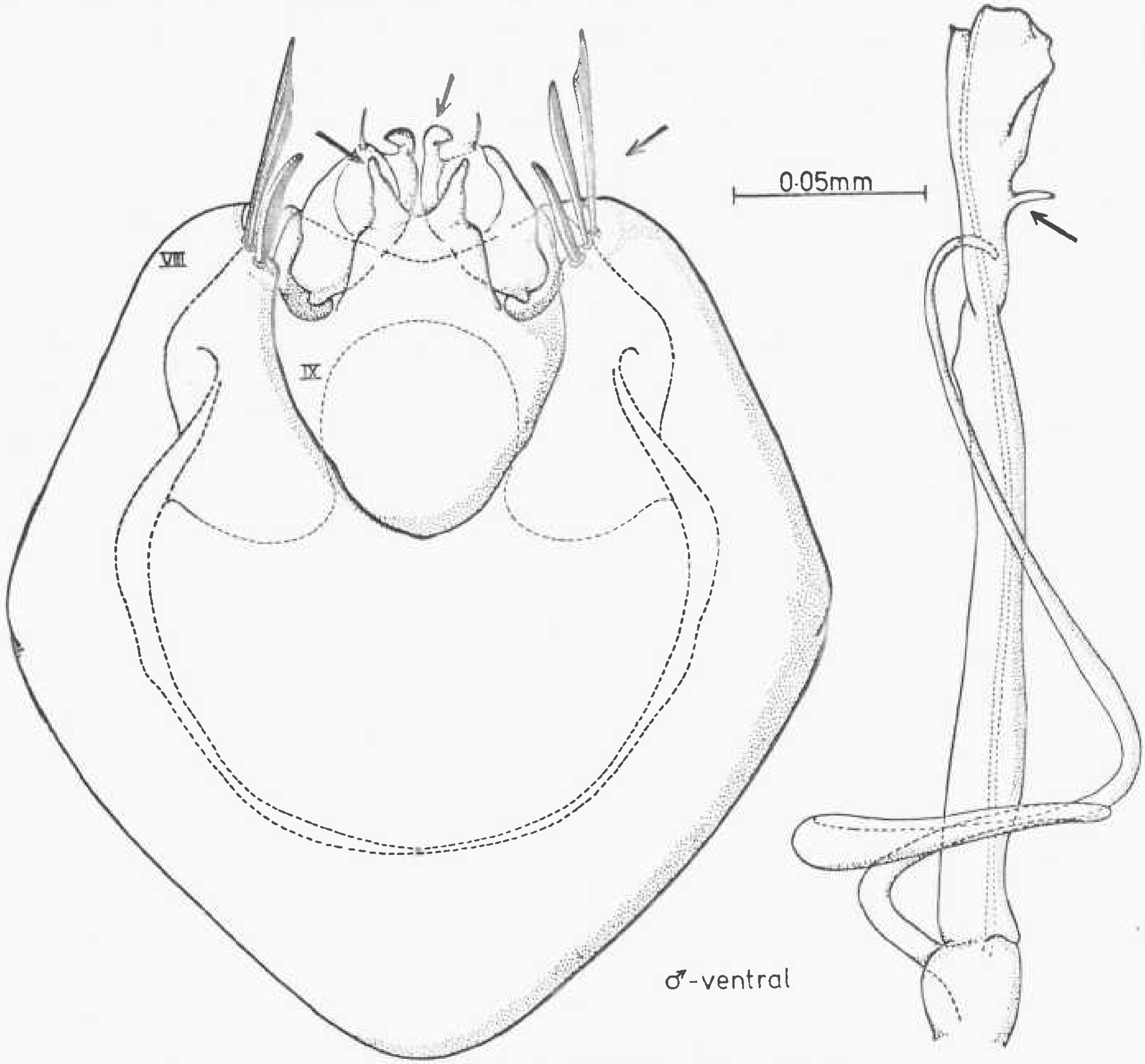
206

Oxyethira simplex Ris



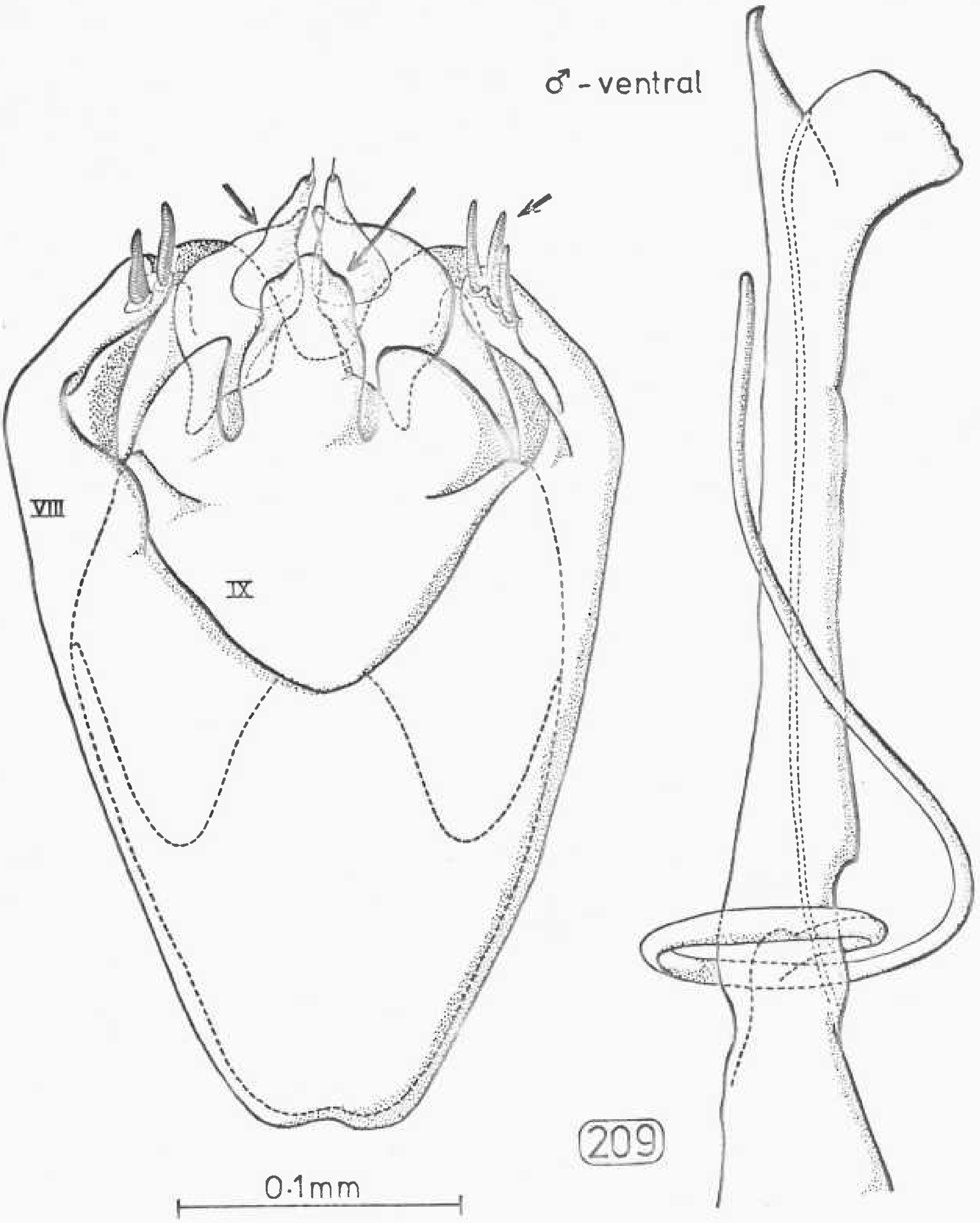
(207)

Oxyethira flavicornis (Pict.)



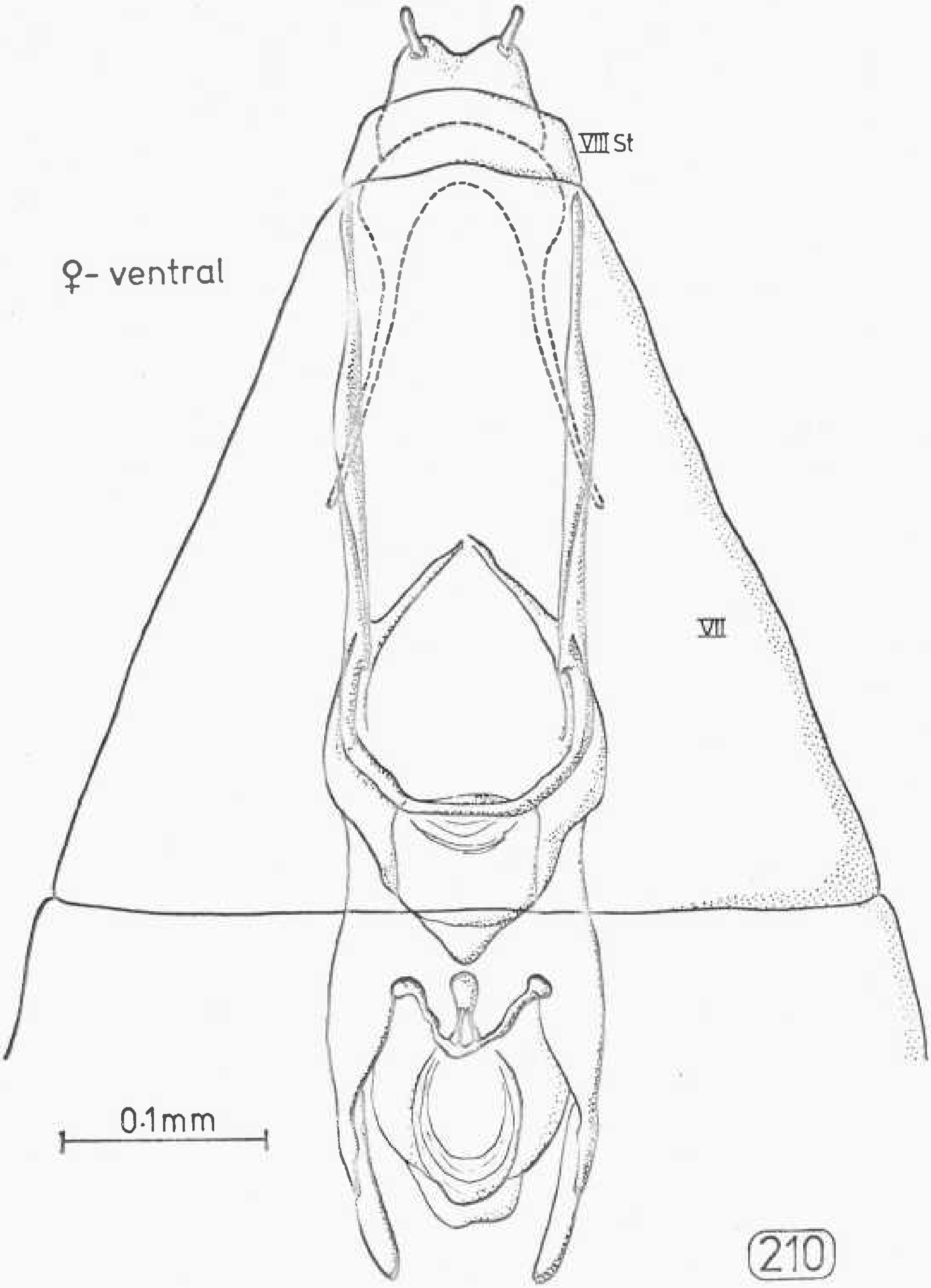
208

Oxyethira frici Klap.



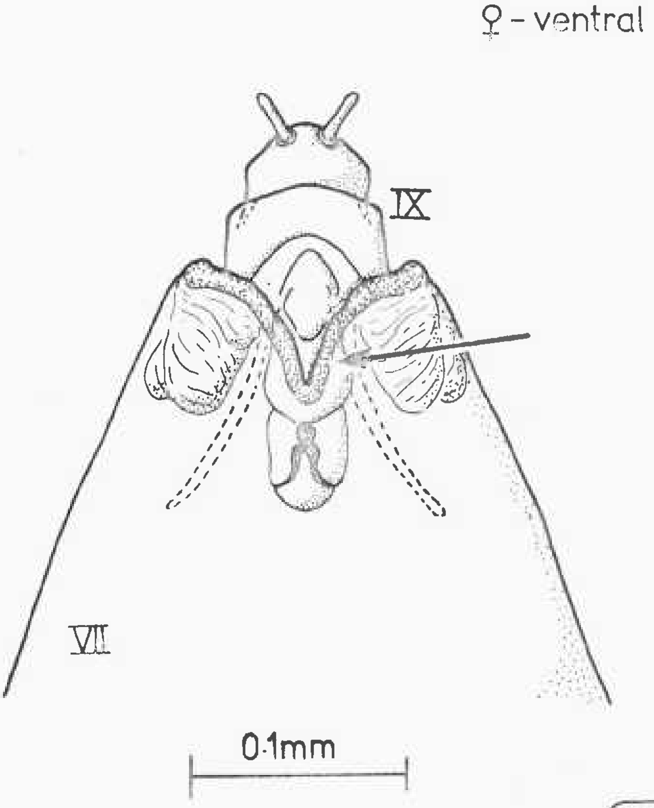
209

Oxyethira falcata Mort.



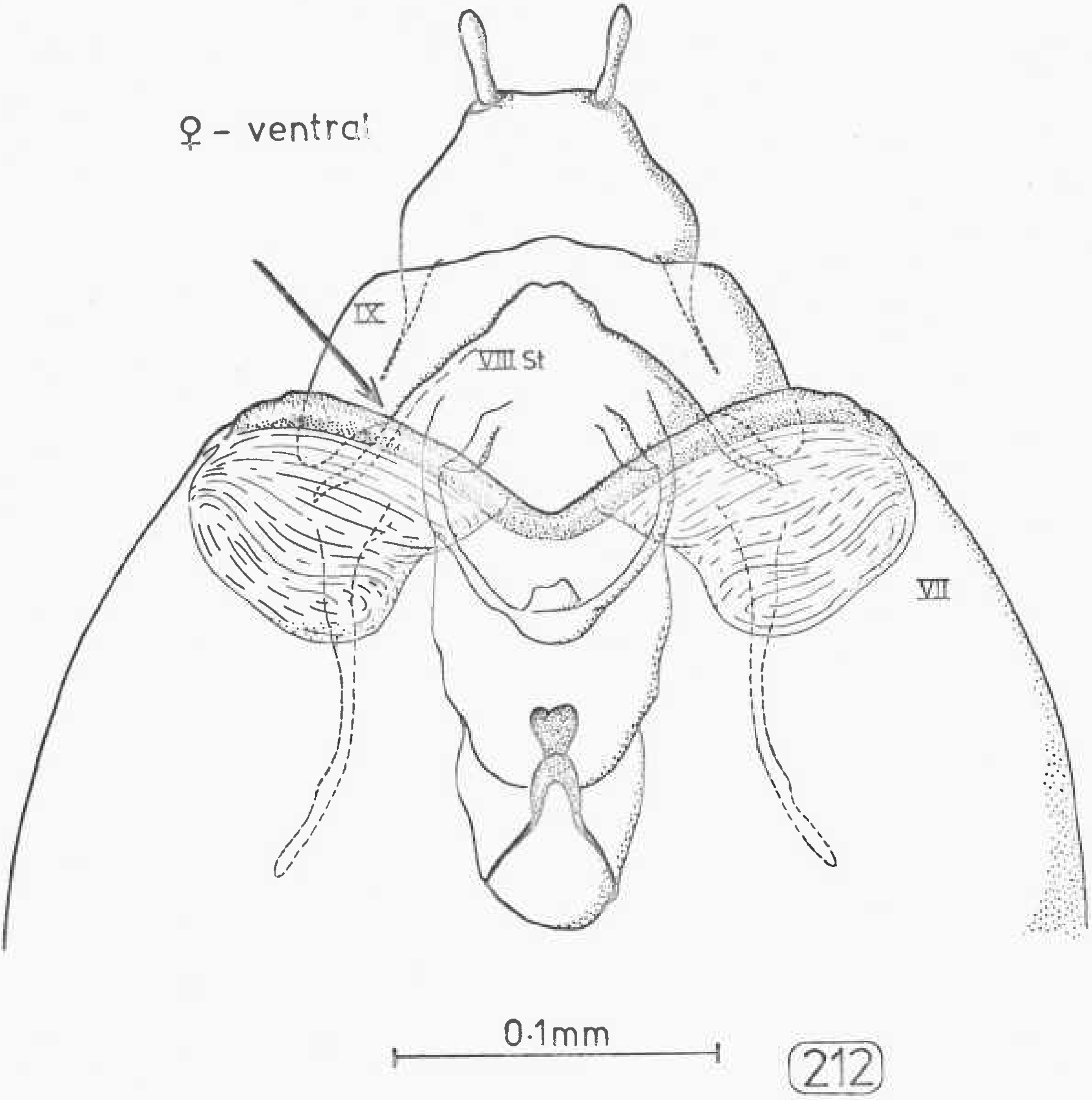
(210)

Oxyethira mirabilis Mort.



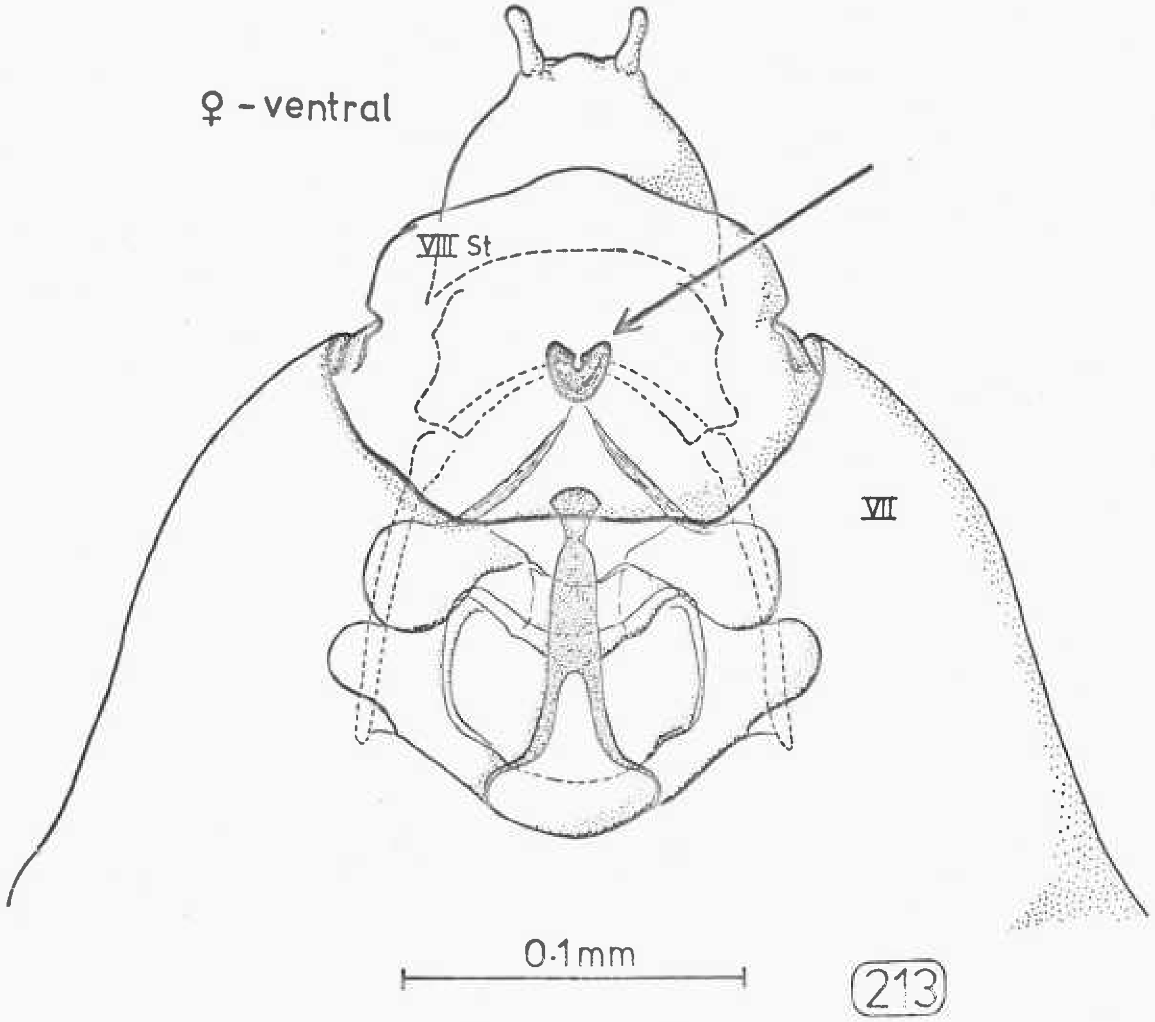
(211)

Oxyethira distinctella McL.



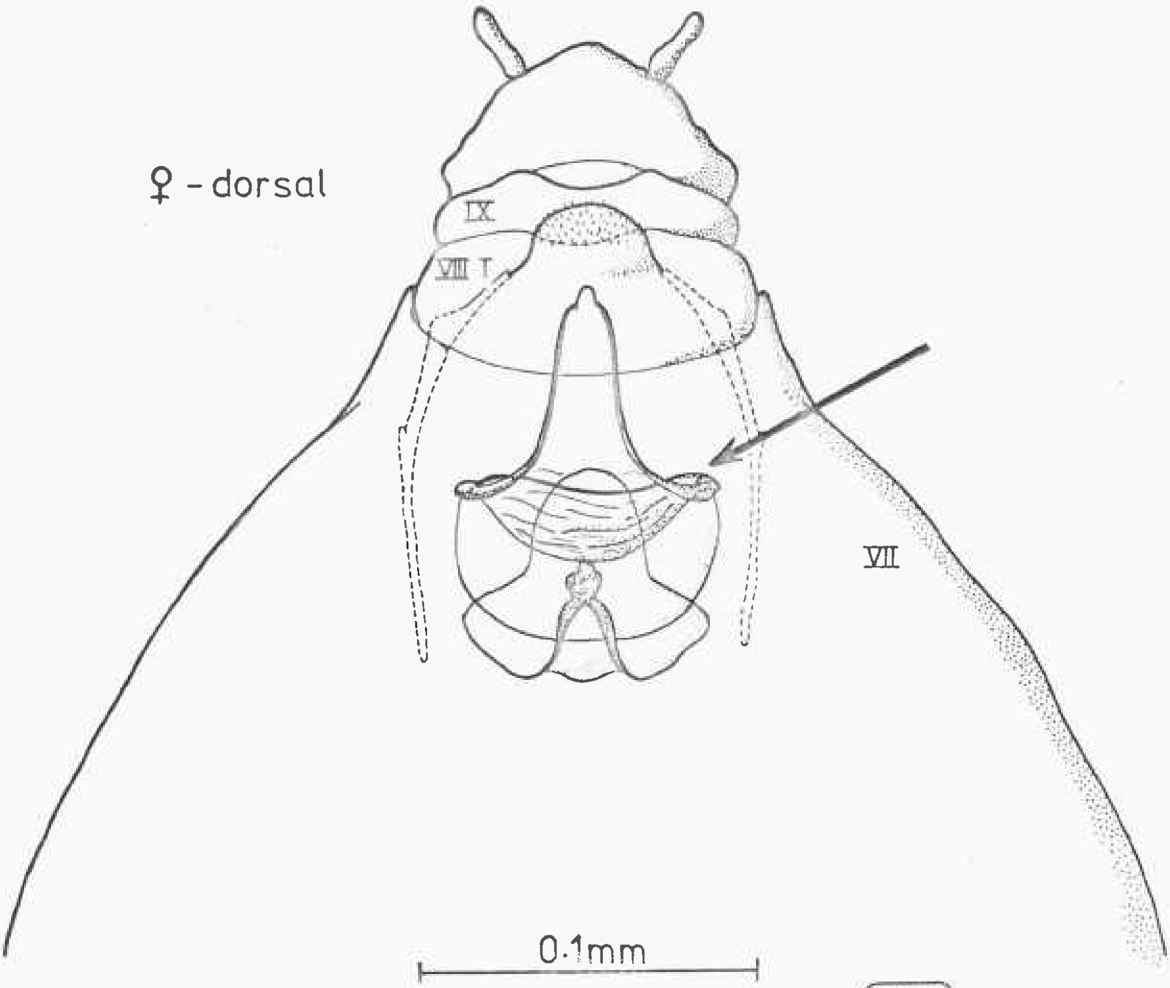
(212)

Oxyethira sagittifera Ris



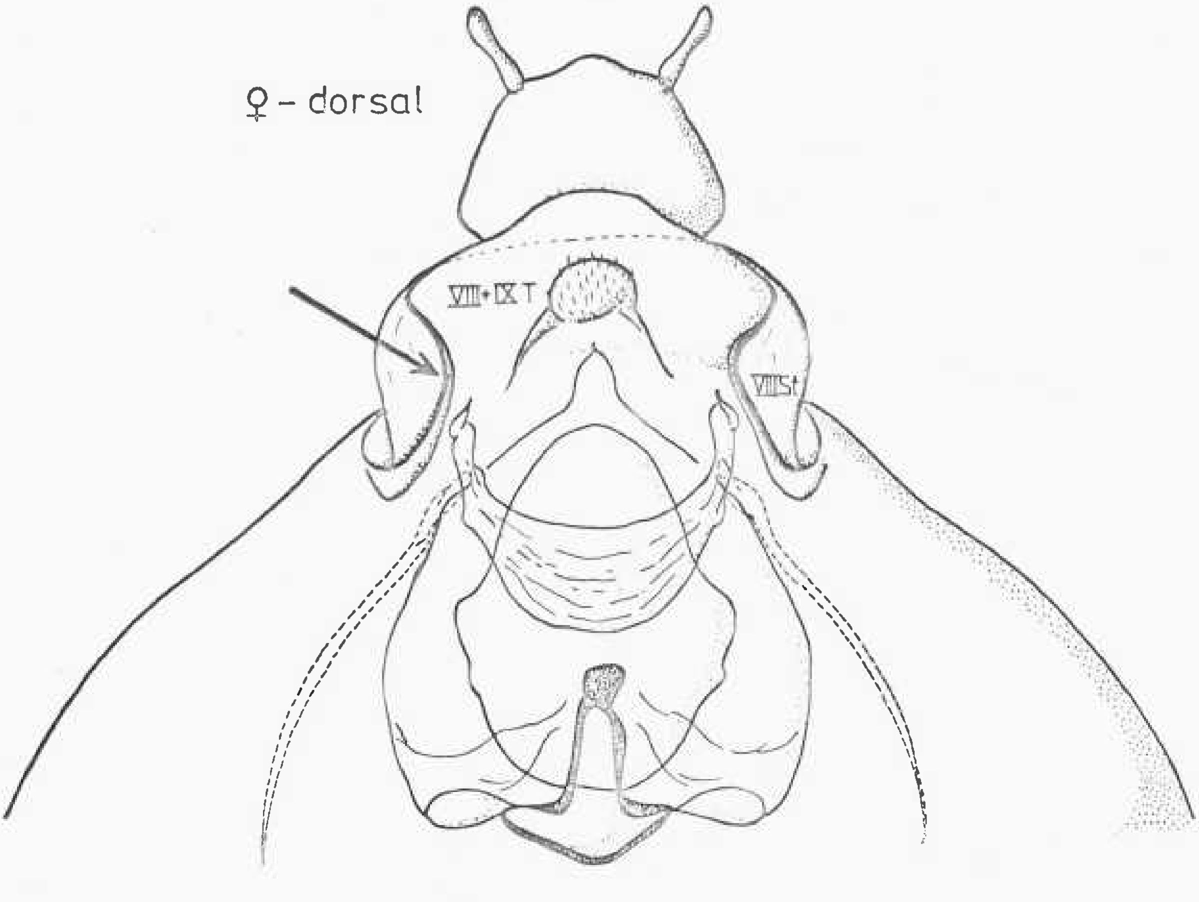
213

Oxyethira tristella Klap.



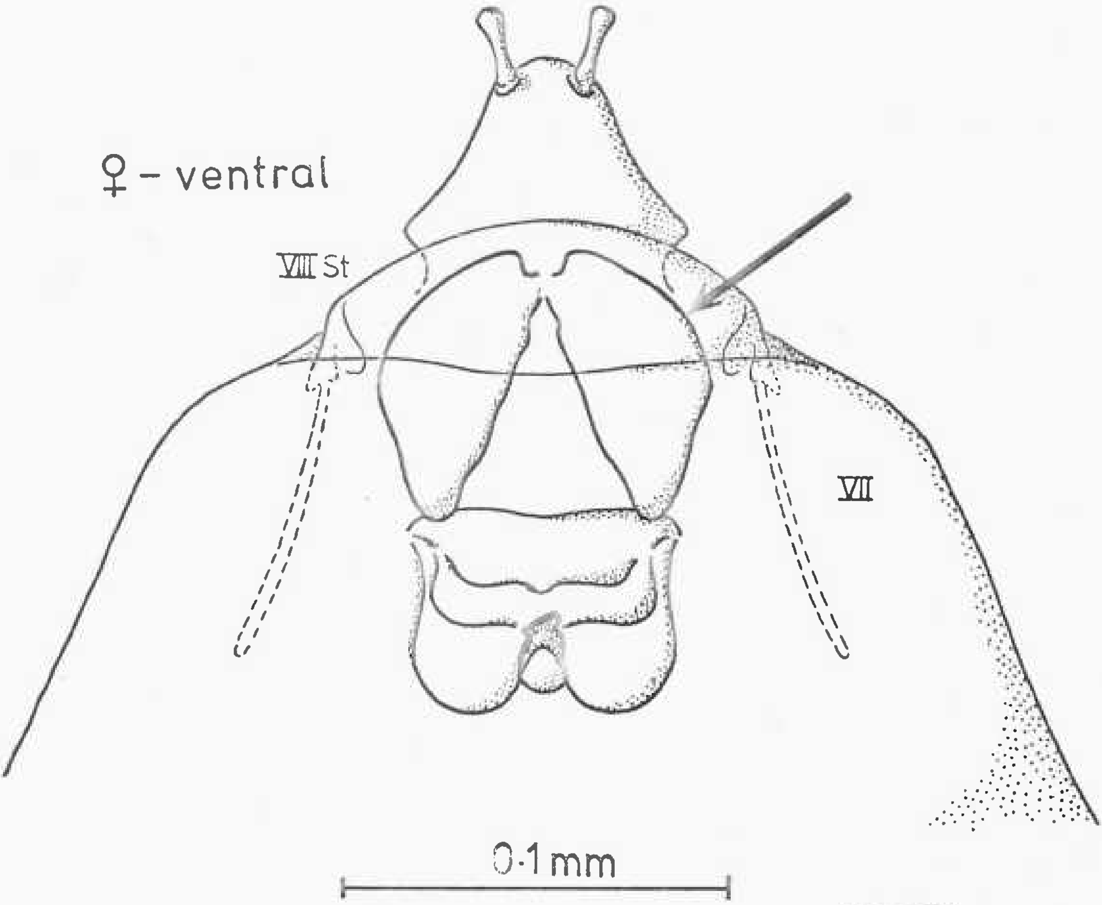
214

Oxyethira simplex Ris



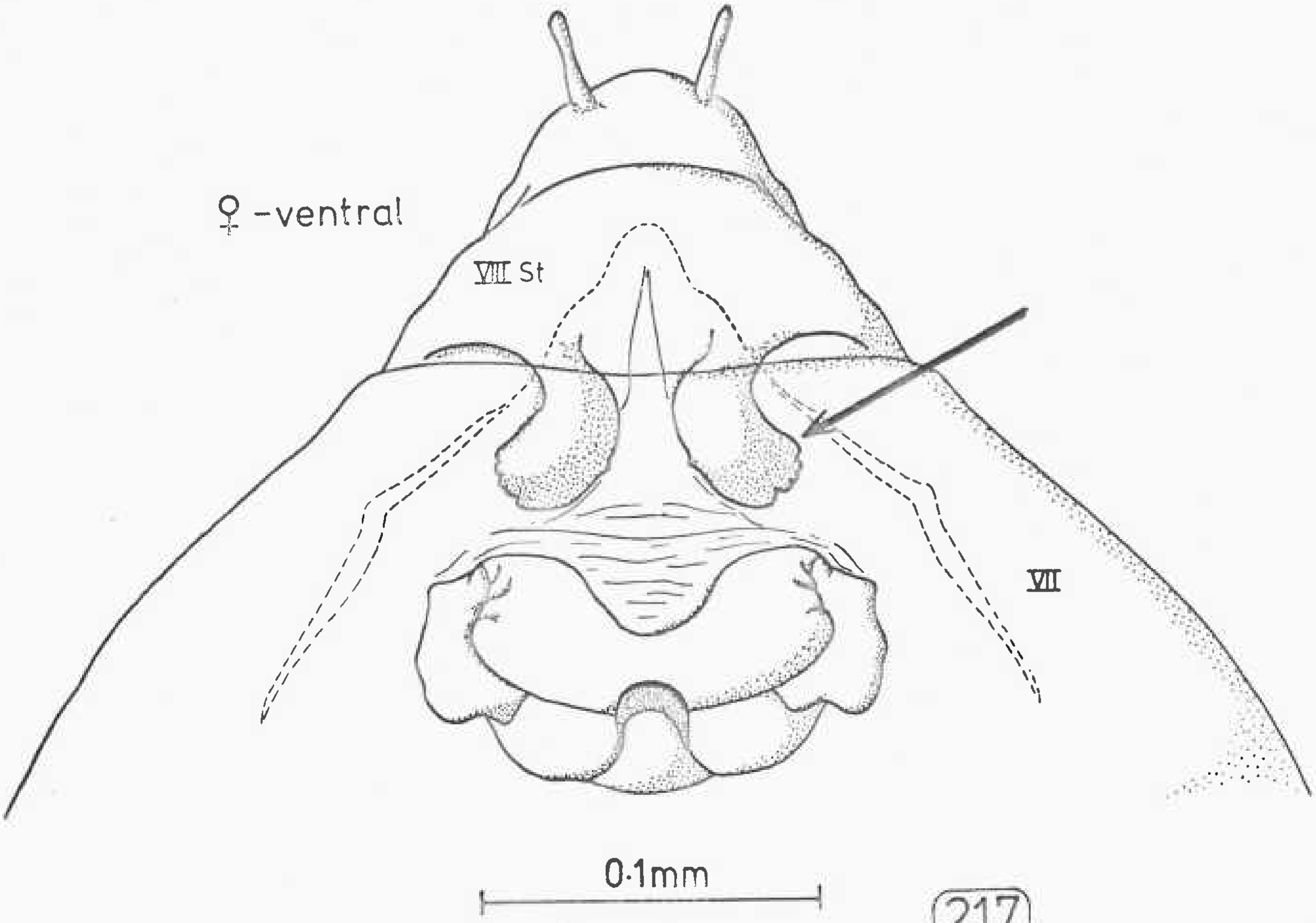
215

Oxyethira flavicornis (Pictet)



216

Oxyethira frici Klap.

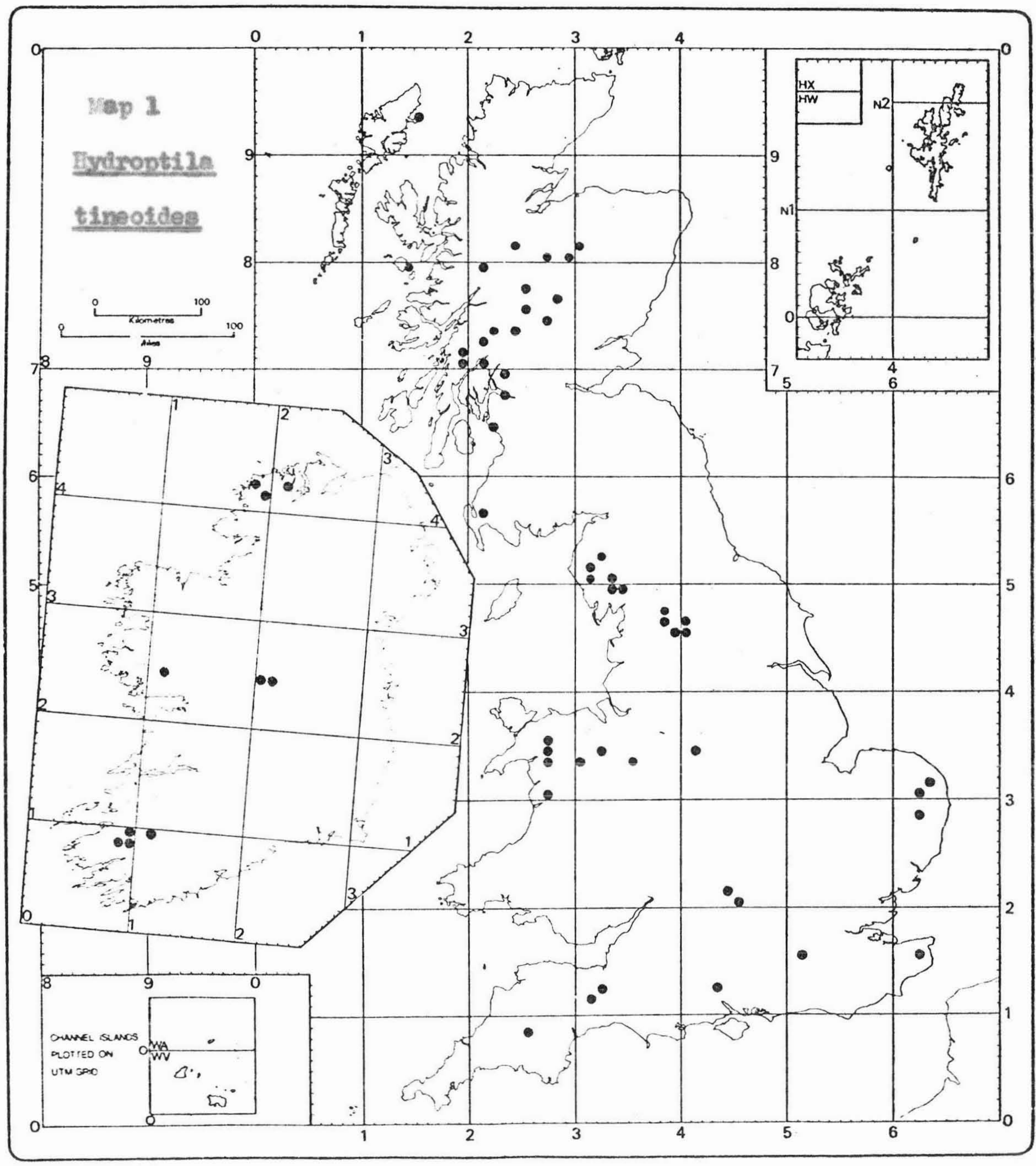


217

Oxyethira falcata Mort.

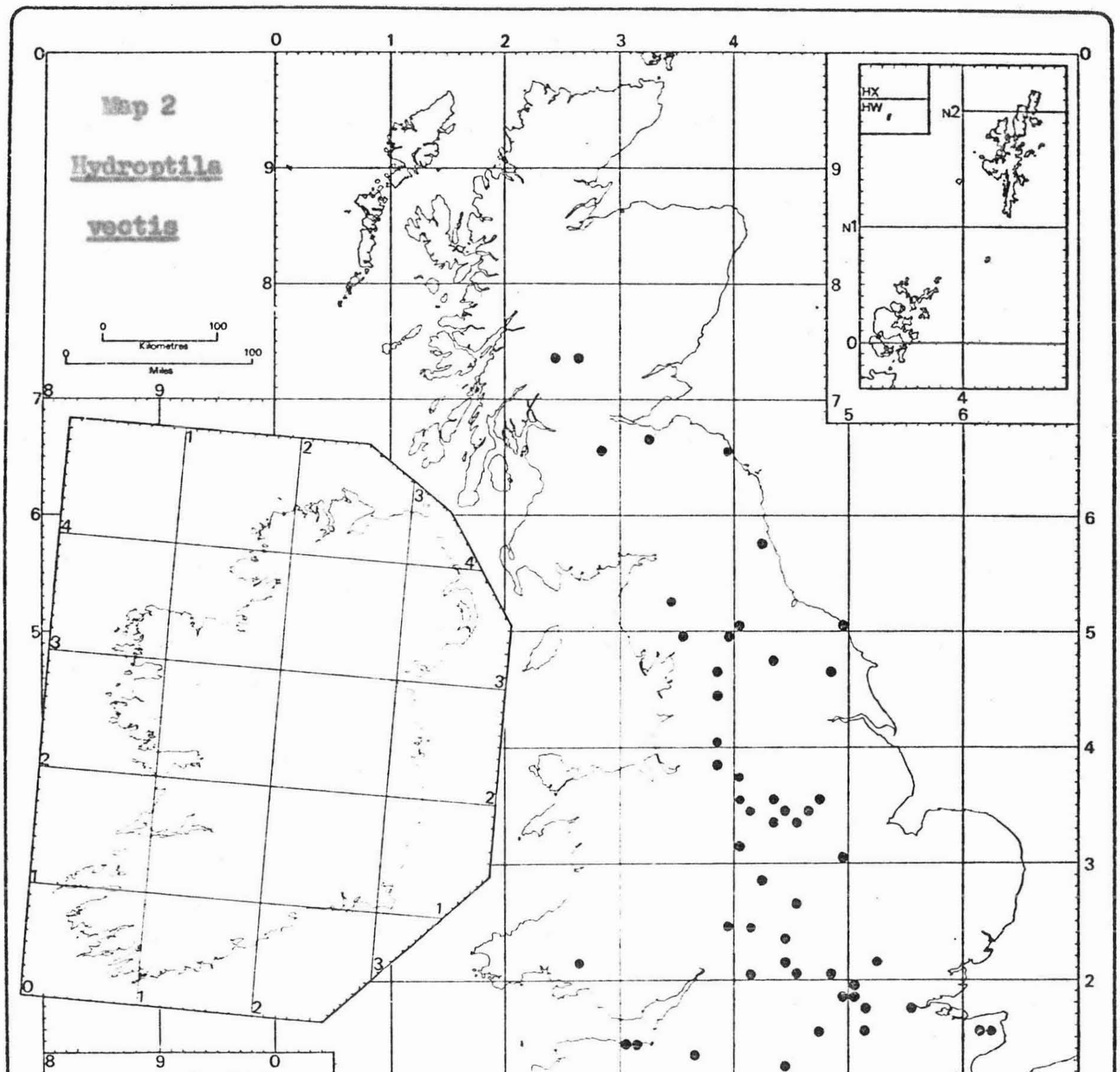
DISTRIBUTION MAPS:

BRITISH SPECIES OF HYDROPTILIDAE



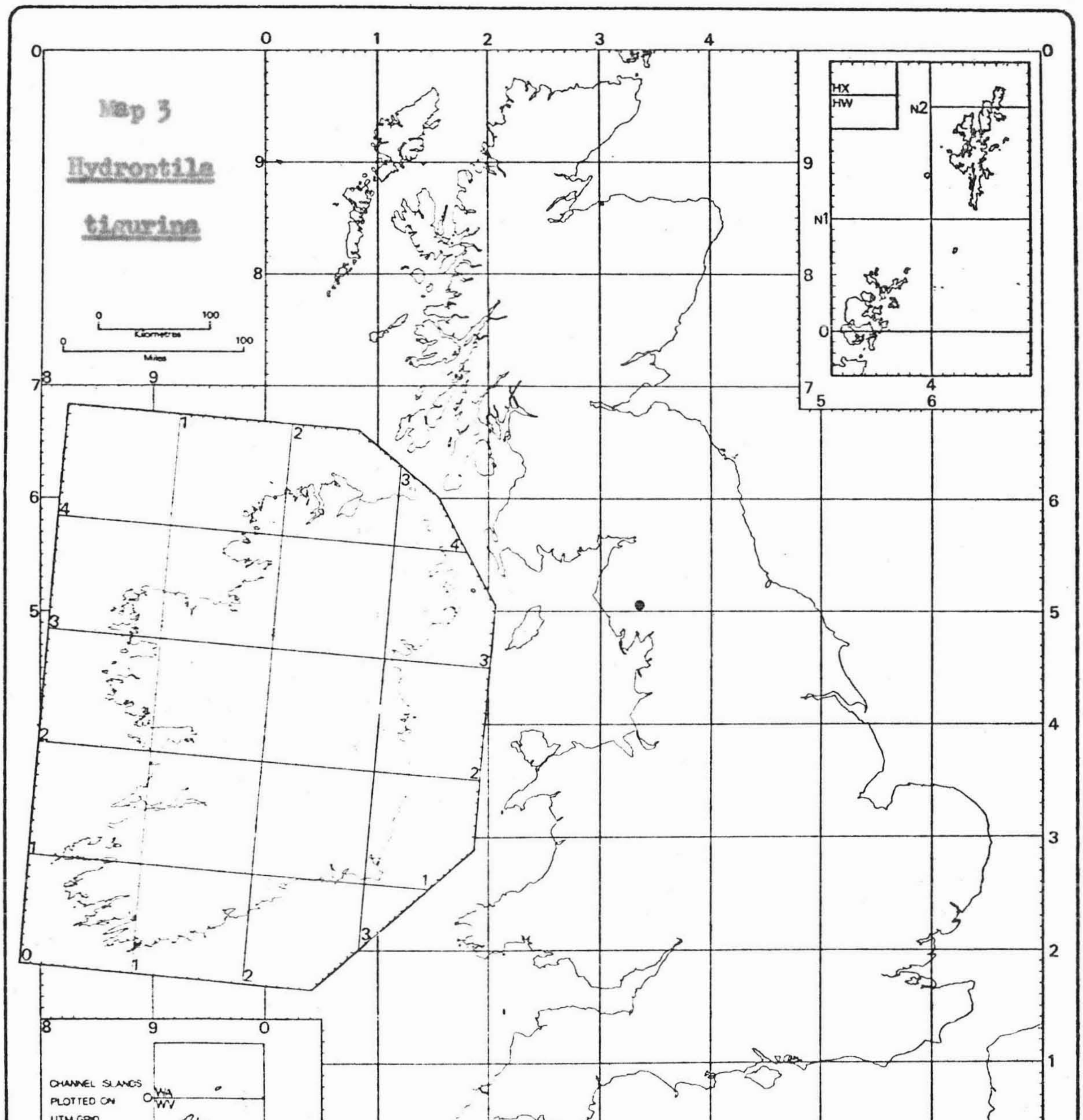
Map 1

Hydroptila tineoides



Map 2

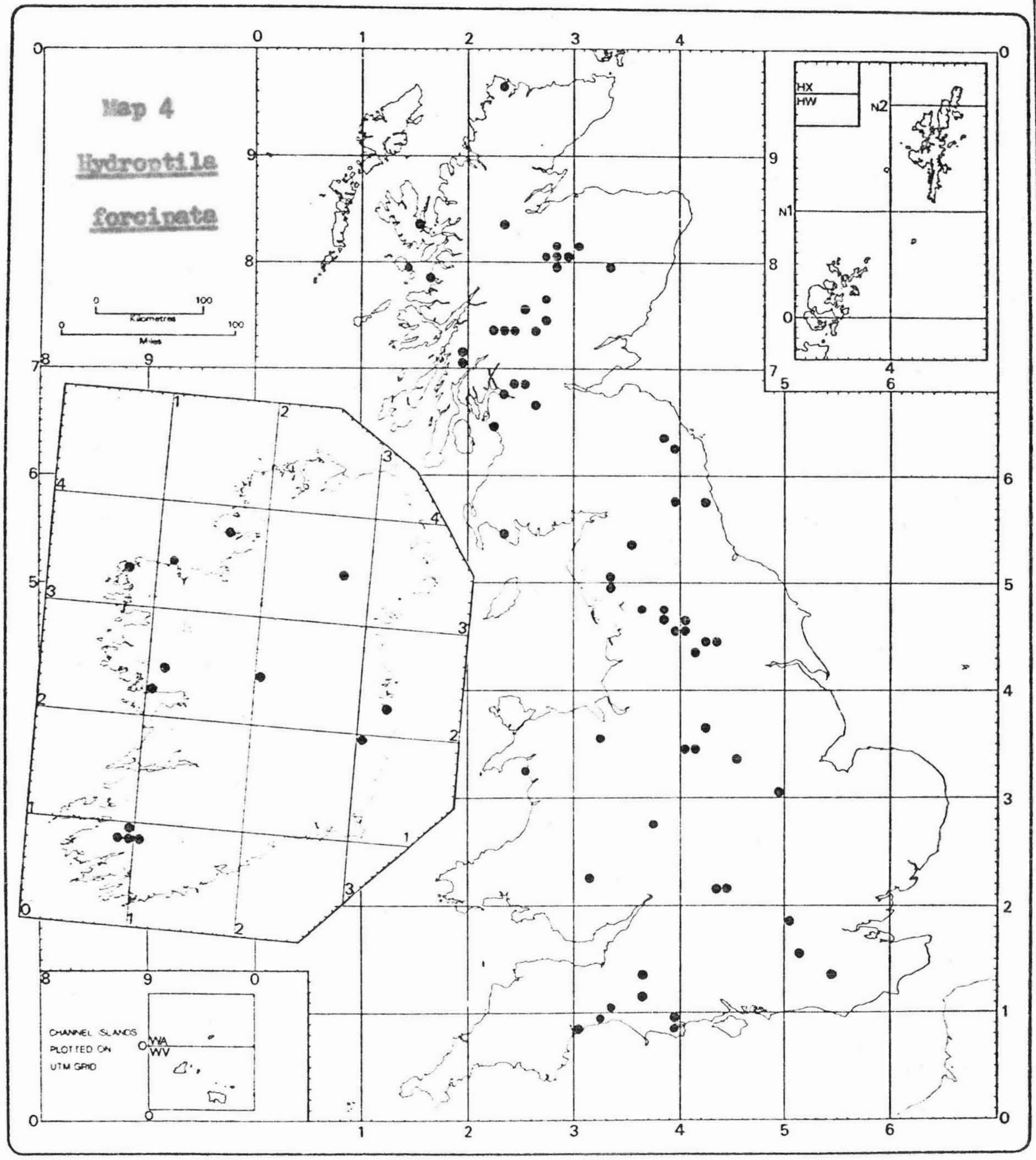
Hydroptila vectis



Map 3

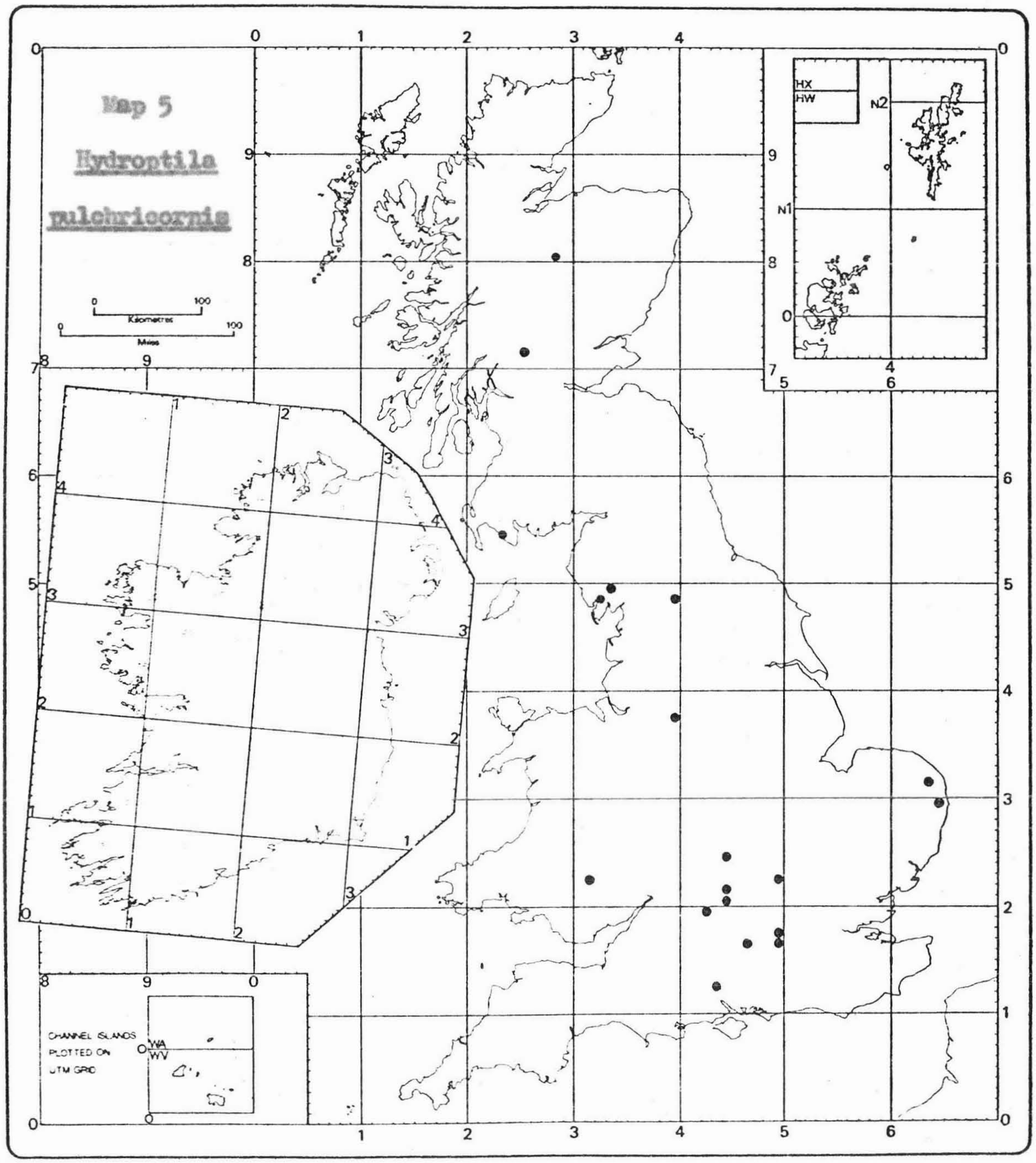
Hydroptila

tigurina



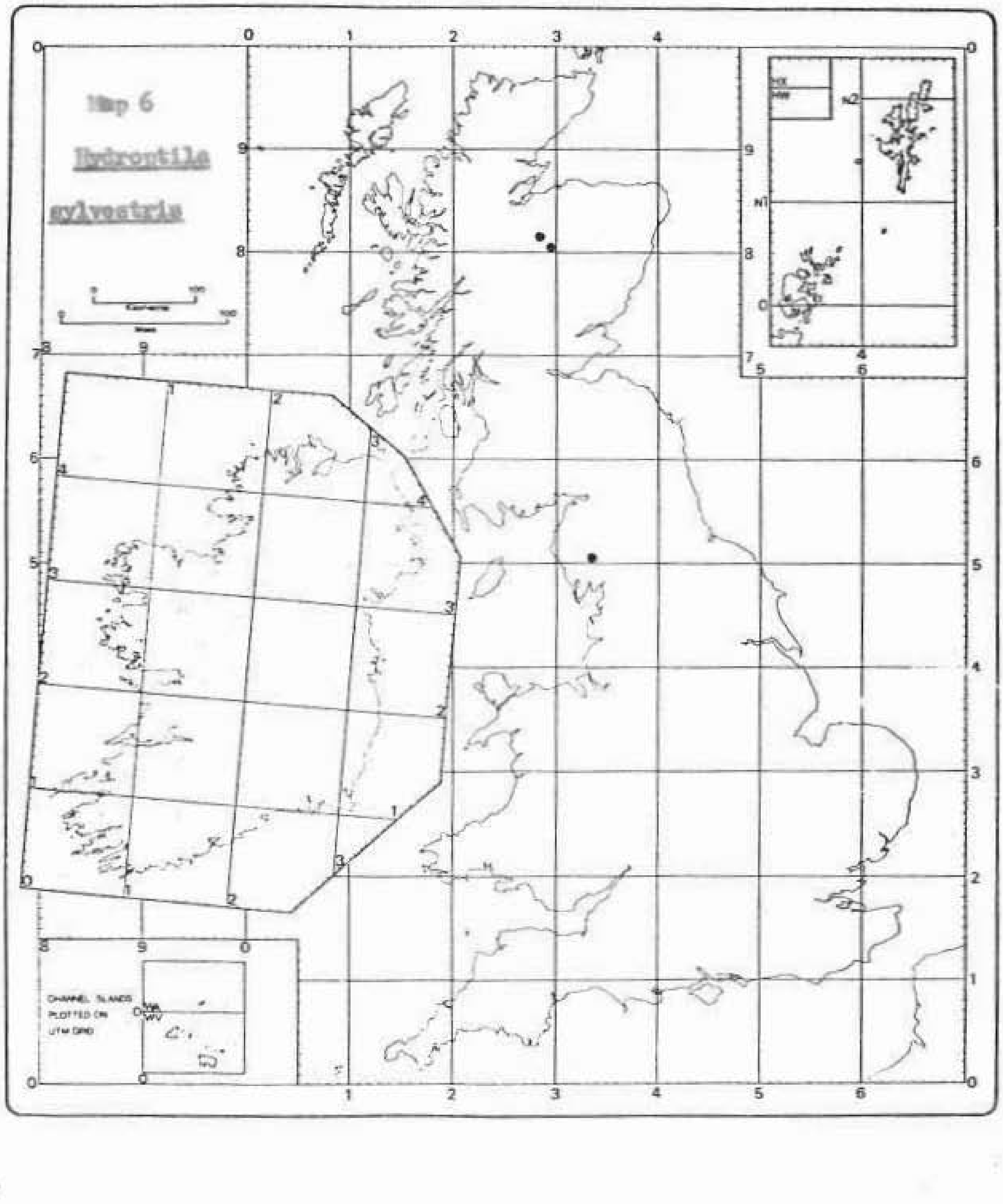
Map 4

Hydroptila forcipata



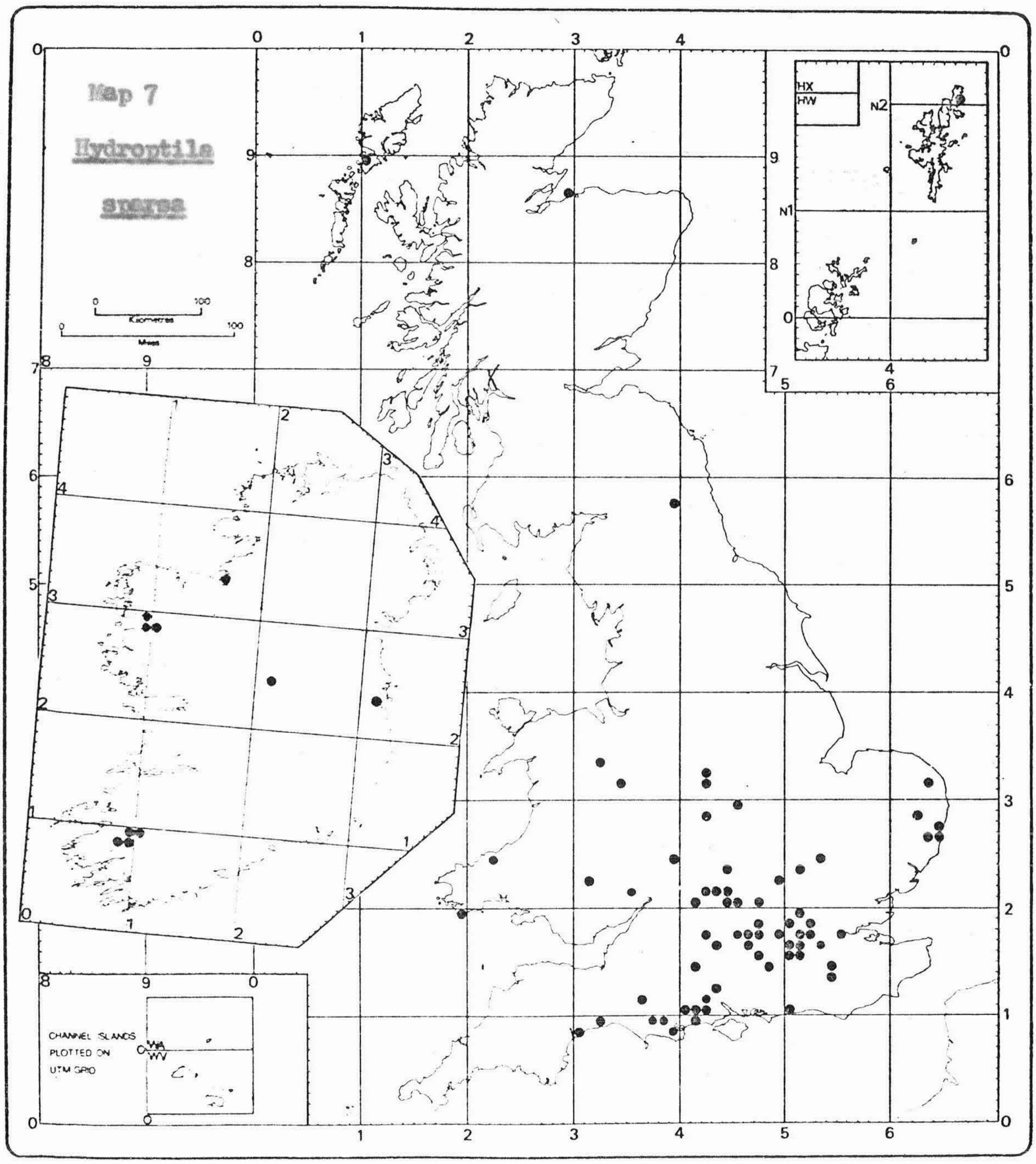
Map 5

Hydroptila pulchricornis



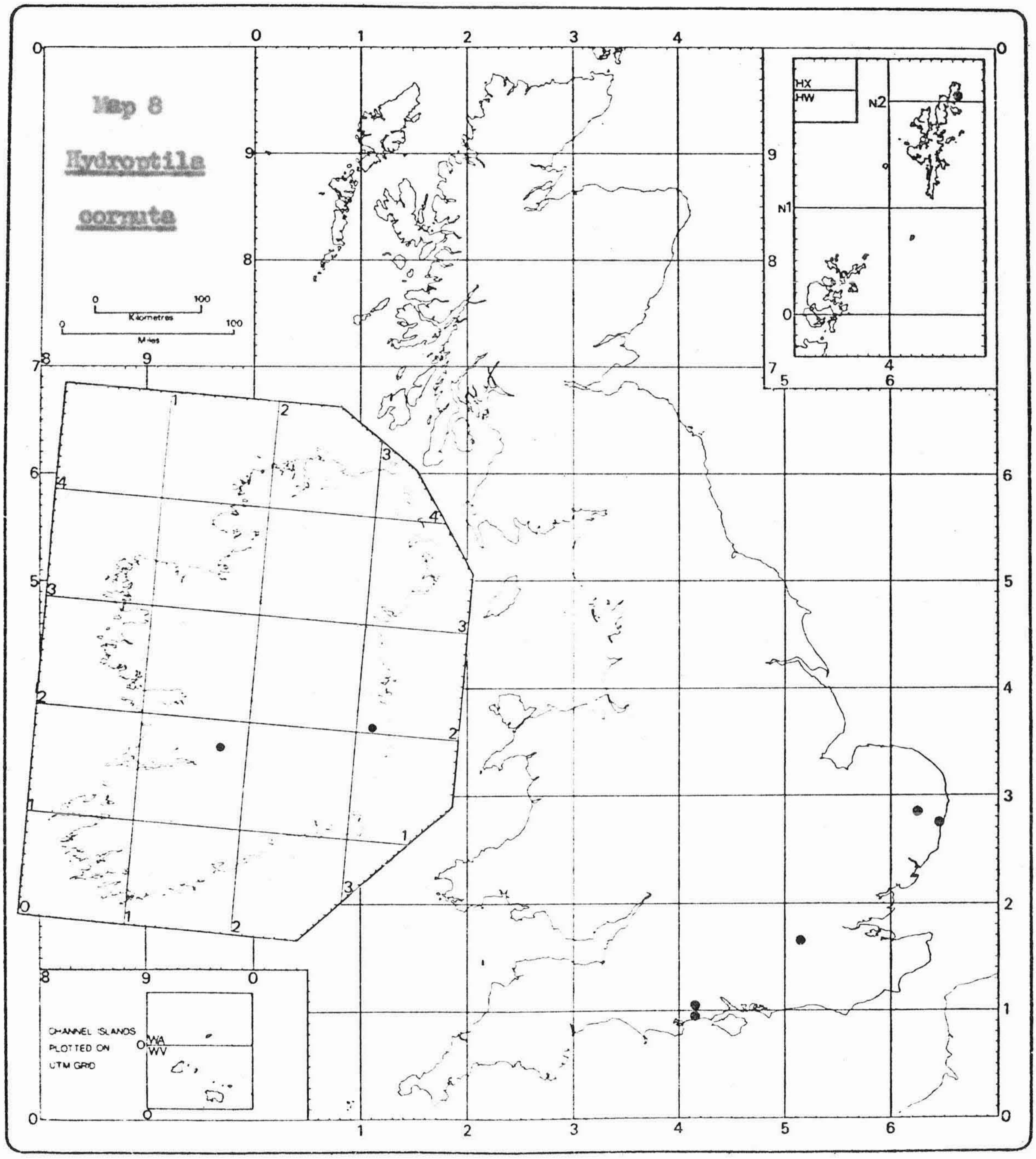
Map 6

Hydroptila sylvestris



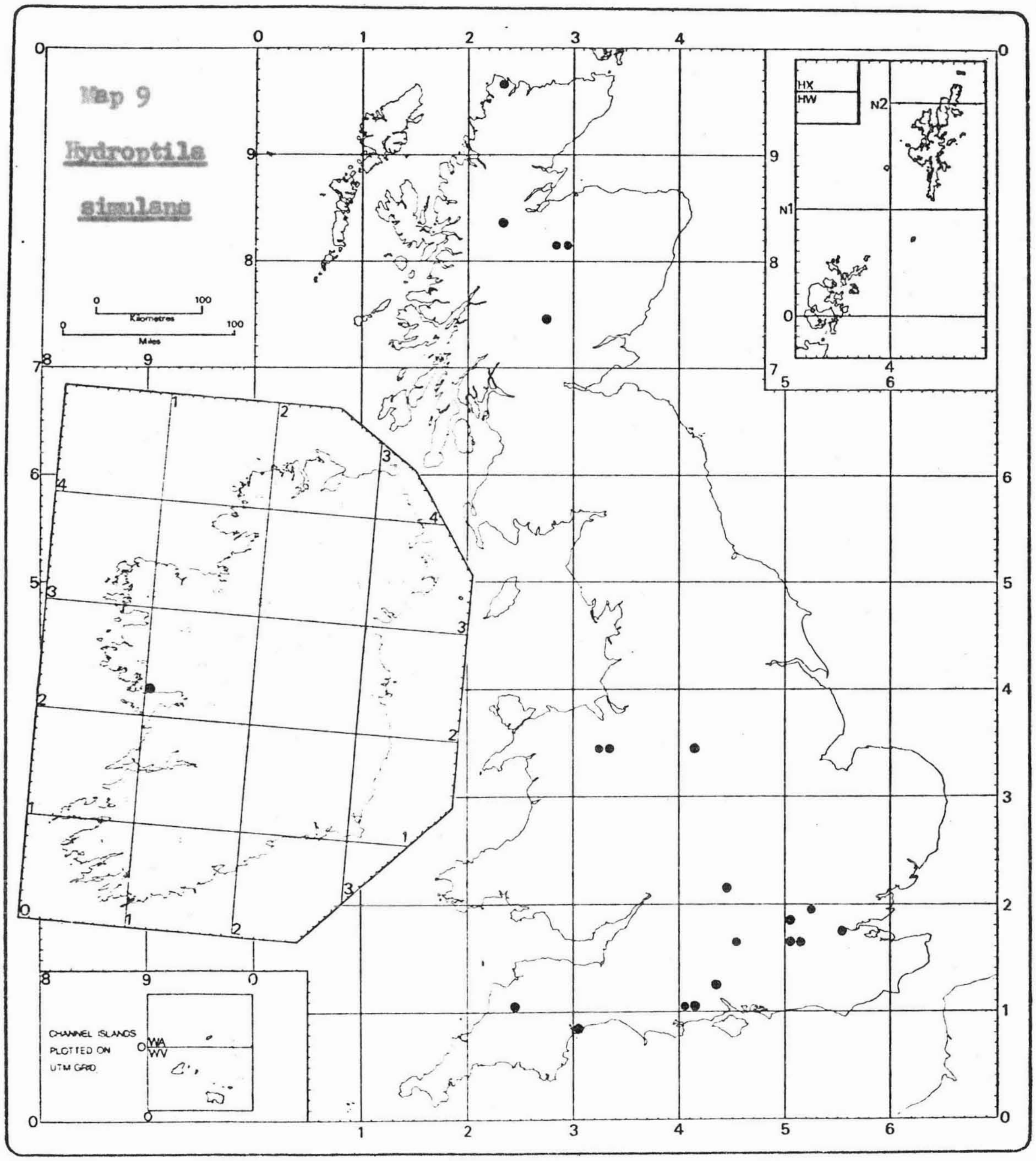
Map 7

Hydroptila sparsa



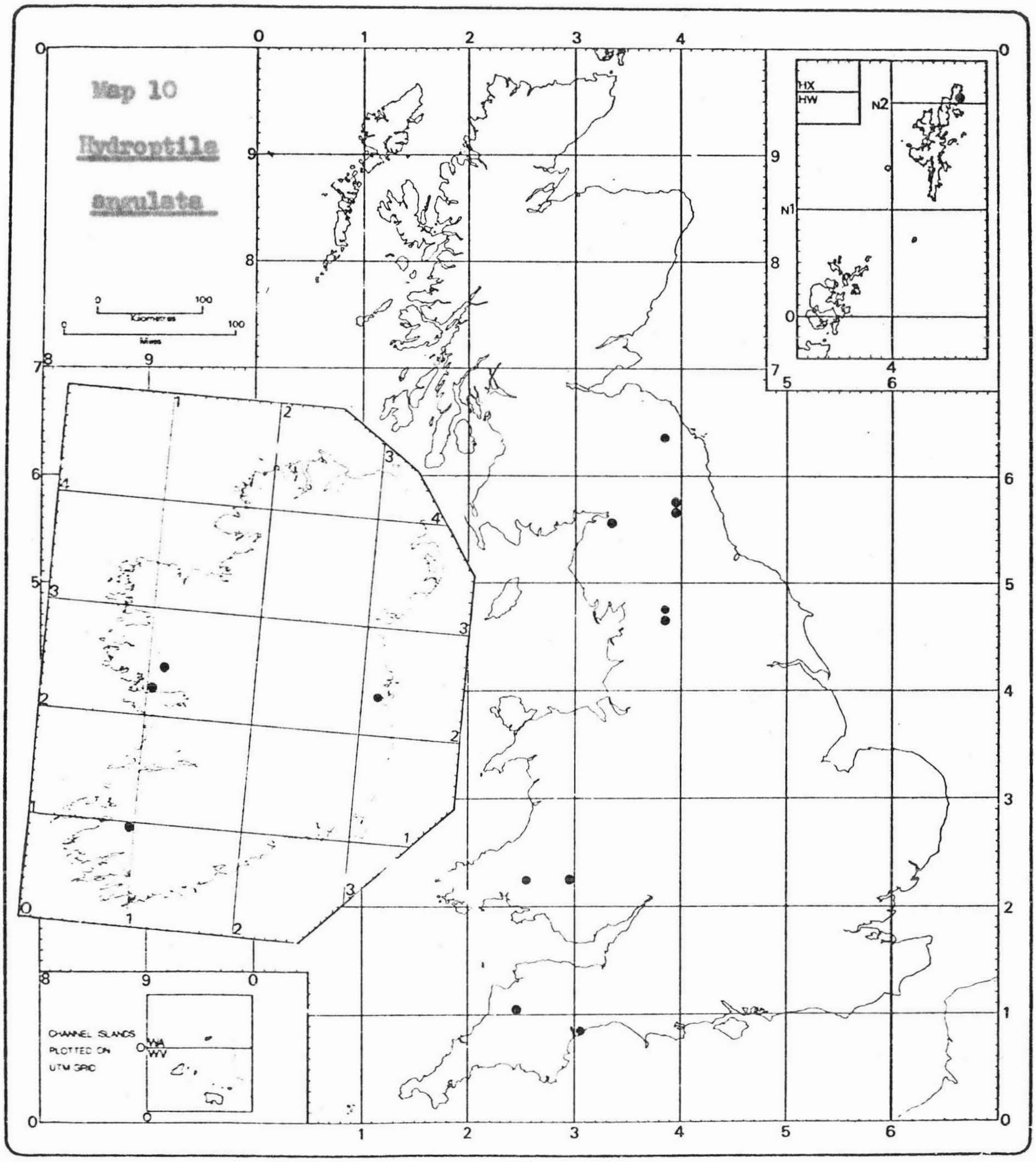
Map 8

Hydroptila cornuta



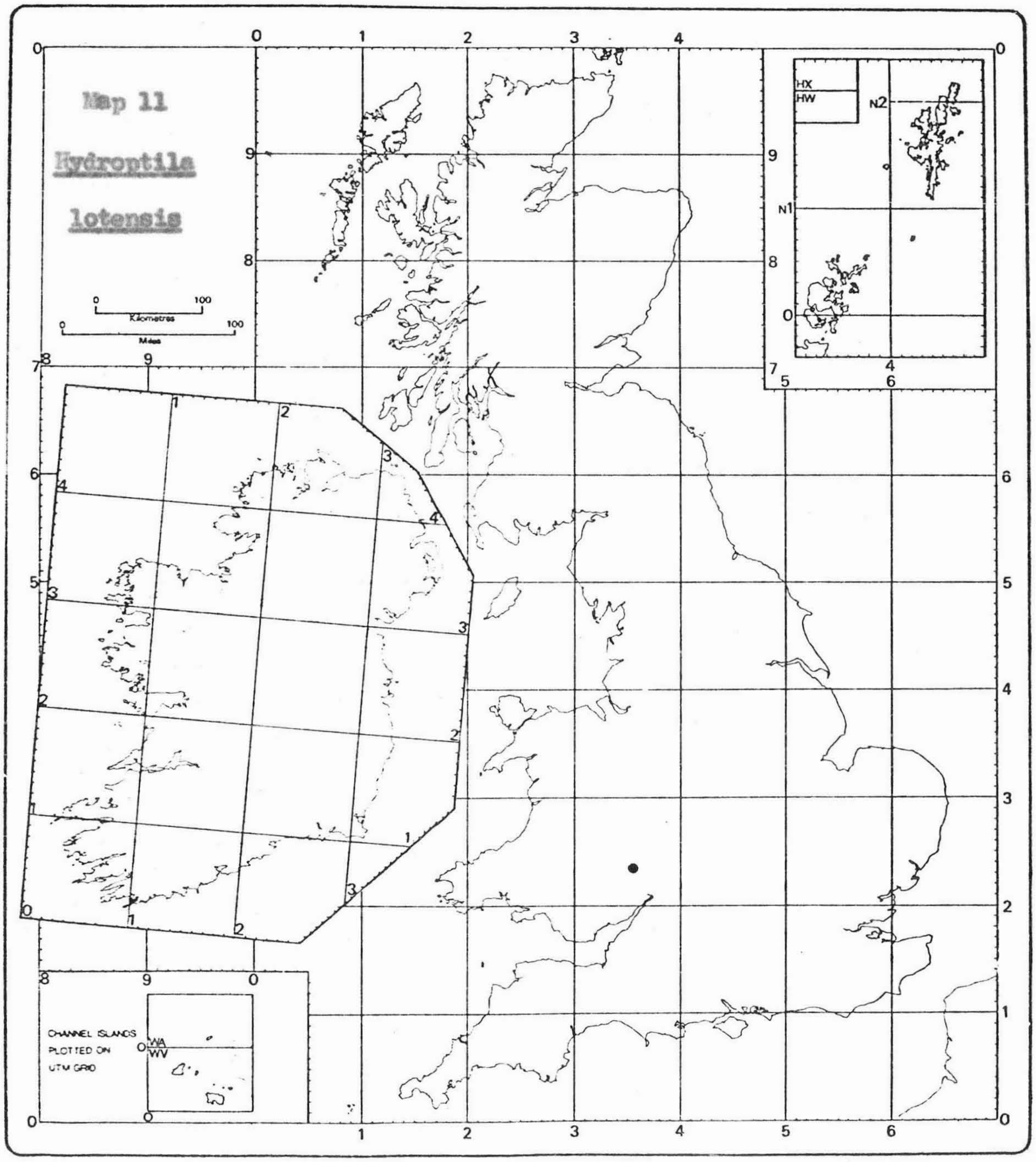
Map 9

Hydroptila simulans



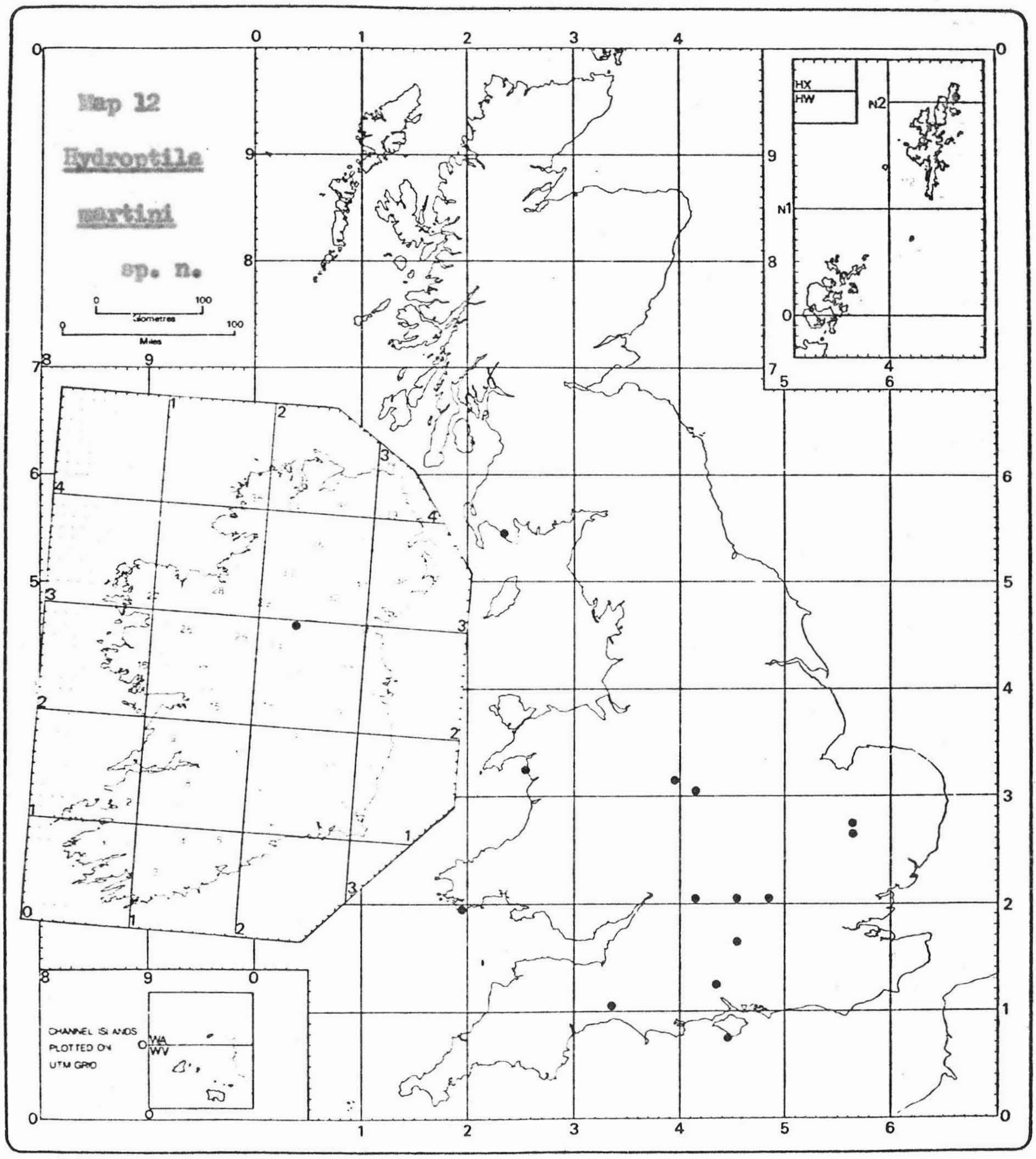
Map 10

Hydroptila angulata

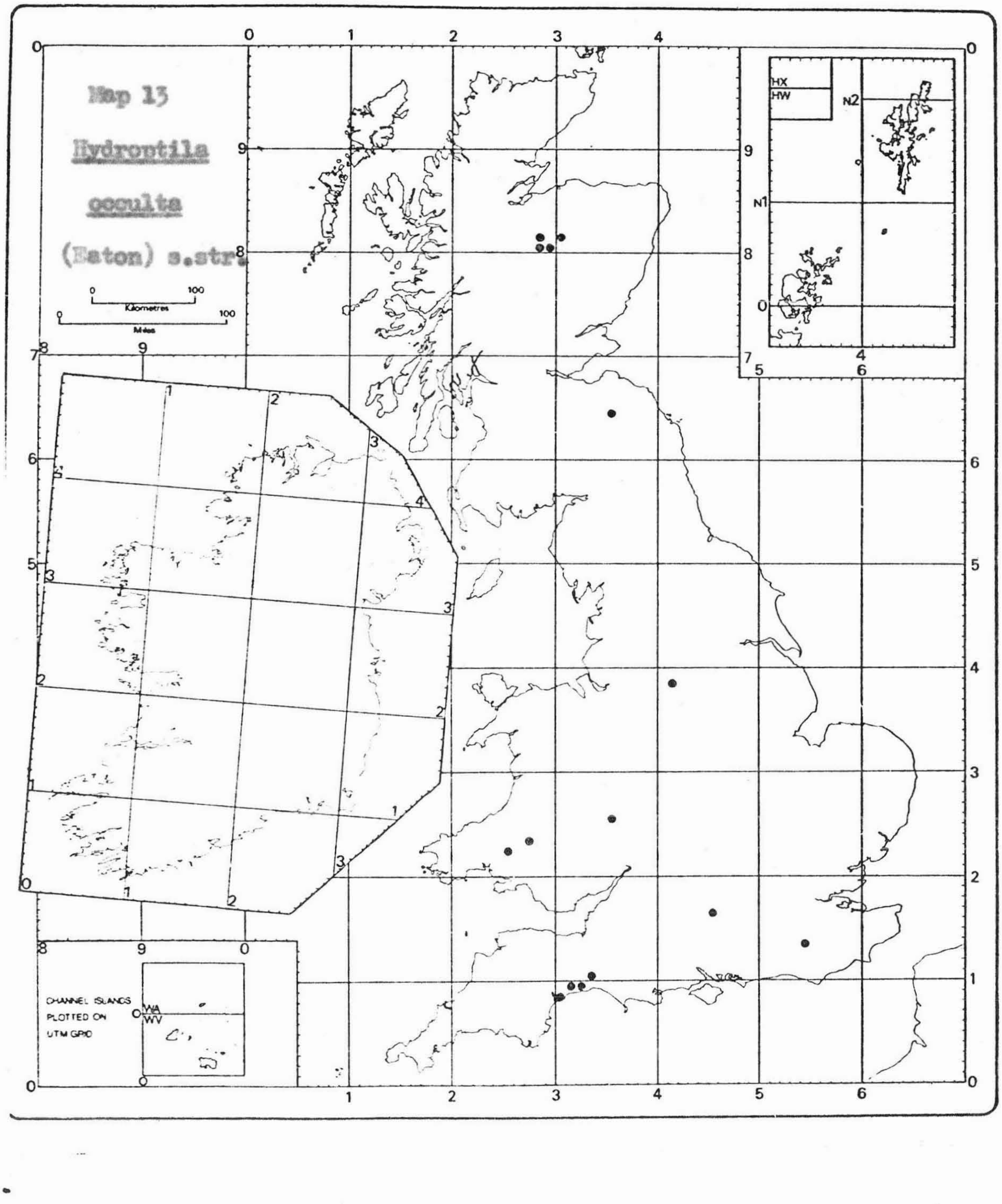


Map 11

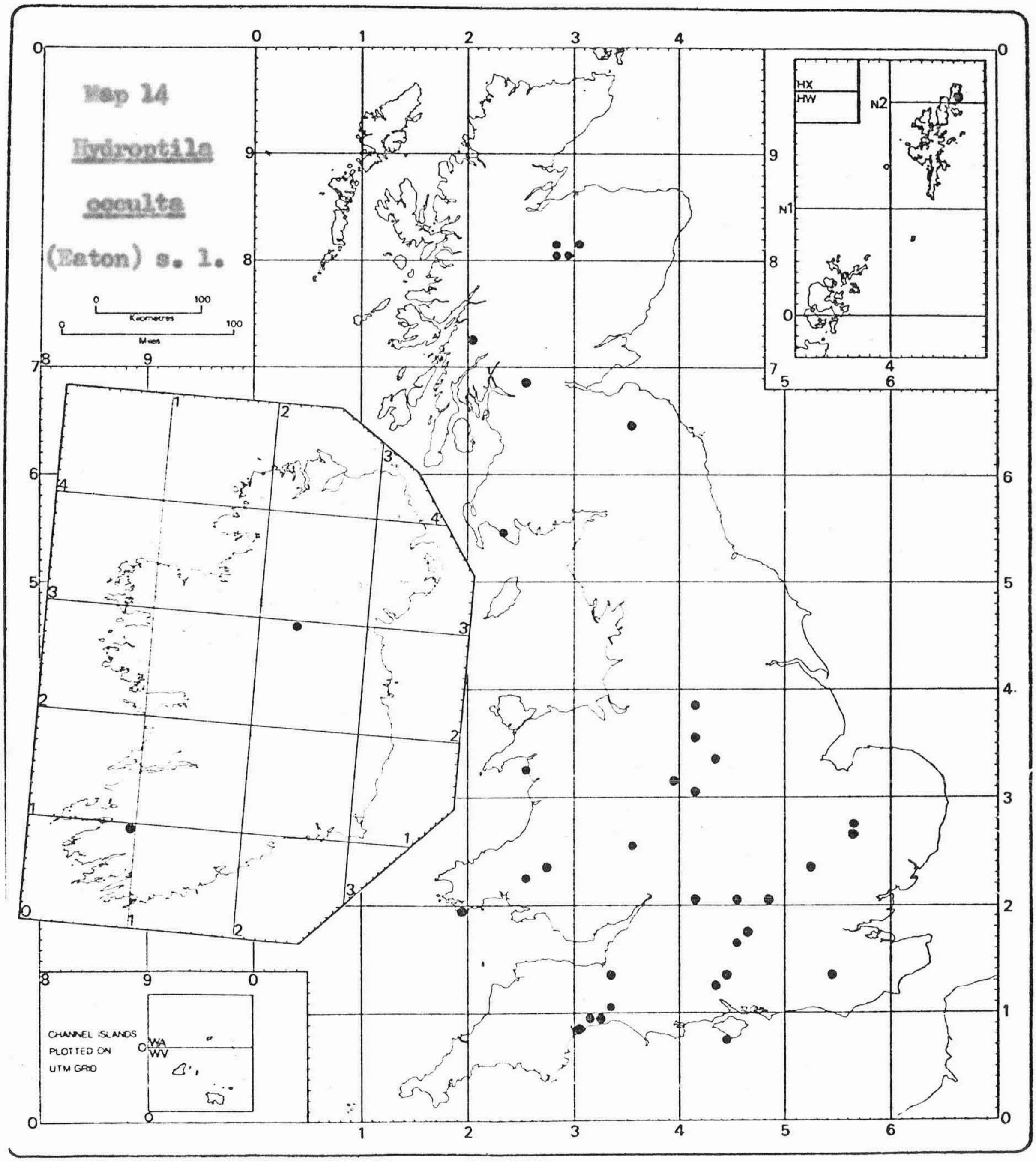
Hydroptila lotensis



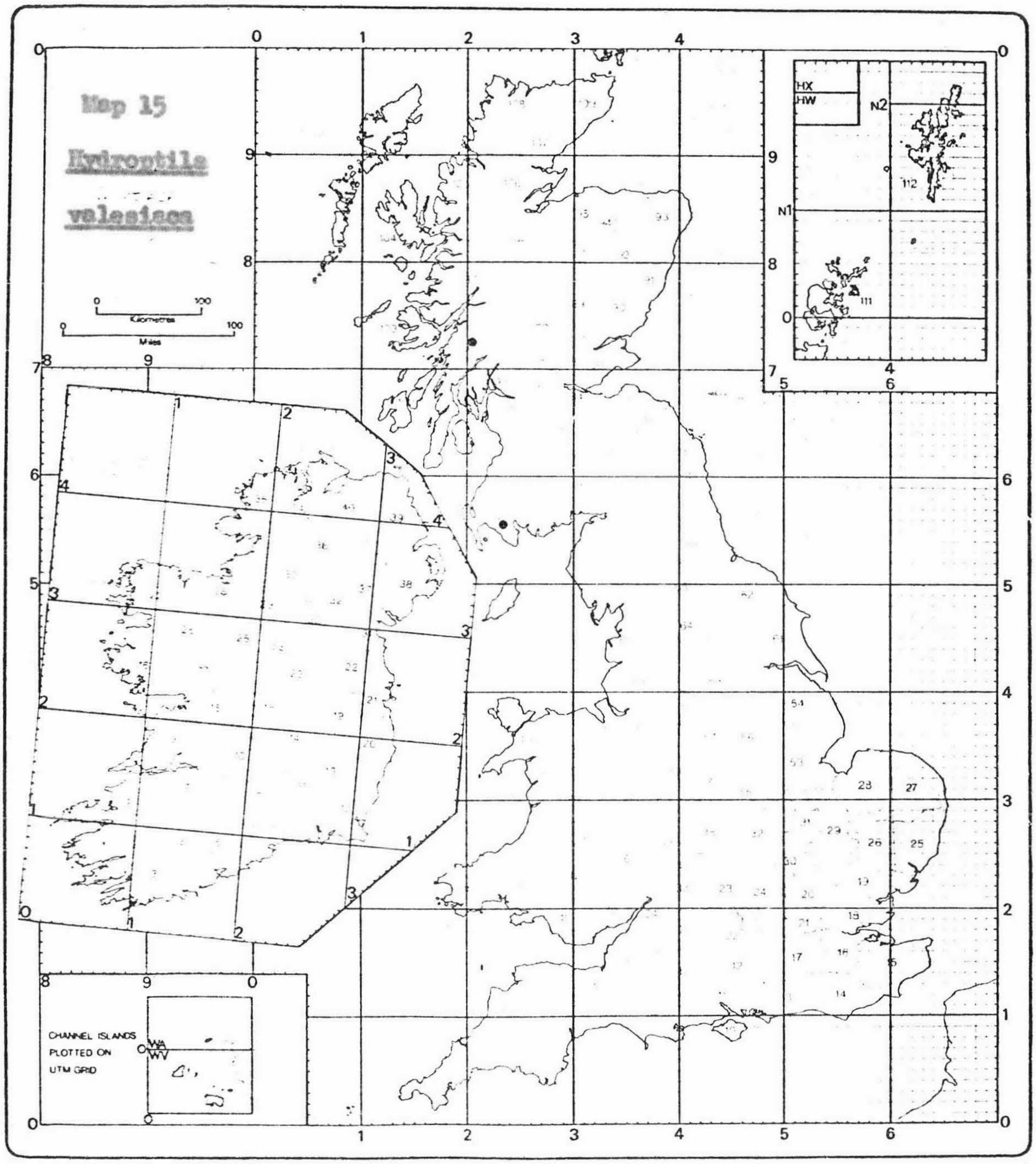
Map 12
Hydroptila
martini
sp. n.



Map 13 *Hydroptila occulta* (Eaton) s.str.

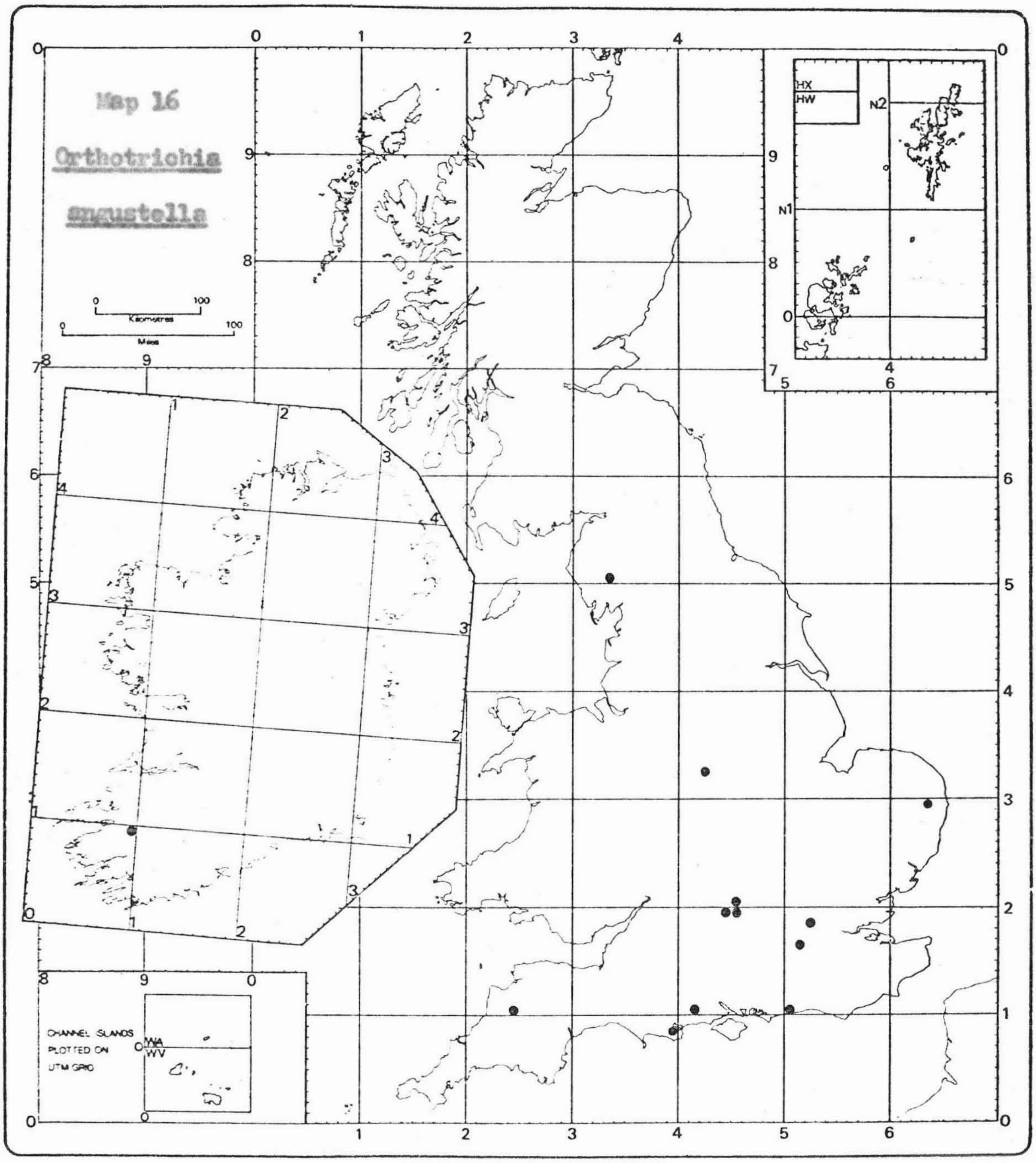


Map 14 Hydroptila occulta (Eaton) s. l.



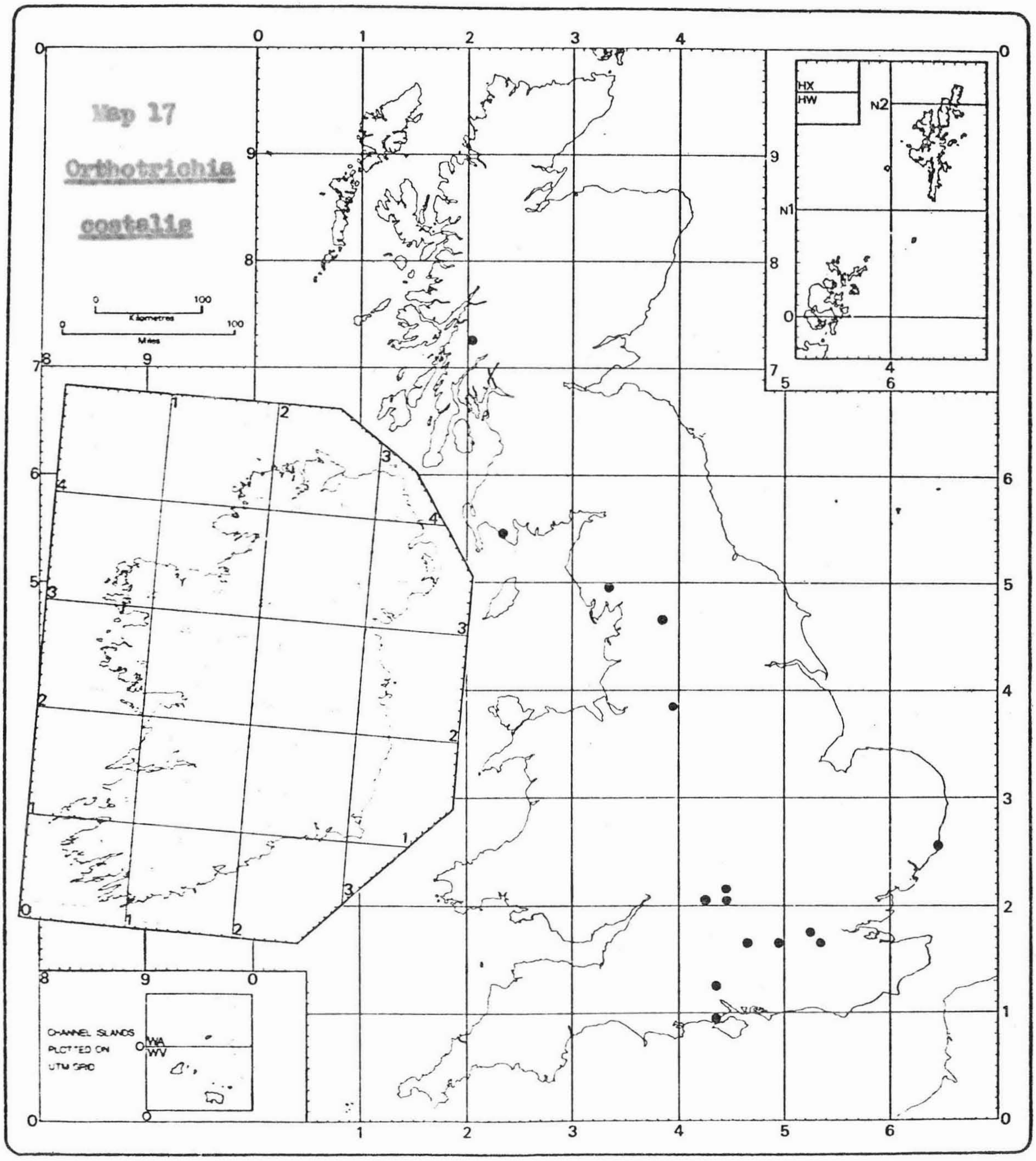
Map 15

Hydroptila valesiaca



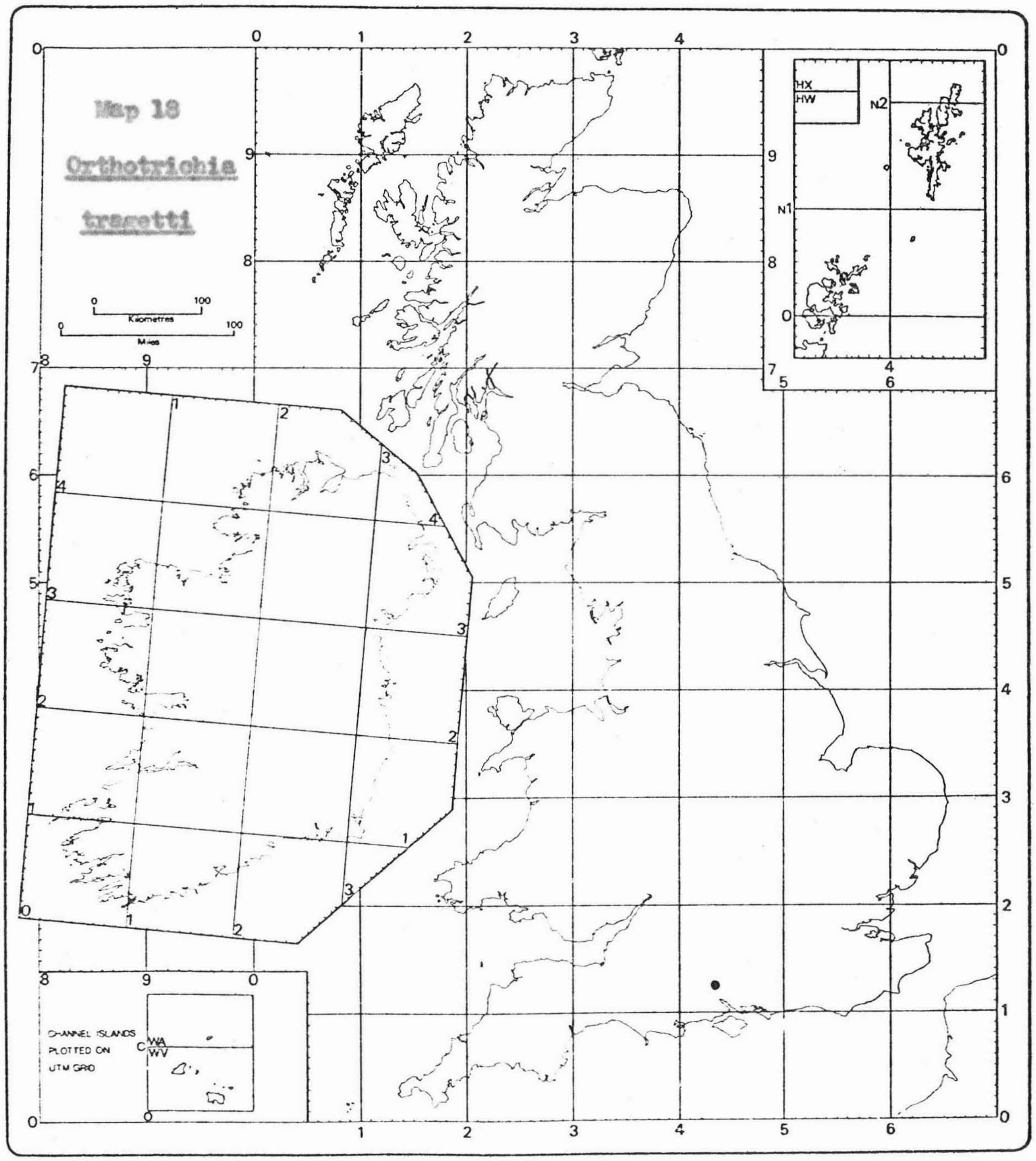
Map 16

Orthotrichia angustella



Map 17

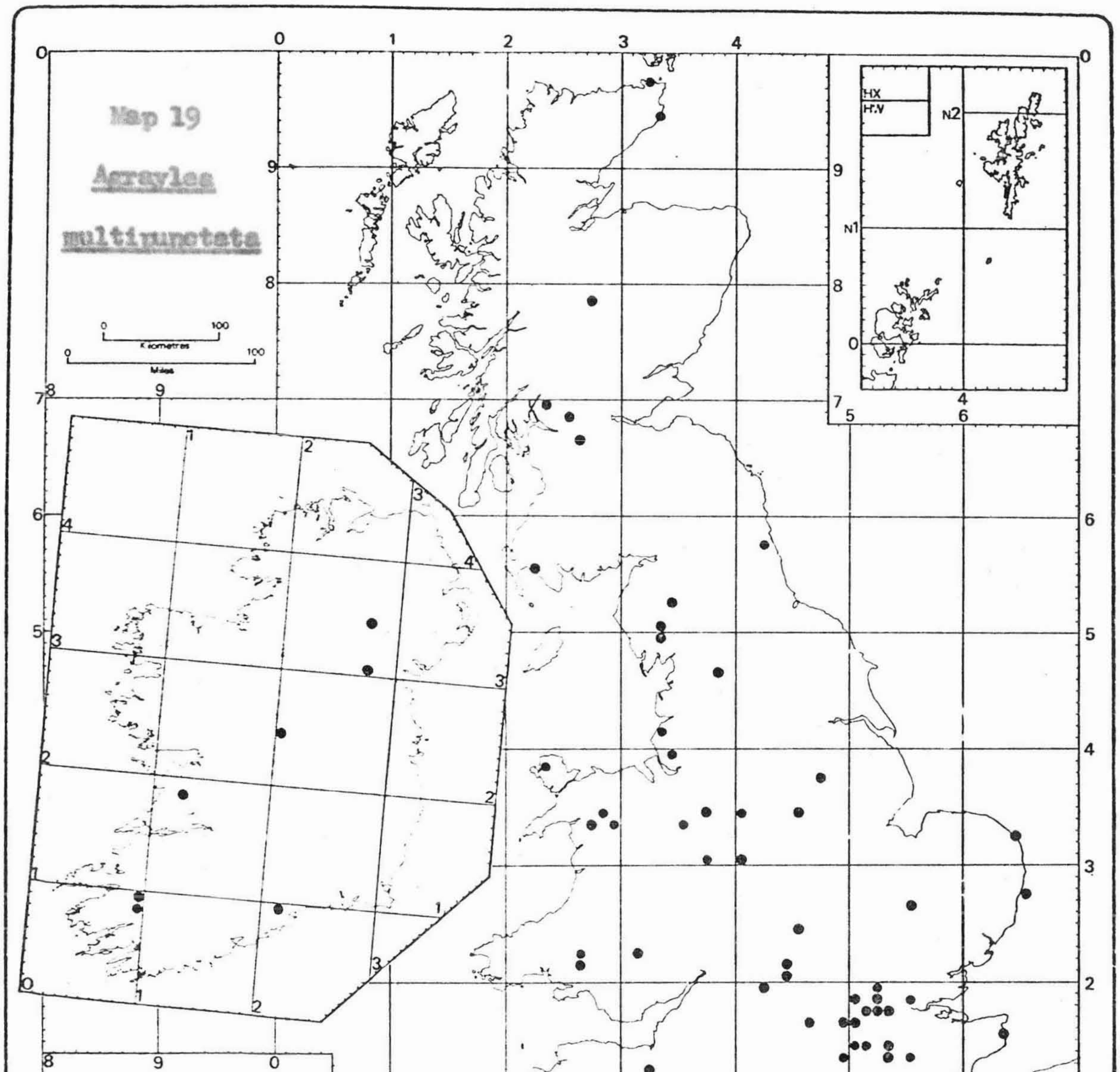
Orthotrichia costalis



Map 18

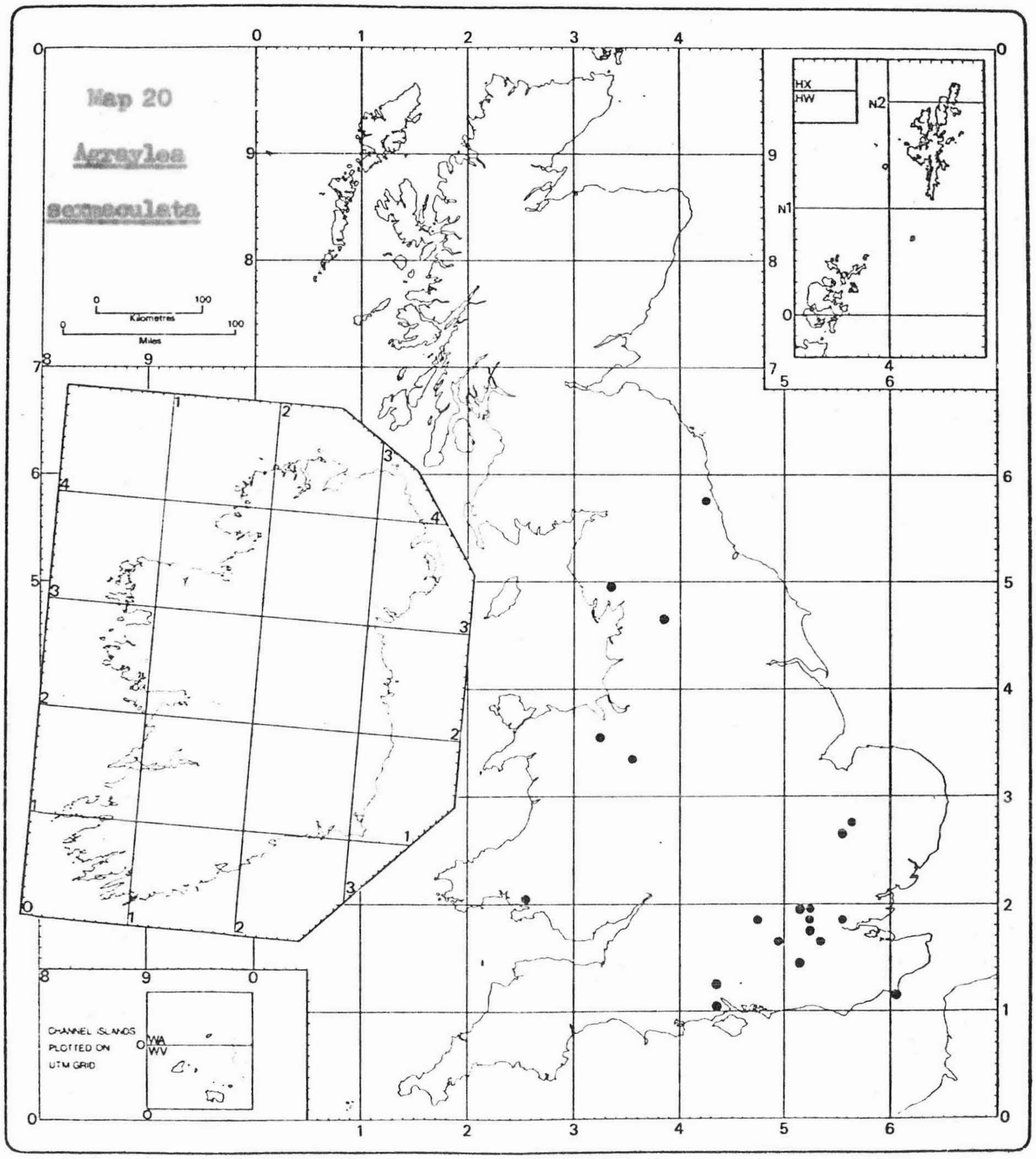
Orthotrichia

tragetti



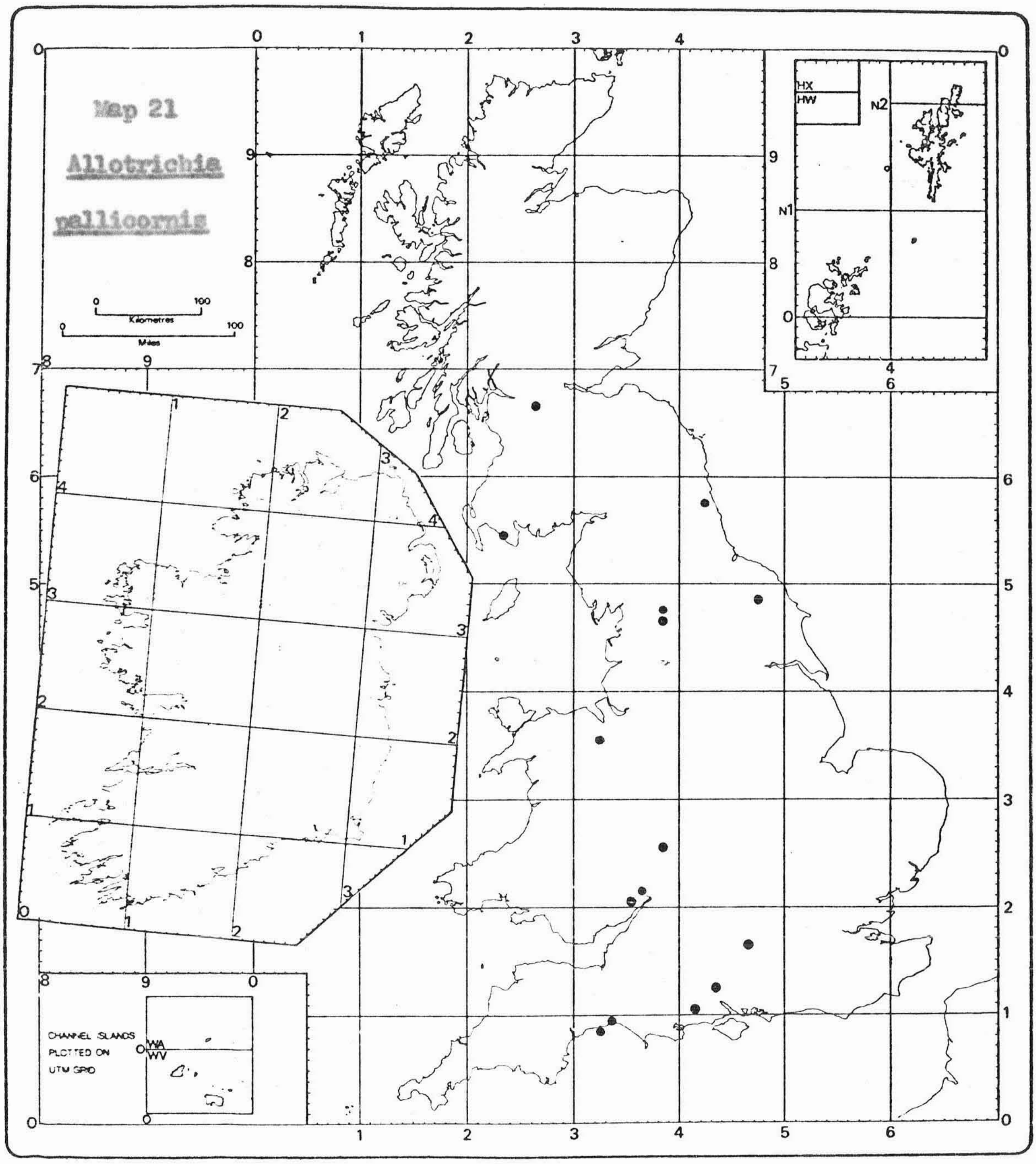
Map 19

Agraylea multipunctata



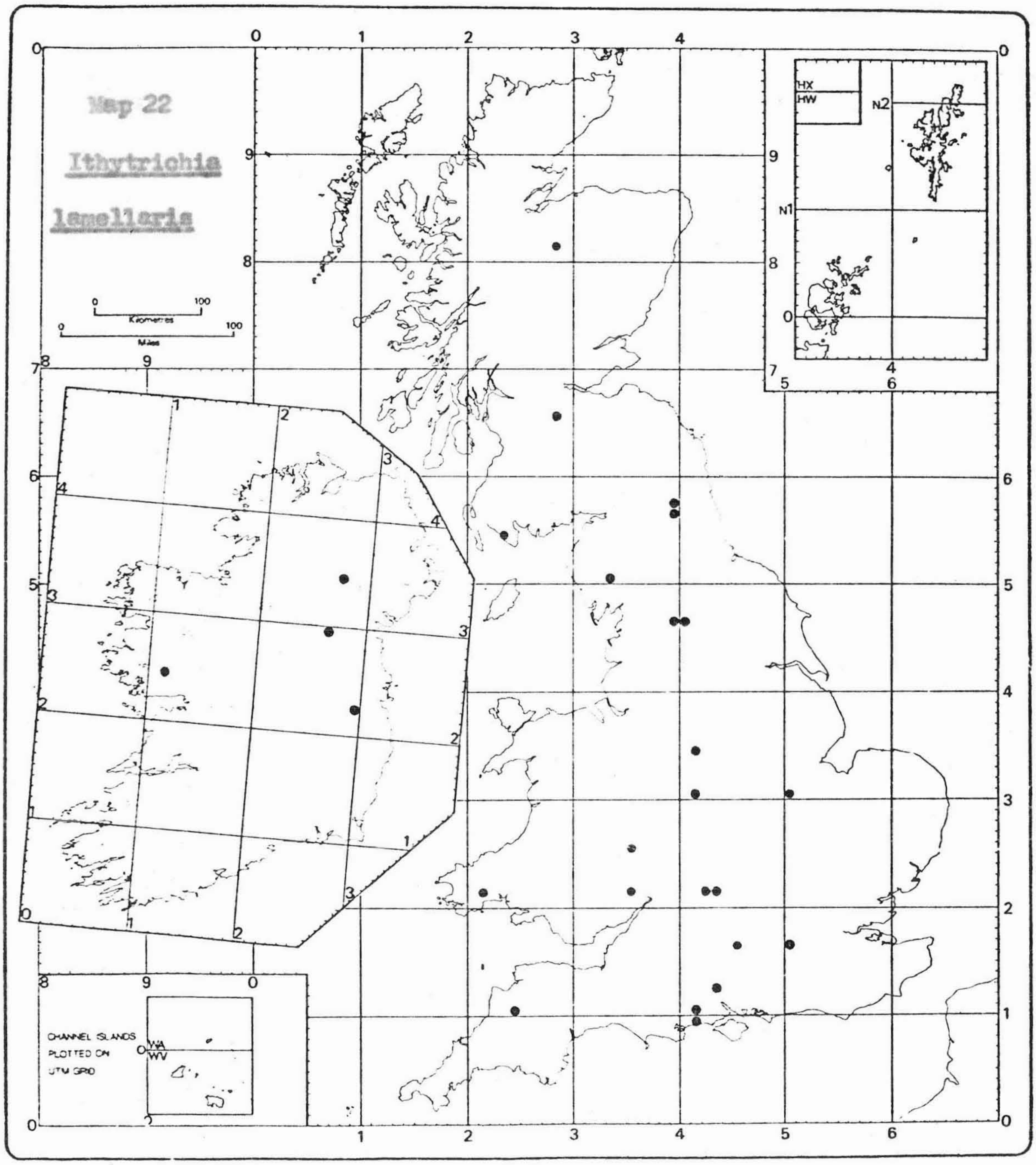
Map 20

Agraylea sexmaculata

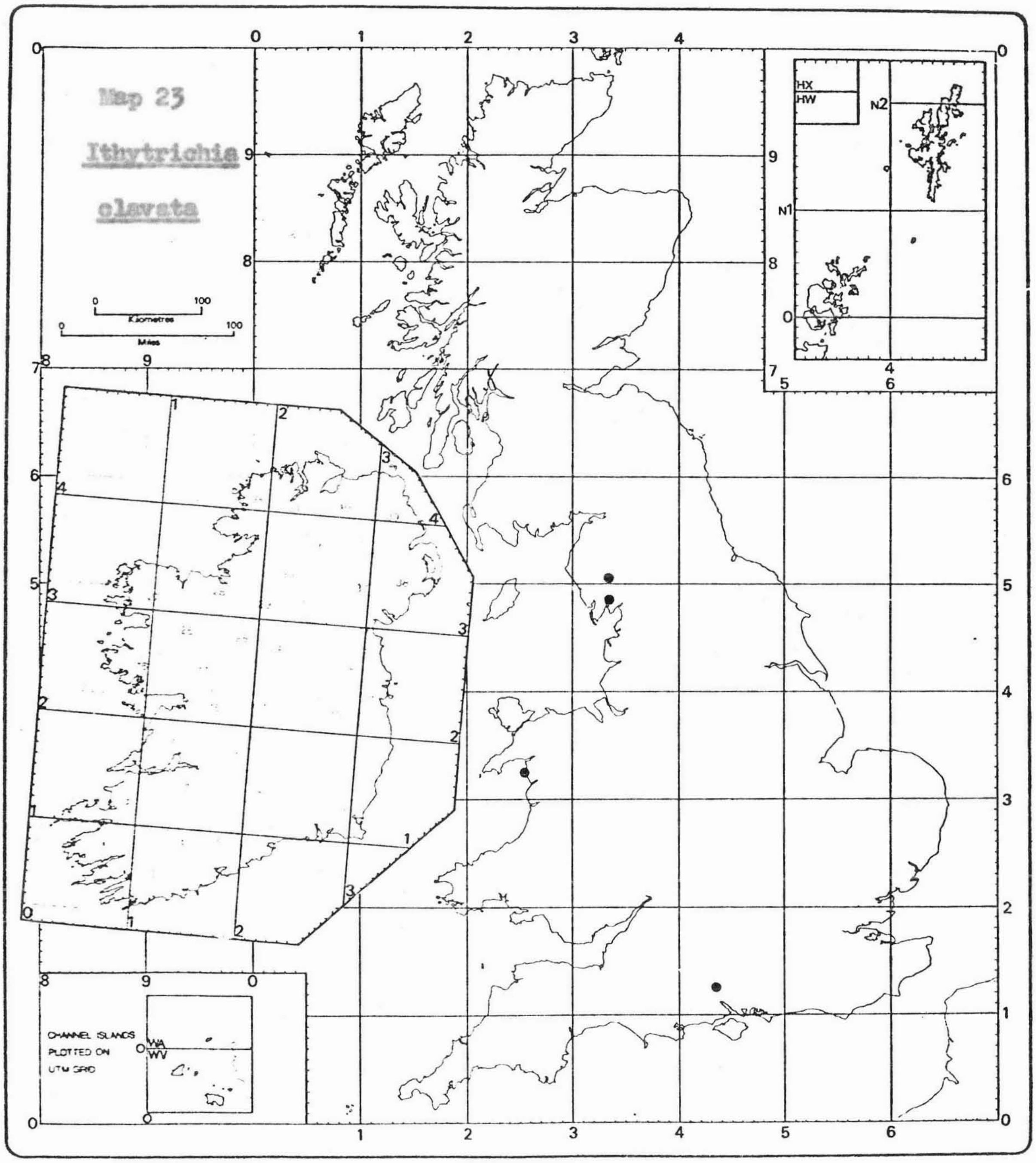


Map 21

Allotrichia pallicornis

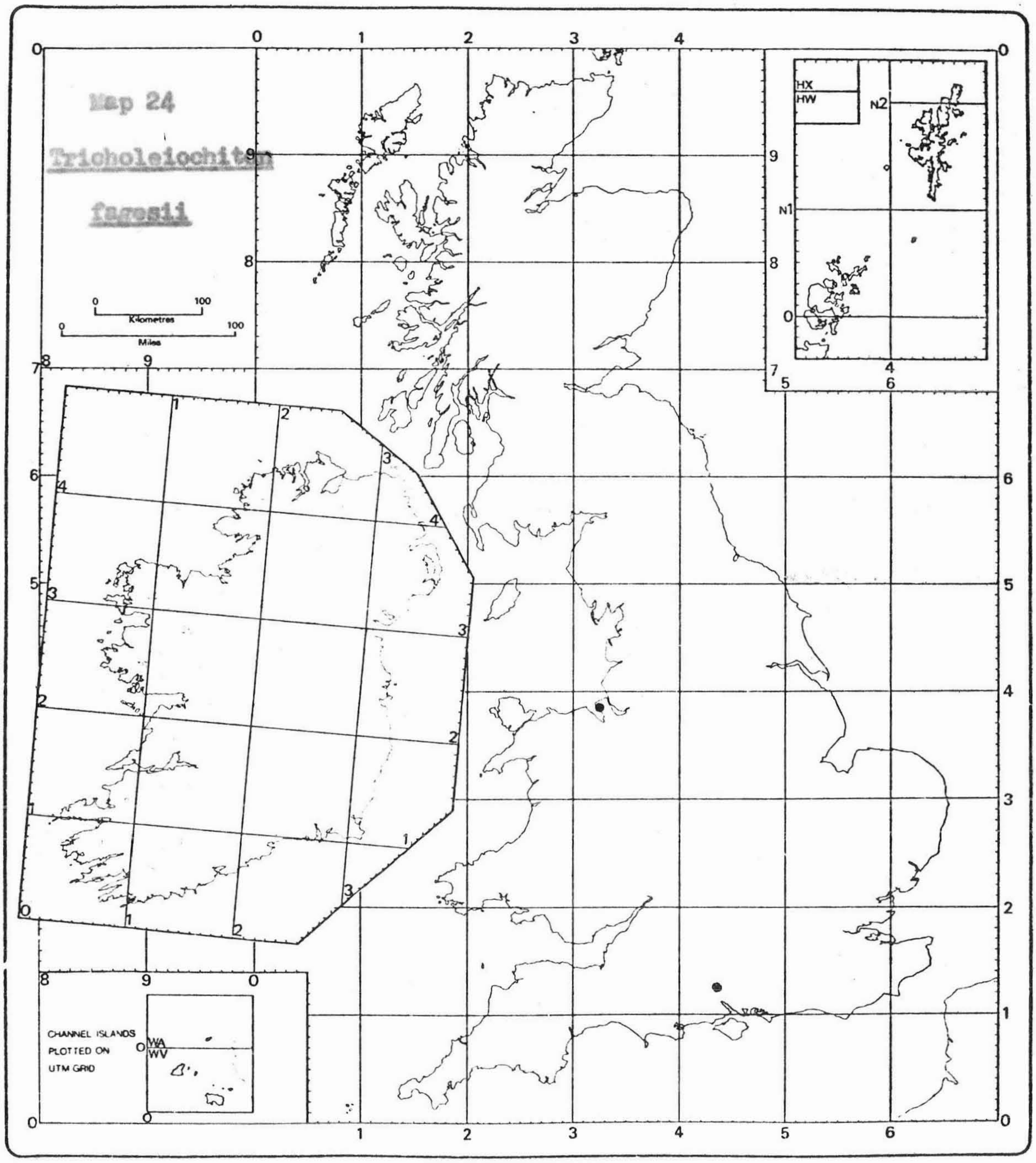

Map 22

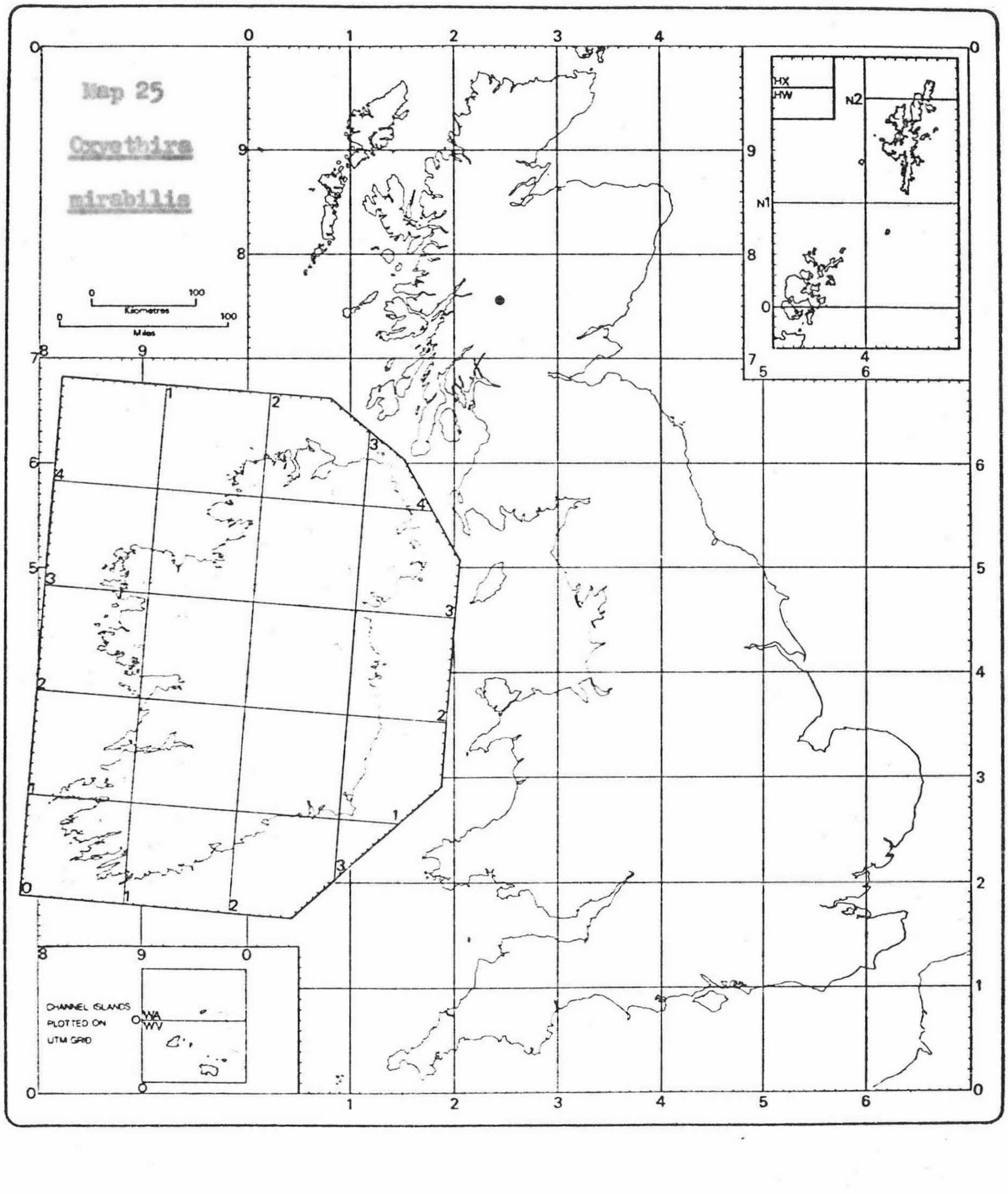
Ithytrichia lamellaris


Map 23
Ithytrichia
clavata
0
100
Kilometres
0
100
Miles
CHANNEL ISLANDS
PLOTTED ON
UTM GRID
WA
WV
HX
HW
N2
N1
0
1
2
3
4
5
6
7
8
9

Map 24

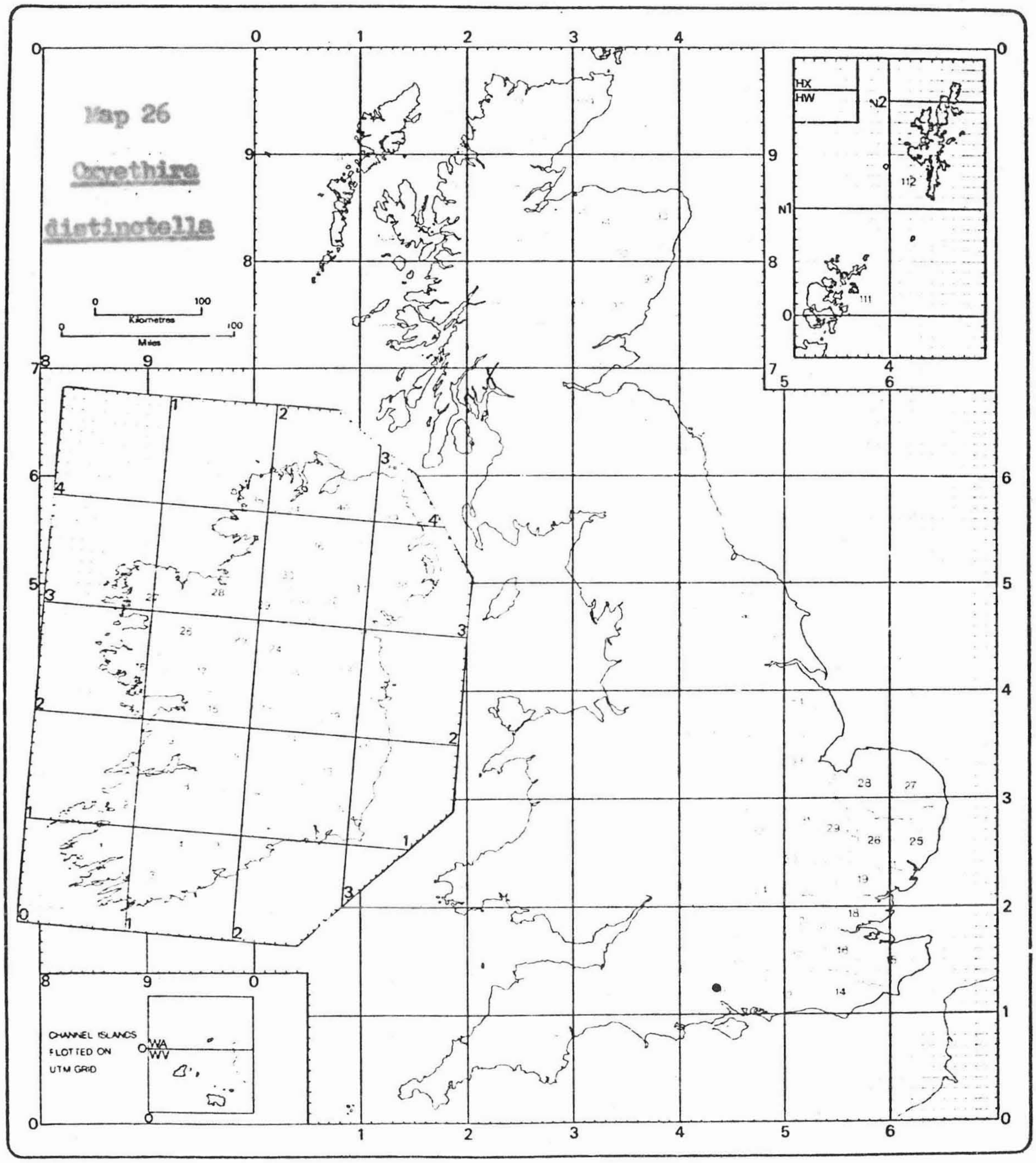
Tricholeiochiton fagesii





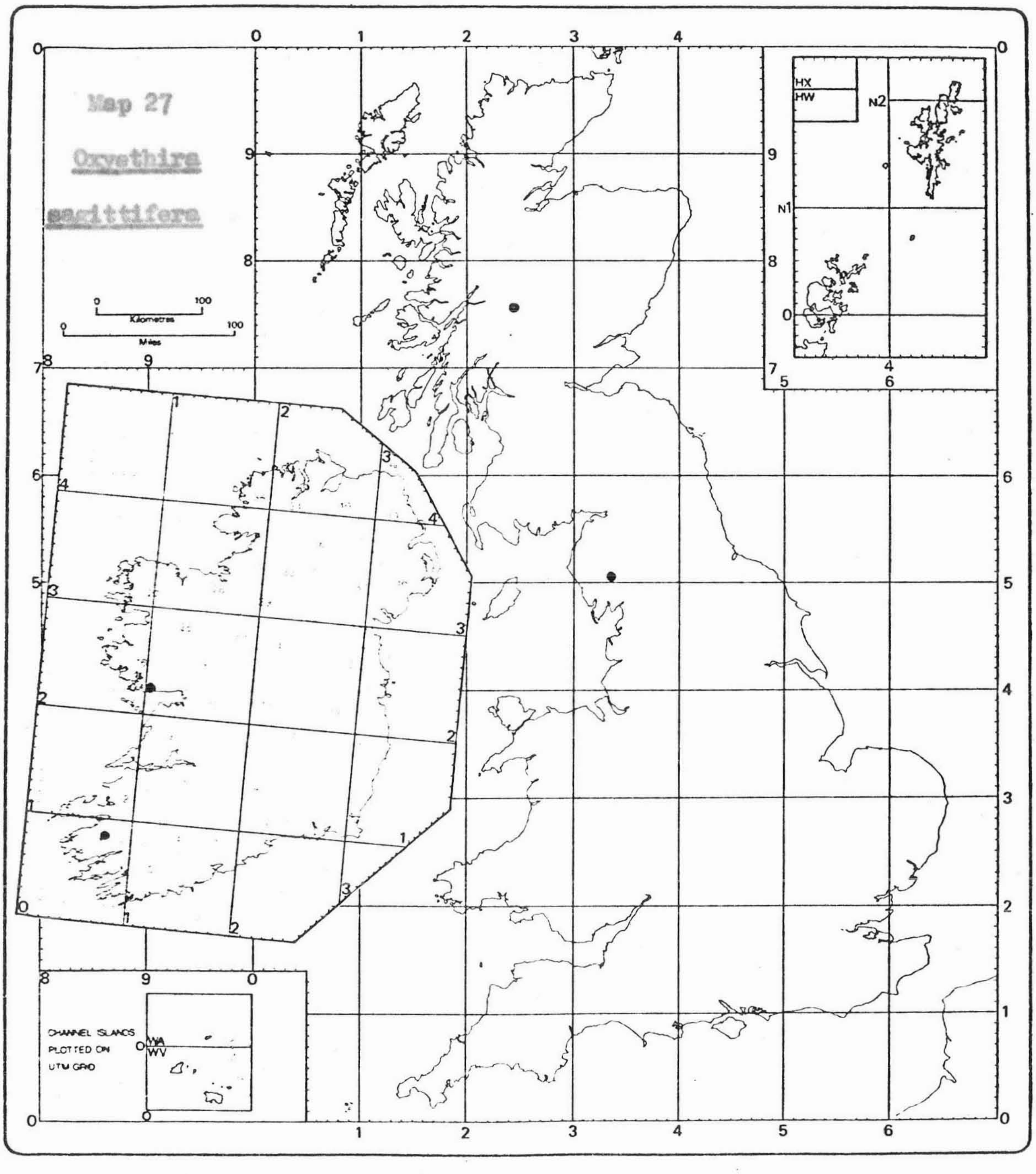
Map 25

Oxyethira mirabilis



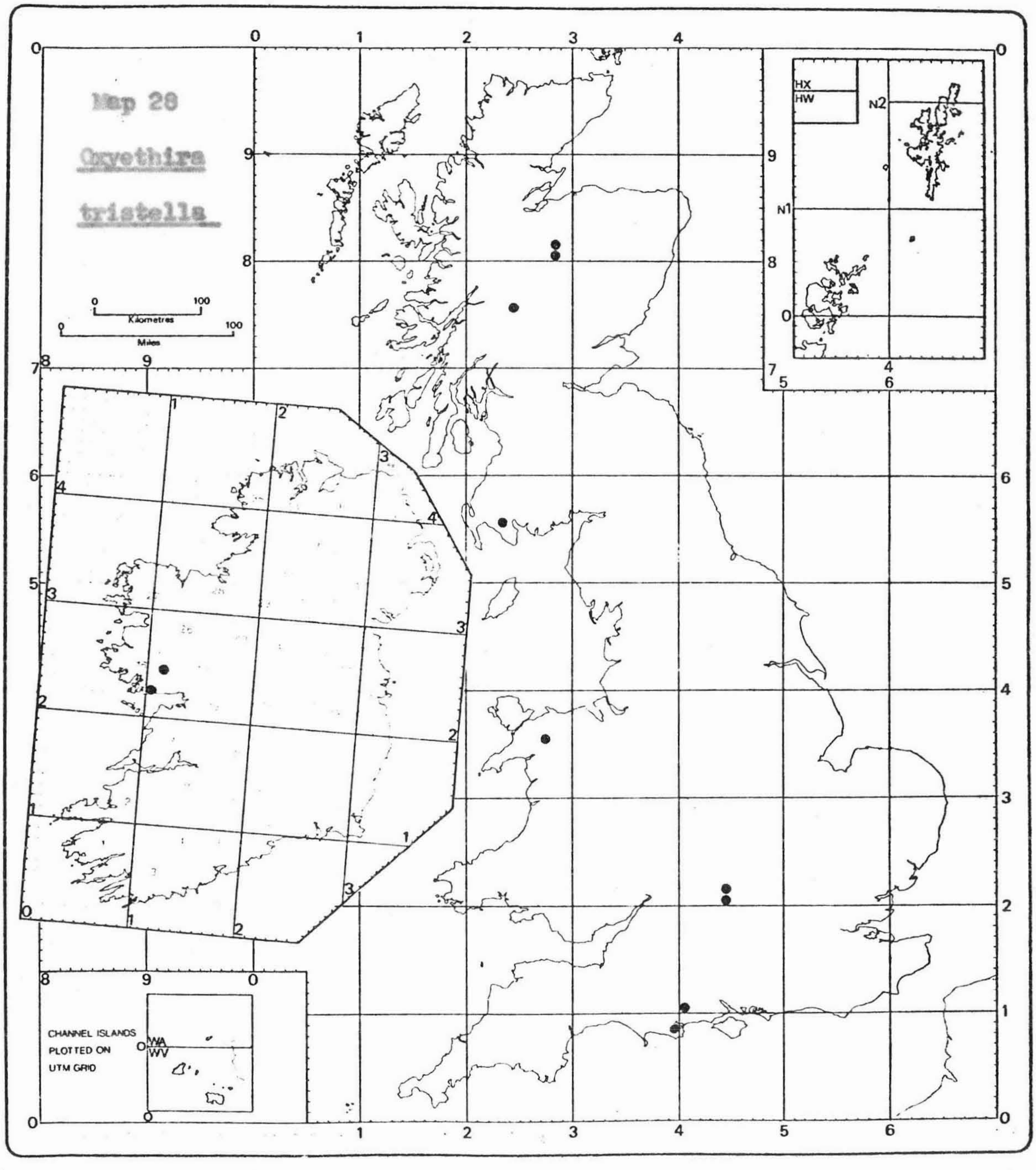
Map 26

Oxyethira distinctella



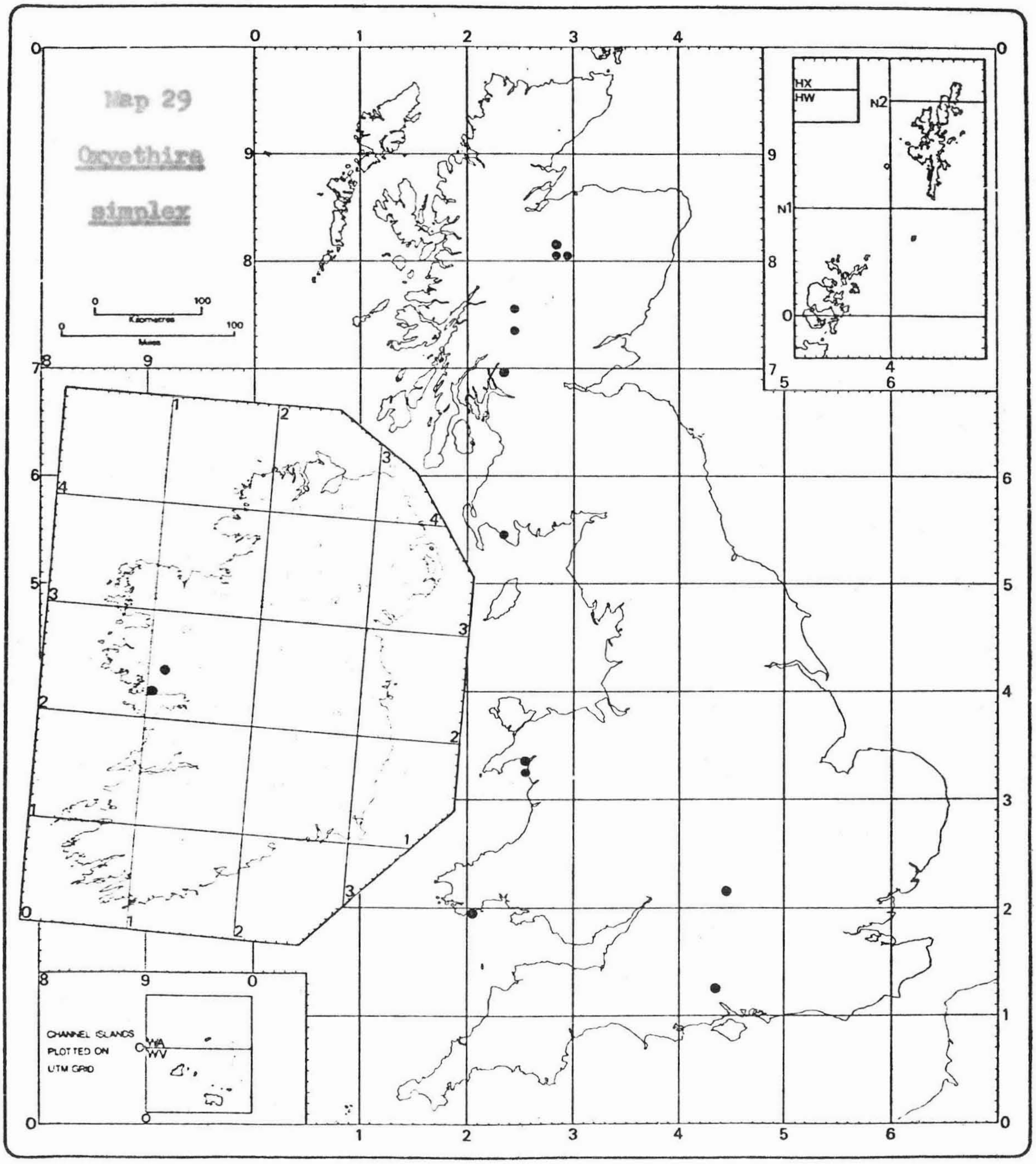
Map 27

Oxyethira sagittifera



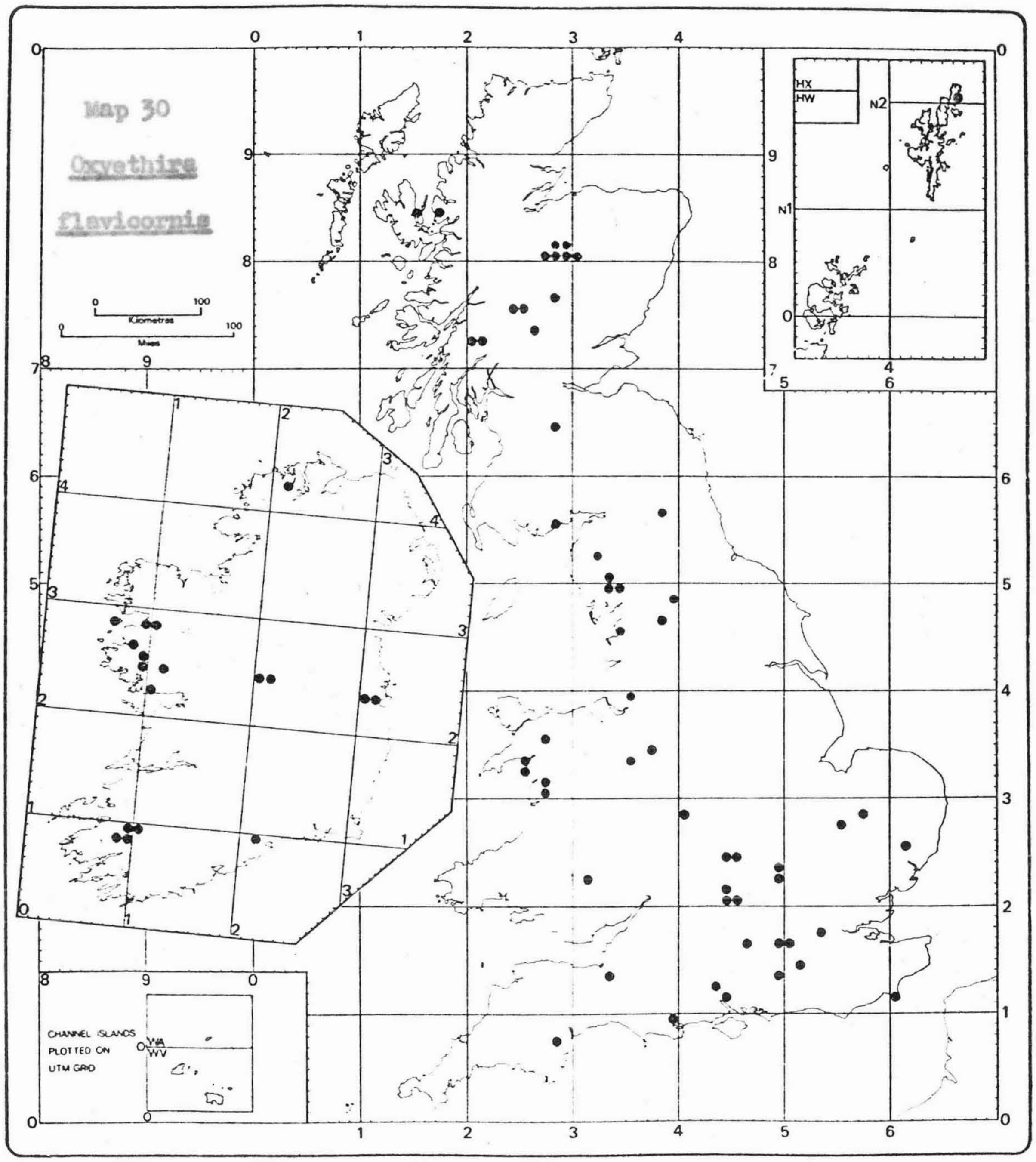
Map 28

Oxyethira tristella



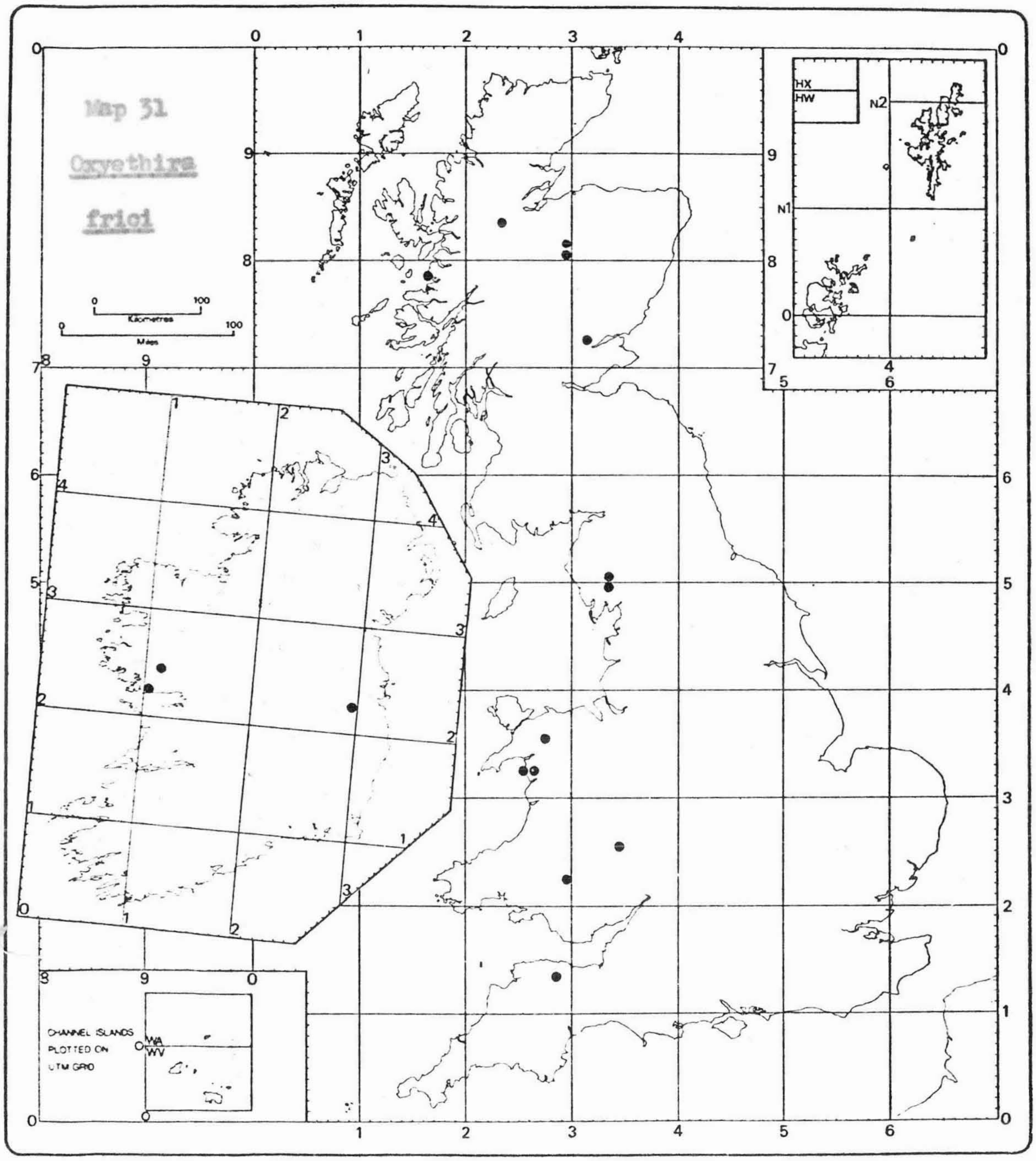
Map 29

Oxyethira simplex



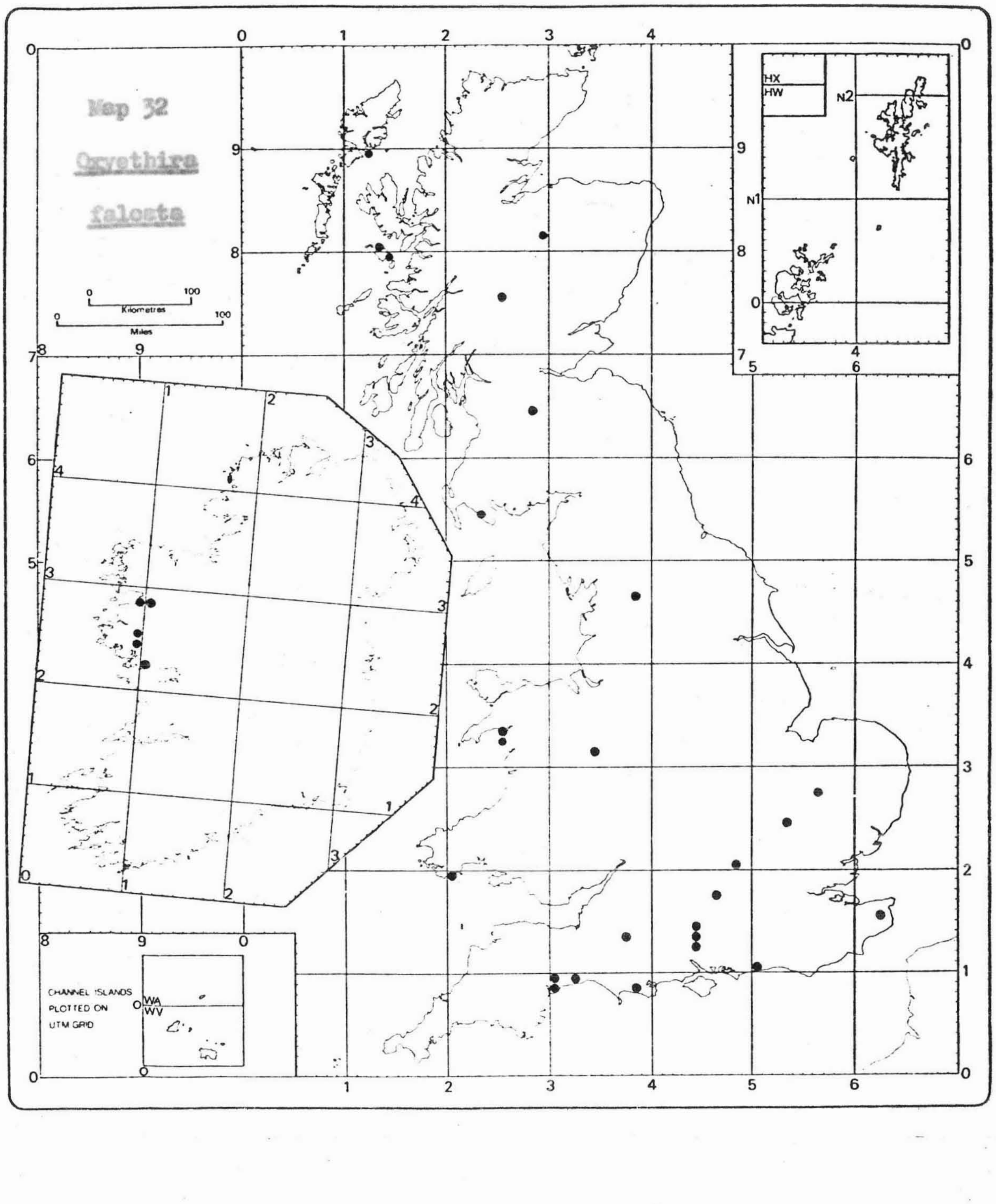
Map 30

Oxyethira flavicornis



Map 31

Oxyethira frici



Map 32

Oxyethira falcata